



Phylogenetic classification of the family Terebridae (Neogastropoda: Conoidea)

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ABSTRACT

The conoidean family Terebridae is an intriguing lineage of marine gastropods, which are of considerable interest due to their varied anatomy and complex venoms. Terebrids are abundant, easily recognizable and widely distributed in tropical and subtropical waters, but our findings have demonstrated that their systematics requires revision. Here we elaborate the classification of Terebridae based on a recently published molecular phylogeny of 154 species, plus characters of the shell and anterior alimentary system. The 407 living species of the family, including seven species described herein, are assigned to three subfamilies: Pellifroniinae new subfamily, Perviciacinae and Terebrinae. The Pellifroniinae comprises five deep-water species in two genera, *Pellifronia* and *Bathyterebra* n. gen. Pellifroniinae possess a radula of duplex marginal teeth, well-developed proboscis and venom gland, and a very small rhynchodeal introvert. The Perviciacinae includes c. 50 species in the predominantly Indo-Pacific genera *Duplicaria* and *Partecosta*. Perviciacinae possess salivary glands, a radula of solid recurved marginal teeth and a weakly developed rhynchodeal introvert, but lack proboscis and venom gland. The remaining Terebridae species are classified into 15 genera in the subfamily Terebrinae (including four genera described herein); nine genera are defined on the basis of phylogenetic data and six solely on shell morphology. The Indo-Pacific genera *Profunditerebra* n. gen., *Maculauger* n. gen. and *Myurellopsis* n. gen. each include about a dozen species. The first is restricted to the deep waters of the Indo-West Pacific, while the latter two range widely in both geographic and bathymetric distribution. *Neoterebra* n. gen. encompasses about 65 species from a range of localities in the eastern Pacific, Caribbean, and Atlantic, and from varying depths. To characterize the highly diversified genera *Terebra*, *Punctoterebra*, *Myurella* and *Duplicaria*, each of which comprise several morphological clusters, we propose the use of DNA-based diagnoses. These diagnoses are combined with more informative descriptions to define most of the supraspecific taxa of Terebridae, to provide a comprehensive revision of the group.

INTRODUCTION

The conoidean family Terebridae, or auger snails, is a diverse lineage of predatory marine gastropods with about 400 currently accepted Recent species (Bratcher & Cernohorsky, 1987; Taylor, 1990; MolluscaBase, 2018). Terebrids are specialized sand and mud dwellers. Although many terebrid species thrive in

the deep sea in both Pacific and Atlantic Oceans, the family reaches its highest diversity in the shallow coastal waters of the Indo-West Pacific (Miller, 1970; Kantor *et al.*, 2012). The local abundance of Terebridae can be remarkable; in some habitats, terebrids by far outnumber other molluscan taxa and can be collected by hundreds per dive (Kantor *et al.*, 2012). Being locally diverse and abundant, and furthermore easily recognizable among other gastropods by their elongate, multiwhorled shells, Terebridae are an excellent model taxon for studying microevolutionary pat-

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terms (Holford *et al.*, 2009; Castelin *et al.*, 2012; Fedosov *et al.*, 2014) or assessing the magnitude of local biodiversity (Kantor *et al.*, 2012; Modica *et al.*, 2014). In addition, there is a growing interest in the family because, like cone snails, terebrids employ complex venoms for hunting—which can be investigated to understand the evolution, function and diversification of venom compounds, and to study their potential pharmacological applications (Imperial *et al.*, 2003, 2007; Puillandre & Holford, 2010; Kendel *et al.*, 2013; Gorson *et al.*, 2015; Gorson & Holford, 2016; Verdes *et al.*, 2016; Ericksson *et al.*, 2018).

The placement of the Terebridae in Conoidea is widely accepted, because of the presence of a toxoglossan envenomation apparatus in most terebrids (Taylor, 1990). Affinities with other Conoidea and relationships within Terebridae have been addressed with both traditional morphological (Rudman, 1969; Taylor, 1990; Taylor, Kantor & Sysoev, 1993) and molecular-phylogenetic approaches (Holford *et al.*, 2009; Puillandre *et al.*, 2011; Castelin *et al.*, 2012). The striking diversity of anterior digestive system anatomies among Terebridae led Rudman (1969) to question the monophyly of the family and to establish the family Pervicaciidae, mainly for species of the genus *Duplicaria* lacking the venom gland and possessing an ancestral radula type. The distinctive features of Pervicaciidae were acknowledged by Taylor (1990), although their independent origin from the rest of Terebridae was rejected, based on an extensive morphological dataset (Taylor *et al.*, 1993). The monophyly of Terebridae (including *Duplicaria*) was further confirmed by molecular studies (Holford *et al.*, 2009; Castelin *et al.*, 2012), which recognized *Duplicaria* as one of the early-diverging lineages of the family, together with an enigmatic deep-water species ‘*Terebra junci*’ (Holford *et al.*, 2009; Castelin *et al.*, 2012). ‘*Terebra junci*’ was subsequently reassigned to a separate genus, *Pellifronia*. However, beyond these partial revisions, little has been done to reconcile the systematics of Terebridae with the emerging phylogenetic framework for the family.

The present day taxonomy of the Terebridae as published by Terry (2007) is largely based on shell characters and no new genus or family group taxa, except *Pellifronia*, have been proposed since 1969. As taxonomic sampling for phylogenetic analyses of Terebridae improved, culminating in the recently published updated phylogeny of the family by Modica *et al.* (2019), the inconsistency between the evolutionary relationships and formal taxonomy of the Terebridae has increased. Given the molecular results, it is now clear that the genus-level classification of the family needs to be revised, because many of the currently recognized genera have been found to be non-monophyletic in published phylogenies (Holford *et al.*, 2009; Castelin *et al.*, 2012; Modica *et al.*, 2014; Modica *et al.*, 2019). Additionally, the growing multidisciplinary interest in the Terebridae warrants a formal revision of the family.

Here we present a revision of the classification of the Terebridae informed by recent phylogenetic analyses. We give a new taxonomic arrangement of terebrid species, with most of the genera defined on the basis of inferred phylogenetic relationships and complete species lists provided for each genus. The change from the traditional shell-based taxonomy to the new classification based largely on phylogenetic relationships, posed some methodological issues, specifically with regard to the provision of informative and useful diagnoses. Many cases of convergent evolution of shell morphology were found, prompting us to introduce diagnoses of supraspecific taxa based on molecular characters. Although the use of molecular characters to diagnose supraspecific taxa remains uncommon, when the molecular data are conclusive it is viewed as a necessary step in the transition to new classifications.

MATERIAL AND METHODS

Rationales for name attribution and ranking of recognized phylogenetic clades

As described by Puillandre *et al.* (2014, 2015), the transformation of a phylogenetic tree to a classification includes several steps, namely (1) delineating putative taxa based on the inferred monophyletic lineages, morphology and phylogeography; (2) attributing names to these groups; and (3) ranking the recognized taxa. Here we followed the same general strategy, using the recently published updated phylogeny of the Terebridae (Modica *et al.*, 2019) as a source of phylogenetic information (Supplementary Material Fig. S1). Only well-supported clades in the phylogenetic analysis are named. A name is attached to a molecular clade primarily based on the inclusion of a type species of a nominal genus in the clade (when several type species are included, priority is given to the oldest generic name). If no such species is included, the name is applied based on concordance in morphological characteristics between the species in the clade and a type species of a nominal genus. If no available names are found for a molecular clade, a new taxon is proposed. Decisions on naming clades are made with the aim of minimal phenotypic variability in a candidate taxon, but avoiding unnecessary subdivision of taxa. We thus followed a conservative approach. For instance, although the names *Cinguloterebra*, *Dimidacus*, *Myurellina* and *Triplostephanus* are available for four well-supported subclades of clade C of Modica *et al.* (2019), all the lineages in clade C are here referred to *Terebra*, a decision substantiated by the observed homogeneity of anatomy and radular morphology across the clade. On the contrary, the six subclades of the major clade E were each assigned generic rank, for which only two names were available (*Myurella* for clade E1 and *Punctoterebra* for clade E2), leading to the naming of four new genera, *Profunditerebra* n. gen. (Clade E3), *Neoterebra* n. gen. (Clade E4), *Maculauger* n. gen. (Clade E5A) and *Myurellopsis* n. gen. (Clade E5B). Recognition of six separate genera within this well-supported clade is justified by the observed substantial differences among subclades in foregut anatomy, radular morphology and distribution.

Two well-supported lineages of the Modica *et al.* (2019) phylogeny, referred to as F1 and F2 therein, share the characteristic ‘*Duplicaria*’ arrangement of foregut structures (Fig. 1; Supplementary Material Fig. S1). However, they are distinctive in shell size, morphology and distribution. *Duplicaria duplicata*, the type species of the genus, is included in clade F1; therefore, the name can be allocated to either clade F1 or to the entire clade F (i.e. F1+F2). Since the recognition of genera recognizable by shell morphology undoubtedly increases the operational ability of a classification, we allocate the name *Duplicaria* to clade F1 only. The name *Partecosta* is available for clade F2, based on the resemblance of sequenced species in this clade to *Terebra fuscobasis*, the type species of *Partecosta*, and is thus applied here. The genetic and anatomical distinctiveness of clade F in relation to other studied Terebridae is sufficient, in our opinion, for recognizing it as a subfamily, for which the name Pervicaciinae is, therefore, restored. Consequently, the two other main clades of Terebridae (clade A and the clade comprising the rest of the Terebridae) are also assigned subfamilial rank: Pellifroniinae n. subfam. for clade A and Terebrinae for the remaining Terebridae (i.e. except clades A and F).

The median estimated times of diversification in each of the recognized genera range from 14 Ma (*Maculauger*) to 29 Ma (*Terebra*), which suggests that diversification of terebrid genera took place in the Oligocene–Miocene (Modica *et al.*, 2019). These estimates fall within the range estimated for the most recent common ancestors in other genera of neogastropods, e.g. in the muricid subfamily Rapaninae (Claremont *et al.*, 2013) and in the family Conidae (Duda & Kohn, 2005; Puillandre *et al.*, 2014).

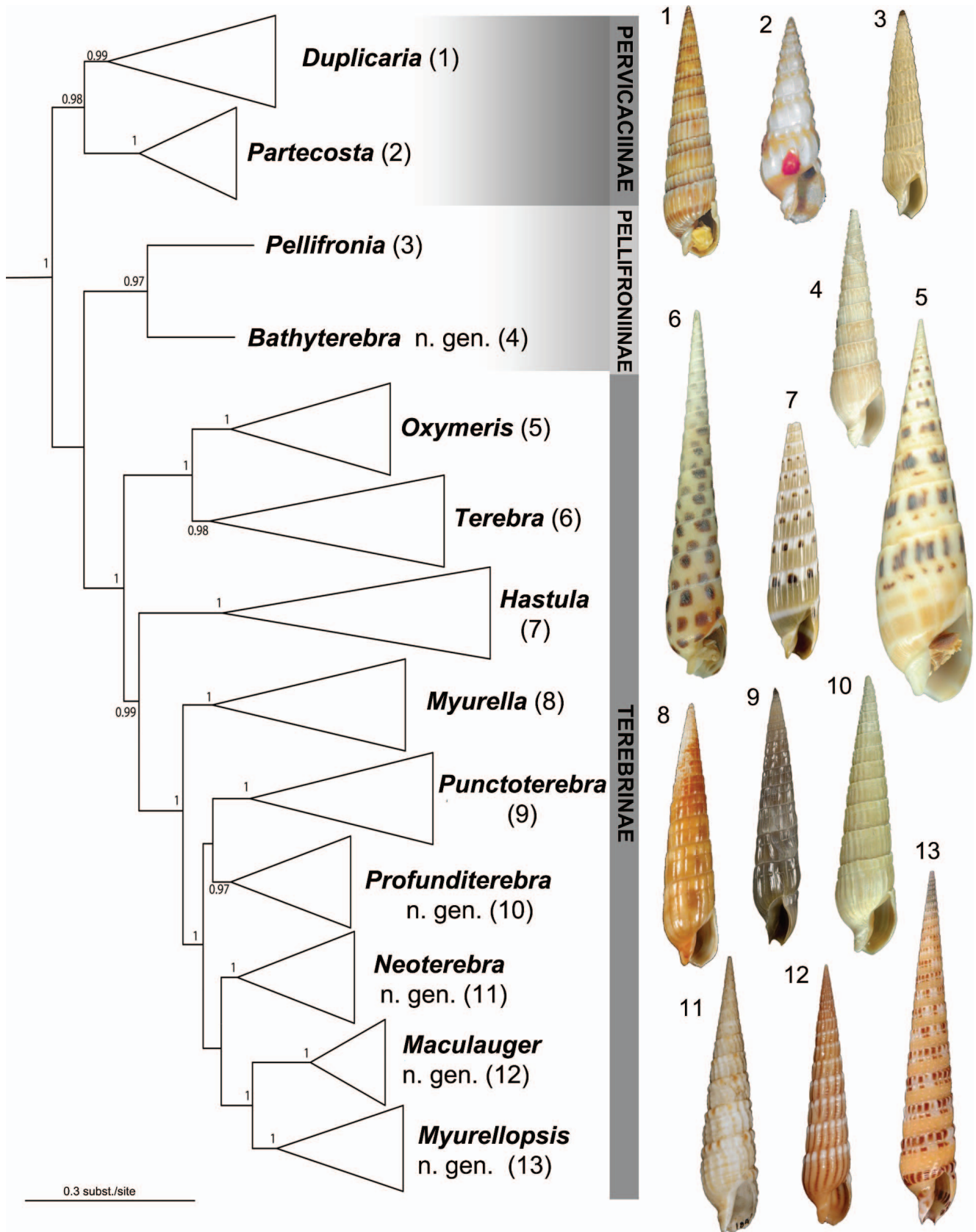


Figure 1. Phylogenetic relationships of the main lineages of Terebridae. Genera are numbered 1–13 in the tree and a shell of the type species of each genus is depicted to the left; see [Supplementary Material Fig. S1](#) for species composition (after [Modica et al., 2019](#)).

Allocation of species to genus-level groups

In identifying the 1400 specimens analysed by [Modica *et al.* \(2019\)](#), we found that the species boundaries, as predicted by shell morphology, in many cases correspond to complexes of closely related species. In most cases, we found that the revealed molecular operational taxonomic units (MOTUs) were distinguishable by shell morphology and, in several cases, we demonstrate that species previously considered to be synonyms actually correspond to distinct species. The phylogenetic analysis of [Modica *et al.* \(2019\)](#) also identified several MOTUs that undoubtedly correspond to undescribed species. Although comprehensive description of all likely new species is not the goal of the present study, those new species that are deemed important for understanding boundaries and identities of the newly introduced genera are described herein. In only one case was a currently accepted species found to be a junior synonym of another species, based on identified and sequenced specimens. Despite many striking parallels in shell morphology uncovered by the phylogenetic analysis (see Discussion), we found that, in general, species with similar morphology predictably grouped together in distinct clusters within a given clade. This confirmed that, for terebrids, shell morphology is a reliable proxy that could be used to allocate species for which no sequence data were available (further discussed below).

Morphological and molecular circumscription of taxa

For the morphological circumscription of taxa, we adopted a three-step approach. In a first, 'indicative' step, we identified species and groups of species with distinctive features in both shell morphology and anatomy within each genus-level clade identified in the phylogenetic tree of [Modica *et al.* \(2019\)](#). The International Code of Zoological Nomenclature ([ICZN, 1999](#)) allows two alternative options for establishing the morphological identity of a taxon: (1) to propose a diagnosis, i.e. "a summary of the characters that differentiate the new nominal taxon from related or similar taxa" (ICZN Recommendation 13 A) or (2) to give a description, in which taxonomically informative and uninformative characters are not separated ([Renner, 2016](#)). In a second, 'diagnostic' step, we were able to use the defined distinctive features to add other nonsequenced species to the proposed taxa and to formulate a description, i.e. a synopsis of morphological characteristics for each genus. Since multiple cases of convergent evolution of shell features have been demonstrated for Terebridae ([Modica *et al.*, 2019](#)), the synopsis was usually not sufficient for unequivocal identification of a primarily phylogenetically defined genus. In each of such cases, a Definition is provided to present our rationale for establishing a taxon with given boundaries, followed by formal Description of shell, and when known, anatomy. Additional information on how the members of each genus can be differentiated from similar but unrelated forms is given in the Remarks sections. In several genera, distinctive subclades were recognized by the phylogenetic analysis and these could have been considered as subgenera. Here we choose to not define subgenera, to avoid the introduction of multiple new names for lineages whose morphological identities are not entirely understood at present. However, we retained in the Remarks brief descriptions of the potential subgroups for reasons of clarity and usability. To avoid ambiguity, we have sometimes made reference to the morphology of individual specimens in the collection of the Museum national d'Histoire naturelle, Paris (MNHN). In a third step, we investigated the species that were difficult to allocate with confidence to the phylogenetically defined genera. We found that in many cases, these species formed groups which, when diagnosed by distinctive morphological features, were found to be attributable to currently accepted genera for which no DNA sequence data were available. As no phylogenetic information is available

on these genera, we cannot resolve their status with certainty and such genera are therefore retained as valid.

We compiled molecular diagnoses to supplement traditional taxonomic diagnoses and descriptions, in response to the fact that recognition of primarily phylogenetically defined genera by morphological means was often problematic. As the four-gene (cytochrome *c* oxidase subunit I (COI), 16S rRNA, 12S rRNA and 28S rRNA) phylogenetic analysis of [Modica *et al.* \(2019\)](#) is not comprehensive for all species and specimens in each clade, the credibility of a molecular diagnosis derived from this dataset could be questioned. To combat this, we used only the COI dataset, including only sequences with no more than five ambiguously called nucleotides (963 records), representing 179 putative species. Initially, species were attributed to predefined clades based on the results of the four-gene analyses and this was consistent with allocations to genera and subfamilies in the classification detailed below. The total length of the COI alignment was 658 base pairs (the 'barcode' fragment defined by the primers of [Folmer *et al.*, 1994](#)), which were thus numbered from 1 to 658. First, an attempt was made to find entirely diagnostic single-nucleotide positions (i.e. at a given position, all the members of the clade, and none of the nonmembers, share a given nucleotide) using the R package SPIDER v. 1.4-1 ([Brown *et al.*, 2012](#)). However, only one diagnostic single-nucleotide character was identified for clades A1 and E5A in [Modica *et al.*'s \(2019\)](#) study, and none for any of the others. Thus, we explored the possibility of providing molecular diagnoses based on diagnostic combinations of nucleotides (i.e. at two or more positions, all the members of the clade, and none of the nonmembers, share a combination of nucleotides). To our knowledge, only CAOS ([Sarkar, Planet & Desalle, 2008](#)) is capable of detecting such diagnostic combinations. However, as CAOS implements a tree-based algorithm, it imposes certain requirements for the data to run efficiently—such as a predefined group is only provided with a diagnosis (referred to as 'characteristic attributes' or CAs by [Sarkar *et al.*, 2008](#); [Rach *et al.*, 2008](#)) if it corresponds to a clade in the provided tree. The tree reconstructed using all the COI sequences of [Modica *et al.* \(2019\)](#) did not retrieve all the subfamilies and genera as monophyletic, thus CAOS was not applicable. Consequently, we developed a customized Python script ([Fedosov *et al.*, 2019](#)) that is based on an alternative, purely statistical approach, and implements an iterated random search to identify diagnostic combinations of COI nucleotides for each predefined group in an assemblage of aligned sequences. This Python script provided the most comprehensive and reproducible results for our dataset, and was used to make species diagnoses.

Abbreviations

Institutional abbreviations:

ANSP, Academy of Natural Sciences of Philadelphia, Drexel University, USA
 GM, private collection of Gavin Malcolm, UK
 JR, private collection of José Rosado, Mozambique
 MMM, Malacologia Mostra Mondiale, Italy
 MNHN, Muséum national d'Histoire naturelle, Paris, France
 NHMUK, Natural History Museum, London
 NMSA, National Museum of South Africa, KwaZulu-Natal Museum, Pietermaritzburg, South Africa
 SG, private collection of Sandro Gori, Italy
 USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
 YT, private collection of Yves Terryn, Belgium

Other abbreviations: dd, dead-collected shell; lv, live-collected specimen.

RESULTS

Levels of confidence in attribution to genera

The valid Recent species entries (401) from the current MolluscaBase database (as per 1 February 2018) were used in our analysis. DNA sequence data (Modica *et al.*, 2019) were available for 135 of these currently accepted species, of which we consider 134 species to be valid [the exception is *Oxymeris troendlei* (Bratcher, 1981), which was found to be a junior synonym of *O. felina* (Dillwyn, 1817)]. These 134 species, as well as seven new species revealed by the phylogenetic analysis of Modica *et al.* (2019) and described herein are allocated to genera with a superscript 1, indicating the highest degree of confidence.

The use of morphological characters in combination with geographic distribution resulted in a nonambiguous placement of 166 further species into one of the groups recognized phylogenetically; these are marked with a superscript 2.

In multiple cases, shell morphology initially appeared to be inconclusive for confident attribution of a species to a genus, because more than one hypothesis on its placement could be proposed; in such cases we suggested a tentative allocation taking into account all available morphological and distribution data. This is the case for 59 species entries marked with a superscript 3.

Of the remaining species, 39 showed no clear affinity to any one of the molecularly defined genera. However, based on the shell morphology alone, each of these species could be allocated to one of six terebrid genera: *Granuliterebra*, *Hasulopsis*, *Pristiterebra*, *Gradaterebra*, *Perirhoe* or *Microtrypetes*. These six genera remain defined solely by shell characters, pending new molecular data.

Six species showed no definite resemblance to any terebrid genus; these are treated as *incertae sedis* and more data are needed to allow credible generic allocations.

Finally, based on the examination of type material, two species, *Terebra walkeri* E. A. Smith, 1899 and *Euterebra mariato* Pilsbry & Lowe, 1932, are excluded from Terebridae and should be reassigned to Cerithiidae and Columbelloidea, respectively. Entries marked with asterisk in species lists are here raised to full species based on the results of the phylogenetic study by Modica *et al.* (2019).

