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Phylogenetic classification of the family Terebridae (Gastropoda: Mollusca)

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PHYLOGENETIC CLASSIFICATION OF TEREBRIDAE

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ABSTRACT

The conoidean family Terebridae Mörch, 1852 is an intriguing lineage of marine gastropods that are of considerable interest due to their multifaceted anatomy and complex venoms. Terebrids are abundant easily recognizable and widely distributed in tropical and subtropical waters, however the systematics of this group requires revision.. Here we elaborate the classification of Terebridae based on a recently published molecular phylogeny including 154 species, shell and anterior alimentary system characters. The 407 living species of the family, including 7 species described herein, are assigned to three subfamilies: Pellifroniinae new subfamily, Pervicaciinae Rudman, 1969 and Terebrinae Mörch, 1852. The new subfamily Pellifroniinae includes five deep-water species in two genera *Pellifronia* Terryn & Holford, 2008 and *Bathyterebra* n. gen.. Pellifroniinae possess radulae of duplex marginal teeth, well developed proboscis and venom gland, and a very small rhynchodeal introvert. The subfamily Pervicaciinae encompasses ~ 50 species in the predominantly Indo-Pacific genera *Duplicaria* Dall, 1908 and *Partecosta* Dance & Earnes, 1966. Pervicaciinae possess salivary glands, a radula of solid recurved marginal teeth and 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 based on the 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, and the latter two range widely in both geographic and bathymetric distribution. The *Neoterebra* n. gen. encompasses about 65 species from a range of localities in the eastern Pacific, Caribbean and Atlantic, and from varying depths.

The highly diversified genera *Terebra* Bruguière, 1789, *Punctoterebra* Bartsch, 1923, *Myurella* Hinds, 1845, and *Duplicaria*, each comprise several morphological clusters. To characterize these genera we propose DNA based diagnoses combined with more informative descriptions in defining 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; WoRMS 2018). Terebrids are specialized sand and mud dwellers. Although many terebrid species thrive in deep sea in both Pacific and Atlantic, the family reaches its highest diversity in 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 molluscs due to their elongate, multi-whorled shells, Terebridae is an excellent model taxon for studying patterns of microevolution (Castelin et al., 2012; Holford et al., 2009; Fedosov et al. 2014), or assessing magnitudes of local biodiversity (Kantor et al. 2012; Modica et al. 2014). Furthermore, there is a growing interest in the Terebridae family as similar to cone-snails, terebrids employ complex venoms for hunting that can be investigated to understand venom evolution, function and diversification, and to discover novel potent bioactive compounds (Puillandre & Holford, 2010; Imperial et al. 2003, 2007; Kendrel et al. 2013; Gorson et al. 2015; 2016; Verdes et. al. 2017).

The placement of the Terebridae into 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 et al. 1993), and molecular phylogenetic approaches (Holford et al. 2009; Puillandre et al. 2011; Castelin et al. 2012). A striking diversity of anterior digestive system anatomies among Terebridae, has led Rudman (1969) to question the monophyly of the family, and 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 further acknowledged by Taylor (1990), however, its 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*’ *jungi* Lai, 2001 (Holford et al. 2009; Castelin et al. 2012). *T. jungi* was subsequently reassigned to a separate genus *Pellifronia* (Holford & Terryn, 2008). However, beyond these punctuated revisions, little has been done to reconcile the systematics of Terebridae with the emerging phylogenetic framework of the family.

The present day taxonomy of the Terebridae as published in Terryn (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 (Gorson et al. submitted), the inconsistency between the evolutionary relationships and systematics of the Terebridae has further increased. Given the molecular efforts, it is now clear that the genus level classification of the family needs to be revised because many of the currently recognized genera were found non-monophyletic in prior published phylogenies (Holford et al. 2009; Castelin et al. 2012, Modica et al. 2014, Gorson et al. submitted). Additionally, the growing multidisciplinary interest in the Terebridae warrants a revision of the family.

Here we present a revision of the Terebridae classification that is informed by recent terebrid phylogenetic analyses. We describe a new taxonomic arrangement of Terebridae, with most genera defined based on the inferred phylogenetic relationships. As the genus level taxonomy undergoes thorough revision, placement of all known terebrid species have been revisited, and complete species lists are provided for each genus. Transition from the traditional shell-based taxonomy to the new classification, which is based largely on the phylogenetic relationships, posed some methodological issues, in particular in the proposition of informative and useful diagnoses. The observed multiple cases of convergent evolution of shell morphology prompted us to introduce molecular character based diagnoses to the recognized taxa of the Terebridae. Although use of molecular characters to diagnose supraspecific taxa remains uncommon, when the molecular data is decisive it is viewed as a necessary step in transition to new classifications as applied here with the Terebridae.

MATERIAL AND METHODS

Rationales for name attribution and ranking of recognized phylogenetic clades

As detailed in Puillandre et al. 2014, transition from the 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 family Terebridae as a source of phylogenetic information (Gorson et al. submitted). Only well-supported clades in the phylogenetic analysis of (Gorson et al. submitted) are named. When molecular clades to be named are identified, a name is pinpointed to a molecular clade primarily based on the inclusion of a type species of a nominative genus in this clade (when several type species are included, priority is given to the oldest genus name). If no such species is included, the name is applied based on concordance in morphological characteristics between the species in a clade and a type species of a nominative genus. If no available names are found for a molecular clade, a new nominative taxon is proposed. Decisions on naming clades are made aiming for minimal phenotypical variability in a candidate taxon, but avoiding unnecessary fragmentation of taxa. We thus followed a conservative approach; for instance, although the names *Cinguloterebra* Oyama, 1961, *Dimidacus* Iredale, 1929, *Myurellina* Bartsch, 1923 and *Triplostephanus* Dall, 1908, are available for four well-supported subclades of the Gorson et al. (submitted) clade C, all the lineages in the clade C are here referred to *Terebra*, a decision substantiated by the observed homogeneity of anatomy and radular morphology across the clade C (Gorson et al. submitted) (Fig. 1). On the contrary, six subclades of the major clade E were each assigned genus rank, leading to naming four new genera, *Profunditerebra* n. gen. (Clade E3), *Neoterebra* n. gen. (Clade E4), *Maculauger* n. gen. (Clade E5A) and *Myurellopsis* n. gen. (Clade E5B), in addition to the names *Myurella* applied to the clade E1 and *Punctoterebra* – to the clade E2. 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.

Fig. 1

Two well-supported lineages of the Gorson et al. (submitted), referred to as F1 and F2 therein, share the characteristic "*Duplicaria*" arrangement of foregut structures (Fig. 1). However, they are distinctive in shell size, morphology and distribution. *Duplicaria duplicata* (Linnaeus, 1958), the type species of the genus, is included in the clade F1, therefore, the name can be allocated to either the clade F1 or the entire clade F (i.e. F1+F2). As proposing genera recognizable by shell morphology undoubtedly increases the operational ability of a classification, we allocate the name *Duplicaria* to the clade F1 of Gorson et al. (submitted) only. The name *Partecosta* Dance & Eames, 1966 is available ffor the phylogenetic lineage F2, based on the notable resemblance of sequenced species in this lineage to *Terebra fuscobasis* E. A. Smith, 1877, the type species of *Partecosta*, and is so applied here. Genetic and anatomical distinctiveness of the Gorson et al. (submitted) clade F in relation to other studied Terebridae is sufficient, in our opinion, for recognizing it as a subfamily; the name Pervicaciinae is therefore restored and applied to it. Consequently, the two other main clades of Terebridae (clade A and the clade comprising the rest of the Terebridae), are also assigned the subfamily rank: Pellifroniinae n. subfam. for clade A, and Terebrinae for the Terebridae except clades A and F.

The median estimated times of diversification in each of the recognized genera range from 14 million years ago (Mya) (*Maculauger*) to 29 Mya (*Terebra*), which suggests that diversification of terebrid genera has taken place in Oligocene-Miocene (Gorson et al. submitted). These estimates fall within the range estimated for the most recent common ancestors in other genera of neogastropods in the muricid subfamily Rapaninae (Claremont et al. 2013) and in the family Conidae (Duda & Kohn 2005; Puillandre et al. 2014).

Allocation of species to genus level groups

In identifying the 1400 sequenced specimens analysed in Gorson et al (2018), we found that the species boundaries as predicted by shell morphology in many cases corresponds to complexes of closely related species (Gorson et al. submitted). In most cases, revealed molecular operational taxonomic units (MOTUs) were distinguishable by shell morphology, and in several cases we demonstrate that species previously considered as synonyms actually correspond to distinct species. We thus raised to species level those that we can confidently identify. Phylogenetic analysis of Gorson et al. (submitted) also identified several MOTUs that undoubtedly correspond to undescribed species. Although massive description of 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 were specimens of a currently accepted species found to be junior synonyms of another species. Despite many striking parallelisms 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 shell morphology is an overall reliable proxy that could be used to allocate species for which no sequence data is available for the proposed taxa (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 based on their distinctive features in both shell morphology and anatomy within each genus-level clade identified in the phylogenetic tree (Gorson et al. submitted). The International Commission on Zoological Nomenclature (ICZN) allows two alternative options for establishing 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 13A), or (2) to propose 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 features to add other non-sequenced species to the proposed taxa and to formulate a synopsis of morphological characteristics for each generic taxon. As multiple cases of convergent evolution of shell features were demonstrated for Terebridae (Gorson et al. submitted), the synopsis content was usually not sufficient for unequivocal identification of a primarily phylogenetically defined genus. In such cases, a formal *Description* was provided, and additional information on how the members of each genus can be differentiated from similar but unrelated forms is to be found in our *Remarks* sections. In several genera, several distinctive subclades were recognized by the phylogenetic analysis, and they could have been considered as subgenera. Here we chose to not define subgenera to avoid 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. 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 for distinctive morphological features, were found to be attributable to currently accepted genera for which no DNA sequence data is available. As no phylogenetic data is available on these genera, we cannot resolve their status with certainty, and thus such genera are retained as valid. In the systematic section below, for each genus we propose a formal diagnosis or description, depending on our ability to identify the characteristics that differentiate a proposed genus from other groups in Terebridae and provide a list of member species.

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 (COI, 18S, 12S, and 23S) phylogenetic analysis (Gorson et. al. submitted) was not comprehensive for all species and specimens per clade, the credibility of a molecular diagnosis derived from this dataset would have been questioned. To combat this we used only the COI dataset including only sequences with no more than 5 ambiguously called nucleotides (963 records), representing 179 putative species. Initially, species were attributed to pre-defined clades based on the results of the four-gene analyses of Gorson et. al. (2018) and that was consistent with allocations to genera and subfamilies in a classification detailed below. The total length of the COI alignment was 658 base pairs (the “barcode” fragment defined by the Folmer et al (1994) primers), which were thus numbered from 1 to 658. First, an attempt was made to find pure diagnostic single-nucleotide positions (i.e. at a given position, all the members of the clade and none of the non-members of the clade share a given nucleotide) using the R package SPIDER 1.4-1 (Brown et al. 2012). However, only one diagnostic single nucleotide character was identified for each of the clades A1 and E5A, and none in 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 non-members of the clade share a combination of nucleotides). To our knowledge, only CAOS (Sarkar et al. 2008) is capable of detecting such diagnostic combinations. However, as CAOS implements a tree-based algorithm, it poses certain requirements to the data to run efficiently, such as a pre-defined group is only provided diagnosis (referred to as characteristic attributes or CA’s by Sarkar et al. 2008 and Rach et al. 2008) if it corresponds to a clade in the provided tree. The tree reconstructed using all our COI sequences (Gorson et al. submitted) did not retrieve all the subfamilies and genera monophyletic, thus making CAOS not applicable. Consequently, we developed a custom Python script (available upon request) that is based on an alternative, purely statistical approach, and implements iterated random search to identify diagnostic combinations of nucleotides for each predefined group in an assemblage of aligned sequences. The in-house Python script provided the most comprehensive and reproducible results for our dataset.

RESULTS

Levels of confidence in attribution to genera

Valid recent species entries (401) from current WoRMS database (as per February 1 2018) were used in our analysis. DNA sequence data were available for 135 currently accepted species (Gorson et al. submitted) that constitute 134 species entries (except *Oxymeris troendlei* (Bratcher, 1981), which was found to be a junior synonym of *O. maculata* (Gmelin, 1791)). These 134 species as well as seven new species revealed by the phylogenetic analysis of Gorson and coauthors (2018) and described herein are allocated to genera with a superscript 1 (^{1}), indicating highest degree of confidence.

The use of morphological characters in combination with geographic distribution resulted in a non-ambiguous placement into one of the groups recognized phylogenetically of 166 more species; these are marked with superscript 2 (^{2}).

In multiple cases, shell morphology initially appeared to be inconclusive for confident attribution of a species to a genus, as more than one hypothesis on its placement was 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 superscript 3 (^{3}).

Of the remaining species, 39 showed no clearly definable affinity to any single molecularly defined genus. However, based on the shell morphology alone, each species could be allocated to one of six terebrid genera *Granuliterebra* Oyama, 1961, *Hastulopsis* Oyama, 1961, *Pristiterebra* Oyama, 1961, *Gradaterebra* Cotton & Godfrey, 1932, *Perirhoe* Dall, 1908, *Microtrypetes* Pilsbry & Lowe, 1932. These six genera remain solely defined by shell characters pending further molecular data.

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

Finally, 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 Columbellidae respectively.

Identification of COI DNA 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 in-house Python script. However, we failed to identify diagnostic combinations of nucleotides for the genera *Terebra* and *Punctoterebra*, and only found diagnostic combinations for *Hastula* H. Adams & A. Adams, 1853, when four sequences with a substitution at the position 181 of the COI fragment were removed from the dataset. As a result, for *Terebra, Punctoterebra,* and *Hastula* taxa we propose separate diagnoses for the inferred phylogenetic clusters within each genus.

SYSTEMATICS

Superfamily Conoidea Fleming, 1822

Family Terebridae Mörch 1852

[Synonyms: Acusidae Gray, 1853]

Description: Shell elongate or conical, multi-whorled, 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 closely set eye tentacles with eye situated near their tips. Rhynchodaeal introvert always present, small to very large. Proboscis, radula, salivary gland, accessory salivary gland, 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 n. subfam.

Fig. 2

(Fig. 2)

Type genus: Pellifronia Terryn & Holford, 2008

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

Table 1

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 1.

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

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

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

Genus *Pellifronia* Terryn & Holford, 2008

(Fig 2. A – D)

Type species: Terebra jungi Lai, 2001; OD.

Definition This genus includes species closely related to *Pellifronia jungi* (Lai, 2001) based on the molecular phylogenetic analysis (Gorson et al. submitted) and those that show a combination of conchological, anatomical and distribution characteristics closely comparable to *Pellifronia jungi* or any genetically proven member of the genus.

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 1.

Description: Shell medium-sized (25-50 mm), elongate, light brown. Protoconch brown, paucispiral, cyrthoconoid, of 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 its tip, shallowly notched; siphonal fasciole weak or indistinct. Aperture elongate, curved.

Anatomy. Rhynchodeal introvert small, proboscis, radular sac, odontophore, salivary and venom glands well developed. Acessory proboscis structure absent. Radula with well-developed membrane, bearing two rows of wide marginal teeth of duplex type.

Distribution: Indo-Pacific, bathyal depths

Remarks: The genus differs from the closely related *Bathyterebra* in having stronger axial sculpture, more flattened whorl outline and last adult whorl constricted to siphonal canal with visible angulation. Species of *Pellifronia* can be distinguished by their coarse sculpture, swollen ribs ends with slightly raised subsutural area. Similar species in other genera, e.g. *Neoterebra puncturosa* (S.S. Berry, 1959), *N. crenifera* (Deshayes, 1859) and *Granuliterebra bathyrhaphe* (E.A. Smith, 1875), normally have a sharper nodular structure on the subsutural band or ribs' endings, or can be separated by the lack of radula (species of *Neoterebra*).

Included species:

Pellifronia brianhayesi (Terryn & Sprague, 2008) [2];
P. jungi (Lai, 2001) [1].

Genus *Bathyterebra* n. gen.

(Fig. 2 E – I)

Type species: Terebra benthalis Dall, 1889; OD herein.

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

Definition: This genus includes species closely related to *Bathyterebra benthalis* (Dall, 1889) based on the molecular phylogenetic analysis (Gorson et al. submitted), and those that show a combination of conchological, anatomical and distribution characteristics closely comparable to *Bathyterebra benthalis* or any genetically proven member of the genus.

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 1.

Description: Shell small, of 12-30 mm, elongate, white to tan. Protoconch paucispiral, cyrthoconoid, of about 1.5 glossy whorls. Sculpture of fine dense orthocline ribs, interrupted by depression in adapical portion of whorl. Axial ribs weakening throughout their height on mature whorls, often forming weak nodules bordering the adapical depression, giving distinctly angulated outline to early spire whorls; late teleoconch whorls gently convex. Last adult whorl evenly convex, transiting to shell base without visible angulation. Siphonal canal stout, slightly recurved at its tip, shallowly notched; siphonal fasciole weak, or rather strong. Aperture elongate, rather wide.

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

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

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

Remarks: Bathyterebra spp. can be differentiated from most other genera of Terebridae by the combination of relatively faint sculpture lacking spiral elements, with weakly defined subsutural band and relatively high last adult whorl with convex outline. In shell proportions the genus somehow resembles *Oxymeris* Dall, 1903; however, the latter genus has more flattened whorls and typically can be easily differentiated by a notably larger size at maturity.

Included species:

Bathyterebra benthalis (Dall, 1889) [1] comb. nov.;
B. coriolisi (Aubry, 1999) [1] comb. nov.;
B. zhongshaensis Malcolm, Terryn & Fedosov [1] sp. nov.

Subfamily **Pervicaciinae Rudman, 1969**

Fig. 3

(Fig. 3)

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

Description: Shells elongate ranging from 10 to 100 mm, with high spire, predominant axial sculpture and wide aperture.

Anatomy. Rhynchodeal introvert rather small, salivary gland 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. 3 A – E)

[Synonyms: *Diplomeriza* Dall, 1919 (Unnecessary nom. nov. pro *Duplicaria* Dall, 1908, by Dall treated as a homonym of the 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: The genus is primarily defined based on the results of the phylogenetic analysis (Gorson et al. submitted), and comprises species which have been demonstrated to form a well-supported clade with the type species *Duplicaria duplicata* (Linnaeus, 1758), and additionally species which show shell morphology, anatomical or genetic characteristics closely comparable to *Duplicaria duplicata* or any genetically proven member of the genus.

Table 2

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 2.

Description: Shell elongate, small to large-sized, adult size 20-100mm, with wide aperture and predominant axial sculpture, either continuous from suture to suture or interrupted by a shallow to deep subsutural indentation. Spiral structure obsolete, sometimes, microscopic striae or weak band joining nodes.

Anatomy. Rhynchodeal introvert rather small, salivary gland 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 and West Africa.

Remarks: By shell morphology 3 distinct clusters can be delineated within *Duplicaria*:

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

Duplicaria tristis (Deshayes, 1859) group. Small shells, adult size 10-30 mm, paucispiral protoconch with sculpture of strong axial ribs, subsutural area weakly impressed.

Duplicaria tricincta (E.A. Smith, 1877) group. Small shells, adult size 10-25 mm, paucispiral protoconch. Strong spiral ribs. A more convex shape with outline flattened due to elevation of ribs below the 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 & Fedosov [1];
D. hiradoensis (Pilsbry, 1921) [2];
D. jukesi (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, 1982[1];
D. silvanae (Aubry, 1999) [3];
D. similis (E. A. Smith, 1873) [2];
D. sowerbyana (Deshayes, 1857) [2];
D. tricincta (E. A. Smith, 1877) [1];
D. tristis (Deshayes, 1859) [1];
D. ustulata (Deshayes, 1857) [2];
D. veronicae (Nicolay & Angioy, 1993) [2].

Genus *Partecosta* Dance & Eames, 1966

(Fig. 3 F – O)

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

Definition: This genus includes species that show a combination of conchological, anatomical and distribution characteristics closely comparable to *Strioterebrum wilkinsi* Dance & Eames, 1966, including all species in the clade F2 of the (Gorson et al. submitted), or any species proven phylogenetically close to them.

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 2.

Description: Shell small, adult size 10-30 mm, pale or tan, often with spiral bands and dark basal area. Protoconch from 1.5 to 3 whorls. Dominant sculpture of axial ribs spanning across whorl's height, resulting in even, slightly convex whorl outline, or (typically) interrupted by depression or narrow groove forming subsutural row of nodules. Spiral sculpture indistinct or represented by fine regular striae. Siphonal canal very short, stout, indistinctly or very shallowly notched, with strong fasciole. Aperture wide, pyriform.

Anatomy. Rhynchodeal introvert rather small; salivary gland 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 depths.

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

Partecosta fuscobasis group with sculpture of strong ribs and clearly delineated subsutural band forming distinct nodules at intersections with ribs (Figs 3F - I). It is closely comparable to species of the New World genus *Neoterebra*, however, can be differentiated by smaller size at maturity, wider aperture, usually with wide anterior notch, and solid curved radular teeth.

Partecosta trilineata (Bozzetti, 2008) group with glossy shells sculptured by strong continuous ribs, no distinct spiral sculpture or subsutural band (Figs 3K, L). Very similar sympatric forms are known in the genus *Punctoterebra* (i.e. *P. solangeae* Bozzetti, 2015 group), that can only be reliably differentiated by anatomical characters (radula of solid curved teeth in *Partecosta* spp. and lacking in *P. solangeae*).

Partecosta macleani (Bratcher, 1988) group with flattened whorl outline, very short and robust siphonal canal, and very weak sculpture represented by rounded, almost indistinct subsutural nodules extended into even less distinct axial folds on whorl periphery (Fig 3M). Some species of *Hastula* are close to *Partecosta macleani*, however, they are commonly larger, have polished surface and retain distinct ribbing at least on the adapical portions of the whorls.

Included species:

Partecosta albofuscata (Bozzetti, 2008) [1] comb. nov.;

P. bozzettii n. sp. Malcolm, Terryn & Fedosov [1];

P. fuscolutea Bozzetti, 2008 [2] comb. nov.;

P. macleani (Bratcher, 1988) [1] comb. nov.;

P. nassoides (Hinds, 1844) [1] comb. nov.;

P. sandrinae (Aubry, 2008) [1] comb. nov.;

P. trilineata (Bozzetti, 2008) [1] comb. nov.;

P. varia (Bozzetti, 2008) [1] comb. nov.;

P. fuscobasis (E. A. Smith, 1877) [2] comb. nov.;

P. fuscocincta (E. A. Smith, 1877) [2] comb. nov.;

P. herosae (Terryn & Rosado, 2011) [2] comb. nov.;

P. macandrewii (E. A. Smith, 1877) [2] comb. nov.;

P. padangensis (Thiele, 1925) [2] comb. nov.;

P. tantilla (E. A. Smith, 1873) [2] comb. nov.;

P. tenera (Hinds, 1844) [3] comb. nov.

P. veliae (Aubry, 1991) [3] comb. nov.

Subfamily Terebrinae Mörch 1852

Type genus: Terebra Bruguière, 1789

Description: Shell elongate, multi-whorled, 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 the rhynchocoel cavity. Radula, proboscis, venom gland, salivary gland and accessory proboscis structure present or absent. Radula when present – consisting of hypodermic, flat, semi-enrolled or very rarely – duplex marginal teeth, never of solid type.

Remarks: Although the subfamily is consistent with a highly supported clade in the phylogenetic tree of Gorson et al. (submitted), its conceptual circumscription (i.e. based on the shared synapomorphic characters) is difficult. Among such characters only the large rhynchodeal introvert that occupies most of the rhynchocoel cavity can be mentioned. Foregut anatomy offers some other characters that can practically facilitate recognition of Terebrinae. Until proven otherwise, all the radula-less terebrids are in the Terebrinae, as well, as all species with flat, semi-enrolled or hypodermic radular teeth. Practically, recognition of the terebrines can be aided by the fact that the two other terebrid subfamilies are notably more compact and are generally clearly delineated; therefore, everything that is definitively not a member of neither Pellifroniinae nor Pervicaciinae is here considered in Terebrinae.

Genus *Terebra* Bruguière, 1789

Fig. 4

(Figs 4, 5)

Fig. 5

Type species: Buccinum subulatum Linnaeus, 1767; Type by subsequent monotypy.

[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; *Dimidacus* Iredale, 1929 (nomen novum pro *Terebrina* Bartsch, 1923, non Rafinesque, 1815); *type species*: *Terebra cingulifera* Lamarck, 1822; by typification of replaced name; *Myurellina* Bartsch, 1923; *type species*: *Terebra ornata* Gray, 1834; OD; *Subula* Schumacher, 1817 (unnecessary replacement name for *Terebra*); *type species*: *Buccinum subulatum*; typification of replacement names; *Terebrina* Bartsch, 1923 (invalid: junior homonym of *Terebrina* Rafinesque, 1815); *type species*: *Terebra cingulifera* Lamarck, 1822; OD; *Terebrum* Montfort, 1810 (unnecessary amendation 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: The genus is primarily defined based on results of the phylogenetic analysis (Gorson et al. submitted), and includes species clustering into a well-supported clade of *Terebra subulata* (Linnaeus, 1767), and species, showing resemblance in shell morphology, anatomy and distribution to any genetically proven member of the genus.

Table 3

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided separately for the seven clades of the genus inferred by Gorson et al. (submitted) in the Table 3.

Description: Shell elongate, medium-sized to large, reaching 192 mm, with truncated base shortly 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 pattern, with spiral elements being stronger or at least pronounced equally with axials. Shell base separated from siphonal canal by concave waist. Aperture elongate to quadrangular.

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

Distribution: Indo Pacific, West Africa, Panamic, Caribbean and Western Atlantic

Remarks: The genus *Terebra* is here established in the boundaries consistent with the clade C of Gorson et al. (submitted). This clade is in turn subdivided into eight lineages, referred to as C1 – C7 (see figure 4), their relationships being not resolved. The clades C1, C2, C3-2, C4, and C7 are well supported; clade C5 comprising one species only – *Terebra argus*. Because of the extreme heterogeneity of the clade C our attempts to provide a molecular diagnosis failed, and therefore, we compiled separate diagnoses for the inferred lineages within C (Table 3). Although lineages C3-1 and C3-2 do not constitute a clade, their affinity is not rejected by the phylogenetic analysis, and here they are grouped together based on the biogeographic considerations. The genus *Terebra* is enormously heterogeneous in regard of shell morphology as well (Fig. 5); some common morphotypes can be delineated based on shell morphology, but their correspondence with inferred phylogenetic groupings is far from being perfect. Below we provide 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 pattern of large spots. Species referable to this morphotype are included in clades C1 (*T. subulata* and *T. guttata* (Röding, 1798)), C4 (*T. ornata* Gray, 1834) and C6 (*T. argus* Hinds, 1844). This morphotype is probably closest to *Oxymeris*, and differentiation of the two lineages is tricky. In most cases *Terebra* spp. can be recognized by the narrower anterior notch; however, examination of the foregut to determine whether proboscis and radula are present is advised for definite allocation.

The *fenestrata* morphotype comprises most heavily sculptured species, which are distinctive because of strong, often elevated gemmate subsutural band which is closely followed by second spiral band of similar morphology, but usually weaker and/or narrower. The lower portion of the whorl is sculptured with spiral cords, or have cancellate pattern. Species exhibiting this morphotype comprise the clade C2, and strikingly similar species can be also found in the clades C7 (*T.* aff. *adamsii* (E. A. Smith, 1873), *T.* aff. *rubrobrunnea* Preston, 1908 MNHN IM-2013-14908, *Terebra anilis* (Röding, 1798)) and C8 (*Terebra cumingi* Deshayes, 1857 species complex). Strong, often elevated, gemmate or beaded spiral elements readily differentiate this morphotype from most terebrid genera. The similar pattern however is present in *Granuliterebra* spp., the species of which being differentiated by the single subsutural band and usually by a prevailing axial sculpture on the lower portion of the whorl.