COI-based diagnoses

Numerous diagnostic combinations were returned for all but three genera and were sorted by length, with priority given to short combinations. The diagnostic nucleotides identified for the clades A1 and E5A by SPIDER were also recovered by our Python script. However, we failed to identify diagnostic combinations of nucleotides for the genera *Terebra* and *Punctoterebra*, and only found diagnostic combinations for *Hastula* when four sequences with a substitution at position 181 of the COI fragment were removed from the dataset. As a result, for *Terebra*, *Punctoterebra* and *Hastula*, we propose separate diagnoses for the inferred phylogenetic clusters within each genus.

SYSTEMATIC DESCRIPTIONS

Superfamily CONOIDEA Fleming, 1822

Family TEREBRIDAE Mörch, 1852

Synonym: Acusidae Gray, 1853

Shell: Elongate or conical, multiwhorled, with very high spire and relatively small last whorl. Aperture small, with anterior siphonal notch, or very short straight siphonal canal. Anal sinus indistinct.

Anatomy: Operculum always present, horny, rounded or leaf-shaped, with terminal nucleus. Head with two very short close-set eye tentacles with eye situated near tip. Rhynchodaeal introvert always present, small to very large. Proboscis, radula, salivary glands, accessory salivary glands, venom gland and accessory proboscis structure present or absent. Radula, when present, composed of marginal teeth only, varying in shape from flat, solid and recurved, semi-enrolled or duplex, to hollow hypodermic.

Subfamily PELLIFRONIINAE new subfamily

(Fig. 2)

Type genus: *Pellifronia* Terry & Holford, 2008

Zoobank registration: urn:lsid:zoobank.org:act:E827742C-E1B3-42DD-B5EB-5D7EAA6E2C95

Diagnosis: Diagnostic nucleotide combinations in Table 1.

Shell: Small to medium-sized (12–50 mm), with predominant axial sculpture. Early teleoconch whorls often with angled profile, later ones flattened or even slightly concave to convex. Sculpture of numerous close-set, evenly spaced, ribs, or forming raised nodules bordering upper or lower suture. Spiral sculpture absent or of very shallow, wide subsutural depression.

Anatomy: Rhynchodaeal introvert small; proboscis, radular sac, odontophore, salivary and venom glands well developed. Radula with well-developed membrane, bearing 2 rows of wide marginal teeth of duplex type. Accessory proboscis structure absent.

Remarks: This subfamily comprises five described species in two genera, *Bathyterebra* and *Pellifronia*, that occur in the Indo-Pacific and Caribbean at bathyal depths. The anatomy of the studied species shows characters that are believed to be ancestral for Terebridae in general, i.e. weakly developed rhynchodaeal introvert and radular teeth of duplex type (Castelin *et al.*, 2012).

Genus *Pellifronia* Terry & Holford, 2008

(Fig. 2A–D)

Type species: *Terebra jungi* Lai, 2001; OD.

Definition: Includes species with combination of conchological, anatomical and distributional characteristics closely comparable with *Pellifronia jungi*, including all species in clade A1 of Modica *et al.* (2019) and any species proven to be a member of this clade.

Diagnosis: Diagnostic nucleotide combinations in Table 1.

Shell: Medium-sized (25–50 mm), elongate, light brown. Protoconch brown, paucispiral, cyrtocoid, 1.5–2.5 whorls. Coarse sculpture of pronounced ribs, orthocline or prosocline, sometimes arcuate on late teleoconch whorls. Axial ribs often thickened in their adapical and/or abapical part(s), giving slightly concave outline to spire whorls. Last adult whorl with flattened adapical portion and short, somewhat angulate transition to shell base. Siphonal canal moderately long, recurved at tip, shallowly notched; siphonal fasciole weak or indistinct. Aperture elongate, curved.

Anatomy: Rhynchodaeal introvert small; proboscis, radular sac, odontophore, salivary and venom glands well developed. Accessory proboscis structure absent. Radula with well-developed membrane, bearing 2 rows of wide marginal teeth of duplex type.

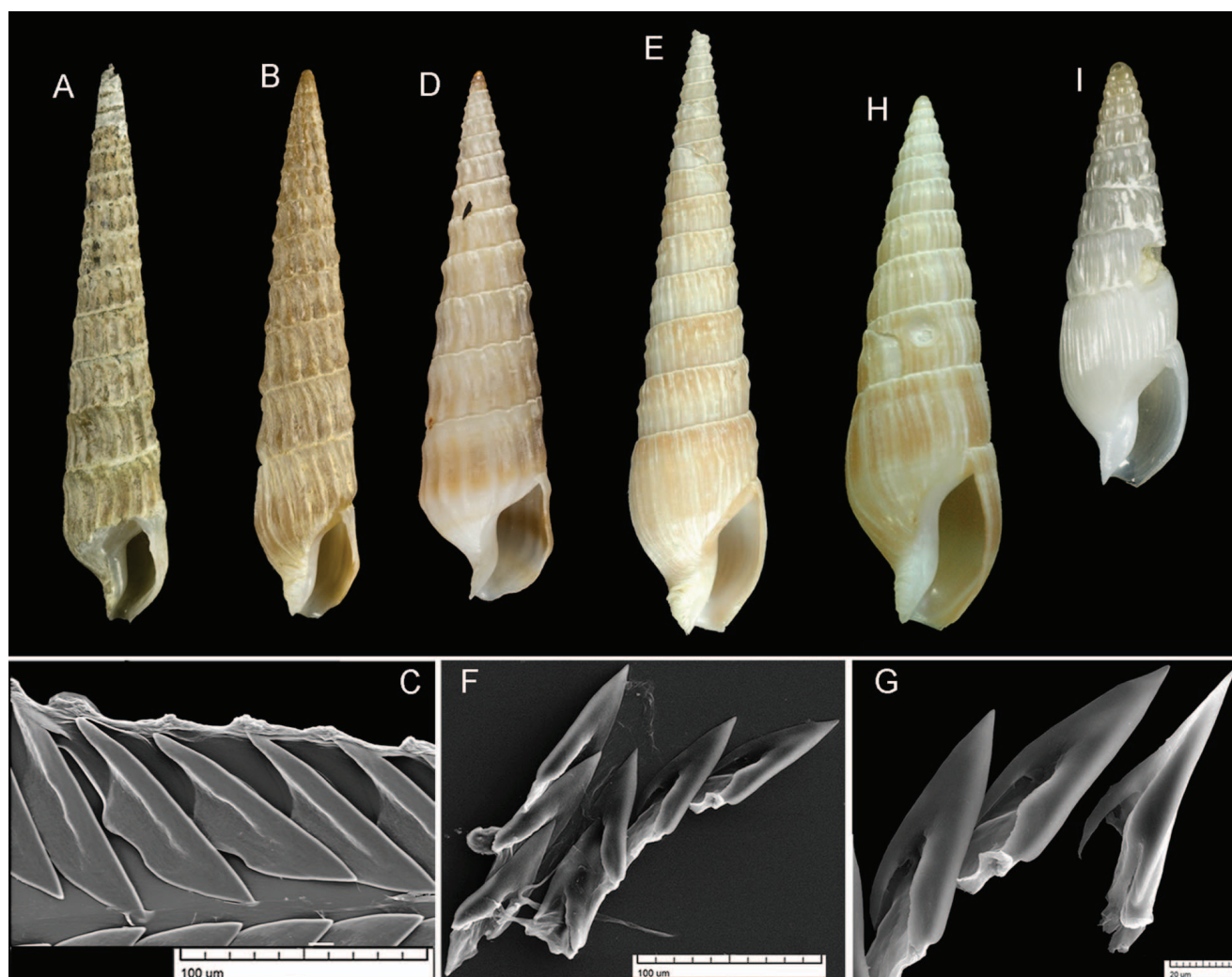


Figure 2. Subfamily Pellifroniinae. **A–C.** *Pellifronia jungi*. **A.** MNHN-IM-2013-52275, NANHAI 2014 Stn DW4102, 15°03'N, 116°31'E, 339–533 m, 25.5 mm. **B.** MNHN-IM-2013-52249, EXBODI Stn CP3831, 22°02'S, 167°09'E, 523–560 m, 24 mm. **C.** MNHN-IM-2007-30591, SALOMON 2 Stn CP2195, 08°26'S, 159°26'E, 543–593 m, 29 mm (broken). **D.** *Pellifronia brianhayesi* holotype, MNHN-IM-2000-20800, S Mozambique, 22.6 mm. **E–G.** *Bathyterebra benthalis*. **E.** MNHN-IM-2013-60185, KARUBENTHOS 2015 Stn CP4524, 16°29'N, 61°42'W, 500–550 m, 35.5 mm. **F, G.** MNHN-IM-2013-61124, KARUBENTHOS 2015 Stn DW4608, 9.3 mm. **H.** *Bathyterebra zhongshaensis* n. sp. holotype, MNHN-IM-2013-61800, ZhongSha 2015 Stn DW4138, 19°13'N, 113°56'E, 470–494 m, 17 mm. **I.** *Bathyterebra coriolisi*, MNHN-IM-2013-52331, CONCALIS Stn DW3001 18°32'S, 163°09'E, 390–400 m, 12.4 mm.

Distribution: Indo-Pacific, bathyal depths.

Remarks: This genus differs from the closely related *Bathyterebra* in having stronger axial sculpture, a more flattened whorl outline and the last adult whorl constricted to the siphonal canal with visible angulation. Species of *Pellifronia* can be distinguished by their coarse sculpture and swollen rib ends with slightly raised subsutural area. Similar species in other genera, e.g. *Neoterebra puncturosa*, *N. crenifera* and *Granuliterebra bathyrhapse*, normally have a sharper nodular structure on the subsutural band or rib endings, or can be separated by the lack of radula (*Neoterebra*).

Included species:

- Pellifronia brianhayesi* (Terry & Sprague, 2008)²;
P. jungi (Lai, 2001)¹.

Genus *Bathyterebra* new genus

(Fig. 2E–I)

Type species: *Terebra benthalis* Dall, 1889.

Zoobank registration: urn:lsid:zoobank.org:act:EF1F9047-25AB-4400-A1D4-C705B757E114

Definition: Includes species with combination of conchological, anatomical and distributional characteristics closely comparable with *Bathyterebra benthalis*, including all species in clade A2 of Modica et al. (2019) and any species proven to be a member of this clade.

Diagnosis: Diagnostic nucleotide combinations in Table 1.

Shell: Small, 12–30 mm, elongate, white to tan. Protoconch paucispiral, cyrthoconoid, about 1.5 glossy whorls. Sculpture of fine dense orthocline ribs, interrupted by depression in adapical portion of whorl. Axial ribs weakening towards anterior throughout their height on mature whorls, often forming weak nodules bordering adapical depression, giving distinctly angulated outline to early spire whorls; late teleoconch whorls gently convex. Last adult whorl evenly convex, transitioning to shell base without visible angulation. Siphonal canal stout, slightly recurved at tip,

Table 1. Subfamily Pellifroniinae and included genera: diagnostic combinations of nucleotides in COI alignment.

| | |
|-----------------------------------|-------------------------------|
| Subfamily Pellifroniinae | |
| Species/sequences analysed | 4/25 |
| Diagnostic nucleotides: | 88: T, 299: G, 334: A, 530: A |
| Genus <i>Pellifronia</i> | |
| Species/sequences analysed | 1/11 |
| Diagnostic nucleotides: | 76: C, 208: T, 299: G, 301: A |
| Genus <i>Bathyterebra</i> n. gen. | |
| Species/sequences analysed | 3/14 |
| Diagnostic nucleotides | 76: T, 88: T, 299: G, 622: C |

shallowly notched; siphonal fasciole weak or strong. Aperture elongate, wide.

Anatomy: Rhynchodeal introvert small; proboscis, radular sac, salivary and venom glands well developed. Accessory proboscis structure absent. Radula with well-developed membrane, bearing 2 rows of wide marinal teeth of duplex type.

Distribution: South China Sea, New Caledonia, Caribbean; bathyal depths.

Etymology: Name refers to bathyal depths, at which three known species of the genus were sampled. Gender feminine.

Remarks: *Bathyterebra* spp. can be differentiated from members of most other genera of Terebridae by the combination of relatively faint sculpture lacking spiral elements, weakly defined subsutural band and relatively high last adult whorl with convex outline. In shell proportions the genus resembles *Oxymetis*; however, the latter has more flattened whorls and typically can be easily differentiated by a larger size at maturity.

Included species:

- Bathyterebra benthalis* (Dall, 1889)¹ n. comb.;
- B. coriolisi* (Aubry, 1999)¹ n. comb.;
- B. zhongshaensis* Malcolm, Terryn & Fedosov¹ n. sp.

Subfamily **PERVICACIINAE Rudman, 1969**

(Fig. 3)

Type genus: *Pervicacia* Iredale, 1924 (= *Duplicaria* Dall, 1908)

Shell: Elongate, 10–100 mm, with high spire, predominant axial sculpture, wide aperture.

Anatomy: Rhynchodeal introvert rather small; salivary glands and radular sac present; radula of solid curved marginal teeth attached to strong membrane. Venom gland, proboscis and accessory proboscis structure absent.

Genus *Duplicaria* Dall, 1908

(Fig. 3A–E)

Synonyms: *Diplomeriza* Dall, 1919 (unnecessary new name for *Duplicaria* Dall, 1908, treated by Dall as homonym of non-existent '*Duplicaria* Rafinesque, 1833'; type species *Buccinum duplicatum* Linnaeus, 1758, by typification of replaced name); *Myurellisca* Bartsch 1923, type species *Myurella duplicatoides*

Bartsch, 1923, OD); *Pervicacia* Iredale, 1924 (type species *Terebra ustulata* Deshayes, 1857, OD).

Type species: *Buccinum duplicatum* Linnaeus, 1758; OD.

Definition: Primarily defined based on phylogenetic analysis, including all species in clade F1 of Modica *et al.* (2019) and, in addition, species that show shell morphology, anatomical or genetic characteristics closely comparable with *Duplicaria duplicata* or any genetically proven member of genus.

Diagnosis. Diagnostic nucleotide combinations in Table 2.

Shell: Elongate, small to large, 20–100 mm, with wide aperture, predominant axial sculpture, either continuous from suture to suture or interrupted by shallow to deep subsutural indentation. Spiral structure obsolete, sometimes microscopic striae or weak band joining nodes.

Anatomy: Rhynchodeal introvert small; salivary glands and radular sac present; radula of solid curved marginal teeth attached to strong membrane. Venom gland, proboscis and accessory proboscis structure absent.

Distribution: Tropical and subtropical Indo-Pacific, West Africa.

Remarks: According to shell morphology, three distinct clusters can be delineated:

Duplicaria duplicata group. Small to large shells, 25–100 mm; paucispiral protoconch; sculpture of strong axial ribs. Deep narrow spiral groove delineating distinct flattened subsutural band; no spiral sculpture. Whorl outline flattened, or shouldered due to elevated ribs below subsutural band.

Duplicaria tristis group. Small shells, 10–30 mm; paucispiral protoconch; sculpture of strong axial ribs, subsutural area weakly impressed.

Duplicaria tricincta group. Small shells, 10–25 mm; paucispiral protoconch; sculpture of strong spiral ribs. A more convex shape with outline flattened due to elevation of ribs below subsutural area. Ribs weakening on mature whorls.

Included species:

- Duplicaria albozonata* (E. A. Smith, 1875)²;
- D. australis* (E. A. Smith, 1873)²;
- D. badia* (Deshayes, 1859)²;
- D. bernardii* (Deshayes, 1857)¹;
- D. brevicula* (Deshayes, 1859)¹;
- D. concolor* (E. A. Smith, 1873)²;
- D. copula* (Hinds, 1844)²;
- D. costellifera* (Pease, 1869)²;
- D. crakei* (Burch, 1965)²;
- D. duplicata* (Linnaeus, 1758)¹;
- D. dussumierii* (Kiener, 1839)²;
- D. evoluta* (Deshayes, 1859)²;
- D. fictilis* (Hinds, 1844)²;
- D. gemmulata* (Kiener, 1839)³;
- D. helenae* (Hinds, 1844)³;
- D. herberti* n. sp. Malcolm, Terryn & Fedosov¹;
- D. hiradoensis* (Pilsbry, 1921)²;
- D. jukesii* (Deshayes, 1857)²;
- D. juliae* (Aubry, 1999)²;
- D. kieneri* (Deshayes, 1859)²;
- D. kirai* (Oyama, 1962)²;
- D. koreana* (Yoo, 1976)²;
- D. morbida* (Reeve, 1860)²;
- D. mozambiquensis* Bratcher & Cernohorsky, 1982¹;
- D. silvanae* (Aubry, 1999)³;
- D. similis* (E. A. Smith, 1873)²;
- D. sowerbyana* (Deshayes, 1857)²;

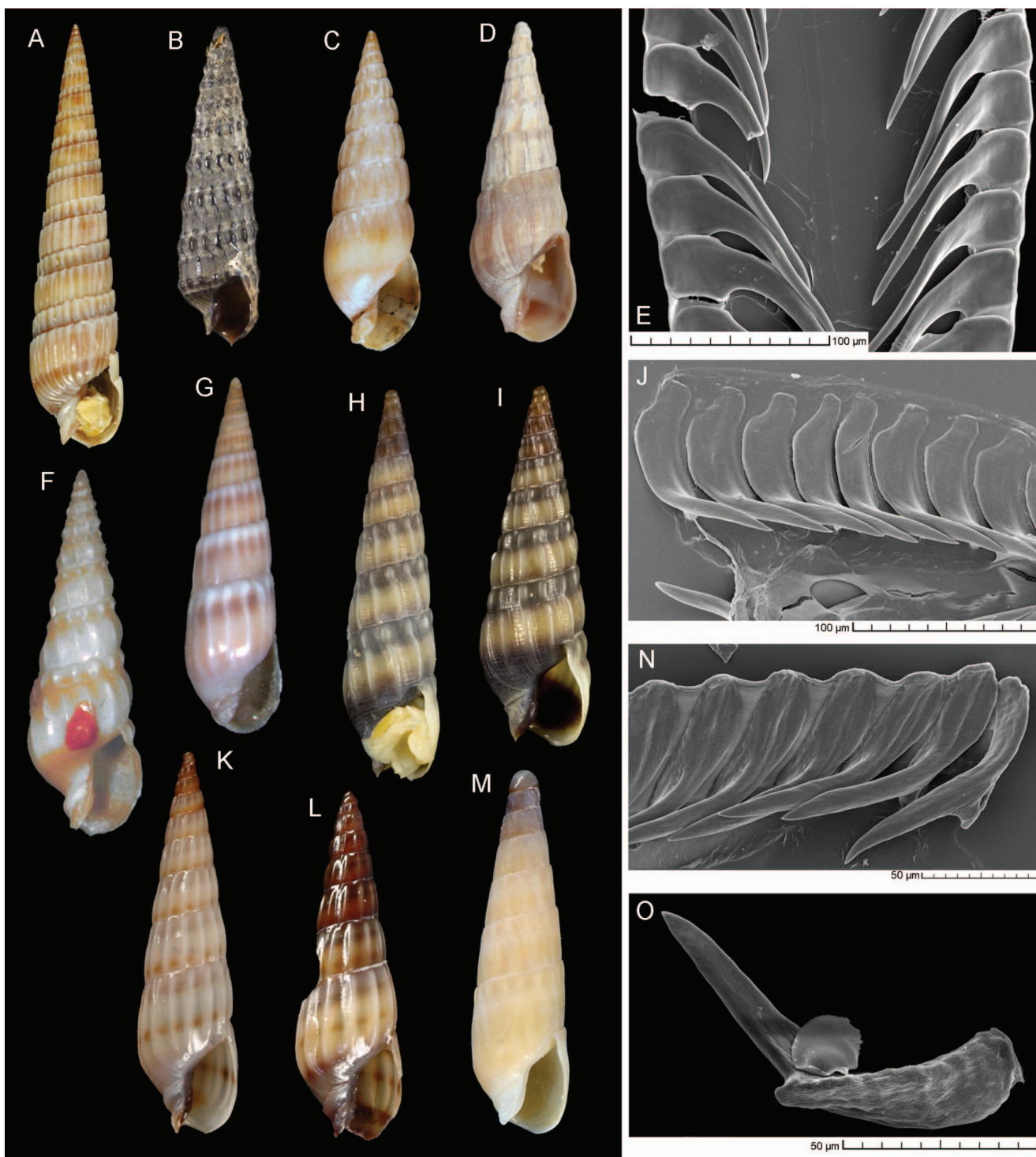


Figure 3. Subfamily Pervicaciinae **A.** *Duplicaria duplicata*, MNHN-IM-2009-29454, WESTERN AUSTRALIA 2011 Stn WB32, 33°33'S, 115°04'E, 5–15 m, 26.7 mm. **B.** *Duplicaria tricineta*, MNHN-IM-2013-5638, PAPUA NIUGINI Stn PD67, 05°15.5'S, 145°46.8'E, 2–6 m, 6.9 mm. **C.** *Duplicaria tristis* lectotype, NHMUK 1979115, 'Seas of Japan', 17.7 mm. **D.** *Duplicaria brevicula*, MNHN-IM-2013-66140, off Namibe, S Angola, 40–60 m, 12.9 mm. **E.** *Duplicaria bernardi* radula, MNHN-IM-2009-10908, Australia, 26°56'607"S; 153°23'813"E, shell broken. **F.** *Terebra fuscobasis* lectotype, NHMUK 1873.7.5.8/1, Persian Gulf, 11.3 mm. **G.** *Terebra nassoides* lectotype, NHMUK 1968251/1, Red Sea, 13.5 mm. **H.** *Partecosta varia*, MNHN-IM-2013-52342, ATIMO VATAE Stn TM27, 24°56.4'S, 47°06.9'E, 0–1 m, 10.4 mm. **I.** *Partecosta sandrinae*, MNHN-IM-2013-52359, INHACA 2011 Stn MM7 PL5, 26°03.7'S, 32°54.1'E, 0–1 m, 8.8 mm. **J.** *Partecosta* n. sp. aff *fuscolutea* radula, MNHN-IM-2009-10133, ATIMO VATAE Stn BS06, 25°26.8'S, 44°54.9'E, 0–27 m, 6.9 mm. **K.** *Partecosta bozzettii* n. sp. paratype, MNHN-IM-2009-10162, ATIMO VATAE Stn TP29, 25°03.7–03.8'S, 46°57.7'E, 3–4 m, 12.4 mm. **L.** *Partecosta trilineata*, MNHN-IM-2009-10164, ATIMO VATAE Stn TP24, 25°03.7–03.8'S, 46°57.6–57.7'E, 2–7 m, 8.2 mm. **M.** *Partecosta macleani*, MNHN-IM-2009-10115 ATIMO VATAE Stn TP19, 25°04.4–04.7'S, 46°55.3–56.3'E, 16–26 m, 8.9 mm. **N, O.** *Partecosta macleani* radula, MNHN-IM-2009-10111, ATIMO VATAE Stn TP19, 25°04.4–04.7'S, 46°55.3–56.3'E, 16–26 m, 12 mm.

Table 2. Genera *Duplicaria* and *Patecosta*: diagnostic combinations of nucleotides in COI alignment.

| | |
|----------------------------|--|
| Genus <i>Duplicaria</i> | |
| Species/sequences analysed | 6/13 |
| Diagnostic nucleotides: | 91: T, 328: A, 436: T, 478: T, 530: A |
| Genus <i>Patecosta</i> | |
| Species/sequences analysed | 8/17 |
| Diagnostic nucleotides: | 31: A, 37: A, 40: T, 55: T, 241: T, 328: T, 343: T, 364: T, 580: T, 604: A, 625: T |

D. trincta (E. A. Smith, 1877)¹;
D. tristis (Deshayes, 1859)¹;
D. ustulata (Deshayes, 1857)²;
D. veronicae (Nicolay & Angioy, 1993)².

Genus *Patecosta* Dance & Eames, 1966

(Fig. 3F–O)

Type species: *Strioterebrum wilkinsi* Dance & Eames, 1966 (= *Terebra fuscobasis* E.A. Smith, 1877); OD.

Definition: Includes species with combination of conchological, anatomical and distributional characteristics closely comparable with *Strioterebrum wilkinsi*, including all species in clade F2 of Modica *et al.* (2019) and any species proven to be a member of this clade.

Diagnosis: Diagnostic nucleotide combinations in Table 2.

Shell: Small, 10–30 mm, pale or tan, often with spiral bands and dark basal area. Protoconch 1.5–3 whorls. Predominant sculpture of axial ribs spanning whorl height, resulting in even, slightly convex whorl outline, typically interrupted by depression or narrow groove forming subsutural row of nodules. Spiral sculpture indistinct or of fine regular striae. Siphonal canal very short, stout, indistinctly or shallowly notched, with strong fasciole. Aperture wide, pyriform.

Anatomy: Rhynchodeal introvert small; salivary glands and radular sac present; radula of solid curved marginal teeth attached to strong membrane. Venom gland, proboscis and accessory proboscis structure absent.

Distribution: Indian Ocean; intertidal and shallow subtidal.

Remarks: Three clusters with varying sculpture patterns can be recognized:

Patecosta fuscobasis group: sculpture of strong ribs and clearly delineated subsutural band forming distinct nodules at intersections with ribs (Fig. 3F–I). Closely comparable with New World genus *Neoterebra*, but can be differentiated by smaller size, wider aperture, usually with wide anterior notch, and solid curved radular teeth.

Patecosta trilineata group: glossy shells sculptured by strong continuous ribs; no distinct spiral sculpture or subsutural band (Fig. 3K, L). Very similar sympatric forms are known in genus *Punctoterebra* (i.e. *Punctoterebra solangeae* Bozzetti, 2015 group) that can only be reliably differentiated by anatomical characters (radula lacking in *P. solangeae*; of solid curved teeth in *Patecosta* spp.).

Patecosta macleani group: flattened whorl outline, very short robust siphonal canal; very weak sculpture of rounded, indistinct subsutural nodules extended into even less distinct axial folds on whorl periphery (Fig. 3M). Some species of *Hastula* are close to *P. macleani*,

but are commonly larger, have polished surface and retain distinct ribbing at least on adapical portions of whorls.

Included species:

Patecosta albofasciata (Bozzetti, 2008)¹ n. comb.;
P. bozzettii n. sp. Malcolm, Terryn & Fedosov¹;
P. fuscolutea Bozzetti, 2008² n. comb.;
P. macleani (Bratcher, 1988)¹ n. comb.;
P. nassoides (Hinds, 1844)¹ n. comb.;
P. sandrinae (Aubry, 2008)¹ n. comb.;
P. trilineata (Bozzetti, 2008)¹ n. comb.;
P. varia (Bozzetti, 2008)¹ n. comb.;
P. fuscobasis (E.A. Smith, 1877)² n. comb.;
P. fuscocincta (E.A. Smith, 1877)² n. comb.;
P. herosae (Terryn & Rosado, 2011)² n. comb.;
P. macandrewii (E.A. Smith, 1877)² n. comb.;
P. padangensis (Thiele, 1925)² n. comb.;
P. tantilla (E.A. Smith, 1873)² n. comb.;
P. tenera (Hinds, 1844)³ n. comb.;
P. veliae (Aubry, 1991)³ n. comb.

Subfamily TEREBRINAE Mörch 1852

Type genus: *Terebra* Bruguière, 1789

Shell: Elongate, multiwhorled, with varying whorl outline, sculpture and colour pattern. Aperture very small relative to shell height, moderately wide to very wide, with short, straight or very weakly recurved, widely open siphonal canal.

Anatomy: Rhynchodeal introvert large, occupying most of rhynchocoel cavity. Radula, proboscis, venom glands, salivary glands and accessory proboscis structure present or absent. Radula (when present) of hypodermic, flat, semi-enrolled or (rarely) duplex marginal teeth, never of solid type.

Remarks: Although the subfamily is consistent with a highly supported clade in the phylogenetic tree of Modica *et al.* (2019), its circumscription (i.e. based on shared synapomorphic characters) is difficult. Among such characters only the large rhynchodeal introvert that occupies most of the rhynchocoel cavity is consistent. Foregut anatomy offers some other characters that can facilitate practical recognition of Terebrinae. Until proved otherwise, all the radula-less terebrids are in the Terebrinae, as well as all species with flat, semi-enrolled or hypodermic radular teeth. In practice, recognition of the terebrines can be aided by the fact that the two other terebrid subfamilies contain few species and are generally clearly delineated; therefore, all species that are definitely not members of either Pellifroniinae or Perviciacinae are here considered in Terebrinae.

Genus *Terebra* Bruguière, 1789

(Figs 4, 5)

Type species: *Buccinum subulatum* Linnaeus, 1767; SD (Lamarck, 1799: 71).

Synonyms: *Triplostephanus* Dall, 1908 (type species *Terebra triseriata* Gray, 1834; OD); *Cinguloterebra* Oyama, 1961 (type species *Terebra hedleyana* Pilsbry, 1905 = *Terebra adamsii* E.A. Smith, 1873; OD); *Dimidacis* Iredale, 1929 (new name for *Terebrina* Bartsch, 1923, non Rafinesque, 1815; type species *Terebra cingulifera* Lamarck, 1822, by typification of replacement name); *Myurellina* Bartsch, 1923 (type species *Terebra ornata* Gray, 1834; OD); *Subula* Schumacher, 1817 (unnecessary replacement name for *Terebra*; type species *Buccinum subulatum*, by typification of replacement name); *Terebrina* Bartsch, 1923 (invalid: junior homonym of

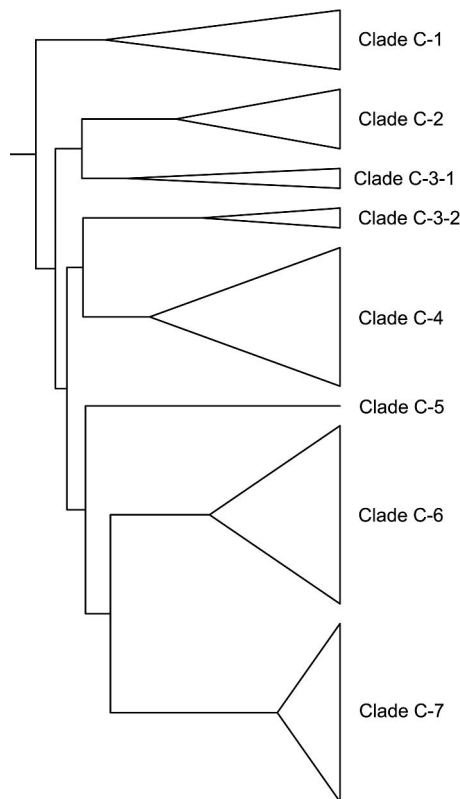


Figure 4. Phylogenetic relationships of the subclades of the genus *Terebra*. Schematic of subclades C1–C7 in the genus *Terebra*; see [Supplementary Material Fig. S1](#) for species composition (after [Modica et al., 2019](#)).

Terebrina Rafinesque, 1815; type species *Terebra cingulifera* Lamarck, 1822, OD); *Terebrum* Montfort, 1810 (unnecessary emendation of *Terebra* Bruguière, 1789; type species *Buccinum subulatum* Linnaeus, 1767, by typification of replaced name); *Paraterebra* Woodring, 1928 (type species *Terebra texana* Dall, 1898; OD); *Panaterebra* Olsson, 1967 (type species *Terebra robusta* Hinds, 1844; OD).

Definition: Primarily defined based on phylogenetic analysis of [Modica et al. \(2019\)](#); includes all species in clade C of [Modica et al. \(2019\)](#), and species showing resemblance in shell morphology, anatomy and distribution to *Terebra subulata* or any genetically proven member of this clade.

Diagnosis: Diagnostic nucleotide combinations (provided separately for the seven clades of the genus inferred by [Modica et al. \(2019\)](#) in Table 3.

Shell: Elongate, medium-sized to large, reaching 192 mm; truncated base abruptly constricted to siphonal canal, sometimes with distinct angulation. Sculpture from very weak, limited to often obsolete subsutural groove, to very strong. Subsutural band simple, or consisting of two closely set cords, often gemmate. Lower whorl portion smooth or with varying sculpture, with spiral elements being as strong or stronger than axials. Shell base separated from siphonal canal by concave waist. Aperture elongate to quadrangular.

Anatomy: Rhynchodeal introvert, proboscis, venom gland, salivary glands and radula well developed. Radula of hypodermic marginal teeth, with only bases attached to strongly reduced membrane. Accessory proboscis structure present or absent.

Distribution: Indo-Pacific, West Africa, tropical East Pacific, Caribbean and Western Atlantic.

Remarks: The genus *Terebra* is here established with boundaries consistent with clade C of [Modica et al. \(2019\)](#). This clade is subdivided into eight lineages, referred to as C1–C7 (Fig. 4), their relationships being unresolved. Clades C1, C2, C3-2, C4 and C7 are well supported; clade C5 comprises one species only—*T. argus*. Because of the extreme heterogeneity of clade C, our attempts to provide a molecular diagnosis failed and, therefore, we compiled separate diagnoses for the inferred lineages within clade C (Table 3). Although lineages C3-1 and C3-2 do not constitute a supported clade, this arrangement is not rejected by the phylogenetic analysis and we have grouped them together based on biogeographic considerations. The genus *Terebra* is also very heterogeneous in regard to shell morphology (Fig. 5); some common morphotypes can be distinguished, but their correspondence with inferred phylogenetic groupings is far from perfect. Below we provide a brief overview of these morphotypes.

Typical *Terebra* are characterized by a weakly sculptured or smooth, medium-sized shell, with gently convex or subcylindrical whorls, often bearing a pattern of large spots. Species referable to this morphotype are included in clades C1 (*T. subulata* and *T. guttata*), C4 (*T. ornata*) and C6 (*T. argus*). This morphotype is closest in appearance to *Oxymeris* and differentiation can be difficult. In most cases *Terebra* species can be recognized by the narrower anterior notch; however, for definite allocation, examination of the foregut is advised to determine whether proboscis and radula are present.

The *fenestrata* morphotype comprises the most heavily sculptured species, with a strong, often elevated, gemmate subsutural band that is closely followed by a second spiral band of similar morphology, but usually weaker and/or narrower. The lower portion of the whorl is sculptured with spiral cords, or has a cancellate pattern. Species exhibiting this morphotype include clade C2, and some strikingly similar species in clades C7 (*T. aff. adamsii*, *T. fenestrata* MNHN IM-2013-14908, *T. anilis*) and C8 (*T. cumingi* species complex). Strong, often elevated, gemmate or beaded spiral elements readily differentiate this morphotype from most terebrid genera. However, a similar pattern is present in *Granuliterebra*, the species of which are differentiated by their single subsutural band and usually by predominantly axial sculpture on the lower portion of the whorl.

The *Triplostephanus* morphotype unifies species with a very high spire and very small, quadrate aperture. Whorls are flattened or slightly concave due to a raised subsutural band and the lower part of the whorl is sculptured by regular cords, while axial sculpture is not developed. Most species in clade C5 exhibit this morphotype; however, species with subcylindrical whorls and stepped spire outline (e.g. *T. laevigata* and *T. funiculata*) are found in C5 as well. The combination of a very high spire and flattened whorl outline makes this morphotype very distinctive among Terebridae.

While the three described morphotypes represent extremes of the conchological diversity of *Terebra*, there is a plethora of intermediate forms. For example, *T. taurina* and *T. fujitai* of clade C3 have a divided ribbed subsutural band, similar to the *fenestrata* morphotype, although notably lower. Similarly, a divided, nodulose subsutural band is present in *T. corrugata*, a species close to *T. subulata* in clade C1. The apparent lack of phylogenetic congruence in the distribution of these morphotypes across clade C precludes assignment of any taxonomic status to them. Moreover, the general lack of homogeneity in shell characteristics within the subclades of *Terebra* makes their establishment as supraspecific taxonomic units pointless as well.

Taking into consideration the great conchological variation within *Terebra*, it is difficult to suggest general diagnostic criteria for this genus. However, it should be noted that the predominantly spiral sculpture below the subsutural band allows differentiation of *Terebra* from most other terebrid genera. Similarly, a divided subsutural band has not been recorded in any species outside *Terebra*.

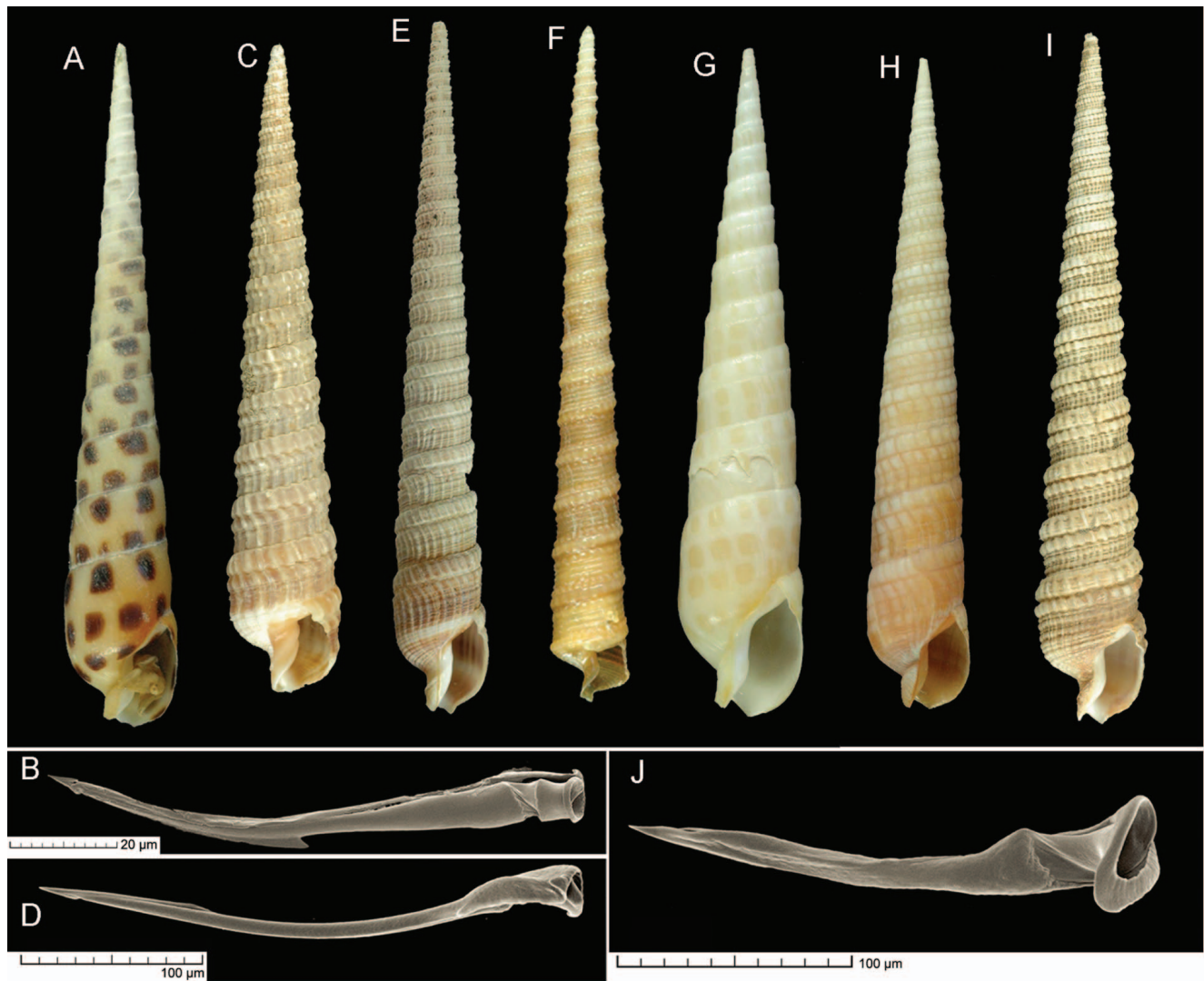


Figure 5. Genus *Terebra*. **A.** *T. subulata* (Subclade C1), MNHN-IM-2013-47287, KAVIENG 2014 Stn KR12, 02°36.3'S, 150°46.3'E, 0 m, 62.8 mm. **B.** *T. guttata* (Subclade C1) radula, MNHN-IM-2007-30376, SANTO 2006 Stn FR08, 15°33.1'S, 167°12.2'E, 3–40 m, 74.6 mm. **C.** *T. aff. fenestrata* (Subclade C2), MNHN-IM-2013-46010, MADEEP Stn CP4330, 06°07.63'S, 149°12.1'E, 315–625 m, 43.5 mm. **D.** *T. aff. fenestrata* 2 (Subclade C2) radula, MNHN-IM-2007-30418, PANGLAO 2005 Stn CP2331, 09°39'N, 123°48'E, 256–268 m, 23.1 mm. **E.** *T. fujitai* (Subclade C3-1), MNHN-IM-2007-15724, PANGLAO 2005 Stn CP2343, 09°27'N, 123°49'E, 273–356 m, 95.7 mm. **F.** *T. triseriata* (Subclade C4), MNHN-IM-2013-51211, KAVIENG 2014 Stn KD13, 02°44.6'S, 150°43.1'E, 0–15 m, 25.6 mm. **G.** *T. argus* (Subclade C5), MNHN-IM-2013-46900, KAVIENG 2014 Stn KR06, 02°36.3'S, 150°46.2'E, 3–12 m, 53.7 mm. **H.** *T. babylonia* (Subclade C6), MNHN-IM-2013-51267, KAVIENG 2014 Stn KR54, 02°42.3'S, 150°39.1'E, 7–10 m, 38.5 mm. **I.** *T. sp. aff. cumingii* (Subclade C7), MNHN-IM-2013-46237, MADEEP Stn CP4335, 06°05'S, 149°18'E, 240–250 m, 62.5 mm. **J.** *T. cingulifera* (Subclade C7) radula, MNHN-IM-2007-30382, SANTO 2006 Stn VM32, 15°26.6'S, 167°15.2'E, 0–1 m, 49.7 mm.

These characters, in combination with the presence of a complete complex of foregut organs and radular teeth of hypodermic type, allow for reliable differentiation of *Terebra* species.