Triplostephanus morphotype unifies species with very high spire and very small, quadrate aperture. Whorls flattened or slightly concave due to raised subsutural band, and lower part of whorl sculptured by regular cords, while axial sculpture is not developed. The clade C5 is mostly represented by species exhibiting this morphotype; however, species with sub-cylindrical whorls and stepped outline of spire (such as *Terebra laevigata* Gray, 1834 and *Terebra funiculata* Hinds, 1844) 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, *Terebra taurina* (Lightfoot, 1786) and *Terebra fujitai* Kuroda & Habe, 1952 of the clade C3 have bifurcate ribbed subsutural band, similar to *fenestrata* morphotype, although notably lower. Similarly, a bifurcate nodulose subsutural band is present in *Terebra corrugata* Lamarck, 1822, a species showing close affinity to *Terebra subulata* in the clade C1. The apparent lack of phylogenetic signal in the distribution of these morphotypes across the clade C precludes assignment of any taxonomic rank to them. Moreover, the general lack of homogeneity in shell characteristics within subclades of *Terebra* makes their establishment as supraspecific taxonomic units pointless as well.

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

Included species:

Terebra achates Weaver, 1960 [2];
T. adamsii (E. A. Smith, 1873) [2];
T. albocancellata Bratcher, 1988 [3];
T. albomarginata Deshayes, 1859 [1];
T. amanda Hinds, 1844 [1];
T. anilis (Röding, 1798) [1];
T. archimedis Deshayes, 1859 [1];
T. argosyia Olsson, 1971 [2];
T. argus Hinds, 1844 [1];
T. babylonia Lamarck, 1822 [1];
T. balabacensis Aubry & Picardal, 2011 [3];
T. bellanodosa Grabau & King, 1928 [3];
T. binii (Aubry, 2014) [2];
T. boucheti (Bratcher, 1981) [2];
T. bratcherae Cernohorsky, 1987 [3];
T. caddeyi (Bratcher & Cernohorsky, 1982) [2];
T. caelata Adams & Reeve, 1850 [1];
T. castaneostriata Kosuge, 1979 [3];
T. cingulifera Lamarck, 1822 [1];
T. circinata Deshayes, 1857 [2];
T. cognata E. A. Smith, 1877 [3];
T. commaculata (Gmelin, 1791) [2];
T. connelli (Bratcher & Cernohorsky, 1985) [2];
T. consobrina Deshayes, 1857 [1];
T. corrugata Lamarck, 1822 [1];
T. cossignanii Aubry, 2008 [2];
T. cumingii (Deshayes, 1857) [1];
T. deshayesii Reeve, 1860 [2];
T. donpisori Terryn, 2017 [3];
T. elliscrossi (Bratcher, 1979) [1];
T. erythraeensis Terryn & Dekker, 2017 [3];
T. eximia (Deshayes, 1859) [2];
T. fenestrata (Hinds, 1844) [1];
T. fernandae Aubry, 1995 [3];
T. fernandesi Bouchet, 1983 [3];
T. fijiensis (E. A. Smith, 1873) 3;
T. floridana (Dall, 1889) [3];
T. formosa Deshayes, 1857 [1];
T. fujitai (Kuroda & Habe, 1952) [1];
T. funiculata Hinds, 1844 [1];
T. gabriellae Aubry, 2008 [3];
T. gaiae Aubry, 2008 [3];
T. giorgioi Aubry, 1999 [3];
T. grayi E. A. Smith, 1877 [3];
T. guineensis Bouchet, 1983 [3];
T. guttata (Röding, 1798) [1];
T. helichrysum Melvill & Standen, 1903 [3];
T. histrio Deshayes, 1857 [3];
T. hoaraui (Drivas & Jay, 1988) [1];
T. insalli (Bratcher & Burch, 1976) [2];

T. irregularis Thiele, 1925 [3];
T. jacksoniana (Garrard, 1976) [3];
T. jenningsi (Burch, 1965) [1];
T. knudseni Bratcher, 1983 [2];
T. laevigata Gray, 1834 [1];
T. lauretanae Tenison-Woods, 1878 [3];
T. levantina Aubry, 1999 [3];
T. ligata Hinds, 1844 [2];
T. lillianae Withney, 1976 [2];
T. lima (Deshayes, 1857) [2];
T. lindae Petuch, 1987 [2];
T. mamillata (Watson, 1886) [2];
T. mariesi (E. A. Smith, 1880) [2];
T. marrowae (Bratcher & Cernohorsky, 1982) [2];
T. montgomeryi Burch, 1965 [2];
T. neglecta (Poppe, Tagaro & Terryn, 2009) [2];
T. nodularis Deshayes, 1859 [3];
T. noumeaensis Aubry, 1999 [3];
T. ornata Gray, 1834 [1];
T. pellyi E. A. Smith, 1877 [3];
T. picta Hinds, 1844 [3];
T. polygonia Reeve, 1860 [3];
T. praelonga Deshayes, 1859 [2];
T. pretiosa Reeve, 1842 [2];
T. pseudopicta Aubry, 2008 [3];
T. pseudoturbonilla Talavera, 1975 [3];
T. punctatostriata Gray, 1834 [2];
T. punctum (Poppe, Tagaro & Terryn, 2009) [2];
T. quoygaimardi Cernohorsky & Bratcher, 1976 [1];
T. raybaudii Aubry, 1993 [2];
T. reticularis (Pecchioli in Sacco, 1891) [3];
T. robusta Hinds, 1844 [1];
T. rosae Aubry, 2015 [3];
T. russetae (Garrard, 1976) [3];
T. salisburyi Drivas & Jay, 1998 [2];
T. stearnsii Pilsbry, 1891 [1];
T. straminea Gray, 1834 [1];
T. subangulata Deshayes, 1859 [3];
T. subulata (Linnaeus, 1767) [1];
T. succinea Hinds, 1844 [3];
T. swobodai Bratcher, 1981 [3];
T. tagaroae Terryn, 2017 [2];
T. taiwanensis Aubry, 1999 [3];
T. taurina (Lightfoot, 1786) [1];
T. tessellata Gray, 1834 [2];
T. tricolor G. B. Sowerby I, 1825 [1];
T. triseriata (Gray, 1834) [1];
T. twilae Bouchet, 1983 [3];
T. unicolor Preston, 1908 [1];
T. vanuatuensis Aubry, 1999 [3];
T. vappereaui Tröndlé, Boutet & Terryn, 2013 [2];
T. venilia Tenison-Woods, 1879 [3];
T. vicdani (Kosuge, 1981) [2];
T. virgo Schepman, 1913 [3];
T. waikikiensis (Pilsbry, 1921) [2];

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

Fig. 6

(Fig. 6 A – E)

Type species: Buccinum strigilatum[1] Linnaeus, 1758; SD Cossmann, (1896: 53).

[Synonyms: *Impages* E. A. Smith, 1873; *type species*: *Terebra caerulescens* 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: This genus includes species closely related to *Hastula strigilata* (Linnaeus, 1758), based on the molecular phylogenetic analysis (Gorson et al. submitted) and those that show a combination of conchological, anatomical and distribution characteristics closely comparable to *Hastula strigilata* or any genetically proven member of the genus.

Table 4

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided for the entire clade with the exception of four specimens of *H. albula* (see Materials and Methods) and separately, for the subclade *H. albula* - *H. natalensis* - *H.* aff. *casta* of the clade D (Table 4).

Description: Shell small to medium-sized, shiny, adult size (12-90 mm). Protoconch pauci- or multispiral of about 1 to 5 whorls. Axial sculpture represented by crenulations on whorl's subsutural portion, or by fine ribs on part or throughout the whorls' height; spiral sculpture represented by single subsutural groove, seldom 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 gland and radula well-developed. Radula consisting of hypodermic marginal teeth attached to thin, reduced membrane. Walls of marginal teeth often with multiple perforations (Figs 6 E, F)

Distribution: Throughout Indo-Pacific, West Africa, Caribbean.

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

Included species:

Hastula aciculina (Lamarck, 1822) [2];
H. acumen (Deshayes, 1859) [1];
H. alboflava Bratcher, 1988 [2];
H. albula (Menke, 1843) [1];
H. androyensis Bozzetti, 2008 [2];
H. anomala (Gray, 1834) [2];
H. anosyana (Bozzetti, 2016) [2];
H. apicitincta (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, 1965 [2];
H. cinerea (Born, 1778) [1];
H. continua Deshayes, 1859 [2];
H. crossii (Deshayes, 1859) [1];
H. cuspidata (Hinds, 1844) [2];
H. denizi Rolán & Gubbioli, 2000 [2];
H. engi Malcolm & Terryn, 2017 [2];
H. escondida (Terryn, 2006) [2];
H. exacuminata Sacco, 1891 [2];
H. filmerae (G. B. Sowerby III, 1906) [2];
H. hamamotoi Tsuchida & Tanaka, 1999 [2];
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. leloeuffi Bouchet, 1983 [2];
H. lepida (Hinds, 1844) [2];
H. marqueti (Aubry, 1994) [2];
H. maryleeae R. D. Burch, 1965 [2];
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. sandrogorii Ryall, Terryn & Rosado, 2017 [2];
H. solida (Deshayes, 1857) [1];
H. strigilata (Linnaeus, 1758) [1];
H. stylata (Hinds, 1844) [1];
H. tenuicolorata Bozzetti, 2008 [1];
H. tiedemani Burch, 1965 [2];
H. venus Aubry, 2008 [2];
H. verreauxi (Deshayes, 1857) [1];
H. westralica (Aubry, 1999) [2];
H. daniae (Aubry, 2008) [3].

Genus *Oxymeris* Dall, 1903

(Fig. 6 F – H)

Type species: Buccinum maculatum Linnaeus, 1758; OD.

[Synonym: *Abretia* H. & A. Adams, 1853 (invalid: junior homonym of *Abretia* Rafinesque, 1814), type species *Terebra cerithina* Lamarck, 1822; SD, Dall, 1908, The Nautilus, 21(11): 125; *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: The genus includes species closely related to *Oxymeris maculata* (Linneaus, 1758), based on the molecular phylogenetic analysis (Gorson et al. submitted) and those that show a combination of conchological, anatomical and distribution features closely comparable to *Oxymeris maculata* (Linnaeus, 1758) or any genetically proven member of the genus.

Table 5

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 5.

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

Anatomy. Rhynchodeal introvert very large, proboscis absent or vestigial, salivary gland 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 (i.e. *O. cerithina*) have spire with convex sides, and superficially resemble medium-sized *Punctoterebra* and *Myurella*. 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 set deep spiral grooves differentiate *Perirhoe* spp. 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, 2016 [2];
O. senegalensis (Lamarck, 1822) [2];
O. strigata (G. B. Sowerby I, 1825) [1];
O. suffusa (Pease, 1869) [2];
O. swinneni Terryn & Ryall, 2014 [2];
O. trochlea (Deshayes, 1857) [2];
O. troendlei (Bratcher, 1981 [1].

Genus *Myurella* Hinds, 1845

Fig. 7

(Fig. 7 A – 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: The genus is primarily defined based on results of the phylogenetic analysis (Gorson et al. submitted), and comprises species which have been demonstrated to form a well-supported clade with the type species *Myurella affinis* (Gray, 1834), and additionally species which show shell morphology, anatomical or genetic characteristics closely comparable to *Myurella affinis* or any genetically proven member of the genus.

Table 6

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 6.

Description: Shell very small to medium-sized, with elongated, with high orthoconoid spire and 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 gland and accessory proboscis structure present in few species.

Distribution: Indo-Pacific, at intertidal to upper bathyal depths.

Remarks: In regard of shell morphology, four distinct clusters can be recognized:

Myurella affinis group. Shell medium-sized; axial sculpture of low and wide, flattened ribs, subsutural band with elongate nodules delineated by punctations, which are also pronounced in interspaces between axial ribs. Similar species that earlier were classified to *Myurella*, but that were found not immediately related to *T. affinis* (i. e. *M. undulata*, *M. columellaris* and *M. kilburni*) are here reclassified to the genus *Myurellopsis*. The typical *Myurella* 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, due to the more elevated ribs in *Myurellopsis* spp., the subsutural band is represented by a row of nodules.

Myurella pseudofortunei group. Shell elongate of variable size (17-60 mm), with very high and 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* Oyama, 1961, of which some smaller species were found to be unrelated lineages, the differences between which are still to be elaborated.

Myurella pygmaea group. Shell small, circa 10 mm, with curving outline, straight sides to whorls and very short, tapering siphonal canal. Axial sculpture of numerous fine oblique ribs; subsutural band, or other spiral elements absent. The group includes one species, the only representative of the former genus *Terenolla*. The very small but rather solid, finely ribbed shell, of *Myurella pygmaea* is easily recognizable amongst terebrids; its recognition is further aided by the color pattern with flesh background and a 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 punctuations, spiral structure 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 within *Hastulopsis* Oyama, 1961. Similar deeper water species are found in the genus *Maculauger* n. gen., most of which can be recognized by having a row of large spots on the periphery. The other similar species remain within the genus *Hastulopsis*, comprising a number of Indian Ocean and Japanese endemic species. Species of *Myurella amoena* group have strong but narrow ribs that are, however, notably stronger than spiral elements. In *Myurellopsis* spp. the ribs are about as strong, but are wider and rounded, with interstices being narrower than ribs themselves. Both *Hastulopsis* and *Maculauger* 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 (Melvill & 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. mindanaoensis (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] comb. nov.;
M. russoi (Aubry, 1991) [2];
M. suduirauti (Terryn & Conde, 2004) [2];
M. wellsilviae (Aubry, 1994) [1].