Included species:

Terebra achates Weaver, 1960²;
T. adamsii (E. A. Smith, 1873)²;
T. albocancellata Bratcher, 1988³;
T. albomarginata Deshayes, 1859¹*;
T. amanda Hinds, 1844¹;
T. anilis (Röding, 1798)¹;
T. archimedis Deshayes, 1859¹*;
T. argosyia Olsson, 1971²;
T. argus Hinds, 1844¹;
T. babylonia Lamarck, 1822¹;
T. balabacensis Aubry & Picardal, 2011³;
T. bellanodosa Grabau & King, 1928³;

T. binii (Aubry, 2014)²;
T. boucheti (Bratcher, 1981)²;
T. bratcherae Cernohorsky, 1987³;
T. caddeyi (Bratcher & Cernohorsky, 1982)²;
T. caelata Adams & Reeve, 1850¹*;
T. castaneostriata Kosuge, 1979³;
T. cingulifera Lamarck, 1822¹;
T. circinata Deshayes, 1857²*;
T. cognata E. A. Smith, 1877³;
T. commaculata (Gmelin, 1791)²;
T. connelli (Bratcher & Cernohorsky, 1985)²;
T. consobrina Deshayes, 1857¹;
T. corrugata Lamarck, 1822¹;
T. cossignanii Aubry, 2008²;
T. cumingii (Deshayes, 1857)¹;
T. deshayesii Reeve, 1860²;
T. donpisorii Terryn, 2017³;

Table 3. Diagnostic combinations of nucleotides for seven subclades of genus *Terebra* in COI alignment. Subclades named as in [Modica et al. \(2019\)](#).

| | |
|----------------------------|--|
| C1 | |
| Species/sequences analysed | 4/30 |
| Diagnostic nucleotides: | 31: A, 242: C, 265: G, 508: T, 547: T, 607: A |
| C2 | |
| Species/sequences analysed | 4/16 |
| Diagnostic nucleotides: | 190: T, 334: A, 536: T, 538: A, 607: G |
| C3 | |
| Species/sequences analysed | 5/34 |
| Diagnostic nucleotides: | 58: T, 94: A, 154: C, 253: A, 283: G, 337: A, 409: T, 433: G, 553: T, 631: T, 641: T |
| C4 | |
| Species/sequences analysed | 9/71 |
| Diagnostic nucleotides: | 58: T, 121: T, 127: T, 278: C, 289: T, 641: C, 643: T |
| C5 | |
| Species/sequences analysed | 1/9 |
| Diagnostic nucleotides: | 61: G, 274: G, 412: T, 508: C |
| C6 | |
| Species/sequences analysed | 8/44 |
| Diagnostic nucleotides: | 88: G, 95: T, 148: A, 278: C, 379: T, 409: T, 481: G, 484: G, 499: G, 562: T |
| C7 | |
| Species/sequences analysed | 10/19 |
| Diagnostic nucleotides: | 76: T, 79: T, 221: G, 222: T |

T. elliscrossi (Bratcher, 1979)¹;
T. erythraensis Terry & Dekker, 2017³;
T. eximia (Deshayes, 1859)²;
T. fenestrata (Hinds, 1844)¹;
T. fernandae Aubry, 1995³;
T. fernandesi Bouchet, 1983³;
T. fijiensis (E. A. Smith, 1873)³;
T. floridana (Dall, 1889)³;
T. formosa Deshayes, 1857¹;
T. fujitai (Kuroda & Habe, 1952)¹;
T. funiculata Hinds, 1844¹;
T. gabriellae Aubry, 2008³;
T. gaeae Aubry, 2008³;
T. giorgioi Aubry, 1999³;
T. grayi E. A. Smith, 1877³;
T. guineensis Bouchet, 1983³;
T. guttata (Röding, 1798)¹;
T. helichrysum Melville & Standen, 1903³;
T. histrio Deshayes, 1857³;
T. hoarui (Drivas & Jay, 1988)¹;
T. insalli (Bratcher & Burch, 1976)²;
T. irregularis Thiele, 1925³;
T. jacksoniana (Garrard, 1976)³;
T. jenningsi (Burch, 1965)¹;
T. knudseni Bratcher, 1983²;
T. laevigata Gray, 1834¹;
T. lauretanae Tenison-Woods, 1878³;
T. levantina Aubry, 1999³;
T. ligata Hinds, 1844²;
T. lillianae Withney, 1976²*;
T. lima (Deshayes, 1857)²;
T. lindae Petuch, 1987²;

T. mamillata (Watson, 1886)²;
T. mariesi (E. A. Smith, 1880)²;
T. marrowae (Bratcher & Cernohorsky, 1982)²;
T. montgomeryi Burch, 1965²;
T. neglecta (Poppe, Tagaro & Terry, 2009)²;
T. nodularis Deshayes, 1859³;
T. noumeaensis Aubry, 1999³;
T. ornata Gray, 1834¹;
T. pellyi E. A. Smith, 1877³;
T. picta Hinds, 1844³;
T. polygonia Reeve, 1860³;
T. praelonga Deshayes, 1859²;
T. pretiosa Reeve, 1842²;
T. pseudopicta Aubry, 2008³;
T. pseudoturbonilla Talavera, 1975³;
T. punctatostrata Gray, 1834²;
T. punctum (Poppe, Tagaro & Terry, 2009)²;
T. quoygaimardi Cernohorsky & Bratcher, 1976¹;
T. raybaudii Aubry, 1993²;
T. reticularis (Pecchioli in Sacco, 1891)³;
T. robusta Hinds, 1844¹;
T. rosae Aubry, 2015³;
T. russetae (Garrard, 1976)³;
T. salisburyi Drivas & Jay, 1998²;
T. stearnsi Pilsbry, 1891¹;
T. straminea Gray, 1834¹*;
T. subangulata Deshayes, 1859³;
T. subulata (Linnaeus, 1767)¹;
T. succinea Hinds, 1844³;
T. swobodai Bratcher, 1981³;
T. tagaroae Terry, 2017²;
T. taiwanensis Aubry, 1999³;
T. taurina (Lightfoot, 1786)¹;
T. tessellata Gray, 1834²;
T. tricolor G. B. Sowerby I, 1825¹;
T. triseriata (Gray, 1834)¹;
T. twilae Bouchet, 1983³;
T. unicolor Preston, 1908¹*;
T. vanuatuensis Aubry, 1999³;
T. vappereau Tröndlé, Boutet & Terry, 2013²;
T. venilia Tenison-Woods, 1879³;
T. vicdani (Kosuge, 1981)²;
T. virgo Schepman, 1913³;
T. waikikiensis (Pilsbry, 1921)².

Genus *Hastula* H. Adams & A. Adams, 1858

(Fig. 6A–E)

Type species: *Buccinum strigilatum* Linnaeus, 1758; SD, [Cossmann \(1896\)](#).

Synonyms: *Impages* E.A. Smith, 1873 (type species *Terebra caerulea* Lamarck, 1822 = *Buccinum hecticum* Linnaeus, 1758; SD, [Cossmann, 1896](#)); *Acuminia* Dall, 1908 (type species *Buccinum lanceatum* Linnaeus, 1767; OD); *Hastulina* Oyama, 1961 (type species *Terebra casta* Hinds, 1844; OD); *Egentelaria* Rehder, 1980 (type species *Terebra stylata* Hinds, 1844; OD).

Definition: Includes all species in clade D of [Modica et al. \(2019\)](#), and those that show a combination of conchological, anatomical and distribution characteristics closely comparable with *Hastula strigilata* or any genetically proven member of the clade.

Diagnosis: Diagnostic nucleotide combinations provided for entire clade with exception of four specimens of *H. albula* (see Material and Methods) and, separately, for subclade *H. albula*–*H. natalensis*–*H. aff. casta* of clade D (Table 4).

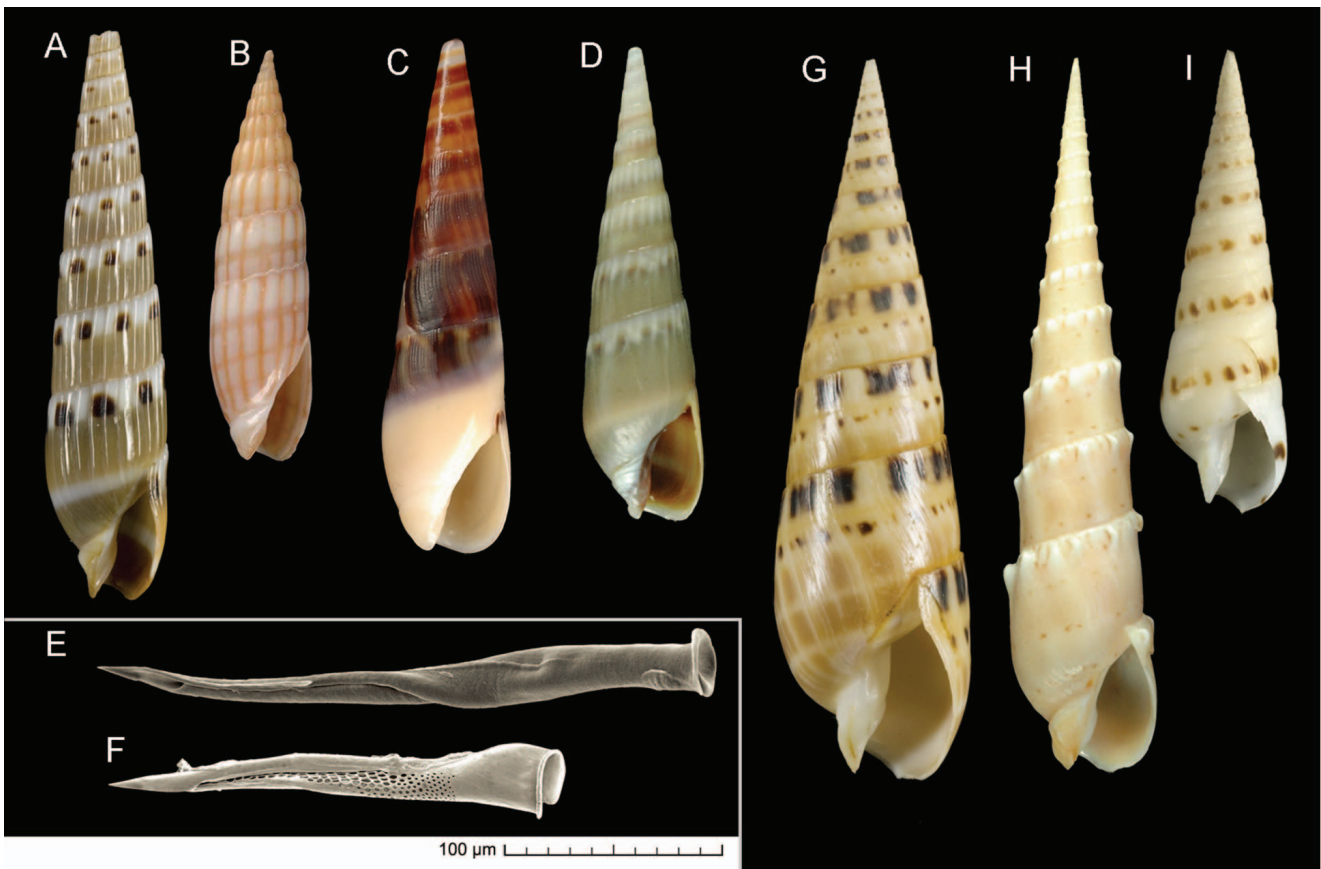


Figure 6. Genera *Hastula* and *Oxymeris*. **A.** *H. strigilata*, MNHN-IM-2013-16102, PAPUA NIUGINI Stn PM41, 05°08.1'S, 145°49.3'E, 0–1 m, 32.4 mm. **B.** *H. solida*, MNHN-IM-2009-07098, Inhaca I., Mozambique, 25°59.0'S, 32°54.5'E, 0 m, 25.6 mm. **C.** *H. hectica*, MNHN-IM-2009-11870, Tahiti, 17°30' 28.28"S, 149°27'0.14"W, 0 m, 35.6 mm. **D.** *H. cinerea*, MNHN-IM-2013-9455, KARUBENTHOS 2012 Stn GM19, 16°21.3'N, 61°44.92'W, 0–1 m, 20.4 mm. **E.** *H. lanceata* radula, MNHN IM-2007-30535, PANGLAO 2004 Stn B1, 9°33.0'N, 123°46.50'E, 8–14 m, 32.5 mm (broken). **F.** *H. hectica* radula., Panglao I., Bohol., Philippines, intertidal. **G.** *O. maculata*, MNHN-IM-2013-40074, Marquesas Is, 113 mm. **H.** *O. crenulata*, MNHN-IM-2013-46877, KAVIENG 2014 Stn KR06, 02°36.3'S, 150°46.2'E, 3–12 m, 85.9 mm. **I.** *O. felina*, MNHN-IM-2013-10283, PAPUA NIUGINI Stn PB05, 05°11.7'S, 145°49.4'E, 0–20 m, 31 mm.

Shell: Small to medium-sized, shiny, 12–90 mm. Protoconch paucispiral or multispiral, about 1–5 whorls. Axial sculpture of crenulations on subsutural portion of whorl, or fine ribs on part or throughout whorl height; spiral sculpture of single subsutural groove, occasionally with additional row of punctations. Siphonal canal stout, very short, with well-developed fasciole. Aperture elongate to rounded.

Anatomy: Rhynchodeal introvert, proboscis, venom gland, salivary glands and radula well developed. Radula of hypodermic marginal teeth attached to thin, reduced membrane; walls of marginal teeth often with multiple perforations (Fig. 6E, F)

Distribution: Indo-Pacific, West Africa, Caribbean.

Remarks: Species of *Hastula* are rather easy to recognize among Terebridae by their typically shiny shells, with fine close-set axial ribs and usually by the lack of a clearly defined subsutural band. The shell morphology in the *Partecosta macleani* group closely resembles that of *Hastula*; however, the latter is usually larger at maturity, while shells of comparable size can be differentiated by texture—a polished surface in *Hastula* vs dull in *Partecosta*. Furthermore, species of *Hastula* possess a venom gland and hypodermic radular teeth, whereas *Partecosta* species lack a venom gland and their radulae teeth are solid.

Table 4. Genus *Hastula*: diagnostic combinations of nucleotides in COI alignment.

| Genus <i>Hastula</i> (except four specimens of <i>H. albula</i>) | |
|---|---|
| Species/sequences analysed | 18/91 |
| Diagnostic nucleotides: | 28: A, 67: T, 95: C, 181: T, 221: C, 222: C, 253: A, 581: T, 598: A |
| Subclade <i>H. albula</i> – <i>H. natalensis</i> – <i>H. aff. casta</i> | |
| Species/sequences analysed | 3/17 |
| Diagnostic nucleotides | 49: G, 347: C, 349: T, 517: T |

Included species:

Hastula aciculina (Lamarck, 1822)²;
H. acumen (Deshayes, 1859)¹;
H. alboflava Bratcher, 1988²;
H. albula (Menke, 1843)¹;
H. androyensis Bozzetti, 2008²;
H. anomala (Gray, 1834)²;
H. anosyana (Bozzetti, 2016)²;
H. apicistincta (G. B. Sowerby III, 1900)²;
H. bacillus (Deshayes, 1859)²;
H. casta (Hinds, 1844)¹;
H. celidonota (Melvill & Sykes, 1898)²;
H. cernohorskyi Burch, 1965²;
H. cinerea (Born, 1778)¹;

H. continua Deshayes, 1859²;
H. crossii (Deshayes, 1859)¹*;
H. cuspidata (Hinds, 1844)²;
H. denizi Rolán & Gubbioli, 2000²;
H. engi Malcolm & Terryn, 2017²;
H. escondida (Terryn, 2006)²;
H. exacuminata Sacco, 1891²;
H. filmerae (G. B. Sowerby III, 1906)²;
H. hamamotoi Tsuchida & Tanaka, 1999²;
H. hastata (Gmelin, 1791)¹;
H. hectica (Linnaeus, 1758)¹;
H. imitatrix (Auffenberg & Lee, 1988)²;
H. inconstans (Hinds, 1844)²;
H. knockeri (E. A. Smith, 1872)²;
H. lanceata (Linnaeus, 1767)¹;
H. leloeufti Bouchet, 1983²;
H. lepida (Hinds, 1844)²;
H. marqueti (Aubry, 1994)²;
H. maryleeae R. D. Burch, 1965²;
H. matheroniana (Deshayes, 1859)¹;
H. nana (Deshayes, 1859)²;
H. natalensis (E. A. Smith, 1903)¹*;
H. parva (Baird, 1873)¹;
H. penicillata (Hinds, 1844)¹;
H. philippiana (Deshayes, 1859)²;
H. puella (Thiele, 1925)¹;
H. raphanula (Lamarck, 1822)¹;
H. rufopunctata (E. A. Smith, 1877)²;
H. salleana (Deshayes, 1859)¹;
H. sandrogarii Ryall, Terryn & Rosado, 2017²;
H. solida (Deshayes, 1857)¹;
H. strigilata (Linnaeus, 1758)¹;
H. stylata (Hinds, 1844)¹;
H. tenuicollata Bozzetti, 2008¹;
H. tiedemani Burch, 1965²;
H. venus Aubry, 2008²;
H. verreauxi (Deshayes, 1857)¹;
H. westralia (Aubry, 1999)²;
H. damiae (Aubry, 2008)³.

Genus *Oxymeris* Dall, 1903

(Fig. 6F–H)

Type species: *Buccinum maculatum* Linnaeus, 1758; OD.

Synonyms: *Abretia* H. & A. Adams, 1853 (invalid, junior homonym of *Abretia* Rafinesque, 1814; type species *Terebra cerithina* Lamarck, 1822; SD, [Dall, 1908](#)); *Abretiella* Bartsch, 1923 (replacement name for *Abretia* H. & A. Adams, 1853; type species *Terebra cerithina* Lamarck, 1822; by typification of replaced name); *Nototerebra* Cotton, 1947 (type species *Terebra albida* Gray, 1834; OD).

Definition: Includes all species in clade B of [Modica et al. \(2019\)](#), and those that show a combination of conchological, anatomical and distribution features closely comparable with *Oxymeris maculata* or any genetically proven member of the clade.

Diagnosis: Diagnostic nucleotide combinations in Table 5.

Table 5. Genus *Oxymeris*: diagnostic combination of nucleotides in COI alignment.

| | |
|----------------------------|---|
| Species/sequences analysed | 11/99 |
| Diagnostic nucleotides: | 46: T, 67: A, 91: T, 127: T, 130: A, 223: T, 250: T, 485: C, 631: T |

Shell: Medium-sized to large, reaching 273 mm; weakly sculptured, typically with orthoconoid spire and rather wide aperture. Protoconch multispiral, 3–3.75 whorls. Sculpture of subsutural band, smooth or with regular crenulations; juvenile sculpture often consisting of axial ribs. Whorls flattened in outline; last adult whorl inflated; siphonal canal short, stout. Aperture wide, elliptic to rounded.

Anatomy: Rhynchodeal introvert very large, proboscis absent or vestigial, salivary glands absent or very small, radula venom gland and accessory proboscis structure absent.

Distribution: Indo-Pacific, tropical East Pacific, West Africa.

Remarks: Species of *Oxymeris* are among the largest terebrids and can usually be easily identified by their large, shiny shells, with an orthoconoid or even slightly acuminate spire, often with a bulbous last whorl, a very wide aperture and a very short siphonal canal separated from the shell base by a deep groove. Nevertheless, some smaller species (e.g. *O. cerithina*) have a spire with convex sides and superficially resemble medium-sized *Punctoterebra* and *Myurella* species. However, in most cases (except *O. crenulata*), the *Oxymeris* species can be recognized by the complete lack of axial sculpture other than growth lines, while axial elements of varying strength and shape are present in *Punctoterebra*, *Myurella* and most other terebrid genera. Finally, widely spaced deep spiral grooves differentiate *Perirhoe* from *Oxymeris*.

Included species:

Oxymeris albida (Gray, 1834)²;
O. areolata (Link, 1807)¹;
O. barbieri (Aubry, 2008)²;
O. caledonica (G. B. Sowerby III, 1909)¹;
O. cerithina (Lamarck, 1822)¹;
O. chlorata (Lamarck, 1822)¹;
O. consors (Hinds, 1844)¹;
O. crenulata (Linnaeus, 1758)¹;
O. dillwynii (Deshayes, 1859)²;
O. dimidiata (Linnaeus, 1758)¹;
O. fatua (Hinds, 1844)²;
O. felina (Dillwyn, 1817)¹;
O. gouldi (Deshayes, 1857)²;
O. lineopunctata (Bozzetti, 2008)²;
O. maculata (Linnaeus, 1758)¹;
O. ngai Thach, 2016²;
O. senegalensis (Lamarck, 1822)²;
O. strigata (G. B. Sowerby I, 1825)¹;
O. suffusa (Pease, 1869)²;
O. swinneni Terryn & Ryall, 2014²;
O. trochlea (Deshayes, 1857)²;
O. troendlei (Bratcher, 1981)¹.

Genus *Myurella* Hinds, 1845

(Fig. 7A–D)

Type species: *Terebra affinis* Gray, 1834; SD, [Cossmann \(1896\)](#).

Synonyms: *Clathroterebra* [Oyama, 1961](#) (type species *Terebra fortunei* Deshayes, 1857; OD); *Decorihastula* [Oyama, 1961](#) (type species *Terebra affinis* Gray, 1834; OD); *Terenolla* Iredale, 1929 (type species *Terebra pygmaea* Hinds, 1844; OD).

Definition: Primarily defined based on phylogenetic analysis of [Modica et al. \(2019\)](#), comprising species in clade E1 of [Modica et al. \(2019\)](#) and additionally those that show shell morphology, anatomical or genetic characteristics closely comparable

with *Myurella affinis* or any genetically proven member of the clade.

Diagnosis: Diagnostic nucleotide combinations in Table 6.

Shell: very small to medium-sized, with elongated, with high orthoconoid spire; sculpture of arcuate or undulating ribs, fine and narrow to flat and wide.

Anatomy: Rhynchodeal introvert very large, proboscis, radula and venom gland absent, salivary glands and accessory proboscis structure present in few species.

Distribution: Indo-Pacific; intertidal to upper bathyal depths.

Remarks: In regard to shell morphology, four distinct groups can be recognized:

Myurella affinis group. Shell medium-sized; axial sculpture of low, wide, flattened ribs; subsutural band with elongate nodules separated by punctations, which are also pronounced in interspaces between axial ribs. Similar species that were earlier classified in *Myurella*, but do not belong in the *T. affinis* clade (i.e. *M. undulata*, *M. columellaris* and *M. kilburni*) are here reclassified in the genus *Myurellopsis*. Typical *Myurella* species can be recognized by the lower axials and shallower interstices between them. Because of the overall flatter axials, the subsutural band is visually continuous in *Myurella*; on the contrary, in *Myurellopsis*, due to the more elevated ribs, the subsutural band is represented by a row of nodules.

Myurella pseudofortunei group. Shell elongate, of variable size (17–60 mm), with very high, slender spire, evenly convex whorls, indistinct subsutural band and narrow, clearly arcuate axial ribs; interspaces with regular striae. Species of this group exhibit a very distinctive morphotype, which has little in common with other species here attributed to *Myurella*. Terebrids with this morphology were previously placed in the genus *Clathroterebra*; however, in the analysis of Modica et al. (2019), they formed several lineages unrelated to *Clathroterebra*; morphological differences between these lineages are still to be studied.