Fig. 8

Table 7

Genus *Punctoterebra* Bartsch, 1923

(Fig. 8)

Type species: Terebra nitida Hinds, 1844; OD.

Definition: The genus is primarily defined based on results of the phylogenetic analysis (Gorson et al. submitted), and comprises species which have been demonstrated to form a well-supported clade with *Punctoterebra nitida* (Hinds, 1844), and additionally species which show shell morphology, anatomical or genetic characteristics closely comparable to *Punctoterebra nitida* or any genetically proven member of the genus.

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided separately for the four phylogenetic clusters of the *Punctoterebra* inferred by Gorson et al. (submitted) in the Table 7 (the deep water lineage composed by two currently undescribed species represented by MNHN IM-2013-52264 and MNHN IM-2013-52293 treated separately from the *Punctoterebra textilis* group).

Description: Shell elongate, small to medium sized (adult size below 50 mm), with high spire and prevailing 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 represented by regular striae in interspaces between axial ribs.Siphonal canal delineated from shell base by distinct concavity, often slightly recurved.

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

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

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

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

Punctoterebra teramachii (Burch, 1965) group. Shells medium sized (<45mm) with dominant structure of orthocline axial ribs; spiral structure absent. Subsutural band clearly defined. Species of this group are conchologically close to the genus *Duplicaria*, from which they can be differentiated by the punctate subsutural groove and narrower aperture, and by morphology of radular teeth that are solid and recurved in *Duplicaria*, and flat (or absent) in *Punctoterebra* spp.

Punctoterebra textilis (Hinds, 1844) group. Shell medium sized (<50mm), heavily sculptured, with gently convex whorls. Sculpture of arcuate ribs, interspaces bearing regular distinct striae; subsutural band delineated by a punctuate groove of varying strength. Syphonal canal typically recurved, delineated from shell base by distinct waist of deep groove. This group is rather heterogeneous in shell morphology, with the core formed by heavily sculptured species of the *Punctoterebra textilis* – *P. succincta* (Gmelin, 1891) complex. Similar heavily sculptured shells characterize typical *Profunditerebra*; 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 bifurcate subsutural bands. The inferred close affinity of the *Punctoterebra lineaperlata* (Terryn & Holford, 2008) to the species in the *P. textilis* group is, however, unexpected and needs further analysis.

Included species:

Punctoterebra arabella (Thiele, 1925) [2] comb. nov.;
P. baileyi (Bratcher & Cernohorsky, 1982) [1] comb. nov.;
P. ballina (Hedley, 1915) [2] comb. nov.;
P. caliginosa (Deshayes, 1859) [1] comb. nov.;
P. caliginosa (Deshayes, 1859) [2] comb. nov.;
P. castaneofusca (Thiele, 1925) [1] comb. nov.;
P. contracta (E. A. Smith, 1873) [1] comb. nov.;
P. exiguoides (Schepman, 1913) [3] comb. nov.;
P. fuscotaeniata (Thiele, 1925) [2] comb. nov.;
P. illustris (Malcolm & Terryn, 2012) [2] comb. nov.;
P. isabella (Thiele, 1925) [2] comb. nov.;
P. japonica (E. A. Smith, 1873) [3] comb. nov.;
P. lineaperlata (Terryn & Holford, 2008) [1] comb. nov.;
P. livida (Reeve, 1860) [3] comb. nov.;
P. longiscata (Deshayes, 1859) [2] comb. nov.;
P. nitida (Hinds, 1844) [1] comb. nov.;
P. paucincisa (Bratcher, 1988) [3] comb. nov.;
P. plumbea (Quoy & Gaimard, 1833) [1] comb. nov.;
P. polygyrata (Deshayes, 1859) [1] comb. nov.;
P. rosacea (Pease, 1869) [3] comb. nov.;
P. roseata (Adams&Reeve, 1850) [1] comb. nov.;
P. solangeae (Bozzetti, 2015) [1] comb. nov.;
P. souleyeti (Deshayes, 1859) [1] comb. nov.;
P. succincta (Gmelin, 1791) [1] comb. nov.;
P. swainsoni (Deshayes, 1859) [2] comb. nov.;
P. teramachii (Burch, 1965) [1] comb. nov.;
P. textilis (Hinds, 1844) [1] comb. nov.;
P. trismacaria (Melvill, 1917) [1] comb. nov.;
P. turrita (E. A. Smith, 1873) [1] comb. nov.;
P. turschi (Bratcher, 1981) [2] comb. nov.

Genus ***Profunditerebra*** n. gen.

Fig. 9

(Fig. 9 A – E)

Type species: Profunditerebra papuaprofundi n. sp.; OD herein.

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

Definition: This genus includes species closely related to *Profunditerebra papuaprofundi* n. sp., based on the molecular phylogenetic analysis (Gorson et al. submitted) and those that show a combination of conchological, anatomical and distribution characteristics closely comparable to *Profunditerebra papuaprofundi* n. sp. or any genetically proven member of the genus.

Table 8

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 8.

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

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

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

Remarks: *Profunditerebra* is the only terebrine genus with duplex radular teeth similar to those in Pellifroniinae; members of the two groups can be easily 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 monophyletic lineage.

Profunditerebra papuaprofundi n. sp. et gen. group. Shell uniformly coloured white to dark brown, heavily sculptured, with distinct subsutural groove and subcylindrical whorls. Sculpture of strong rounded ribs forming a 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 in *Neoterebra* (i.e. *N. armillata*) exhibit overall similar sculpture pattern, but can be differentiated from *Profunditerebra* by their flattened whorls. The *Punctoterebra textilis* group also includes some similar forms (see Remarks section under *Punctoterebra*).

Profunditerebra orientalis (Aubry, 1999) group. Shells with flattened whorl profile, and 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 delineated by shallow punctuate groove. Species of this group can be easily differentiated from congeners that either lack spiral elements, or display an overall much coarser sculpture. Both *Profunditerebra orientalis* and *Profunditerebra hiscocki* closely resemble species in the genus *Maculauger* from which they can be confidently differentiated only by anatomy (all studied species of *Maculauger* are radula-less) or molecular characters.

Profunditerebra anseeuwi (Terryn, 2005) group. Shells with flattened whorl outline, subsutural band represented by short ribs or indentation. Sculpture of axial ribs pronounced throughout whorl's 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. Besides, these lineages can be confidently differentiated by the radular teeth morphology, with *Duplicaria* having solid and recurved teeth, *Profunditerebra* – duplex teeth, and *Punctoterebra* – flat teeth.

Profunditerebra brazieri (Angas, 1871) stands apart from other species in the clade, being an endemic of subtropical shallow waters off Tasmania. Morphologically, it is close to the *Profunditerebra anseeuwi* group, but has a very weakly defined subsutural band.

Etymology: The genus name refers to the considerable depths, at which all known species of the genus occur. Gender feminine.

Included species:

Profunditerebra anseeuwi (Terryn, 2005) [1] comb. nov.;

P. brazieri (Angas, 1871) [1] comb. nov.;

P. evelynae (Clench & Aguayo, 1939) [3] comb. nov.;

P. macclesfieldensis n. sp. Malcolm, Terryn & Fedosov [1] sp. nov.;

P. orientalis (Aubry, 1999) [1] comb. nov.;

P. papuaprofundi n. sp. Malcolm, Terryn & Fedosov [1] sp. nov.;

P. poppei (Terryn, 2003) [1] comb. nov.;

P. hiscocki (Sprague, 2004) [1] comb. nov.

Genus *Neoterebra* n. gen.

(Fig. 9 F – H)

Type species: Terebra specillata Hinds, 1844; OD herein.

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

Definition: The genus is primarily defined based on results of the phylogenetic analysis (Gorson et al. submitted), and comprises species which have been demonstrated to form a well-supported clade with *Neoterebra specillata* (Hinds, 1844), and additionally species which show shell morphology, anatomical or genetic characteristics closely comparable to *Neoterebra specillata* or any genetically proven member of the genus.

Table 9

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 9.

Description: Shell small to medium-sized (<60 mm) uniformly creamy-white to light brown or bearing pattern of brown blotches, with pointed multi- or paucispiral protoconch of 1.5 – 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 shortly constricted to siphonal canal. Canal clearly separated from shell base, bearing well-pronounced fasciole.

Anatomy. Radula absent; proboscis, venom gland and accessory proboscis structure typically absent; salivary gland typically present.

Distribution: Panamic and Caribbean, off Brazil, intertidal to upper bathyal depths, typically shallow.

Remarks: Shallow-water species of the *Neoterebra* differ notably from their congeners described from deep water of Brazil and Caribbean – the former being larger at maturity and sharing characteristic sculpture of strong axial ribs forming elevated, sometimes axially elongated nodules on subsutural band. Caribbean species have notably weaker subsutural band, and species 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.

Etymology: The name is a contraction of *neo* (*latin*: new) and *Terebra*, referring to the fact that species of this new genus only occur in East Pacific, Caribbean and off Brazil, constituting the majority of the New World terebrid fauna.

Included species:

Neoterebra acrior (Dall, 1889) [2] comb. nov.;

N. alagoensis (Lima, Tenorio & Barros, 2007) [2] comb. nov.;

N. alba (Gray, 1834) [2] comb. nov.;
N. allyni (Bratcher & Burch, 1970) [2] comb. nov.;
N. angelli (J. Gibson-Smith & W. Gibson-Smith, 1984) [2] comb. nov.;
N. arcas (Abbott, 1954) [2] comb. nov.;
N. armillata (Hinds, 1844) [1] comb. nov.;
N. assu (Simone, 2012) [2] comb. nov.;
N. berryi (Campbell, 1961) [2] comb. nov.;
N. biminiensis (Petuch, 1987) [2] comb. nov.;
N. brandi (Bratcher & Burch, 1970) [2] comb. nov.;
N. brasiliensis (E. A. Smith, 1873) [2] comb. nov.;
N. bridgesi (Dall, 1908) [3] comb. nov.;
N. carolae (Bratcher, 1979) [2] comb. nov.;
N. churea (Campbell, 1964) [2] comb. nov.;
N. colombiensis (Simone & Gracia, 2006) [2] comb. nov.;
N. concava (Say, 1826) [2] comb. nov.;
N. corintoensis (Pilsbry & Lowe, 1932) [2] comb. nov.;
N. crassireticula (Simone, 1999) [2] comb. nov.;
N. crenifera (Deshayes, 1859) [1] comb. nov.;
N. curacaoensis (De Jong & Coomans, 1988) [2] comb. nov.;
N. dislocata (Say, 1822) [1] comb. nov.;
N. doellojuradoi (Carcelles, 1953) [2] comb. nov.;
N. elata (Hinds, 1844) [1] comb. nov.;
N. frigata (Hinds, 1844) [2] comb. nov.;
N. glauca (Hinds, 1844) [2] comb. nov.;
N. glossema (Schwengel, 1942) [1] comb. nov.;
N. guadeloupensis n. sp. Malcolm, Terryn & Fedosov [1] sp. nov.;
N. guayaquilensis (E. A. Smith, 1880) [2] comb. nov.;
N. hancocki (Bratcher & Burch, 1970) [2] comb. nov.;
N. hemphilli (Vanatta, 1924) [2] comb. nov.;
N. hondurasiensis (Gargiulo, 2016) [2] comb. nov.;
N. intertincta (Hinds, 1844) [3] comb. nov.;
N. intumescyra (Lima, Tenorio & Barros, 2007) [2] comb. nov.;
N. jacquelinae (Bratcher & Burch, 1970) [2] comb. nov.;
N. juanica (Dall & Simpson, 1901) [2] comb. nov.;
N. lamyi (Terryn, 2011) [2] comb. nov.;
N. larvaeformis (Hinds, 1844) [1] comb. nov.;
N. leptapsis (Simone, 1999) [2] comb. nov.;
N. limatula (Dall, 1889) [1] comb. nov.;
N. lucana (Dall, 1908) [2] comb. nov.;
N. mugridgeae (García, 1999) [2] comb. nov.;
N. nassula (Dall, 1889) [2] comb. nov.;
N. pacei (Petuch, 1987) [2] comb. nov.;
N. panamensis (Dall, 1908) [2] comb. nov.;
N. pedroana (Dall, 1908) [2] comb. nov.;
N. petiveriana (Deshayes, 1857) [2] comb. nov.;
N. plicata (Gray, 1834) [2] comb. nov.;
N. protexta (Conrad, 1846) [2] comb. nov.;
N. puncturosa (Berry, 1959) [1] comb. nov.;
N. rancheria (Bratcher, 1988) [2] comb. nov.;
N. riosi (Bratcher & Cernohorsky, 1985) [2] comb. nov.;
N. roperi (Pilsbry & Lowe, 1932) [3] comb. nov.;
N. rushii (Dall, 1889) [2] comb. nov.;
N. sanjuanense (Pilsbry & Lowe, 1932) [2] comb. nov.;
N. shyana (Bratcher & Burch, 1970) [2] comb. nov.;
N. simonei (Lima, Tenorio & Barros, 2007) [2] comb. nov.;
N. specillata (Hinds, 1844) [1] comb. nov.;
N. spirosulcata (Simone, 1999) [2] comb. nov.;
N. sterigma (Simone, 1999) [2] comb. nov.;
N. sterigmoides (Simone & Gracia, 2006) [1] comb. nov.;
N. stohleri (Bratcher & Burch, 1970) [2] comb. nov.;
N. tiarella (Deshayes, 1857) [3] comb. nov.;
N. variegata (Gray, 1834) [1] comb. nov.;
N. vinosa (Dall, 1889) [2] comb. nov.

Genus *Maculauger* n. gen.

(Fig. 7 E, F)

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

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

Definition: This genus includes species closely related to: *Maculauger pseudopertusus* (Bratcher & Cernohorsky, 1985), based on the molecular phylogenetic analysis (Gorson et al. submitted) and those that show a combination of conchological, anatomical and distribution characteristics closely comparable to *Maculauger pseudopertusus* or any genetically proven member of the genus.

Table 10

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 10.