Myurella pygmaea group. Shell small, c. 10 mm; convex spire profile, straight sides to whorls; very short, tapering siphonal canal. Axial sculpture of numerous fine oblique ribs; subsutural band and other spiral elements absent. The group includes one species, *M. pygmaea*, formerly classified in the monotypic genus *Terenolla*. The very small but rather solid, finely ribbed shell is easily recognizable among terebrids; its recognition is further aided by the pattern of flesh-colour background with contrasting dark brown spiral line just below the suture.

Myurella amoena group. Shell medium-sized; sculptured with fine to strong ribs, subsutural band defined by line of punctations, spiral sculpture of narrow grooves or cords. The species of this group form a well-supported clade and exhibit a shallow-water morphotype that was formerly classified in *Hastulopsis*. Similar deeper-water species are found in *Maculager* n. gen., most of which can be recognized by having a row of large spots on the periphery. The other similar species remain within *Hastulopsis*, comprising a number of Indian Ocean and Japanese endemic species. Species of the *M. amoena* group have strong but narrow ribs that are notably stronger than spiral elements. In *Myurellopsis* the ribs are about as strong as in the *M. amoena* group, but are wider and rounded, with interstices narrower than the ribs. Both *Hastulopsis* and *Maculager* comprise species with axial and spiral elements of comparable strength, resulting in a rather cancellate pattern, and a continuous subsutural band.

Included species:

- Myurella affinis* (Gray, 1834)¹;
- M. amoena* (Deshayes, 1859)¹;

- M. andamanica* (Melville & Sykes, 1898)¹*;
- M. bilineata* (Sprague, 2004)¹;
- M. brunneobandata* (Malcolm & Terryn, 2012)¹;
- M. burchi* (Bratcher & Cernohorsky, 1982)¹;
- M. conspersa* (Hinds, 1844)¹;
- M. dedonderi* (Terryn, 2003)¹;
- M. eburnea* (Hinds, 1844)¹;
- M. flavofasciata* (Pilsbry, 1921)¹;
- M. fortunei* (Deshayes, 1857)¹;
- M. mactanensis* (Bratcher & Cernohorsky, 1982)²;
- M. mindanaensis* (Aubry, 2008)¹;
- M. multistriata* (Schepman, 1913)¹;
- M. nebulosa* (G. B. Sowerby I, 1825)¹;
- M. pertusa* (Born, 1778)¹;
- M. picardali* (Aubry, 2011)²;
- M. pseudofortunei* (Aubry, 2008)¹;
- M. pygmaea* (Hinds, 1844)¹ n. comb.;
- M. russoi* (Aubry, 1991)²;
- M. suduirauti* (Terryn & Conde, 2004)²;
- M. wellsilviae* (Aubry, 1994)¹.

Genus *Punctoterebra* Bartsch, 1923

(Fig. 8)

Type species: *Terebra nitida* Hinds, 1844; OD.

Definition: Primarily defined based on phylogenetic analysis of Modica et al. (2019), comprising species that belong to clade E2 of Modica et al. (2019) and additionally species that show shell morphology, anatomical or genetic characteristics closely comparable with *Punctoterebra nitida* or any genetically proven member of the clade.

Diagnosis. Diagnostic nucleotide combinations are provided separately for the four phylogenetic clusters of the *Punctoterebra* clade inferred by Modica et al. (2019) in Table 7.

Shell: Elongate, small to medium-sized (<50 mm), with high spire and predominantly axial sculpture. Protoconch paucispiral or multispiral, of varying morphology. Axial ribs strong on spire whorls, sometimes becoming obsolete on last whorl. Spiral sculpture limited to a weak punctuate groove delineating subsutural band, or well-developed and represented by regular striae in interspaces between axial ribs. Siphonal canal demarcated from shell base by distinct concavity; often slightly recurved.

Anatomy: Proboscis, venom gland, radula and salivary glands typically present; radula, when present, of flat marginal teeth. Accessory proboscis structure absent.

Distribution: Indo-Pacific; intertidal to upper bathyal depths (to 405 m), but typically shallow water.

Remarks: With regard to shell morphology, species of this genus form three distinct groups that are consistent with three of the phylogenetic lineages inferred by Modica et al. (2019).

Punctoterebra nitida group. Shell small to medium-sized (<50 mm), polished, with subsutural band demarcated by deep punctures or short grooves; sculpture predominantly of axial ribs. The small species of the group (*P. plumbea* and *P. solangeae*) are conchologically very close to some species of *Partecosta* (see Remarks on the latter genus).

Punctoterebra teramachii group. Shells medium-sized (<45 mm), with dominant sculpture of orthocline axial ribs; spiral sculpture absent; subsutural band clearly defined. Species of this group are conchologically close to *Duplicaria*, from which they can be differentiated by the punctate subsutural groove and narrower aperture, and by radular teeth that are solid and recurved in *Duplicaria*, but flat (or absent) in *Punctoterebra*.



Figure 7. Genera *Myurella*, *Macaulaiger* n. gen. and *Myurellopsis* n. gen. **A.** *Myurella affinis*, MNHN-IM-2013-17860, PAPUA NIUGINI Stn PR196, 05°12.3'S, 145°48.8'E, 0 m, 39.8 mm. **B.** *Myurella fortunei*, MNHN-IM-2013-58677, KAVIENG 2014 Stn DW4468, 02°45'S, 150°37'E, 190–472 m, 25.2 mm. **C.** *Myurella amoena*, MNHN-IM-2013-46861, KAVIENG 2014 Stn KR02, 02°37.5'S, 150°46.5'E, 10–14 m, 24.9 mm. **D.** *Myurella pygmaea*, MNHN-IM-2009-10121, off Lovanono, S Madagascar, 0–5 m, 6.1 mm. **E.** *Macaulaiger pseudopertusa*, MNHN-IM-2009-9954, MIRIKY Stn DW3230, 13°25'S, 47°57'E, 71–158 m, 42.9 mm. **F.** *Macaulaiger campbelli*, MNHN-IM-2013-52252, EXBODI Stn CP3836, 22°08'S, 167°11'E, 415–420 m, 20.5 mm. **G.** *Myurellopsis undulata*, MNHN-IM-2013-10252 PAPUA NIUGINI Stn PR07, 05°12.5'S, 145°48.5'E, 2–17 m, 31.9 mm. **H.** *Myurellopsis kilburni*, MNHN-IM-2013-12712, PAPUA NIUGINI Stn PS11, 05°04.7'S, 145°48.9'E, 0–5 m, 24.8 mm. **I.** *Myurellopsis joserosadoi*, MNHN-IM-2013-52369, INHACA 2011 Stn MR13, 25°59.7'S, 32°54.5'E, 2–5 m, 17.9 mm.

Punctoterebra textilis group. Shell medium-sized (<50 mm), heavily sculptured, with gently convex whorls. Sculpture of arcuate ribs; interspaces bearing distinct regular striae; subsutural band

demarcated by punctate groove of varying strength. Syphonal canal typically recurved, separated from shell base by distinct waist or deep groove. This group is rather heterogeneous in shell

Table 6. Genus *Myurella*: diagnostic combination of nucleotides in COI alignment.

| | |
|----------------------------|--|
| Species/sequences analysed | 21/161 |
| Diagnostic nucleotides: | 49: T, 56: C, 157: T, 263: C, 334: T, 433: T, 485: C, 494: A, 538: T, 539: C, 565: T |

morphology, with its core formed by heavily sculptured species of the *P. textilis*–*P. succincta* complex. Similar heavily sculptured shells characterize typical *Profunditerebra* species; however, these can be distinguished by more rounded ribs, a row of nodules on the subsutural band and by straight siphonal canal. The heavily sculptured species of *Terebra* in the *T. amanda* group can be readily differentiated by their divided subsutural bands. The inferred membership of *P. lineaperlata* in the *P. textilis* group is, however, unexpected and needs further analysis.

Included species:

- Punctoterebra arabella* (Thiele, 1925)² n. comb.;
- P. baileyi* (Bratcher & Cernohorsky, 1982)¹ n. comb.;
- P. ballina* (Hedley, 1915)² n. comb.;
- P. caliginosa* (Deshayes, 1859)¹ n. comb.;
- P. castaneofusca* (Thiele, 1925)¹ n. comb.;
- P. contracta* (E. A. Smith, 1873)¹ n. comb.;
- P. exiguides* (Schepman, 1913)³ n. comb.;
- P. fuscotaeniata* (Thiele, 1925)² n. comb.;
- P. illustris* (Malcolm & Terry, 2012)² n. comb.;
- P. isabella* (Thiele, 1925)² n. comb.;
- P. japonica* (E. A. Smith, 1873)³ n. comb.;
- P. lineaperlata* (Terry & Holford, 2008)¹ n. comb.;
- P. livida* (Reeve, 1860)³ n. comb.;
- P. longiscata* (Deshayes, 1859)² n. comb.;
- P. nitida* (Hinds, 1844)¹ n. comb.;
- P. paucincisa* (Bratcher, 1988)³ n. comb.;

- P. plumbea* (Quoy & Gaimard, 1833)¹ n. comb.;
- P. polygyrata* (Deshayes, 1859)¹ n. comb.;
- P. rosacea* (Pease, 1869)³ n. comb.;
- P. roseata* (Adams & Reeve, 1850)¹* n. comb.;
- P. solangeae* (Bozzetti, 2015)¹ n. comb.;
- P. souleyeti* (Deshayes, 1859)¹* n. comb.;
- P. succincta* (Gmelin, 1791)¹ n. comb.;
- P. swainsoni* (Deshayes, 1859)² n. comb.;
- P. teramachii* (Burch, 1965)¹ n. comb.;
- P. textilis* (Hinds, 1844)¹ n. comb.;
- P. trismacaria* (Melville, 1917)¹ n. comb.;
- P. turrita* (E. A. Smith, 1873)¹ n. comb.;
- P. turschi* (Bratcher, 1981)² n. comb.

Genus *Profunditerebra* new genus

(Fig. 9A–E)

Type species: *Profunditerebra papuaprofundii* n. sp.

Zoobank registration: urn:lsid:zoobank.org:act:A5A78A3D-AB11-41C3-86F0-7C1451512FF4

Definition: Includes all species included in clade E3 of Modica *et al.* (2019) and those that show a combination of conchological, anatomical and distribution characteristics closely comparable with *Profunditerebra papuaprofundii* n. sp. or any genetically proven member of the clade.

Diagnosis: Diagnostic nucleotide combinations provided in Table 8.

Shell: Small to medium-sized (<45 mm), with multispiral protoconch and slender siphonal canal. Whorls subcylindrical or flattened. Sculpture varying greatly; axial sculpture of rounded ribs, weak to very strong and elevated; spiral sculpture typically limited to striae in interstices and a subsutural groove, but may be absent or represented by strong cords generating overall cancellate pattern.

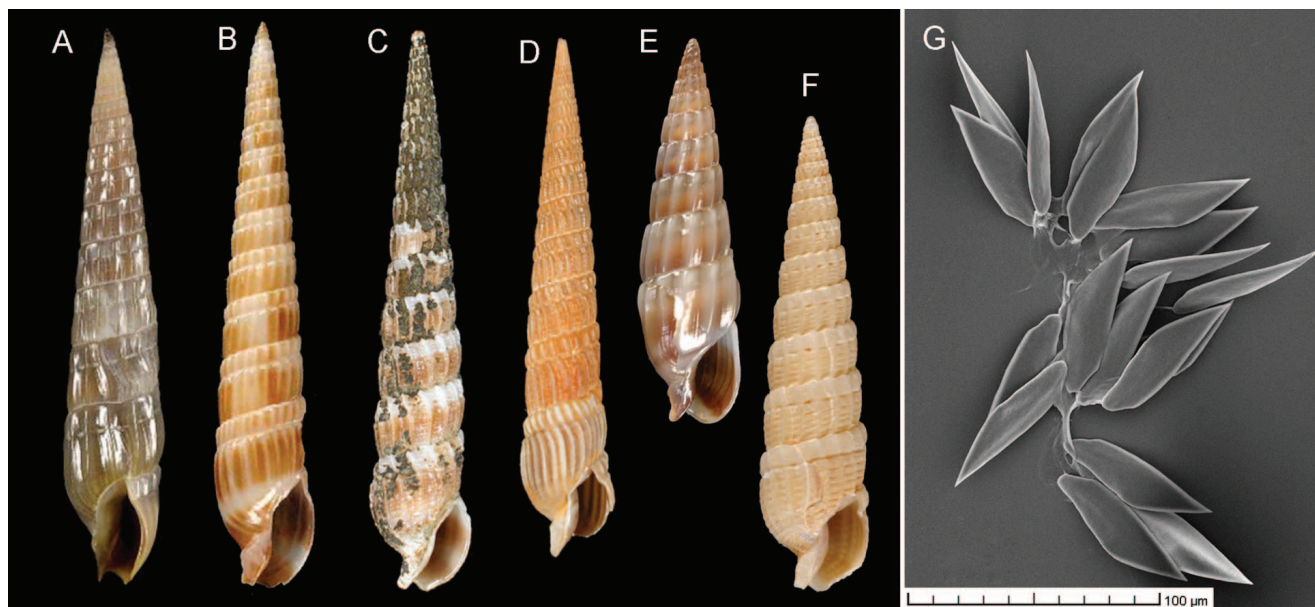


Figure 8. Genus *Punctoterebra*. **A.** *P. nitida*, MNHN-IM-2013-13332, PAPUA NIUGINI Stn PD32, 05°04.4'S, 145°48.7'E, 1–8 m, 26.5 mm. **B.** *P. teramachii*, MNHN-IM-2009-9973, TERRASSES Stn DW3093, 22°06'S, 167°03'E, 190–200 m, 27.5 mm. **C.** *P. polygyrata*, MNHN-IM-2007-30424, SALOMON 2 Stn CP2282, 08°37'S, 157°21'E, 150–160 m, 22.3 mm. **D.** *P. succincta*, MNHN-IM-2007-30385, SANTO 2006 Stn VM32, 15°26.6'S, 167°15.2'E, 0–1 m, 42.9 mm. **E.** *P. solangeae*, MNHN-IM-2009-10122, ATIMO VATAE Stn BP18, 25°26.1–26.4'S, 44°55.2–55.6'E, 17–20 m, 10.2 mm. **F.** *P. sp. aff. textilis*, MNHN-IM-2009-10093, MIRIKY Stn CP3274, 15°30.15'S, 46°04.3'E, 29–36 m, 16.8 mm. **G.** *P. souleyeti* radula, MNHN-IM-2007-30547, SANTO 2006 Stn LD21, 15°31.3'S, 167°09.9'E, 1–6 m, 27 mm.

Table 7. Diagnostic combinations of nucleotides in four subgroups of genus *Punctoterebra* in COI alignment.

| | |
|---------------------------------------|---|
| <i>Punctoterebra nitida</i> group | |
| Species/sequences analysed | 8/48 |
| Diagnostic nucleotides: | 28: A, 43: T, 67: A, 91: A, 112: A, 145: A, 160: A, 184: A, 214: A, 263: C, 265: T, 295: T, 562: T, 580: T, 655: A |
| <i>Punctoterebra teramachii</i> group | |
| Species/sequences analysed | 5/8 |
| Diagnostic nucleotides: | 50: C, 74: C, 184: G, 304: T, 382: T |
| <i>Punctoterebra</i> clade 3 | |
| Species/sequences analysed | 2/4 |
| Diagnostic nucleotides: | 14: C, 34: G, 499: A, 592: G, 622: T |
| <i>Punctoterebra textilis</i> group | |
| Species/sequences analysed | 13/72 |
| Diagnostic nucleotides: | 14: T, 40: T, 50: T, 64: T, 92: T, 106: T, 205: T, 235: T, 250: T, 295: T, 343: T, 433: T, 494: A, 517: A, 541: T, 548: T, 581: T, 607: T, 637: T |

Anatomy: Proboscis, radula, venom gland and salivary glands present. Radula of duplex marginal teeth (Fig. 9E). Accessory proboscis structure absent.

Distribution: Almost exclusively deep water (typically 150–600 m) of tropical Indo-West Pacific from Taiwan to New Caledonia; one species known from shallow water of South Australia.

Remarks: *Profunditerebra* is the only terebrine genus with duplex radular teeth similar to those in Pellifroniinae; however, members of the two groups can easily be differentiated by shell characters. Species of *Profunditerebra* can be separated into four clusters based on their shell morphology; however, only the first cluster corresponds to a phylogenetic lineage.

Profunditerebra papuaprofundum n. sp. group. Shell uniformly coloured white to dark brown; heavily sculptured, with distinct subsutural groove and subcylindrical whorls. Sculpture of strong rounded ribs forming row of prominent nodules on subsutural band. Spiral sculpture of fine striae limited to interstices between axials, or overriding them to form fine continuous cords (including on subsutural band), or coarse cancellate pattern. Species of *Neoterebra* (e.g. *N. armillata*) exhibit a similar sculpture, but can be differentiated from *Profunditerebra* by their flattened whorls. The *Punctoterebra textilis* group also includes some similar forms (see Remarks on *Punctoterebra*).

Profunditerebra orientalis group. Shell with flattened whorl profile; variegated colour pattern. Sculpture of fine orthocline ribs intersected by cords of about equal strength or slightly weaker than axials, to form delicate cancellate pattern. Subsutural band demarcated by shallow punctuate groove. Species of this group can easily be differentiated from congeners that either lack spiral elements, or display an overall much coarser sculpture. Both *P. orientalis* and *P. hiscocki* closely resemble species of *Maculauger*, from which they can confidently be differentiated only by anatomy (all studied species of *Maculauger* lack a radula) or molecular characters.

Profunditerebra anseeuwi group. Shell with flattened whorl outline; subsutural band represented by short ribs or indentation. Sculpture of axial ribs, pronounced throughout whorl height, but weakening and becoming obsolete on later whorls; spiral sculpture absent. Species of this group are conchologically close to *Duplicaria* and to the *Punctoterebra teramachii* group; however, they can be differentiated from both by the overall weaker sculpture. In addition, these

lineages can confidently be differentiated by the radular teeth morphology, *Duplicaria* having solid and recurved teeth, *Profunditerebra* duplex teeth and *Punctoterebra* flat teeth.

Profunditerebra brazieri stands apart from other species in the genus, being endemic to temperate shallow water off Tasmania. Morphologically, it is close to the *P. anseeuwi* group, but has a very weakly defined subsutural band.

Etymology: Name refers to the considerable depths at which almost all known species of the genus occur. Gender feminine.

Included species:

Profunditerebra anseeuwi (Terry, 2005)¹ n. comb.;
P. brazieri (Angas, 1871)¹ n. comb.;
P. evelynae (Clench & Aguayo, 1939)³ n. comb.;
P. macclesfieldensis n. sp. Malcolm, Terry & Fedosov¹ n. sp.;
P. orientalis (Aubry, 1999)¹ n. comb.;
P. papuaprofundum n. sp. Malcolm, Terry & Fedosov¹ n. sp.;
P. poppei (Terry, 2003)¹ n. comb.;
P. hiscocki (Sprague, 2004)¹ n. comb.

Genus *Neoterebra* new genus

(Fig. 9F–H)

Type species: *Terebra specillata* Hinds, 1844.

Zoobank registration: urn:lsid:zoobank.org:act:68993F36-2AD1-4DDE-A853-8832B4A9EE30

Definition: Includes all species included in clade E4 of Modica et al. (2019) and those that show a combination of conchological, anatomical and distribution characteristics closely comparable with *Neoterebra specillata* or any genetically proven member of the clade.

Diagnosis: Diagnostic nucleotide combinations in Table 9.

Shell: Small to medium-sized (<60 mm); uniformly creamy-white to light brown or with pattern of brown blotches; pointed multi-spiral or paucispiral protoconch, 1.5 to about 3 whorls. Axial sculpture of orthocline or arcuate ribs, forming axially elongated subsutural nodules on well-defined band. Spiral sculpture from weak striae in interspaces between ribs to distinct cords, overriding ribs, often forming nodes at intersection or on lower portion of ribs. Last whorl typically abruptly constricted to siphonal canal. Canal clearly separated from shell base, bearing pronounced fasciole.

Anatomy: Radula, proboscis, venom gland typically absent. Radula, when present, of hypodermic type. Salivary glands typically present. Accessory proboscis structure absent.

Distribution: Tropical East Pacific, Caribbean, off Brazil; intertidal to upper bathyal depths, but typically shallow water.

Remarks: Shallow-water species of *Neoterebra* differ from their congeners from deep water of Brazil and the Caribbean, being larger at maturity and sharing characteristic sculpture of strong axial ribs that form elevated, sometimes axially elongated nodules on the subsutural band. Caribbean species have a weaker subsutural band; those from deep water commonly lack a recognizable subsutural band and display a fine cancellate pattern of narrow axial riblets, intersected by spiral cords of equal strength. Although the affinity of Panamic and Caribbean species is suggested by the analysis of COI, further studies are needed to document relationships and delineate major groupings within the genus.