Description: Shell small to medium-sized (<60mm), 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 the whorl by narrow groove of row of punctations. Axial and spiral sculpture elements of about equal strength producing cancellate sculpture below subsutural band.

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

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

Remarks: The newly established genus *Maculauger* comprises several species that were formerly placed in *Hastulopsis*, and can be differentiated by the equal pronunciation of spiral and axial spiral elements, producing a fine cancellate sculpture when compared to similar species in *Myurella*. The species in *Hastulopsis* have very weak sculpture and are found in the Indian Ocean or endemic to Japan. Some species of *Maculauger,* such as *Maculauger campbelli*, are conchologically very close to *Profunditerebra orientalis* – a case where only anatomical and molecular characters can ensure correct identification (see Remarks section under *Profunditerebra*).

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

Included species:

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

Genus *Myurellopsis* n. gen.

(Fig. 7 G – I)

Type species: Terebra undulata Gray, 1834; OD herein.

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

Definition: This genus includes species closely related to: *Myurellopsis undulata* (Gray, 1834), based on the molecular phylogenetic analysis (Gorson et al. submitted) and those that show a combination of conchological, anatomical and distribution characteristics closely comparable to *Myurellopsis undulata* or any genetically proven member of the genus.

Diagnosis. Diagnostic nucleotide combinations in the COI barcode region provided in the Table 10.

Description: Shell small to medium-sized (<50mm), pinkish or orange, often with white subsutural band. Protoconch multispiral. Sculpture of strong rounded slightly undulating ribs, polished in appearance. Row of punctuations with groove partially cutting ribs forming subsutural band. Interstices between ribs deep and narrow, bearing regular striae and often darkly colored. Adapical 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 found in species of the genus: either all typical foregut structures present, or all are lacking; in the latter case accessory proboscis structure present.

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

Remarks: Species in genus *Myurellopsis* n. gen. are closest to the *Myurella* spp., but can be differentiated by the sharper more elevated ribs often with nodes on the subsutural band or top of the whorls.

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

Included species:

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

GENERA DEFINED BASED ON CONCHOLOGICAL CHARACTERS

Genus *Granuliterebra* Oyama, 1961

Fig. 10

(Fig. 10 A)

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

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

Distribution: Indian Ocean and western Pacific.

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

Included species:

Granuliterebra bathyrhaphe (E. A. Smith, 1875) [4];
G. constricta (Thiele, 1925) [4];
G. eddunhami Terryn & Holford, 2008 [4];
G. oliverai Terryn & Holford, 2008 [4];
G. palawanensis (Aubry & Picardal, 2011) [4];
G. persica (E. A. Smith, 1877) [4].

Genus *Hastulopsis* Oyama, 1961

(Fig. 10 B)

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

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

Distribution: Indian Ocean and western Pacific

Remarks: The genus comprises two groups of shallow water species found along eastern coast of Africa to the Arabian Gulf and a group found in mainland Japan waters to Australia. Similar deeper water species are found in the genus *Maculauger* n. gen., most of which can be recognized by having a row of large spots on the periphery. The species within *Myurella* have a much stronger and more distinct sculpture features, and generally a brown basal area.

Included species:

Hastulopsis baliensis Terryn & Dekker, 2017 [4];
H. blanda (Deshayes, 1859) [4];
H. cebuensis Gargiulo, 2014 [4];
H. elialae (Aubry, 1994) [4];
H. gotoensis (E. A. Smith, 1879) [4];
H. loisae (E. A. Smith, 1903) [4];
H. maestratii Terryn & Rosado, 2011 [4];
H. marmorata (Deshayes, 1859) [4];
H. masirahensis Terryn & Rosado, 2016 [4];
H. melanacme (E. A. Smith, 1873) [4];
H. mirbatensis Terryn & Rosado, 2016 [4];
H. suspensa (E. A. Smith, 1904) [4];
H. whiteheadae (Aubry & Marquet, 1995) [4].

Genus *Pristiterebra* Oyama, 1961

(Fig. 10 C)

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 outline flattened to convex with predominant pustulose, or seldom cancellate sculpture. Whorl periphery shifted abapically, leading to truncated appearance of shell, with shell base shortly constricted to short siphonal canal. Aperture wide, especially in its anterior portion.

Distribution: Western Pacific

Remarks: A characteristic truncated outline with a short siphonal canal and broad aperture allows for easy recognition of the *Pristiterebra* spp. among other terebrid genera. Species in *Pristiterebra* are nearest to the nodulose species of *Neoterebra*, i.e. *N. tuberculosa*, *N. glauca* and *N. petiveriana*, which can be recognised 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 dominating axial sculpture or, rarely, complete lack of sculpture, and (*Partecosta*) by generally smaller adult size.

Included species:

Pristiterebra bifrons (Hinds, 1844)[4];
P. frausseni Poppe, Tagaro & Terryn, 2009[4] comb. nov.;
P. milelinae (Aubry, 1999)[4] comb. nov.;
P. miranda (E. A. Smith, 1873)[4] comb. nov.;
P. pustulosa (E. A. Smith, 1879)[4] comb. nov.;
P. tuberculosa (Hinds, 1844)[4] comb. nov..

Genus *Gradaterebra* Cotton & Godfrey, 1932

(Fig. 10 D)

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

Diagnosis: Small (<25 mm) often dull coloured shells with flattened to bulbous whorls, axial structure of prominent ribs, spiral structure absent, microscopical or represented by fine cords; last whorl inflated.

Distribution: Indian Ocean and SW Pacific

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

Included species:

Gradaterebra scalariformis (Cotton & Godfrey, 1932)[4] comb. nov.;
G. assecla (Iredale, 1924)[4] comb. nov.;
G. capensis (E. A. Smith, 1873)[4] comb. nov.;
G. easmithi (Aubry, 1999)[4] comb. nov.;
G. kowiensis (Turton, 1932)[4] comb. nov.;
G. lightfooti (E. A. Smith, 1899)[4] comb. nov.;
G. ninfae (Campbell, 1961)[4] comb. nov.;
G. pilsbryi (Aubry, 1999)[4] comb. nov.;
G. planecosta (Barnard, 1958)[4] comb. nov.;
G. severa (Melvill, 1897)[4] comb. nov.;
G. sorrentense (Aubry, 1999)[4] comb. nov.;
G. taylori (Reeve, 1860)[4] comb. nov.

Genus *Perirhoe* Dall, 1908

(Fig. 10 E)

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

[Synonym: None.]

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

Distribution: Southern 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 whorl's height. The sculpture pattern of widely set spiral grooves in *Perirhoe* resembles 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) [4];

Perirhoe valentinae (Aubry, 1999) [4] comb. nov.

Genus *Microtrypetes* Pilsbry & Lowe, 1932

(Fig. 10 F)

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

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

Distribution: Eastern Pacific.

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

Included species:

Microtrypetes iola Pilsbry & Lowe, 1932 [4];

M. polypenus (Pilsbry & Lowe, 1932) [4] comb. nov.

DESCRIPTIONS OF NEW SPECIES

Abbreviations

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 of the United Kingdom, London, UK;

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, D.C.;

YT: Private collection of Yves Terryn, Belgium.

Bathyterebra zhongshaensis **Malcolm, Terryn & Fedosov new species**

(Fig. 2H)

Type material: Holotype, MNHN IM-2013-61800, 17.4 x 4.8 mm.

Type locality: 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

Table 11

Diagnostic nucleotide positions in COI alignment: see Table 11.

Description: Shell small with orthocline spire and rather wide apical angle. Protoconch wide paucispiral, comprising 2.5 whorls with small nucleus. Teleoconch of 9 whorls Early teleoconch whorls convex in outline with strong sharply convex ribs; subsequent whorl's outline with narrow constriction formed by indentation with straight ribs below the suture. Suture distinct and ragged. Mature whorls with less convex outline, weaker and more numerous ribs, 30 on the penultimate whorl. Spiral sculpture of very weak threads. Last whorl bulbous at its 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: Found at depths between 470-494 m.

Distribution: Only known from type locality.

Etymology: Named for the Zhongsha sand bars, which form a subsurface atoll that sits on top of the Macclesfield Bank.

Remarks: Bathyterebra zhongshaensis n. sp. is similar to the deep-water species *Bathyterebra coriolisi* (Aubry, 1999) and *Bathyterebra benthalis* (Dall, 1889). *Bathyterebra coriolisi* (Fig. 2E) is similar in colour, in the sculpture of the early whorls and in the shape of its aperture. However, *Bathyterebra 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 and 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 the *Bathyterebra zhongshaensis* n. sp. in the outline of its mature whorls being flat and the ribs on the early whorls are extremely convex creating nodes which dominate the profile of the early whorls.

Duplicaria herberti Malcolm, Terryn & Fedosov new species

Fig. 11

(Fig. 11 A – C)

Duplicaria mozambiquensis Bratcher & Cernohorsky, 1982 - Aubry 1992: fig. 9; Aubry et al. 2006: pl. 16.

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

Type Locality: Mozambique, 26°00.0'S - 32°54.4'E, 4 m [INHACA 2011 Stn MR15]

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

Diagnostic nucleotide positions in COI alignment: see Table 11.

Description: Shell of medium size, protoconch paucispiral consisting of about 1.0-1.5 broad whorls. Teleconch of holotype with 11 whorls. Outline of teleoconch whorls straight. Spiral sculpture absent. Subsutural band beset with axially elongated nodes corresponding to axial ribs on the remainder of the whorl. Subsutural band bordered by deep and wide depression lacking punctations. Straight axial ribs stretching across whorl, sharply angular adapically and becoming more rounded abapically. Axial 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 blackish brown, lighter coloured early whorls and a spiraling whitish line at the periphery.

Habitat: Retrieved from depths between 0 and 55 m.

Distribution: Known from South Mozambique to off Durban, RSA.

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

Remarks: Shell colour varies: juveniles have shiny beige to fawn colour; also lighter brown coloured specimens are known. This species has always been confused with *Duplicaria mozambiquensis* Bratcher & Cernohorsky, 1982, even by its authors. The holotype of *Duplicaria mozambiquensis* (NMSA H7843/T2541) is a small, slender shell of 22.3 mm. The type series of *Duplicaria mozambiquensis* shows a large discrepancy in many features between the holotype and all the paratypes which are specimens of *Duplicaria herberti* n. sp. Subsequent authors have to our knowledge always featured specimens of *Duplicaria herberti* n. sp. as *Duplicaria mozambiquensis* which should be considered a rarely encountered species.

The whorls of *Duplicaria mozambiquensis* (Fig. 11D) have a narrower apical angle, its convex axial ribs giving the outline an extremely rounded convex impression, the subsutural band comprises round nodes, compared to elongated nodes on *D. herberti* n. sp. The axial ribs of *Duplicaria herberti* n. sp. become straight creating an angular projection posteriorly. The peripheral white band in *Duplicaria 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 *Duplicaria herberti* n. sp. We have no confirmation that *Duplicaria mozambiquensis* has ever been found in the south of Mozambique while specimens of *D. herberti* n. sp. are found extensively in the south of Mozambique and South Africa. Within *Duplicaria*, several species change the sculpture of their whorls as they grow and do so at variable rates of change. However a comparison of the early whorls of the two species highlights differences in the early whorls and protoconch of *Duplicaria mozambiquensis* and *D. herberti*. The protoconch of *Duplicaria mozambiquensis* is about 30% less wide 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 to convex ribs on *D. herberti* n. sp.

Partecosta bozzettii **Malcolm, Terryn & Fedosov new species**

(Figs 3K, 11 E)

Type material: Holotype, MNHN IM-2009-10163, 12.5 mm. Paratype 1, Type locality, MNHN IM-2009-10162, 1 lv, 11.8 mm.

Type Locality: S Madagascar, Port d'Ehoala, 25°03'43.9"S; 46°57'42.9"E, 3-4 m [ATIMO VATAE Stn TP29].

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

Diagnostic nucleotide positions in COI alignment: see Table 11.

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

Habitat: In sand at 3-4 m.

Distribution: Known only from the type locality.

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

Remarks: The species resembles *Partecosta trilineata* (Bozzetti, 2008) (Fig. 11F) but differs from the latter by its more globose and convex whorls and by having a single row of brown blotches instead of two. Moreover, the protoconch of *Partecosta trilineata* is differently shaped, has 2 whorls with a medium nucleus. The phylogenetic analysis shows significant genetic distance between the two species. *Partecosta bozzettii* n. sp. shares some resemblance to *Partecosta albofuscata* (Bozzetti, 2008) but again differs from the latter by its more convex whorls, distinct axial ribbing and shell color pattern. *Partecosta bozzettii* n. sp. is similar in general morphology and shell colour pattern to *Hastula daniae* (Aubry, 2008) (Fig. 2G) described from West Africa but the latter species has a multispiral protoconch and more globose mature whorls.

Profunditerebra papuaprofundi **Malcolm, Terryn & Fedosov new species**

Fig. 12

(Fig. 12 A, B)

Type material: Holotype, MNHN IM-2013-58123, 19 x 4.4 mm. Paratype 1, W Buka Is, N Bougainville, N/O *Alis*, 5°43'S; 154°03'E, 490-530 m [MADEEP Stn DW4278], MNHN IM-2013-45571, 1 lv, 29.5 x 6.3 mm; Paratype 2, same locality MNHN IM-2013-59946, 1 lv, 25.6 x 5.1 mm; Paratype 3, same locality, MNHN IM-2013-59944, 1 lv, 13.7 x 3.7 mm. Paratype 4: W Buka Is, N Bougainville, N/O *Alis*, 5°35'S; 153°58'E, 623-640 m, [MADEEP Stn DW4271], MNHN IM-2013-59945, 1 lv, 16.3 x 4.3 mm. Paratype 5: W Buka Is, N Bougainville, N/O *Alis*, 5°37'S; 153°59'E, 421m, [MADEEP Stn DW4270], MNHN IM-2013-45509, 1 lv, 27.1 x 5.8 mm. Paratype 6: SW Santa Isabel Is., N/O *Alis*, 8°24'S; 159°27'E, 362-432 m [SALOMON 2 Stn CP2193], MNHN IM-2013-30574, 1 lv, 33 x 6.1 mm (broken).