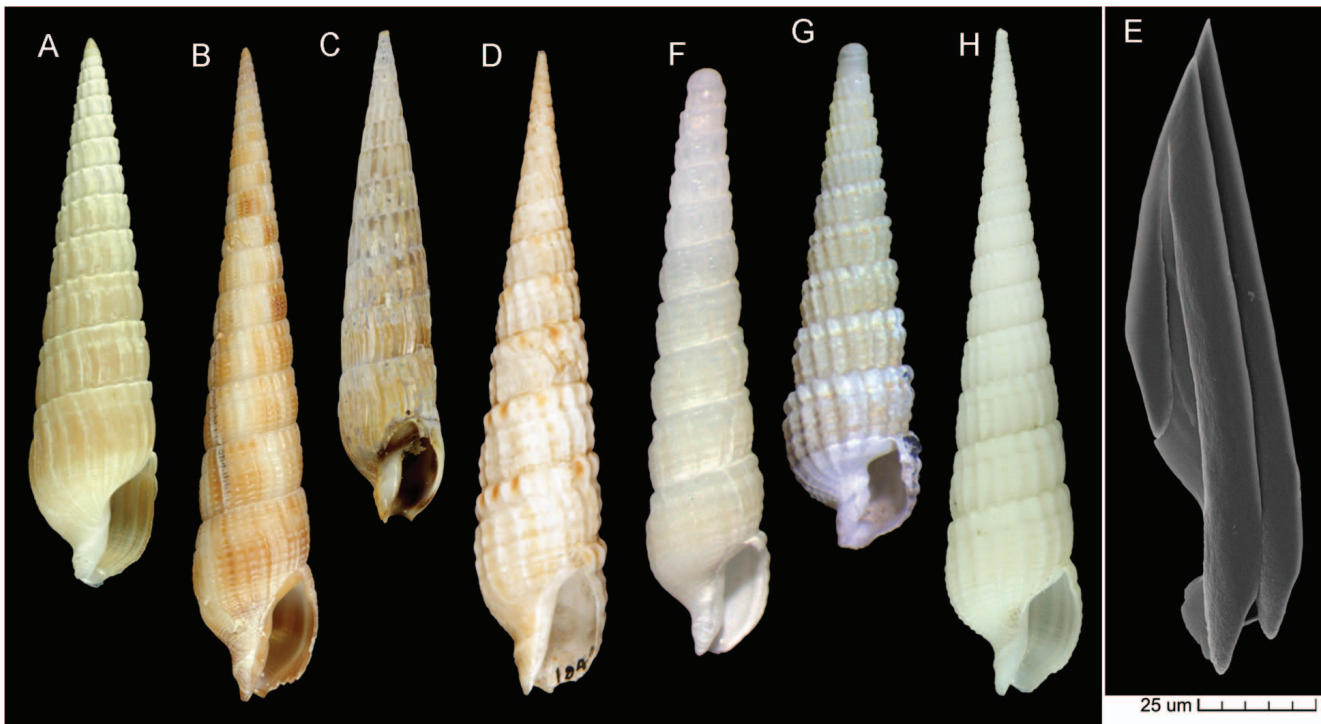


Figure 9. Genera *Profunditerebra* n. gen. and *Neoterebra* n. gen. **A.** *P. papuaprofundii* n. sp., MNHN-IM-2013-58123, KAVIENG 2014 Stn CP4422, 02°21'S, 150°38'E, 496–609 m, 19.2 mm. **B.** *P. orientalis*, MNHN-IM-2009-29153, EXBODI Stn DW3930, 18°37'S, 164°26'E, 448–464 m, 39.6 mm. **C.** *P. brazieri*, MNHN-IM-2013-55861, MORRISON AUSTRALIA Stn TA22, 43°10.4'S, 147°51.3'E, 1–7 m, 32.4 mm. **D.** *Terebra specillata* lectotype, NHMUK 1844.6.7.84, San Blas, Mexico, 7 fms (= 12.8 m), 39.3 mm. **E.** *P. poppei* radula, MNHN-IM-2007-30546, SANTO 2006, Stn AT44, 15°36'S, 167°03'E, 86–118 m, broken. **F.** *Terebra assu* holotype, MNHN-IM-2000-25244, off Conceição da Barra, Espírito Santo, Brazil MD55, Stn DC75, 18°59'S, 37°50'W, 295 m, 9.8 mm. **G.** *Terebra alagoensis* holotype, MZSP 84238, continental slope off Alagoas, Brazil, 10°05'57"S, 35°46'24"W, 720 m, 9.8 mm. **H.** *Neoterebra sterigmoides*, MNHN-IM-2013-20352, KARUBENTHOS 2012 Stn GD02, 16°22.57'N, 61°34.12'W, 0–80 m, 29.6 mm.

Table 8. Genus *Profunditerebra* n. gen.: diagnostic combination of nucleotides in COI alignment.

| | |
|----------------------------|---|
| Species/sequences analysed | 11/39 |
| Diagnostic nucleotides: | 22: A, 154: T, 313: A, 349: G, 379: T, 382: A, 388: A, 496: G, 533: T, 631: A |

Table 9. Genus *Neoterebra* n. gen.: diagnostic combination of nucleotides in COI alignment.

| | |
|----------------------------|---|
| Species/sequences analysed | 12/45 |
| Diagnostic nucleotides: | 52: A, 157: T, 181: T, 295: T, 334: T, 379: T, 401: T, 415: T, 485: C, 487: T, 494: A, 502: A, 557: C, 583: A |

Etymology: The name is a combination of *neo* (Latin: new) and *Terebra*, referring to the fact that species of this new genus only occur in the New World, constituting the majority of the terebrid fauna in the region.

Included species:

Neoterebra acrior (Dall, 1889)² n. comb.;
N. alagoensis (Lima, Tenorio & Barros, 2007)² n. comb.;
N. alba (Gray, 1834)² n. comb.;
N. allyni (Bratcher & Burch, 1970)² n. comb.;
N. angelli (J. Gibson-Smith & W. Gibson-Smith, 1984)² n. comb.;
N. arcas (Abbott, 1954)² n. comb.;
N. armillata (Hinds, 1844)¹ n. comb.;
N. assu (Simone, 2012)² n. comb.;
N. berryi (Campbell, 1961)² n. comb.;
N. biniensis (Petuch, 1987)² n. comb.;
N. brandi (Bratcher & Burch, 1970)² n. comb.;
N. brasiliensis (E. A. Smith, 1873)² n. comb.;
N. bridgesi (Dall, 1908)³ n. comb.;
N. carolae (Bratcher, 1979)² n. comb.;
N. churea (Campbell, 1964)² n. comb.;

N. colombiensis (Simone & Gracia, 2006)² n. comb.;
N. concava (Say, 1826)² n. comb.;
N. corintoensis (Pilsbry & Lowe, 1932)² n. comb.;
N. crassireticula (Simone, 1999)² n. comb.;
N. crenifera (Deshayes, 1859)¹ n. comb.;
N. curacaoensis (De Jong & Coomans, 1988)² n. comb.;
N. dislocata (Say, 1822)¹ n. comb.;
N. doellojuradoi (Carcelles, 1953)² n. comb.;
N. elata (Hinds, 1844)¹ n. comb.;
N. frigata (Hinds, 1844)² n. comb.;
N. glauca (Hinds, 1844)² n. comb.;
N. glossema (Schwengel, 1942)¹ n. comb.;
N. guadeloupensis n. sp. Malcolm, Terryn & Fedosov¹ n. sp.;
N. guayaquilensis (E. A. Smith, 1880)² n. comb.;
N. hancocki (Bratcher & Burch, 1970)² n. comb.;
N. hemphilli (Vanatta, 1924)² n. comb.;
N. hondurasiensis (Gargiulo, 2016)² n. comb.;
N. intertincta (Hinds, 1844)³ n. comb.;
N. intumescens (Lima, Tenorio & Barros, 2007)² n. comb.;
N. jacquelinae (Bratcher & Burch, 1970)² n. comb.;
N. juanica (Dall & Simpson, 1901)² n. comb.;

N. lamyi (Terry, 2011)² n. comb.;
N. larvaeformis (Hinds, 1844)¹ n. comb.;
N. leptapsis (Simone, 1999)² n. comb.;
N. limatula (Dall, 1889)¹ n. comb.;
N. lucana (Dall, 1908)² n. comb.;
N. mugridgeae (García, 1999)² n. comb.;
N. nassula (Dall, 1889)² n. comb.;
N. pacei (Petuch, 1987)² n. comb.;
N. panamensis (Dall, 1908)² n. comb.;
N. pedroana (Dall, 1908)² n. comb.;
N. petiveriana (Deshayes, 1857)² n. comb.;
N. plicata (Gray, 1834)² n. comb.;
N. protecta (Conrad, 1846)² n. comb.;
N. puncturosa (Berry, 1959)¹ n. comb.;
N. rancheria (Bratcher, 1988)² n. comb.;
N. riosi (Bratcher & Cernohorsky, 1985)² n. comb.;
N. roperi (Pilsbry & Lowe, 1932)³ n. comb.;
N. rushii (Dall, 1889)² n. comb.;
N. sanjuanense (Pilsbry & Lowe, 1932)² n. comb.;
N. shyana (Bratcher & Burch, 1970)² n. comb.;
N. simonei (Lima, Tenorio & Barros, 2007)² n. comb.;
N. specillata (Hinds, 1844)¹ n. comb.;
N. spirosulcata (Simone, 1999)² n. comb.;
N. sterigma (Simone, 1999)² n. comb.;
N. sterigmoides (Simone & Gracia, 2006)¹ n. comb.;
N. stohleri (Bratcher & Burch, 1970)² n. comb.;
N. tiarella (Deshayes, 1857)³ n. comb.;
N. variegata (Gray, 1834)¹ n. comb.;
N. vinosa (Dall, 1889)² n. comb.

Genus *Maculauger* new genus

(Fig. 7E, F)

Type species: *Terebra pseudopertusa* Bratcher & Cernohorsky, 1985.

Zoobank registration: urn:lsid:zoobank.org:act:3565DB17-E4EF-478B-8757-3A682BB8F6CF

Definition: Includes all species included in clade E5A of *Modica et al.* (2019) and those that show a combination of conchological, anatomical and distribution characteristics closely comparable with *Maculauger pseudopertusus* or any genetically proven member of the clade.

Diagnosis: Diagnostic nucleotide combinations in Table 10.

Shell: Small to medium-sized (<60 mm); typically, orange-brown with irregular maculations on subsutural band. Whorl outline flattened or gently convex. Subsutural band lightly ribbed or flattened, separated from lower portion of whorl by narrow groove or row of punctations. Axial and spiral sculpture of about equal strength, producing cancellate sculpture below subsutural band.

Anatomy: Proboscis, radula, venom gland and accessory proboscis structure absent; salivary glands present or absent.

Distribution: Indo-Pacific; subtidal and bathyal depths to about 600 m.

Remarks: The new genus *Maculauger* comprises several species, formerly placed in *Hastulopsis*, that can be differentiated from similar species in *Myurella* by the equal prominence of spiral and axial spiral elements, producing a fine cancellate sculpture. *Hastulopsis* species have very weak sculpture and are found in the Indian Ocean or Japan. Some species of *Maculauger*, such as *M. campbelli*, are conchologically very close to *Profunditerebra orientalis*—a case

where only anatomical and molecular characters can ensure correct identification (see Remarks on *Profunditerebra*).

Etymology: The name combines ‘macula’ (Latin: spot, blotch), referring to the commonly maculated subsutural band in the species of the genus, with ‘auger’, the English epithet for Terebridae (‘auger shells’). Gender masculine.

Included species:

Maculauger alveolatus (Hinds, 1844)¹ n. comb.;
M. campbelli (R. D. Burch, 1965)¹ n. comb.;
M. castigatus (A. H. Cooke, 1885)¹ n. comb.;
M. cinctella (Deshayes, 1859)³ n. comb.;
M. minipulcher (Bozzetti, 2008)¹ n. comb.;
M. pseudopertusus (Bratcher & Cernohorsky, 1985)¹ n. comb.;
M. sudchinskiensis n. sp. Malcolm, Terry & Fedosov¹ n. sp.

Genus *Myurellopsis* new genus

(Fig. 7G–I)

Type species: *Terebra undulata* Gray, 1834.

Zoobank registration: urn:lsid:zoobank.org:act:EC3F14B2-3595-482B-9890-399BA78A7631

Definition: Includes all species included in the clade E5B of *Modica et al.* (2019) and those that show a combination of conchological, anatomical and distribution characteristics closely comparable with *Myurellopsis undulata* or any genetically proven member of the genus.

Diagnosis: Diagnostic nucleotide combinations in Table 10.

Shell: Small to medium-sized (<50 mm), pinkish or orange, often with white subsutural band. Protoconch multispiral. Sculpture of strong, rounded, slightly undulating ribs, polished in appearance. Row of punctations with groove partially cutting ribs forming subsutural band. Interstices between ribs deep, narrow, bearing regular striae, often darkly coloured. Apical parts of ribs forming one row of rounded nodules, separated from their lower portions by shallow depression or partial groove. Siphonal canal moderately long, tapering, with weakly developed fasciole.

Anatomy: Two distinct states—either all typical foregut structures present, or all lacking; in latter case, accessory proboscis structure present.

Distribution: Throughout Indo-Pacific; intertidal to upper bathyal depths (to 358 m), typically shallow.

Remarks: Species in *Myurellopsis* n. gen. appear conchologically close to *Myurella* species, but can be differentiated by the sharper,

Table 10. Genera *Maculauger* and *Myurellopsis*: diagnostic combinations of nucleotides in COI alignment.

| | |
|-----------------------------|---|
| <i>Maculauger</i> n. gen. | |
| Species/sequences analysed | 8/26 |
| Diagnostic nucleotides: | 214: T, 242: C, 520: G, 580: G, 592: T |
| <i>Myurellopsis</i> n. gen. | |
| Species/sequences analysed | 8/65 |
| Diagnostic nucleotides: | 25: G, 40: T, 50: C, 199: A, 304: A, 307: T, 328: T, 349: A, 379: T, 494: A, 643: A |

more elevated ribs, often with nodes on the subsutural band or top of the whorls.

Etymology: The name refers to the close resemblance between its members and species in the genus *Myurella*. Gender feminine.

Included species:

Myurellopsis alisi (Aubry, 1999)³ n. comb.;
M. columellaris (Hinds, 1844)¹ n. comb.;
M. guphila (Poppe, Tagaro & Terryn, 2009)¹ n. comb.;
M. joserosadoi (Bozzetti, 2001)¹ n. comb.;
M. kilburni (R. D. Burch, 1965)¹ n. comb.;
M. monicae (Terryn, 2005)² n. comb.;
M. nathaliae (Drivas & Jay, 1988)¹ n. comb.;
M. parkinsoni (Bratcher & Cernohorsky, 1976)¹ n. comb.;
M. paucistriata (E. A. Smith, 1873)¹ n. comb.;
M. undulata (Gray, 1834)¹ n. comb.;
M. vaubani (Aubry, 1999)³ n. comb.

Genera defined based on conchological characters

Genus *Granuliterebra* Oyama, 1961

(Fig. 10A)

Type species: *Terebra bathyrhapse* E.A. Smith, 1875; OD.

Diagnosis: Shell of small size (<36 mm), slender, sculptured by strong ribs, bearing nodules on subsutural band and on bottom of ribs, giving concave outline to whorls. Protoconch of 2.5–4 whorls.

Distribution: Indian and western Pacific Oceans.

Remarks: Species in the genus *Pellifronia* are similar in having a concave whorl outline, but have notably weaker nodules and a less clearly defined subsutural band. Species with similar nodulose sculpture exist in the genus *Neoterebra*, but generally these have a wider apical angle or a very shiny texture. *Duplicaria tricineta* has similar sculpture, but including two raised, thin, spiral cords.

Included species:

Granuliterebra bathyrhapse (E. A. Smith, 1875)⁴;
G. constricta (Thiele, 1925)⁴;
G. eddunhami Terryn & Holford, 2008⁴;
G. oliverai Terryn & Holford, 2008⁴;
G. palawanensis (Aubry & Picardal, 2011)⁴;
G. persica (E. A. Smith, 1877)⁴.

Genus *Hastulopsis* Oyama, 1961

(Fig. 10B)

Type species: *Terebra melanacme* E. A. Smith, 1873; OD.

Diagnosis: Shell small to medium-sized (to 60 mm), shiny, faintly axially ribbed, with numerous fine spiral incisions. Subsutural band generally not spirally decorated, bordered by relatively deep incision (Terryn, 2007).

Distribution: Indian and western Pacific Oceans.

Remarks: The genus comprises two groups of shallow-water species, one found from the eastern coast of Africa to the Arabian Gulf and another in waters of mainland Japan to Australia. Similar, but deeper-water species are found in the genus *Macaulager* n. gen., most of which can be recognized by having a row of large spots

on the periphery. The species of *Myurella* have much stronger and more distinct sculpture features, and generally a brown basal area.

Included species:

Hastulopsis baliensis Terryn & Dekker, 2017⁴;
H. blanda (Deshayes, 1859)⁴;
H. cebuensis Gargiulo, 2014⁴;
H. elialae (Aubry, 1994)⁴;
H. gotoensis (E. A. Smith, 1879)⁴;
H. loisae (E. A. Smith, 1903)⁴;
H. maestratii Terryn & Rosado, 2011⁴;
H. marmorata (Deshayes, 1859)⁴;
H. masirahensis Terryn & Rosado, 2016⁴;
H. melanacme (E. A. Smith, 1873)⁴;
H. mirbatensis Terryn & Rosado, 2016⁴;
H. suspensa (E. A. Smith, 1904)⁴;
H. whiteheadae (Aubry & Marquet, 1995)⁴.

Genus *Pristiterebra* Oyama, 1961

(Fig. 10C)

Type species: *Terebra tsuboiana* Yokoyama, 1922[†]; OD.

Synonym: *Laeviacus* Oyama, 1961 (type species *Terebra chibana* Yokoyama, 1922; OD).

Diagnosis: Shell small to medium-sized (20–65 mm). Whorls flattened to convex, with predominant pustulose or seldom cancellate sculpture. Whorl periphery shifted abapically, leading to truncated appearance of shell, with shell base abruptly constricted to short siphonal canal. Aperture wide, especially in anterior portion.

Distribution: Western Pacific.

Remarks: A characteristic truncated outline with a short siphonal canal and broad aperture allow for easy recognition of *Pristiterebra* among other terebrid genera. Species in *Pristiterebra* are nearest to the nodulose species of *Neoterebra* (*N. tuberculosa*, *N. glauca*, *N. petiveriana*), which can be recognized by the presence of a distinct subsutural groove. Some species of *Gradaterebra* and *Partecosta* have similar shell outline, but both can be differentiated from *Pristiterebra* by dominant axial sculpture or, rarely, complete lack of sculpture, and (in *Partecosta*) by generally smaller size.

Included species:

Pristiterebra bifrons (Hinds, 1844)⁴;
P. frausseni Poppe, Tagaro & Terryn, 2009⁴ n. comb.;
P. miranda (E. A. Smith, 1873)⁴ n. comb.;
P. pustulosa (E. A. Smith, 1879)⁴ n. comb.;
P. tuberculosa (Hinds, 1844)⁴ n. comb.

Genus *Gradaterebra* Cotton & Godfrey, 1932

(Fig. 10D)

Type species: *Gradaterebra scalariformis* Cotton & Godfrey, 1932; OD.

Diagnosis: Shell small (<25 mm), often dull-coloured, with flattened to bulbous whorls; axial sculpture of prominent ribs; spiral sculpture absent, microscopic or represented by fine cords; last whorl inflated.

Distribution: Indian and SW Pacific Oceans.

Remarks. The genus mainly comprises small species from Australia and South Africa, which can be differentiated based on adult size <25 mm.

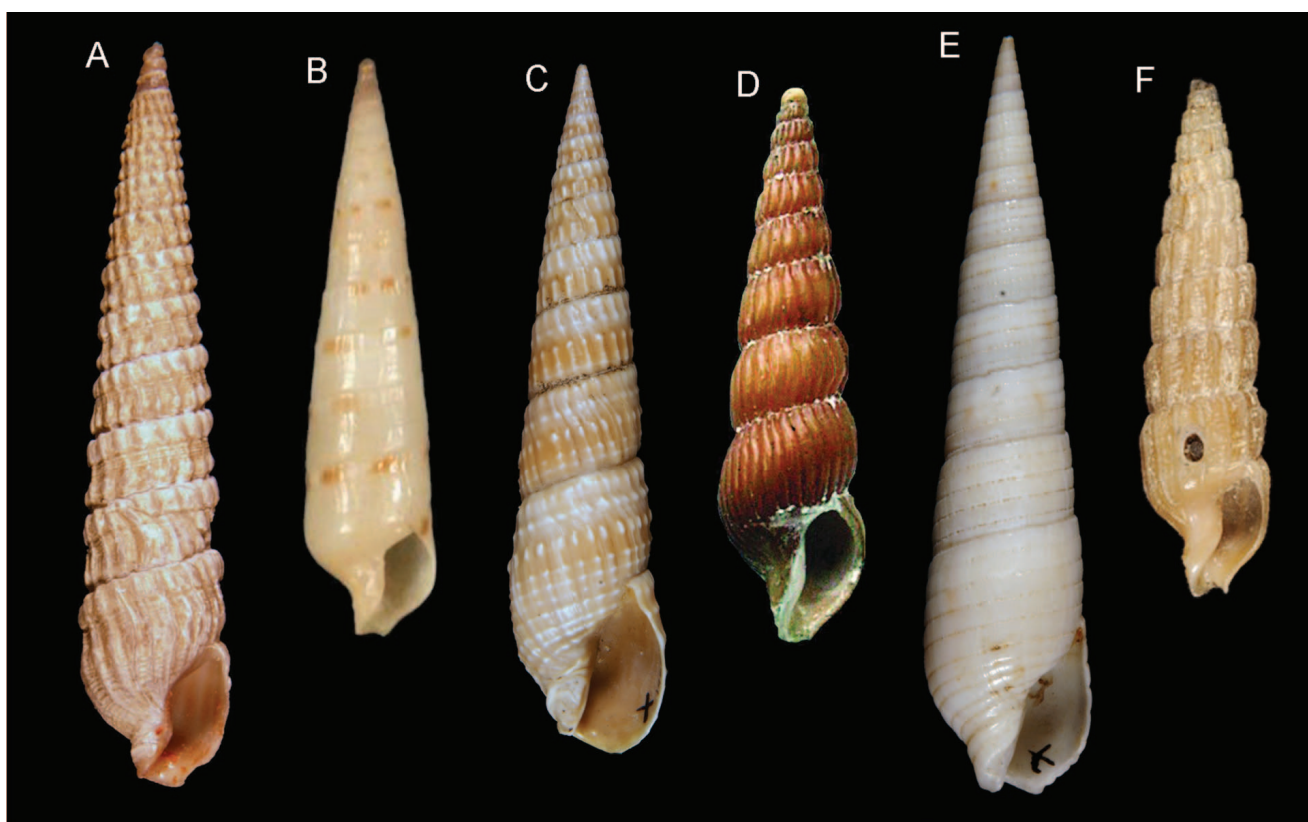


Figure 10. Genera defined solely by shell morphology. **A.** *Terebra bathyrhaphae* lectotype, NHMUK 1873.8.6.10/1, Gulf of Yedo, 35°35'N, 139°48'E, 6–25 fms (= 11–46 m), 24.8 mm. **B.** *Hastulopsis melanachne* lectotype, NMHUK 1873.8.6.11/1, Cape Sima, Japan, 18 fms (= 33 m), 17.8 mm. **C.** *Terebra bifrons* holotype, NHMUK 1968237, Japan, 51.0 mm. **D.** *Gradaterebra scalariformis*, SAM D-110176, Newland Head, S Australia, 20 fms (= 37 m), 12.1 mm. **E.** *Terebra circumcincta* holotype, NHMUK 1978150, Red Sea (erroneous?), 38.0 mm. **F.** *Microtrypetes iola* holotype, ANSP 155289, Mazatlan, Mexico, 20 fms (= 37 m), 14.0 mm.