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

Type locality: Papua New Guinea, off New Ireland, 2°21'S; 150°38'E, 496-609 m [KAVIENG 2014 Stn CP4422].

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

Diagnostic nucleotide positions in COI alignment: 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: Found at depths from 350-600 m.

Distribution: Known from Papua New Guinea, the Solomon Islands and Taiwan.

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

Remarks: The only sequenced specimen of *Profunditerebra papuaprofundi* n. sp. with intact protoconch was designated as a holotype. It is notably smaller than other sequenced type specimens that reach shell length of 42 mm. The larger specimens demonstrate the increased curvature of ribs and increased number and density of ribs to 25 on penultimate whorl. *Profunditerebra papuaprofundi* n. sp. is phylogenetically closest to *Profunditerebra orientalis* (Aubry, 1999) and *Profunditerebra anseeuwi* (Terryn, 2005). *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 intersections. Specimens of *Profunditerebra papuaprofundi* n. sp. with more numerous curving ribs are similar to *Maculauger cinctella* (Deshayes, 1859) and *Terebra textilis* Hinds, 1844 (Salvador & Pickering 2017). However *M. cinctella* (Fig. 12C) has a shorter protoconch of 2.5 whorls, a much narrower nodded subsutural band and many spiral striae within the interspaces between ribs on its whorls. In turn, *Terebra textilis* (Fig. 12D) differs in having a spiral groove defined by deep punctuations or partially cutting ribs and has several spiral striae in the interspaces between ribs.

Profunditerebra macclesfieldensis Malcolm, Terryn & Fedosov new species

(Fig. 12 E, F)

Type material: Holotype, MNHN IM-2013-61875, 22.4 x 4.3 mm. Paratype 1, type locality, MNHN IM-2013-61877, 1 lv, 22.2 x 4.2 mm; Paratype 2, type locality, MNHN IM-2013-61995, 1 lv, 27.2 x 5.1mm. Paratype 3, New Ireland, 2°26'S; 149°55'E, 240-242 m [KAVIENG 2014 Stn DW4485], MNHN IM-2013-58887, 1 lv, 19.2 x 3.9 mm. Paratype 4, South China Sea. YT, 200 m, 1 dd, 23.1 mm. Paratype 5 – 7, Philippines, off Aliguay Island, YT, dredged at 150-200 m, 3 lv, 20.6-29.5 mm.

Type locality: N Macclesfield bank; South China Sea 16°07'N; 114°23'E, 161-m [ZhongSha 2015 Stn DW4144].

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

Diagnostic nucleotide positions in COI alignment: see Table 11.

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

Habitat: Found at 160-240 m.

Distribution: Known from the 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 *Profunditerebra macclesfieldensis* n.sp. is most similar to *Profunditerebra anseeuwi* (Terryn, 2005) (Fig. 12G), *Duplicaria duplicata* (Linneaus, 1758) (Fig. 3A), and *Punctoterebra teramachii* (R.D. Burch, 1965) (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 and 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, Terryn & Fedosov new species**

Fig. 13

(Fig. 13 A, B)

Type material: Holotype, MNHN IM2013-61448: 17.2 x 3.5 mm. Paratypes: Guadeloupe, off Fajou, 16°22'N; 61°34', 80 m [KARUBENTHOS 2012 Stn GD02]. Paratype 1, MNHNIM-2013-20542, 1 lv, 6.5 x 2 mm; Paratype 2, MNHNIM-2013-20541, 1 lv, 5.7 x 2 mm; Paratype 3, MNHN IM-2013-20539, 1 lv, 10.4 mm x 2.6 mm. Paratype 4, Guadeloupe, Port Louis, 16° 22' 46'N; 61°34'W, 66 m [KARUBENTHOS 2012 Stn GD35], MNHN IM-2013-9110, 1 lv, 7 x 2.1 mm.

Type Locality: S Marie-Galante, Guadeloupe. 15°50'N, 61°19'W, 305-312 m [N/O *Antea*, KARUBENTHOS 2015 Stn DW4638].

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

Diagnostic nucleotide positions in COI alignment: see 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 whorls 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, two strongly projecting spiral cords at top and middle of whorl dominating sculpture forming a reticulate pattern of deep indentations with thin ribs. The upper cord projects in outline beyond the subsutural band. On the mature whorls interspaces sometimes with one or two 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 Terebridae species have been described from the Western Atlantic and Caribbean seas which have a similar strong reticulate sculpture. These include *Neoterebra limatula* (Dall, 1889) which has more than 2 strong spiral cords in addition to the subsutural band (Fig. 13C) and has a paucispiral protoconch. *Neoterebra colombiensis* (Simone & Gracia, 2006) is very similar to *Neoterebra guadeloupensis* n. sp. but the spiral sculpture in the former species is less dominant giving a more uniform reticulate sculpture with nodes at intersections. Furthermore, *Neoterebra colombiensis* has a paucispiral protoconch in comparison to the multispiral protoconch of the *N. guadeloupensis* n. sp. *Neoterebra simonei* (De Lima, Tenorio & De Barros, 2007) is similar in colour and sculpture, however, it 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. *Neoterebra intumescyra* (De Lima, Tenorio & De Barros, 2007), *Neoterebra alagoensis* (De Lima, Tenorio & De Barros, 2007) (Fig. 9F) all have paucispiral protoconchs and differing sculpture patterns.

Maculauger sudchinensis **Malcolm, Terryn & Fedosov new species**

(Fig. 13 D, E)

Type material: Holotype, MNHN IM-2013-61887, 19.9 x 3.9 mm. Paratypes, South China Sea, N Macclesfield Bank, 16°08’N, 114°19'E, 180-226 m [ZhongSha 2015 Stn CP4145], Paratype 1, 1 lv, MNHN IM-2013-61902, 20.2 x 3.2 mm; Paratype 2, 1 lv, MNHN IM-2013-61895, 20.7 x 3.7 mm.
Other examined material: South China Sea, N Macclesfield Bank, 16°07’N;114°19’E, 218-281 m **[**ZhongSha 2015 Stn CP4148], 2 dd.
Type Locality: South China Sea, N Macclesfield Bank, 16°07'N; 114°23'E, 161 m [ZhongSha 2015 Stn DW4144].

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

Diagnostic nucleotide positions in COI alignment: see Table 11.

Description: Shell sized to 21 mm, with rather narrow apical angle. Protoconch paucispiral of 1.5 translucent whorls. Teleoconch of holotype with 14 whorls; outline of teleoconch whorls slightly convex. Subsutural band formed by deep punctures. Axial ribs narrow with wide interspaces; ribs circa 18-20 on penultimate whorl, straight on subsutural band, becoming oblique at subsutural groove and then curved on abapical part of whorls. Axial ribs intersected by 2 to 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 the N Macclesfield Bank.

Habitat: Found at depths of 160-220 m.

Etymology: Named after the South China Sea.

Remarks: Maculauger campbelli (R.D. Burch, 1965) has a similar protoconch and slender overall shape with slightly convex whorls but in comparison with *Maculauger 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* (Melvill & Standen, 1903) (Fig. 13F), which however has a much shorter curved columella, a multispiral protoconch of 3.5 whorls, its whorls are shorter and it has an mottled orange colour pattern. *Terebra levantina* (Aubry, 1999) (Fig. 13G) has similar sculpture, but its whorls are much shorter, there are 4-6 spiral grooves on its whorls, and it has a mottled colour pattern.

DISCUSSION

Terebridae systematics: a case study for integratived taxonomy This work describes the systematic revision of the venomous conoidean marine snail 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 recognition of clusters of closely related species, thus defining content of future taxa, but provides no means of ICZN valid circumscription of these taxa. Additionally, existing taxonomic practices are still deeply rooted in traditional morphology based alpha-taxonomy. Therefore, an informative morphology based diagnosis and / or description remains 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 operationability 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 vain we applied the recent 154 species molecular phylogenetic analyses of the Terebridae (Gorson et. al. submitted) to elaborate the classification of Terebridae in combintation with shell and anterior alimentary system characters. Our results placed the 407 living species of the family, including 7 species described herein, into three subfamilies: Pellifroniinae new subfamily, Pervicaciinae Rudman, 1969 and Terebrinae Mörch, 1852. Additionally, we devised an in-house computational method for analyzing COI fragments to propose DNA based diagnoses to define most of the supraspecific taxa of Terebridae. Using this approach we propose separate diagnoses for the inferred phylogenetic clusters within *Terebra, Punctoterebra*, and *Hastula* genera.

Challenges of 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 a significant amount of rigor and validation to the process of species delimitation. However, when shell-based and DNA findings are incongruent, deciphering a robust diagnoses is an arduous task. The notable discrepancies between morphology-based and DNA-based hypotheses of terebrid genera challenged our ability to formally establish these taxa following traditional taxonomic practices. Morphological variation in some phylogenetic lineages of Terebridae were so notable that it was extremely difficult to propose an inclusive diagnosis that would still be informative. A perfect example of such distinct conchological clusters can be found in the genus *Punctoterebra,* where *P. solangeae* is hardly distinguishable from the sympatric species of *Partecosta*. Species of the *Punctoterebra teramachii* complex demonstrate shell characteristics typical of *Duplicaria,* and the *Punctoterebra textilis* group would perfectly fit in a cluster of heavily sculptured *Terebra*. To cope with this situation and satisfy requirements of ICZN, we provided inclusive descriptions of genera and elaborated guidelines for their differentiation in *Remarks*. In cases similar to the one 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 would argue that splitting such heterogeneous groups could have been a reasonable solution, leading at least to narrower and more robust generic diagnoses. Nevertheless, informative and seemingly more practical 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 (~ 1/3 of currently accepted), and morphologically readily attributable species (~ 1/3 of species) are distributed among about 25-30 clearly defined genera, the remaining 20-30 percent of ‘problematic’ species, which do not match any proposed genus, end up in *incertae sedis*, which greatly compromises any proposed classification. However, the option of broadly defined genera, although not straightforward, allows for generally plausible placement of such divergent species. The proposed classification can be seen as a transition version that can be further elaborated with minimal rearrangement of the principal scheme established herein. The classification presented here although enclosing some compromises, fulfills its role 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 that would allow its unmistakable recognition. However, there no reliable expectation that phylogenetically defined lineages will necessarily be readily distinguishable morphologically (Bickford et al. 2007; Jörger & Schrödl, 2013). The comprehension that molecular and morphological characters do not necessarily evolve with comparable rate underpins the concept of cryptic species that has profoundly changed our estimates of the global species diversity on the planet (Knowlton, 1993; Bickford et al. 2007). It is to be expected that mechanisms which are accounted for morphological crypticism at the species level, be it morphological stasis or convergent evolution, can also act at a higher taxonomic level. On the contrary, descendants of a relatively recent radiation may exhibit wide range of morphologies under influence of different selection pressures on the diverging lineages as demonstrated in the terebrid genera *Duplicaria, Myurella* and *Punctoterebra*. Such cases of rapid divergence may lead to the erroneous phylogenetic hypotheses, if based solely on the morphology. Therefore, as shown with this revision of the Terebridae, the integrative approach is crucial to reconstruct phylogenetic relationships, when the molecular and morphological data considered separately lead to conflicting hypotheses of relatedness.

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CAPTIONS

Figure 1. Phylogenetic relationships of the main Terebridae lineages. All genera are numbered 1-13 in the tree and a shell of the type species corresponding to each genus is depicted by number (1-13) to the left of the phylogenetic tree.

Figure 2. Subfamily Pellifroniinae.

A. MNHN-IM-2013-52275 *Pellifronia jungi* NANHAI 2014 Stn DW4102 15°03'N; 116°31'E, 339-533 m, 25.5 mm;

B. MNHN-IM-2013-52249 *Pellifronia jungi* EXBODI Stn CP3831 22°02'S; 167°09'E, 523-560 m, 24 mm;

C. MNHN-IM-2007-30591 *Pellifronia jungi* SALOMON 2 Stn CP2195 08°26'S; 159°26'E, 543-593 m, 29 mm (broken);

D. MNHN-IM-2000-20800 *Pellifronia brianhayesi* holotype, Southern Mozambique, 22.6 mm;

E. MNHN-IM-2013-60185 *Bathyterebra benthalis* KARUBENTHOS 2015 Stn CP4524 16°29'N; 61°42'W, 500-550 m, 35.5 mm;

F, **G**. MNHN-IM-2013-61124 *Bathyterebra benthalis* KARUBENTHOS 2015 Stn DW4608, 9.3 mm;

H. MNHN-IM-2013-61800 *Bathyterebra zhongshaensis* n.sp. holotype ZhongSha 2015 Stn DW4138 19°13'N; 113°56'E, 470-494 m, 17 mm;

I. MNHN-IM-2013-52331 *Bathyterebra coriolisi* CONCALIS Stn DW3001 18°32'S; 163°09'E, 390-400 m, 12.4 mm.

Figure 3. Subfamily Pervicaciinae

A. MNHN-IM-2009-29454 *Duplicaria duplicata* WESTERN AUSTRALIA 2011 Stn WB32 33°33'S; 115°04'E, 5-15 m, 26.7 mm;

B. MNHN-IM-2013-5638 *Duplicaria tricincta* PAPUA NIUGINI Stn PD67 05°15.5'S; 145°46.8'E, 2-6 m, 6.9 mm;

C. NHMUK 1979115 *Duplicaria tristis* Lectotype, ‘Seas of Japan’, 17.7 mm;

D. MNHN-IM-2013-66140 *Duplicaria brevicula* Off Namibe, Southern Angola, 40-60 m, 12.9 mm;

E. MNHN-IM-2009-10908 *Duplicaria bernardi* Australia, 26°56'607"S; 153°23'813"E, shell broken;

F. NHMUK 1873.7.5.8/1 *Terebra fuscobasis* Lectotype, Persian Gulf, 11.3 mm;

G. NHMUK 1968251/1 *Terebra nassoides* Lectotype, Red Sea, 13.5 mm;

H. MNHN-IM-2013-52342 *Partecosta varia* ATIMO VATAE Stn TM27 24°56.4'S; 47°06.9'E, 0-1 m, 10.4 mm;

I. MNHN-IM-2013-52359 *Partecosta sandrinae* INHACA 2011 Stn MM7 PL5 26°03.7'S; 32°54.1'E, 0-1 m, 8.8 mm;

J. MNHN-IM-2009-10133 *Partecosta* n.sp. aff *fuscolutea* ATIMO VATAE Stn BS06 25°26.8'S; 44°54.9'E, 0-27 m, 6.9 mm;

K. MNHN-IM-2009-10162 *Partecosta bozzettii* n.sp. paratype ATIMO VATAE Stn TP29 25°03.7-03.8'S; 46°57.7'E, 3-4 m, 12.4 mm;

L. MNHN-IM-2009-10164 *Partecosta trilineata* ATIMO VATAE Stn TP24 25°03.7-03.8'S; 46°57.6-57.7'E, 2-7 m, 8.2 mm;

M. MNHN-IM-2009-10115 *Partecosta macleani* ATIMO VATAE Stn TP19 25°04.4-04.7'S; 46°55.3-56.3'E, 16-26 m, 8.9 mm;

N, **O**. MNHN-IM-2009-10111 *Partecosta macleani* ATIMO VATAE Stn TP19 25°04.4-04.7'S; 46°55.3-56.3'E, 16-26 m, 12 mm.

Figure 4. Phylogenetic relationships of the subclades of the genus *Terebra*. Schematic of subclades C1-C7 in the *Terebra* genus.

Figure 5. Genus *Terebra*.

A. MNHN-IM-2013-47287 *Terebra subulata* (Subclade C-1) KAVIENG 2014 Stn KR12 02°36,3'S; 150°46,3'E, 0 m, 62.8 mm;

B. MNHN-IM-2007-30376 *Terebra guttata* (Subclade C-1) SANTO 2006 Stn FR08 15°33,1'S; 167°12,2'E, 3-40 m, 74.6 mm;

C. MNHN-IM-2013-46010 *Terebra* aff *fenestrata* (Subclade C-2) MADEEP Stn CP4330 06°07.63'S; 149°12.1'E, 315-625 m, 43.5 mm;

D. MNHN-IM-2007-30418 *Terebra* sp. aff *fenestrata* 2 (Subclade C-2) PANGLAO 2005 Stn CP2331 09°39'N; 123°48'E, 256-268 m, 23.1 mm;

E. MNHN-IM-2007-15724 *Terebra fujitai* (Subclade C-3-1) PANGLAO 2005 Stn CP2343 09°27'N; 123°49'E, 273-356 m, 95.7 mm;

F. MNHN-IM-2013-51211 *Terebra triseriata* (Subclade C-4) KAVIENG 2014 Stn KD13 02°44,6'S; 150°43,1'E, 0-15 m, 25.6 mm;

G. MNHN-IM-2013-46900 *Terebra argus* (Subclade C-5) KAVIENG 2014 Stn KR06 02°36,3'S; 150°46,2'E, 3-12 m, 53.7 mm;

H. MNHN-IM-2013-51267 *Terebra babylonia* (Subclade C-6) KAVIENG 2014 Stn KR54 02°42,3'S; 150°39,1'E, 7-10 m, 38.5 mm;

I. MNHN-IM-2013-46237 *Terebra* n.sp. aff *cumingii* (Subclade C-7) MADEEP Stn CP4335 06°05'S; 149°18'E, 240-250 m, 62.5 mm;

J. MNHN-IM-2007-30382 *Terebra cingulifera* (Subclade C-7) SANTO 2006 Stn VM32 15°26,6'S; 167°15,2'E, 0-1 m, 49.7 mm.

Figure 6. Genera *Hastula* and *Oxymeris*.

A. MNHN-IM-2013-16102 *Hastula strigilata* PAPUA NIUGINI Stn PM41 05°08.1'S; 145°49.3'E, 0-1 m, 32.4 mm;

B. MNHN-IM-2009-07098 *Hastula solida* Inhaca Is, 25°59.0'S; 32°54.5'E, 0 m, 25.6 mm;

C. MNHN-IM-2009-11870 *Hastula hectica* Tahiti, 17°30'28.28"S; 149°27'0.14"W, 0 m, 35.6 mm;

D. MNHN-IM-2013-9455 *Hastula cinerea* KARUBENTHOS 2012 Stn GM19 16°21.3'N; 61°44.92'W, 0-1 m, 20.4 mm;

E. MNHN IM-2007-30535 *Hastula lanceata* radula PANGLAO 2004 Stn B1, 9°33.0'N, 123°46.50'E, 8-14 m, 32.5 mm (broken);

F. *Hastula hectica* radula, The Philippines, Bohol, Panglao, Is, intertidal, radula;

G. MNHN-IM-2013-40074 *Oxymeris maculata* PAKAIHI I TE MOANA Marqueses I, exact locality unknown, 113 mm;

H. MNHN-IM-2013-46877 *Oxymeris crenulata* KAVIENG 2014 Stn KR06 02°36.3'S; 150°46.2'E, 3-12 m, 85.9 mm;

I. MNHN-IM-2013-10283 *Oxymeris felina* PAPUA NIUGINI Stn PB05 05°11.7'S; 145°49.4'E, 0-20 m, 31 mm.

Figure 7. Genera *Myurella*, *Maculauger* n. gen. and *Myurellopsis* n. gen.

A. MNHN-IM-2013-17860 *Myurella affinis* PAPUA NIUGINI Stn PR196 05°12.3'S; 145°48.8'E, 0 m, 39.8 mm;

B. MNHN-IM-2013-58677 *Myurella fortunei* KAVIENG 2014 Stn DW4468 02°45'S; 150°37'E, 190-472 m, 25.2 mm;

C. MNHN-IM-2013-46861 *Myurella amoena* KAVIENG 2014 Stn KR02 02°37.5'S; 150°46.5'E, 10-14 m, 24.9 mm;

D. MNHN-IM-2009-10121 *Myurella pygmaea* S Madagascar off Lovanono, 0-5 m, 6.1 mm;

E. MNHN-IM-2009-9954 *Maculauger pseudopertusa* MIRIKY Stn DW3230 13°25'S; 47°57'E, 71-158 m, 42.9 mm;

F. MNHN-IM-2013-52252 *Maculauger campbelli* EXBODI Stn CP3836 22°08'S; 167°11'E, 415-420 m, 20.5 mm;

G. MNHN-IM-2013-10252 *Myurellopsis undulata* PAPUA NIUGINI Stn PR07 05°12.5'S; 145°48.5'E, 2-17 m, 31.9 mm;

H. MNHN-IM-2013-12712 *Myurellopsis kilburni* PAPUA NIUGINI Stn PS11 05°04.7'S; 145°48.9'E, 0-5 m, 24.8 mm;

I. MNHN-IM-2013-52369 *Myurellopsis joserosadoi* INHACA 2011 Stn MR13 25°59.7'S; 32°54.5'E, 2-5 m, 17.9 mm.

Figure 8. Genus *Punctoterebra*.

A. MNHN-IM-2013-13332 *Punctoterebra nitida* PAPUA NIUGINI Stn PD32 05°04.4'S; 145°48.7'E, 1-8 m, 26.5 mm;

B. MNHN-IM-2009-9973 *Punctoterebra teramachii* TERRASSES Stn DW3093 22°06'S; 167°03'E, 190-200 m, 27.5 mm;

C. MNHN-IM-2007-30424 *Punctoterebra polygyrata* SALOMON 2 Stn CP2282 08°37'S; 157°21'E, 150-160 m, 22.3 mm;

D. MNHN-IM-2007-30385 *Punctoterebra succincta* SANTO 2006 Stn VM32 15°26.6'S; 167°15.2'E, 0-1 m, 42.9 mm;

E. MNHN-IM-2009-10122 *Punctoterebra solangeae* ATIMO VATAE Stn BP18 25°26.1-26.4'S; 44°55.2-55.6'E, 17-20 m, 10.2 mm;

F. MNHN-IM-2009-10093 *Punctoterebra* sp. aff *textilis* MIRIKY Stn CP3274 15°30.15'S; 46°04.3'E, 29-36 m, 16.8 mm;

G. MNHN-IM-2007-30547 *Punctoterebra souleyeti* SANTO 2006 Stn LD21 15°31,3'S, 167°09,9'E, 1-6 m, 27 mm, radula.

Figure 9. Genera *Profunditerebra* n. gen. and *Neoterebra* n. gen.

A. MNHN-IM-2013-58123 *Profunditerebra papuaprofundi* n.sp. KAVIENG 2014 Stn CP4422 02°21'S; 150°38'E, 496-609 m, 19.2 mm;

B. MNHN-IM-2009-29153 *Profunditerebra orientalis* EXBODI Stn DW3930 18°37'S; 164°26'E, 448-464 m, 39.6 mm;

C. MNHN-IM-2013-55861 *Profunditerebra brazieri* MORRISON AUSTRALIA Stn TA22 43°10.4'S; 147°51.3'E, 1-7 m, 32.4 mm;

D. NHMUK 1844.6.7.84 *Terebra specillata* Lectotype, San Blas, Mexico, 7 fms (=12.8 m), 39.3 mm;

E. MNHN-IM-2007-30546, *Profunditerebra poppei* SANTO 2006, Stn AT44 15°36'S, 167°03'E, 86-118 m, (broken), radula;

F. MNHN-IM-2000-25244 *Terebra assu* holotype, Brazil, Espírito Santo, off Conceição da Barra Stn MD55, stn DC75 18°59’S, 37°50’W , 295 m, 9.8 mm;

G. MZSP 84238 *Terebra alagoensis* holotype, Brazil, continental slope off Alagoas, 10°05'57"S, 35°46'24"W, 720 m, 9.8 mm;

H. MNHN-IM-2013-20352 *Neoterebra sterigmoides* KARUBENTHOS 2012 Stn GD02 16°22.57'N; 61°34.12'W, 0-80 m, 29.6 mm.

Figure 10. Genera defined solely by means of shell morphology.

A. NHMUK 1873.8.6.10/1 *Terebra bathyrhaphe* Lectotype, Gulf of Yedo Stn 35°35’N; 139°48'E, 6-25 fms (=11-45.7 m), 24.8 mm;

B. NMHUK 1873.8.6.11/1, *Hastulopsis melanachme* Lectotype, Cape Sima, Japan, 18fms (=33 m), 17.8 mm;

C. NHMUK 1968237, *Terebra bifrons* holotype, Japan, 51.0 mm;

D. SAM D-110176, *Gradaterebra scalariformis* Newland Head, S. Australia, 20 fms (=36.6 m), 12.1 mm;

E. NHMUK 1978150 *Terebra circumcincta* holotype, Red Sea(erroneous?), no depth), 38.0 mm;

F. ANSP 155289, *Microtrypetes iola* holotype, Mazatlan, Mexico, 20 fms (=36.6 m), 14.0 mm.

Figure 11. *Duplicaria herberti* n. sp., *Partecosta bozzettii* n.sp. and morphologically similar species.

A. MNHN-IM-2013-52381 *Duplicaria herberti* n. sp. holotype, INHACA 2011 Stn MR15 26°00.0'S; 32°54.4'E, 0-1 m), 29.7 mm;

B. MNHN-IM-2013-52366 *Duplicaria herberti* n. sp. INHACA 2011 Stn MM1 26°02.3'S; 32°54.1'E, 0-1 m), 12.4 mm;

C. NMSA 566 *Duplicaria herberti* n. sp. Paratype of *D. mozambiquensis*, 27 mm;

D. YT *Duplicaria mozambiquensis* Quelimane Pebane, 35-45 m, 19.6 mm;

E. MNHN-IM-2009-10163 *Partecosta bozzettii* n.sp. holotype ATIMO VATAE Stn TP29 25°03'43.9"S; 46°57'42.9"E, 3-4 m, 12.5 mm;

F. MNHN-IM-2000-21473 *Partecosta trilineata* holotype, S Madagascar, Lavanono, 8.85 mm;

G. *Partecosta daniae* MMM, holotype, Farol das Lagostas, Luanda, Angola, 12 mm.

Figure 12. *Profunditerebra papuaprofundi* n.sp., *Profunditerebra macclesfieldensis* n. sp. and morphologically similar species.

A. MNHN-IM-2013-58123 *Profunditerebra papuaprofundi* n.sp. holotype, KAVIENG 2014 Stn CP4422 02°21'S; 150°38'E, 496-609 m, 19.0 mm;

B. MNHN-IM-2013-45571 *Profunditerebra papuaprofundi* n.sp. paratype 1, same locality, 29.5 mm;

C. NHMUK 197988/1 *Terebra cinctella* Lectotype, Mouth of the Indus', 27.8 mm;

D. NHMUK 1844.6.7.80 T*erebra textilis* Lectotype, ‘Str Macassar', 25.7 mm;

E. MNHN-IM-2013-61875 *Profunditerebra macclesfieldensis* n. sp. holotype, ZhongSha 2015 Stn DW4144 16°6'N; 114°23'E, 160-200 m, 22.4 mm;

F. MNHN-IM-2013-61877 *Profunditerebra macclesfieldensis* n. sp. Paratype 1, same locality, 22.2 mm;

G. MNHN-IM-2000-6224 *Profunditerebra anseeuwi* holotype, Philippines, Aliguay Island, Sulu Sea, 80-150 m, 29.8 mm.

Figure 13. *Neoterebra guadeloupensis* n. sp., *Maculauger sudchinensis* n. sp. and morphologically similar species.