Included species:

Gradaterebra scalariformis (Cotton & Godfrey, 1932)[†] n. comb.;
G. assecla (Iredale, 1924)[†] n. comb.;
G. capensis (E. A. Smith, 1873)[†] n. comb.;
G. easmithi (Aubry, 1999)[†] n. comb.;
G. kowiensis (Turton, 1932)[†] n. comb.;
G. lightfooti (E. A. Smith, 1899)[†] n. comb.;
G. ninfæ (Campbell, 1961)[†] n. comb.;
G. pilsbryi (Aubry, 1999)[†] n. comb.;
G. planecosta (Barnard, 1958)[†] n. comb.;
G. severa (Melvill, 1897)[†] n. comb.;
G. sorrentense (Aubry, 1999)[†] n. comb.;
G. taylori (Reeve, 1860)[†] n. comb.

Genus *Perirhoe* Dall, 1908

(Fig. 10E)

Type species: *Perirhoe circumcincta* (Deshayes, 1857); OD.

Diagnosis: Shell small to medium-sized (<50 mm), solid; axial sculpture weak to obsolete; spiral sculpture of irregular punctate grooves; subsutural band weakly defined.

Distribution: S Pacific, particularly New Caledonia.

Remarks: *Perirhoe* is close to the genus *Oxymeris* in terms of shell proportions; however, it can be readily differentiated from species of the latter by the distinct spiral grooves throughout the whorls' height. The sculpture pattern of widely set spiral grooves in *Perirhoe*

resembles that in some species of *Terebra*, but the latter group has notably more slender shells, with higher spire and less robust siphonal canal.

Included species:

Perirhoe circumcincta (Deshayes, 1857)[†];
Perirhoe valentinae (Aubry, 1999)[†] n. comb.

Genus *Microtrypetes* Pilsbry & Lowe, 1932

(Fig. 10F)

Type species: *Microtrypetes iola* Pilsbry & Lowe, 1932; OD.

Diagnosis: Shell small (<20 mm), dull, with turreted outline due to subcylindrical to clearly cylindrical whorl outline. Sculpture of strong, straight to finely curving axial ribs and fine spiral striae. Subsutural band indistinct or weakly defined. Siphonal canal long, curved.

Distribution: E Pacific.

Remarks: The genus can be differentiated from other New World genera of Terebridae by the stepped appearance of the spire, due to the cylindrical or subcylindrical whorl outline, by the generally indistinct subsutural band and by the siphonal canal that is rather long for the family.

Included species:

Microtrypetes iola Pilsbry & Lowe, 1932[†];
M. polyphenus (Pilsbry & Lowe, 1932)[†] n. comb.

Descriptions of new species

***Bathyterebra zhongshaensis* Malcolm, Terryn & Fedosov
new species**
(Fig. 2H)

Type material: Holotype: MNHN IM-2013-61800, 17.4 mm; South China Sea, Helen Shoal, 19°13'N, 113°55'E, 470–494 m (ZhongSha 2015 Stn DW4138).

Zoobank registration: urn:lsid:zoobank.org:act:C8461C7A-BF53-48D4-BE1B-EF23F17413F8

Diagnostic nucleotide positions: Table 11.

Description: Shell small, with orthocone spire, wide apical angle. Protoconch wide, paucispiral, 2.5 whorls, with small nucleus. Teleoconch 9 whorls. Early whorls convex in outline with strong, sharply convex ribs; subsequent whorls with narrow constriction formed by indentation, with straight ribs below suture; suture distinct, ragged; mature whorls with less convex outline, weaker and more numerous ribs, 30 on penultimate whorl. Spiral sculpture of very weak threads. Last whorl bulbous at base, but elongate with wide aperture. Columella straight, with weak fold. Overall colour white, with extensive patches of light-tan axial flammules on mature whorls.

Habitat: Depths of 470–494 m.

Distribution: Only known from type locality.

Etymology: Named for the Zhongsha sand bars, which form a sub-surface atoll on top of the Macclesfield Bank.

Remarks: *Bathyterebra zhongshaensis* n. sp. is similar to the deep-water species, *B. coriolisi* and *B. benthalis*. *Bathyterebra coriolisi* (Fig. 2E) is similar in colour, in the sculpture of the early whorls and in the shape of its aperture. However, *B. coriolisi* differs in having a much narrower shape, with a strong subsutural groove and fewer ribs on

the early whorls, creating a band with nodes. Its subsutural groove becomes weaker, with just a slight indentation on mature whorls. *Bathyterebra benthalis* (Fig. 2I) is similar in colour and in overall sculpture of the shell, but differs from *B. zhongshaensis* n. sp. in the outline of its mature whorls being flat and the ribs on the early whorls extremely convex, creating nodes that dominate the profile of the early whorls.

***Duplicaria herberti* Malcolm, Terryn & Fedosov new species**
(Fig. 11A–C)

Duplicaria mozambiquensis—Aubry, 1992: Fig. 9. Aubry *et al.*, 2006: pl. 16. (Both not Bratcher & Cernohorsky, 1982).

Type material: Holotype: MNHN IM-2013-52381, lv, 29.7 mm; Inhaca I., Mozambique, 26°00.0'S, 32°54.4'E, 4 m (INHACA 2011 Stn MR15). Paratypes 1–3: Inhaca I., Mozambique, 26°03.1'S, 33°01.0'E, 50–53 m (INHACA 2011, Stn MD13). Paratype 1: MNHN IM-2013-52373, lv, 17.4 mm. Paratype 2: MNHN IM-2013-52379, lv, 23.0 mm. Paratype 3: MNHN IM-2013-52383, lv, 28.2 mm. Paratype 4: MNHN IM-2013-52385, 1 lv, 30.8 mm; type locality. Paratype 5: MNHN IM-2013-52405, lv, 24.0 mm; 26°05.0'S, 32°59.0'E, 0–35 m (INHACA 2011 Stn MA15). Paratypes 6–19: YT, 14 lv, 22.4–32.5 mm; Inhaca I., Mozambique, 6–8 m. Paratype 20: SG, lv, 24.0 mm; off Inhaca I., Mozambique, 25°59'59.3"S, 32°54'43.2"E, 4 m. Paratypes 21–25: JR, 4 lv, 30.0–39.5 mm; off Inhaca I., Mozambique, 4–8 m. Paratype 26: GM, lv, 26 mm; Inhambane, Mozambique. Paratype 27: YT, dd, 32.0 mm; off Durban Bluff, Natal, South Africa, in sand dredging at bay-head dump.

Zoobank registration: urn:lsid:zoobank.org:act:C26159E5-4A5A-4218-AC7F-A76103809749

Diagnostic nucleotide positions: Table 11.

Description: Shell of medium size. Protoconch paucispiral, about 1.0–1.5 broad whorls. Teleoconch of holotype 11 whorls. Outline of teleoconch whorls straight. Spiral sculpture absent. Subsutural band with axially elongated nodes corresponding to axial ribs on remainder of whorl. Subsutural band bordered by deep and wide depression lacking punctations. Straight axial ribs stretching across whorl, sharply angular apically and becoming more rounded abapically; ribs half as wide as interspaces; 17 ribs on penultimate whorl of holotype. Axial growth lines pronounced throughout whorl height. Aperture wide, somewhat quadrate, brown with white band; columella straight with visible fold. Shell colour dark, later whorls blackish brown with spiral whitish line at the periphery.

Habitat: Depth 0–55 m.

Distribution: S Mozambique to off Durban, South Africa.

Etymology: The species honours Dr David G. Herbert (formerly Chief Curator of Mollusca, NMSA), who contributed with detailed observations on the *D. mozambiquensis* type series at NMSA and provided additional historical information.

Remarks: Shell colour varies: juveniles are beige to fawn, but light brown specimens are known. This species has been confused with *D. mozambiquensis*. The holotype of *D. mozambiquensis* (NMSA H7843/T2541) is a small, slender shell of 22.3 mm, but the type series shows a large discrepancy in many features between this holotype and all the paratypes—which are specimens of *D. herberti* n. sp. Subsequent authors have to our knowledge always featured

Table 11. Diagnostic combinations of nucleotides in COI alignment for new species of Terebridae described herein.

Bathyterebra zhongshaensis n. sp.

Sequences analysed: 1

Diagnostic nucleotides: 34: G, 223: G, 373: A, 487: C, 499: C, 581: C

Duplicaria herberti n. sp.

Sequences analysed: 6

Diagnostic nucleotide: 43: G, 184: T, 232: A, 241: A, 277: T, 451: G, 526: A

Partecosta bozzettii n. sp.

Sequences analysed: 3

Diagnostic nucleotides: 85: A, 121: G, 271: A, 301: G, 350: T, 541: G

Profunditerebra papuaprofundii n. sp.

Sequences analysed: 1

Diagnostic nucleotides: 169: G, 397: C, 457: G, 622: C, 658: C

Profunditerebra macclesfieldensis n. sp.

Sequences analysed: 3

Diagnostic nucleotides: 61: C, 367: C, 400: C, 445: C, 457: C, 487: G

Neoterebra guadeloupensis n. sp.

Sequences analysed: 14

Diagnostic nucleotides: 439: T, 493: A, 526: G, 580: A, 604: C, 628: A

Maculauger sudchinensis n. sp.

Sequences analysed: 3

Diagnostic nucleotides: 85: C, 217: G, 238: G, 256: A, 514: T, 625: G

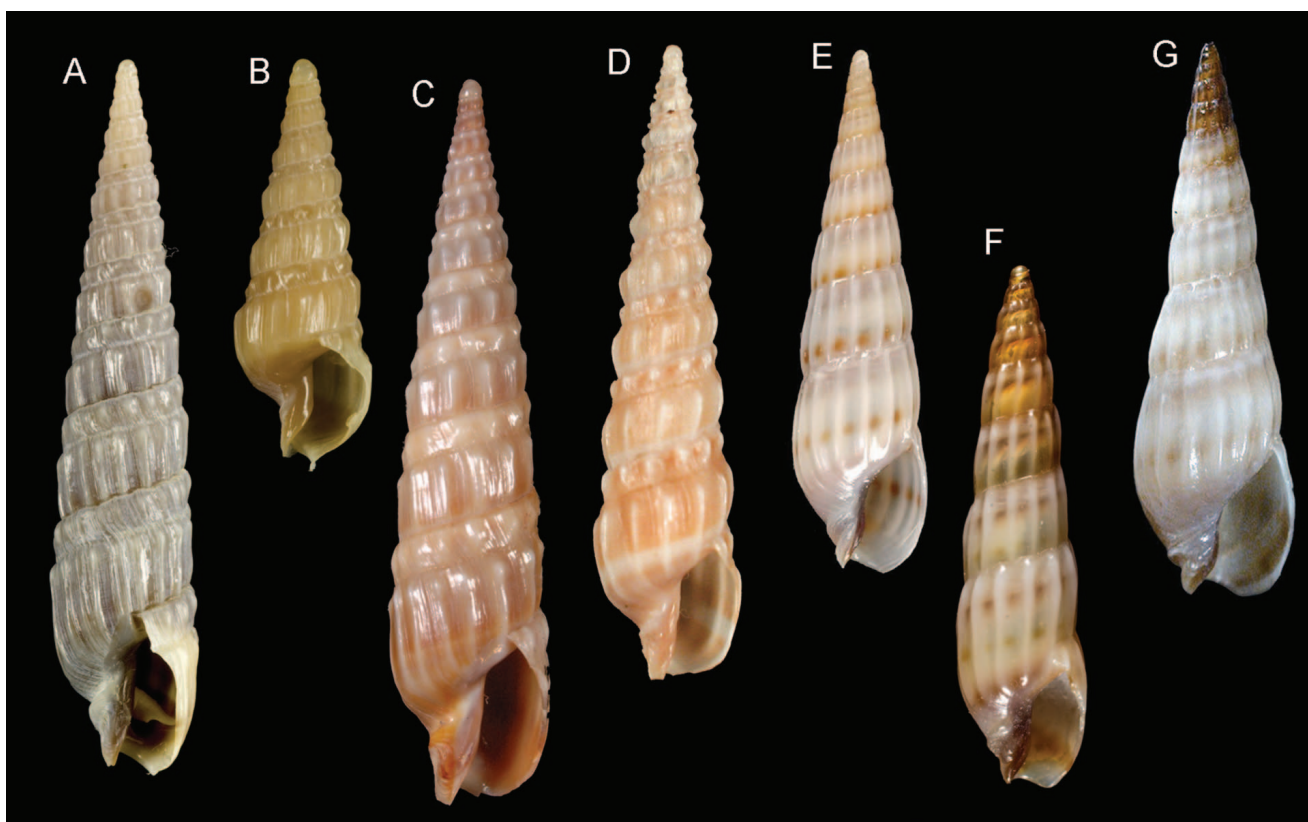


Figure 11. *Duplicaria herberti* n. sp., *Partecosta bozzettii* n. sp. and morphologically similar species. **A.** *D. herberti*, holotype, MNHN-IM-2013-52381, INHACA 2011 Stn MR15, 26°00.0'S, 32°54.4'E, 0–1 m, 29.7 mm. **B.** *D. herberti*, MNHN-IM-2013-52366, INHACA 2011 Stn MM1, 26°02.3'S, 32°54.1'E, 0–1 m, 12.4 mm. **C.** *D. herberti* (paratype of *D. mozambiquensis*), NMSA 566, 27 mm. **D.** *D. mozambiquensis*, YT, Quelimane Pebane, Mozambique, 35–45 m, 19.6 mm. **E.** *Partecosta bozzettii* holotype, MNHN-IM-2009-10163, ATIMO VATAE Stn TP29, 25°03'43.9"S, 46°57'42.9"E, 3–4 m, 12.5 mm. **F.** *Partecosta trilineata* holotype, MNHN-IM-2000-21473, S Madagascar, Lavanono, 8.85 mm. **G.** *P. daniae* holotype, MMM, Farol das Lagostas, Luanda, Angola, 12 mm.

specimens of *D. herberti* n. sp. as '*D. mozambiquensis*', which should be considered a rarely encountered species.

The whorls of *D. mozambiquensis* (Fig. 11D) have a narrower apical angle, its convex axial ribs giving an extremely rounded convex outline. The subsutural band comprises round nodes, compared with elongated nodes on *D. herberti* n. sp. The axial ribs of *D. herberti* n. sp. become straight, creating an angular projection posteriorly. The peripheral white band in *D. mozambiquensis* is wider and more clearly defined. Both have a subsutural furrow with minute axial growth striae, appearing as a punctate groove in *D. mozambiquensis*, while this feature is not present in *D. herberti* n. sp. We have no confirmation that *D. mozambiquensis* has ever been found in southern Mozambique, while specimens of *D. herberti* n. sp. are found extensively in southern Mozambique and South Africa. Within *Duplicaria*, several species change the sculpture of their whorls as they grow and do so at variable rates. However, a comparison of the two species highlights differences in the early whorls and protoconch. The protoconch of *D. mozambiquensis* is about 30% narrower than that of *D. herberti* n. sp. and the latter has a broader, inflated shape. The early whorls of *D. mozambiquensis* have distinctive round nodes compared with convex ribs on *D. herberti* n. sp.

***Partecosta bozzettii* Malcolm & Terry new species**
(Figs 3K, 11E)

Type material: Holotype: MNHN IM-2009-10163, lv, 12.5 mm; Port d'Ehoala, S Madagascar, 25°03'43.9"S, 46°57'42.9"E, 3–4 m

(ATIMO VATAE Stn TP29). Paratype 1: MNHN IM-2009-10162, lv, 11.8 mm; type locality.

Zoobank registration: urn:lsid:zoobank.org:act:6E3E67B5-1B55-4A99-8D39-6517DA4D065C

Diagnostic nucleotide positions: Table 11.

Description: Shell small. Protoconch paucispiral, 1 whorl, with broad nucleus. Holotype 9 teleoconch whorls; outline of whorls weakly convex. No subsutural band, or demarcation thereof, except for minor indentation of ribs; no visible spiral sculpture. Axial sculpture of almost straight, thin ribs, 14 on penultimate whorl, stretching across whorl height; interspaces wider than ribs. Last whorl elongate, tapering towards base. Columella straight, aperture elongate. Shell colour off-white with darker-tinged spiral band adapically on whorls and below periphery; brownish blotches between the axial ribs abapically on whorls; inner columella dark brown or purplish.

Habitat: In sand at 3–4 m.

Distribution: Known only from type locality.

Etymology: The species honours Luigi Bozzetti (Italy), who has contributed tremendously to the knowledge of the molluscan fauna of S Madagascar.

Remarks: The species resembles *P. trilineata* (Fig. 11F), but differs by its more globose and convex whorls and by having a single row of

brown blotches instead of two. In addition, the protoconch of *P. trilineata* is differently shaped, having two whorls and a medium nucleus. The phylogenetic analysis of Modica *et al.* (2019) shows significant genetic distance between the two species. *Partecosta bozzettii* n. sp. shows some resemblance to *P. albofasciata*, but again differs by its more convex whorls, distinct axial ribbing and shell colour pattern. *Partecosta bozzettii* n. sp. is similar in general morphology and shell colour pattern to *Hastula daniæ* (Fig. 2G) from West Africa, but the latter has a multispiral protoconch and more globose mature whorls.

***Profunditerebra papuaprofundii* Malcolm, Terry & Fedosov new species**

(Fig. 12A, B)

Type material: Holotype: MNHN IM-2013-58123, 1 lv, 19.0 mm; off New Ireland, Papua New Guinea, 2°21'S, 150°38'E, 496–609 m (KAVIENG 2014 Stn CP4422). Paratype 1: MNHN IM-2013-45571, 1 lv, 29.5 mm; W Buka I., N Bougainville, Papua New Guinea, 5°43'S, 154°03'E, 490–530 m (MADEEP Stn DW4278). Paratype 2: MNHN IM-2013-59946, 1 lv, 25.6 mm; same locality. Paratype 3: MNHN IM-2013-59944, 1 lv, 13.7 mm; same locality. Paratype 4: MNHN IM-2013-59945, 1 lv, 16.3 mm; W Buka I., N Bougainville, 5°35'S, 153°58'E, 623–640 m (MADEEP Stn DW4271). Paratype 5: MNHN IM-2013-45509, 1 lv, 27.1 mm; W Buka I., N Bougainville, 5°37'S, 153°59'E, 421 m (MADEEP Stn DW4270). Paratype 6: MNHN IM-2013-30574, 1 lv, 33 mm (broken); SW Santa Isabel I., Solomon Islands, 8°24'S, 159°27'E, 362–432 m (SALOMON 2 Stn CP2193).

Other material examined: Taiwan, 15°03'N; 116°31'E (NANHAI 2014 Stn DW4102), IM-2013-52276, 1 lv.

Zoobank registration: urn:lsid:zoobank.org:act:ABAFB4A7-FCD6-4632-A07C-E9945D21EA7A

Diagnostic nucleotide positions: see Table 11.

Description (holotype): Shell of moderate size, to 42 mm. Protoconch of 4 narrow, conical whorls with small nucleus. Teleoconch of 12 whorls; teleoconch whorl outline convex constricted abapically at the suture. Subsutural groove represented by weak indentation on early whorls becoming sharper groove cutting through the ribs on mature whorls. Sculpture of strong slightly convex narrow axial ribs on subsutural band aligned with those on succeeding portion of whorls, varying significantly between specimens in spacing, and in number from 18 to 25 (20 ribs on penultimate whorl). No spiral sculpture in interspaces except for striae on base below periphery. Last whorl cup-shaped, becoming more elongate on mature specimens. Aperture wide with slight callus; columella straight with 2 folds. Colour off-white with tinges of yellow or pink with shiny white columella.

Habitat: Depths of 350–600 m.

Distribution: Papua New Guinea, Solomon Islands and Taiwan.

Etymology: Named after its deep-water habitat in Papua New Guinea.

Remarks: The only sequenced specimen of *P. papuaprofundii* n. sp. with intact protoconch was designated as the holotype. It is notably smaller than the sequenced paratypes, which reach shell lengths of 42 mm. The larger specimens demonstrate the increased curvature of ribs and increased number and density of ribs to 25 on the penultimate whorl. *Profunditerebra papuaprofundii* n. sp. is phylogenetically closest to *P. orientalis* and *P. anseeuwi*. *Profunditerebra*

anseeuwi has a weaker subsutural groove, straight and oblique ribs and a mottled colour pattern. *Profunditerebra orientalis* has more axial ribs, a mottled colour pattern, and a sculpture of ribs and spiral cords creating nodes at their intersections. Specimens of *P. papuaprofundii* n. sp. with more numerous curving ribs are similar to *Maculager cinctella* and *Terebra textilis* (Salvador & Pickering, 2017). However, *M. cinctella* (Fig. 12C) has a shorter protoconch of 2.5 whorls, a much narrower noded subsutural band and many spiral striae within the interspaces between the ribs. In turn, *T. textilis* (Fig. 12D) differs in having a spiral groove defined by deep punctations or partially cutting the ribs, and has several spiral striae in the interspaces between the ribs.

***Profunditerebra macclesfieldensis* Malcolm, Terry & Fedosov new species**

(Fig. 12E, F)

Type material: Holotype: MNHN IM-2013-61875, 1 lv, 22.4 mm; N Macclesfield Bank; South China Sea, 16°07'N, 114°23'E, 161 m (ZhongSha 2015 Stn DW4144). Paratype 1: MNHN IM-2013-61877, 1 lv, 22.2 mm; type locality. Paratype 2: MNHN IM-2013-61995, 1 lv, 27.2 mm; type locality. Paratype 3: MNHN IM-2013-58887, 1 lv, 19.2 mm; New Ireland, 2°26'S, 149°55'E, 240–242 m (KAVIENG 2014 Stn DW4485). Paratype 4: 1 dd, 23.1 mm; South China Sea. YT, 200 m. Paratypes 5–7: YT, 3 lv, 20.6–29.5 mm; off Aliquay I., Philippines, dredged at 150–200 m.

Zoobank registration: urn:lsid:zoobank.org:act:F1081F38-DB65-4EDF-B73C-8743D92009A9

Diagnostic nucleotide positions: Table 11.

Description: Shell to 30 mm. Protoconch multispiral, 4 translucent amber whorls, small nucleus. Holotype of 12 teleoconch whorls. Teleoconch whorls with straight outline. Subsutural band defined by continuous punctate groove. Axial ribs thin compared with interspaces, gradually becoming more numerous, resulting in about 25 ribs on penultimate whorl of holotype. Ribs only intersected by punctate groove, extended onto flat subsutural band. On last whorl, ribs fade at periphery. No spiral sculpture visible between ribs. Aperture long, creating elongate rounded shape to last whorl. Columella straight, with callus in mature specimens. Colour brown to white with some brown markings.

Habitat: Depths of 160–240 m.

Distribution: South China Sea, Philippines and Papua New Guinea.

Etymology: Named after the type locality, the Macclesfield Bank in the South China Sea.

Remarks: In terms of shell morphology, *P. macclesfieldensis* n. sp. is most similar to *P. anseeuwi* (Fig. 12G), *Duplicaria duplicata* (Fig. 3A) and *Punctoterebra teramachii* (Fig. 8B). *Profunditerebra anseeuwi* is the most similar in shell morphology; it has a much shorter columella, creating a cup-shape to the last whorl; its ribs are set at an oblique angle; its colour is white, with broad brown spiral bands between the ribs and dark spots on the subsutural band. *Duplicaria duplicata* differs in having a paucispiral protoconch of 1.5 whorls, a shorter aperture, and its ribs are broad and closely packed. *Punctoterebra teramachii* has a much narrower apical angle, the profile of its whorls is more rounded and the subsutural band narrower.

***Neoterebra guadeloupensis* Malcolm, Terry & Fedosov new species**

(Fig. 13A, B)

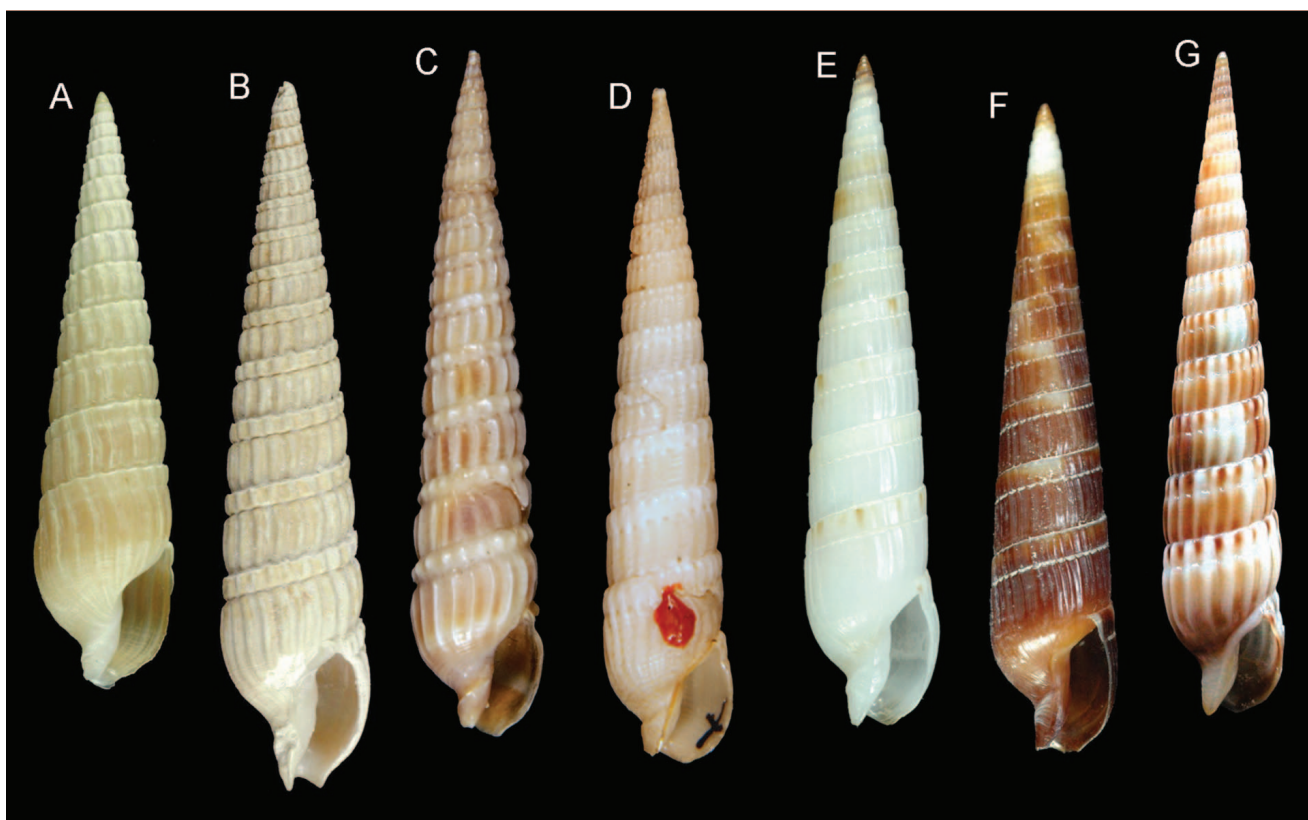


Figure 12. *Profunditerebra papuaprofundus* n. sp., *P. macclesfieldensis* n. sp. and morphologically similar species. **A.** *P. papuaprofundus* holotype, MNHN-IM-2013-58123, KAVIENG 2014 Stn CP4422, 02°21'S, 150°38'E, 496–609 m, 19.0 mm. **B.** *P. papuaprofundus* paratype 1, MNHN-IM-2013-45571, same locality, 29.5 mm. **C.** *Terebra cinclella* lectotype, NHMUK 197988/1, 'Mouth of the Indus', 27.8 mm. **D.** *Terebra textilis* lectotype, NHMUK 1844.6.7.80, 'Str Macassar', 25.7 mm. **E.** *P. macclesfieldensis* holotype, MNHN-IM-2013-61875, ZhongSha 2015 Stn DW4144, 16°6'N, 114°23'E, 160–200 m, 22.4 mm. **F.** *P. macclesfieldensis* paratype 1, MNHN-IM-2013-61877, same locality, 22.2 mm. **G.** *P. anseeuwi* holotype, MNHN-IM-2000-6224, Aliquay I., Philippines, 80–150 m, 29.8 mm.

Type material: Holotype: MNHN IM-2013-61448, 1 lv, 17.2 mm; S Marie-Galante, Guadeloupe, 15°50'N, 61°19'W, 305–312 m (N/O *Antea*, KARUBENTHOS 2015 Stn DW4638). Paratypes 1–3: off Fajou, Guadeloupe, 16°22'N, 61°34'W, 80 m (KARUBENTHOS 2012 Stn GD02). Paratype 1: MNHN IM-2013-20542, 1 lv, 6.5 mm. Paratype 2: MNHN IM-2013-20541, 1 lv, 5.7 mm. Paratype 3: MNHN IM-2013-20539, 1 lv, 10.4 mm. Paratype 4: MNHN IM-2013-9110, 1 lv, 7 × 2.1 mm; Port Louis, Guadeloupe, 16° 22' 46'N, 61°34'W, 66 m (KARUBENTHOS 2012 Stn GD35).

Zoobank registration: urn:lsid:zoobank.org:act:57E995EE-24F0-47A0-9DDC-E9D54948B056

Diagnostic nucleotide positions: Table 11.

Description: Shell small. Protoconch multispiral, transparent with 3 whorls tinged yellow; protoconch/teleoconch transition clear-cut with visible sinusigera. Teleoconch of holotype with 15 whorls; overall whorl outline straight to convex. Weak axial sculpture of 15 narrow axial ribs with wider interspaces, increasing with maturity to 25 on penultimate whorl. Deep subsutural groove crossed obliquely by ribs. Subsutural band with strong elongate nodes; subsequently, 2 strongly projecting spiral cords at top and middle of whorl dominating sculpture, forming reticulate pattern of deep indentations with thin ribs; the upper cord projects in outline beyond subsutural band. On mature whorls interspaces sometimes with 1 or 2 weak spiral striae. Reticulate sculpture continuing on shell base. Aperture long with weak callus; columella with 2 weak folds. Shell lacks any pattern; coloured in shades of white to yellow.

Habitat: Deep water, 60–310 m.

Distribution: Only known from off Guadeloupe.

Etymology: Named after the type locality, the French Caribbean island of Guadeloupe.

Remarks: A number of species of Terebridae have been described from the Western Atlantic and Caribbean Sea that have a similar strong reticulate sculpture. These include *N. limatula* that has more than 2 strong spiral cords in addition to the subsutural band (Fig. 13C) and a paucispiral protoconch. *Neoterebra colombiensis* is very similar to *N. guadeloupensis* n. sp., but the spiral sculpture in the former is less dominant, giving a more uniform reticulate sculpture with nodes at the intersections. In addition, *N. colombiensis* has a paucispiral protoconch in comparison with the multispiral protoconch of *N. guadeloupensis* n. sp. *Neoterebra simonei* is similar in colour and sculpture, but has 3 spiral cords in addition to the subsutural band and has a distinctive paucispiral protoconch of 1.5 whorls. Other similar species from the region, e.g. *N. intumescens* and *N. alagoensis* (Fig. 9F), all have paucispiral protoconchs and different sculpture.

***Macaulager sudchinensis* Malcolm, Terry & Fedosov
new species
(Fig. 13D, E)**

Type material: Holotype: MNHN IM-2013-61887, 1 lv, 19.9 mm; N Macclesfield Bank, S China Sea, 16°07'N, 114°23'E, 161 m (ZhongSha 2015 Stn DW4144). Paratypes: N Macclesfield Bank,

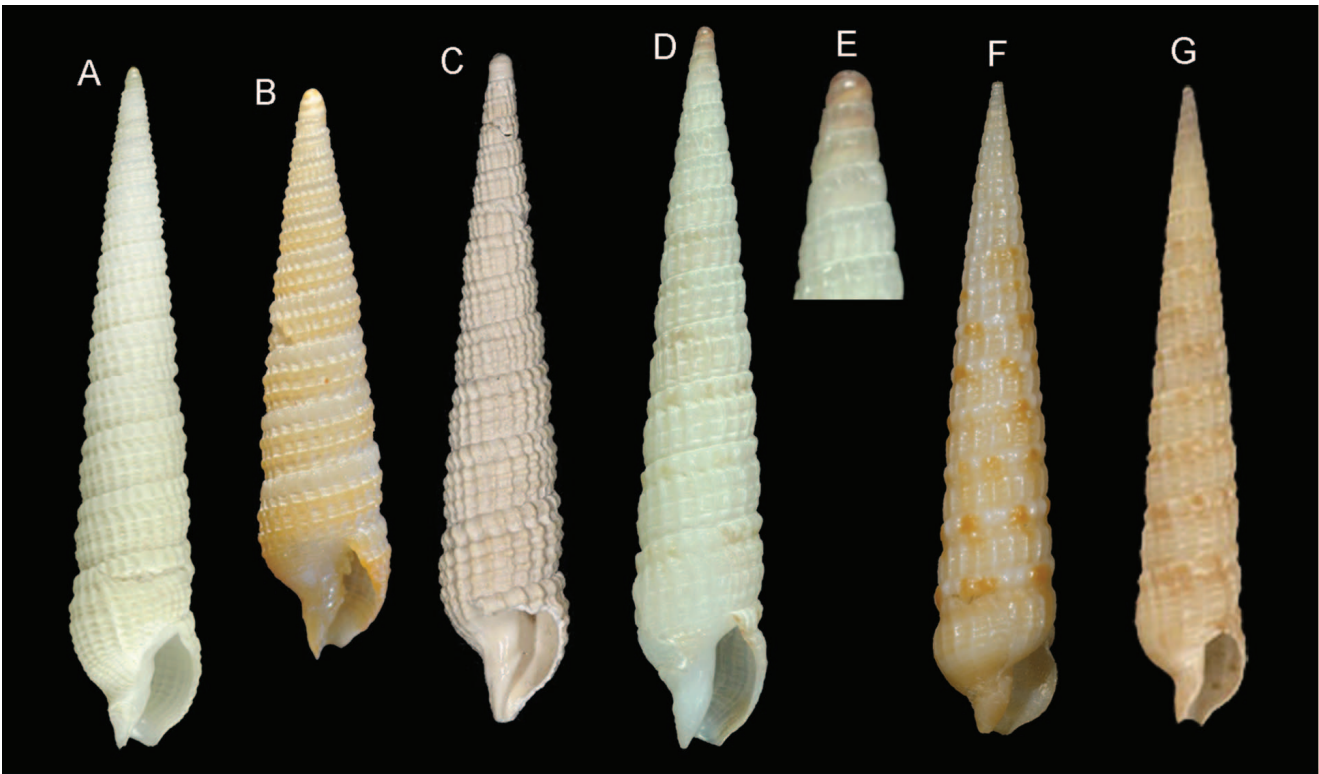


Figure 13. *Neoterebra guadeloupensis* n. sp., *Maculauger sudchinensis* n. sp. and morphologically similar species. **A.** *N. guadeloupensis* n. sp. holotype, MNHN-2013-61448, KARUBENTHOS 2015 Stn DW4638, 15°50'N, 61°18'W, 305–312 m, 17.2 mm. **B.** MNHN-IM-2013-20531, KARUBENTHOS 2012 Stn GD55, 16°22.48'N, 61°35.46'W, 85 m, 9.4 mm. **C.** *Terebra limatula* syntype, USNM93971, Apalachicola Bay, FL, 17.8 mm. **D, E.** *M. sudchinensis* n. sp., holotype, MNHN-IM-2013-61887, ZhongSha 2015 Stn CP4144, 16°6'N, 114°23'E, 160–200 m, 19.9 mm. **F.** *Terebra helichrysum* lectotype, NHMUK 1903.12.15.117, Mussandam, Persian Gulf, 47 fms (= 86 m), 24.5 mm. **G.** *Terebra levantina* holotype, MNHN-IM-2000-2812, MUSORSTOM 2 Stn CP59, 14°00'N, 120°16'E, 186–190 m, 24.2 mm.

S China Sea, 16°08'N, 114°19'E, 180–226 m (ZhongSha 2015 Stn CP4145). Paratype 1: MNHN IM-2013-61902, 1 lv, 20.2 mm. Paratype 2: MNHN IM-2013-61895, 1 lv, 20.7 mm.

Other examined material: N Macclesfield Bank, S China Sea, 16°07'N, 114°19'E, 218–281 m (ZhongSha 2015 Stn CP4148), 2 dd.

Zoobank registration: urn:lsid:zoobank.org:act:BB5F5C93-C9FE-44F0-B1EC-C00AA31EFF23

Diagnostic nucleotide positions: Table 11.

Description: Shell to 21 mm; narrow apical angle. Protoconch paucispiral, 1.5 translucent whorls. Teleoconch of holotype with 14 whorls; outline of whorls slightly convex. Subsutural band formed of deep pits. Axial ribs narrow with wide interspaces; ribs *c.* 18–20 on penultimate whorl, straight on subsutural band, becoming oblique at subsutural groove, then curved on abapical part of whorls. Axial ribs intersected by 2–3 evenly spaced spiral grooves. Aperture long, with straight columella. Ground colour chalky white, sometimes with vague brown marks on subsutural band.

Distribution: Only known from N Macclesfield Bank.

Habitat: Depths of 160–220 m.

Etymology: Named after the South China Sea.

Remarks: *Maculauger campbelli* has a similar protoconch and slender overall shape with slightly convex whorls, but in comparison with *M. sudchinensis* n. sp. has a more continuous subsutural groove, less

pronounced sculpture, with 5–7 spiral grooves and a distinctive pattern of straw colour with random square spots. *Maculauger sudchinensis* n. sp. is similar to *Terebra helichrysum* (Fig. 13F), which however has a much shorter curved columella, a multispiral protoconch of 3.5 whorls, shorter whorls and a mottled orange colour pattern. *Terebra levantina* (Fig. 13G) has similar sculpture, but its whorls are much shorter, with 4–6 spiral grooves and it has a mottled colour pattern.

DISCUSSION

Systematics of Terebridae: a case study for integrative taxonomy

This work describes the systematic revision of the venomous conoidean marine gastropod family Terebridae using an integrated molecular, morphological and anatomical approach. With the increasing role of DNA sequence analysis in systematic studies, a critical step is the transition from inferred clades to formally described taxa. A phylogenetic tree allows the recognition of clusters of closely related species, thus defining the content of future taxa, but provides no means of circumscription of the setaxa. Additionally, existing taxonomic practices are still deeply rooted in traditional morphology-based alpha-taxonomy. Therefore, an informative morphology-based diagnosis and/or description remain central for the formal establishment of new taxa. Similarly, when contents of previously known taxa are redefined based on a phylogenetic analysis, provision of reliable diagnostic morphological characters consistent with inferred phylogenetic relationships is challenging, but notably increases the operational value of the revised taxonomic arrangement. Thus, knowing the phylogenetic relationships provides necessary insight, as it enables

a 'guided' detection of inconspicuous and previously likely ignored features that may prove to be very important for understanding the morphological identity of a taxon.

In this vein, we used the recent 154-species molecular-phylogenetic analyses of the Terebridae (Modica *et al.*, 2019) to elaborate the classification of Terebridae, in combination with shell and anterior alimentary-system characters. Our results placed the 407 living species of the family, including seven species described herein, into three subfamilies: Pellifroniinae n. subfam., Perviaciinae and Terebrinae. Additionally, we devised a computational method for analysing COI fragments to propose DNA-based diagnoses in order to define most of the supraspecific taxa of Terebridae. Using this approach, we also proposed separate diagnoses for the inferred phylogenetic clusters within the large genera *Terebra*, *Punctoterebra* and *Hastula*.

Challenges for transition from shell-based to DNA-based taxonomy

Traditional molluscan shell-based taxonomy is increasingly being challenged by DNA-based methods. When these two methods are in agreement, it adds rigour and robustness to the process of species delimitation. However, when shell-based and DNA findings are incongruent, formulating a robust diagnosis is an arduous task. The cases of discrepancy between morphology-based and DNA-based hypotheses of terebrid genera challenged our ability to establish these taxa formally using traditional taxonomic practices. Morphological variation in some phylogenetic lineages of Terebridae was so great that it was extremely difficult to propose an inclusive diagnosis that would still be informative. Good examples are found in the genus *Punctoterebra*, in which *P. solangeae* is hardly distinguishable from the sympatric species of *Partecosta*, species of the *P. teramachii* complex demonstrate shell characteristics typical of *Duplicaria*, and the *P. textilis* group would perfectly fit in a cluster of heavily sculptured *Terebra* species. To cope with this situation and satisfy the requirements of the ICZN, we provided inclusive descriptions of genera and gave guidelines for their differentiation in *Remarks*. In cases similar to that of *Punctoterebra*, we treated several morphological groups included in a phylogenetic genus separately, as each of them appeared morphologically more similar to one or several unrelated lineages, than to inferred congeners. One could argue that splitting such heterogeneous groups would have been a reasonable solution, leading to narrower if more robust generic diagnoses. Nevertheless, more informative diagnoses would have been the only advantage of such a scheme, since they would not have made the task of delineating a morphological cluster from similar but unrelated lineages any easier. On the other hand, when sequenced species (*c.* 1/3 of those currently accepted) and morphologically readily-attributable species (*c.* 1/3 of species) are distributed among about 25–30 clearly defined genera, the remaining 'problematic' species, which do not match any proposed genus, would end up *incertae sedis*, which would greatly compromise the proposed classification. We, therefore, employed the option of broadly defined genera which, although not straightforward, allows for generally plausible placement of such 'problematic' species. Our proposed classification can be seen as a transitional scheme that can be further elaborated with minimal rearrangement of the principal genera. The classification presented here, although involving some compromises, fulfills its aim to establish a framework consistent with the state-of-the-art phylogenetic relationships within Terebridae, and provides an account of morphological and molecular diversity in each proposed genus and subfamily, facilitating correct allocation of specimens and species.

Accounting for varying selection pressures and rates of evolution in species delimitation

Ideally, a set of morphological characteristics would be found for each delineated taxon, allowing for its unmistakable recogni-

tion. However, there is no expectation that phylogenetically defined lineages will necessarily be readily distinguishable morphologically (Bickford *et al.*, 2007; Jörger & Schrödl, 2013). The acknowledgement that molecular and morphological characters do not necessarily evolve at comparable rates underpins the concept of cryptic species, which has profoundly changed our estimates of global species diversity (Knowlton, 1993; Bickford *et al.*, 2007). It is to be expected that mechanisms such as morphological stasis or convergent evolution, which account for morphological crypsis at the species level, can also act at a higher taxonomic level. On the other hand, descendants of a relatively recent radiation may exhibit a wide range of morphologies under the influence of divergent selection pressures, as demonstrated in the terebrid genera *Duplicaria*, *Myurella* and *Punctoterebra*. In such cases of rapid morphological divergence, phylogenetic hypotheses based solely on morphological characters may be erroneous. Therefore, as shown with this revision of the Terebridae, an integrative approach is crucial to reconstruct phylogenetic relationships, when the molecular and morphological data considered separately lead to conflicting hypotheses of relatedness.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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