A. MNHN-2013-61448 *Neoterebra guadeloupensis* n. sp. holotype KARUBENTHOS 2015 Stn DW4638 15°50'N; 61°18'W, 305-312 m, 17.2 mm;

B. MNHN-IM-2013-20531 *Neoterebra guadeloupensis* n. sp KARUBENTHOS 2012 Stn GD55 16°22,48'N; 61°35,46'W, 85 m, 9.4 mm;

C. USNM93971 *Terebra limatula* syntype Apalachicola Bay, Florida, USA, 17.8 mm;

D, **E**. MNHN-IM-2013-61887 *Maculauger sudchinensis* n. sp. Holotype, ZhongSha 2015 Stn CP4144 16°6'N; 114°23'E, 160-200 m, 19.9 mm;

F. NHMUK 1903.12.15.117 *Terebra helichrysum* Lectotype Persian Gulf, Mussandam, 47 fms (=86 m) , 24.5 mm;

G. MNHN-IM-2000-2812 *Terebra levantina* holotype MUSORSTOM 2 Stn CP59 14°00'N; 120°16'E, 186-190 m, 24.2 mm.

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

Subfamily Pellifroniinae	
Species / sequences analyzed	4 /25
Diagnostic nucleotide combinations	[299: 'G']
	[334: 'A', 382: 'G', 607: 'T']
	[88: 'T', 100: 'T', 379: 'A']
	[163: 'T', 313: 'A', 530: 'A']
	[118: 'T', 265: 'T', 415: 'G']
Genus *Pellifronia*	
Species / sequences analyzed	1 / 11
Diagnostic nucleotide combinations	[76: 'C']
	[208: 'T', 553: 'A']
	[301: 'A', 337: 'G']
	[121: 'G', 205: 'G']
	[334: 'A', 350: 'T']
	[299: 'G', 304: 'T']
	[22: 'T', 359: 'C']
	[67: 'G', 88: 'T']
	[325: 'T', 547: 'C']
	[415: 'G', 565: 'A']
	[238: 'A', 508: 'A']
	[562: 'G', 622: 'T']
Genus *Bathyterebra*	
Species / sequences analyzed	3 / 14
Diagnostic nucleotide combinations	[76: 'T', 100: 'T']
	[299: 'G', 454: 'A']
	[50: 'C', 88: 'T']
	[415: 'G', 622: 'C']
	[74: 'C', 485: 'T', 562: 'A']
	[73: 'A', 265: 'T', 334: 'A']
	[35: 'C', 382: 'G', 530: 'A']
	[349: 'A', 496: 'T', 565: 'G']
	[110: 'C', 508: 'G', 547: 'T']

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

Genus *Duplicaria*	
Species / sequences analyzed	6 / 13
Diagnostic nucleotide combinations:	[328: 'A', 415: 'T', 530: 'A'] [7: 'A', 172: 'A', 478: 'T'] [263: 'C', 328: 'A', 478: 'T'] [265: 'T', 370: 'T', 478: 'T'] [172: 'A', 418: 'T', 478: 'T'] [301: 'T', 478: 'T', 530: 'A'] [91: 'T', 265: 'T', 301: 'T', 494: 'C'] [202: 'T', 418: 'T', 436: 'T', 485: 'T']
Genus *Partecosta*	
Species / sequences analyzed	8 / 17
Diagnostic nucleotide combinations:	[37: 'A', 40: 'T', 328: 'T', 343: 'T'] [37: 'A', 40: 'T', 50: 'T', 328: 'T'] [31: 'A', 37: 'A', 40: 'T', 343: 'T', 520: 'A'] [31: 'A', 37: 'A', 40: 'T', 343: 'T', 580: 'T'] [37: 'A', 55: 'T', 328: 'T', 343: 'T', 448: 'T'] [37: 'A', 55: 'T', 160: 'A', 343: 'T', 625: 'T']

Table 3. Genus *Terebra*, diagnostic combinations of nucleotides in the COI alignment.

C1	
Species / sequences analyzed	4 / 30
Diagnostic nucleotide combinations:	[508: 'T', 607: 'A'] [265: 'G', 547: 'T'] [28: 'A', 37: 'T', 547: 'T'] [31: 'A', 37: 'T', 313: 'A'] [31: 'A', 547: 'T', 631: 'T'] [67: 'T', 547: 'T', 631: 'T'] [133: 'T', 242: 'C', 607: 'A']
C2	
Species / sequences analyzed	2 / 16
Diagnostic nucleotide combinations:	[536: 'T', 607: 'G'] [91: 'T', 536: 'T'] [334: 'A', 538: 'A'] [538: 'A', 607: 'G'] [334: 'A', 536: 'T'] [508: 'T', 607: 'G'] [190: 'T', 538: 'A'] [190: 'T', 536: 'T']
C3	
Species / sequences analyzed	5 / 34
Diagnostic nucleotide combinations:	[74: 'T', 307: 'A', 337: 'A', 631: 'T'] [94: 'A', 154: 'C', 283: 'G', 520: 'A'] [154: 'C', 163: 'T', 535: 'A', 631: 'T'] [253: 'A', 337: 'A', 520: 'A', 631: 'T'] [58: 'T', 154: 'C', 469: 'A', 631: 'T']
C4	
Species / sequences analyzed	9/71
Diagnostic nucleotide combinations:	[643: 'T'] [58: 'T', 127: 'T'] [278: 'C', 289: 'T', 550: 'A'] [34: 'T', 121: 'T', 641: 'C'] [56: 'C', 127: 'T', 641: 'C'] [100: 'T', 121: 'T', 127: 'T'] [121: 'T', 127: 'T', 202: 'T']
C5	
Species / sequences analyzed	1 / 9
Diagnostic nucleotide combinations:	[274: 'G'] [238: 'C', 412: 'T'] [181: 'G', 595: 'C'] [151: 'C', 313: 'T'] [43: 'G', 289: 'G'] [292: 'G', 424: 'G'] [37: 'T', 61: 'G'] [95: 'T', 622: 'C'] [376: 'C', 607: 'A']
C6	
Species / sequences analyzed	8 / 44
Diagnostic nucleotide combinations:	[22: 'G', 379: 'T', 499: 'G'] [95: 'T', 499: 'G', 562: 'T'] [95: 'T', 409: 'T', 499: 'G'] [278: 'C', 379: 'T', 499: 'G'] [379: 'T', 499: 'G', 562: 'T'] [484: 'G', 499: 'G', 562: 'T'] [278: 'C', 499: 'G', 562: 'T']
C7	
Species / sequences analyzed	10 / 19
Diagnostic nucleotide combinations:	[222: 'T'] [221: 'G'] [28: 'G', 76: 'T'] [76: 'T', 158: 'C'] [79: 'T', 592: 'T'] [109: 'G', 278: 'C', 535: 'G'] [16: 'A', 37: 'T', 100: 'A'] [106: 'C', 148: 'G', 211: 'A']

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

Genus *Hastula* (except four specimens of *H. albula*)	
Species / sequences analyzed	18 / 91
Diagnostic nucleotide combinations:	[67: 'T', 181: 'T', 221: 'C', 253: 'A']
	[67: 'T', 95: 'C', 181: 'T', 598: 'A']
	[67: 'T', 181: 'T', 222: 'C', 253: 'A']
	[28: 'A', 67: 'T', 181: 'T', 253: 'A']
	[67: 'T', 95: 'C', 181: 'T', 253: 'A']
	[28: 'A', 67: 'T', 181: 'T', 581: 'T', 598: 'A']
	[67: 'T', 181: 'T', 221: 'C', 581: 'T', 598: 'A']
	[67: 'T', 181: 'T', 222: 'C', 581: 'T', 598: 'A']
subclade *H. albula* - *H. natalensis* - *H*. aff. *casta*	
Species / sequences analyzed	3 / 21
Diagnostic nucleotide combinations	[349:'T']
	[127:'T', 223:'A']
	[49:'G', 547:'T']
	[347:'C', 517:'T']
	[202:'G', 205:'G']
	[43:'A', 610:'C']
	[148:'A', 157:'C', 376:'A']
	[211:'G', 307:'T', 337:'G']

Table 5. Genus *Oxymeris*, diagnostic combinations of nucleotides in the COI alignment.

Species / sequences analyzed	11 / 99
Diagnostic nucleotide combinations:	[127: 'T', 631: 'T']
	[67: 'A', 127: 'T', 250: 'T']
	[46: 'T', 67: 'A', 631: 'T']
	[67: 'A', 91: 'T', 631: 'T']
	[50: 'T', 127: 'T', 202: 'T', 250: 'T']
	[67: 'A', 455: 'A', 487: 'T', 631: 'T']

Table 6. Genus *Myurella*, diagnostic combinations of nucleotides in the COI alignment

Species / sequences analyzed	21 / 161
Diagnostic nucleotide combinations:	[485: 'C', 494: 'A', 565: 'T']
	[56: 'C', 433: 'T', 485: 'C', 565: 'T']
	[334: 'T', 433: 'T', 485: 'C', 565: 'T']
	[263: 'C', 433: 'T', 485: 'C', 539: 'C', 565: 'T']
	[263: 'C', 433: 'T', 485: 'C', 538: 'T', 565: 'T']
	[263: 'C', 334: 'T', 485: 'C', 538: 'T', 565: 'T']
	[49: 'T', 263: 'C', 433: 'T', 485: 'C', 565: 'T']

Table 7. Diagnostic nucleotide combinations in the COI alignment in subgroups of the genus *Punctoterebra*.

Punctoterebra nitida **group**	
Species / sequences analyzed	8 / 48
Diagnostic nucleotide combinations:	[91: 'A', 184: 'A', 265: 'T', 542: 'T', 562: 'T', 580: 'T']
	[76: 'A', 160: 'A', 181: 'T', 265: 'T', 268: 'A', 562: 'T']
	[130: 'A', 160: 'A', 184: 'A', 265: 'T', 530: 'G', 562: 'T']
	[130: 'A', 160: 'A', 184: 'A', 265: 'T', 295: 'T', 530: 'G']
	[91: 'A', 184: 'A', 229: 'G', 265: 'T', 562: 'T', 580: 'T']
	[112: 'A', 160: 'A', 184: 'A', 265: 'T', 557: 'C', 562: 'T']
	[160: 'A', 184: 'A', 229: 'G', 265: 'T', 562: 'T', 580: 'T']
Punctoterebra teramachii **group**	
Species / sequences analyzed	5 / 6
Diagnostic nucleotide combinations:	[304: 'T', 382: 'T']
	[50: 'C', 163: 'A', 184: 'G']
	[74: 'C', 100: 'G', 223: 'T']
	[376: 'T', 412: 'G', 469: 'G', 520: 'A']
	[82: 'A', 169: 'A', 316: 'G', 379: 'A']
	[46: 'G', 158: 'T', 322: 'A', 655: 'G']
Punctoterebra multistriata **group**	
Species / sequences analyzed	2 / 3
Diagnostic nucleotide combinations:	[46: 'G', 421: 'C']
	[124: 'C', 319: 'G']
	[115: 'C', 542: 'C']
	[14: 'C', 385: 'C']
	[193: 'C', 517: 'G']
	[25: 'A', 163: 'G', 229: 'A']
	[100: 'G', 130: 'G', 530: 'A']
Punctoterebra textilis **group**	
Species / Sequences analyzed	13 / 72
Diagnostic nucleotide combinations:	[40: 'T', 50: 'T', 494: 'A', 517: 'A', 548: 'T']
	[40: 'T', 50: 'T', 92: 'T', 494: 'A', 517: 'A']
	[40: 'T', 50: 'T', 494: 'A', 517: 'A', 581: 'T']
	[14: 'T', 40: 'T', 50: 'T', 485: 'C', 494: 'A', 581: 'T']
	[50: 'T', 106: 'T', 295: 'T', 343: 'T', 517: 'A', 607: 'T']
	[50: 'T', 343: 'T', 494: 'A', 517: 'A', 541: 'T', 581: 'T']
	[14: 'T', 40: 'T', 50: 'T', 56: 'C', 92: 'T', 494: 'A']

Table 8. Genus *Profunditerebra*, diagnostic combinations of nucleotides in the COI alignment.

Species / sequences analyzed	10 / 39
Diagnostic nucleotide combinations:	[154: 'T', 382: 'A', 388: 'A', 496: 'G']
	[139: 'T', 349: 'G', 379: 'T', 533: 'T', 631: 'A']
	[313: 'A', 349: 'G', 382: 'A', 496: 'G', 533: 'T']
	[154: 'T', 313: 'A', 349: 'G', 379: 'T', 631: 'A']
	[229: 'G', 298: 'A', 349: 'G', 379: 'T', 631: 'A']
	[22: 'A', 181: 'T', 313: 'A', 379: 'T', 382: 'A']
	[256: 'T', 298: 'A', 349: 'G', 379: 'T', 631: 'A']

Table 9. Genus *Neoterebra*, diagnostic combinations of nucleotides in the COI alignment.

Sequences analyzed	10 / 42
Diagnostic nucleotide combinations:	[52: 'A', 379: 'T', 401: 'T', 487: 'T', 494: 'A']
	[52: 'A', 379: 'T', 401: 'T', 485: 'C', 494: 'A', 502: 'A']
	[52: 'A', 151: 'T', 157: 'T', 295: 'T', 379: 'T', 415: 'T', 487: 'T']
	[52: 'A', 157: 'T', 222: 'C', 379: 'T', 485: 'C', 502: 'A', 557: 'C']
	[52: 'A', 157: 'T', 379: 'T', 415: 'T', 485: 'C', 502: 'A', 559: 'T']
	[157: 'T', 181: 'T', 379: 'T', 487: 'T', 494: 'A', 502: 'A', 557: 'C']
	[157: 'T', 181: 'T', 221: 'C', 379: 'T', 485: 'C', 502: 'A', 559: 'T']:

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

Maculauger	
Species / sequences analyzed	8 / 26
Diagnostic nucleotide combinations	[214: 'T']
	[94: 'A', 520: 'G', 592: 'T']
	[212: 'C', 242: 'C', 592: 'T']
	[199: 'G', 580: 'G', 592: 'T']
	[242: 'C', 583: 'A', 592: 'T']
	[94: 'A', 388: 'G', 592: 'T']
	[212: 'C', 494: 'A', 592: 'T']
Myurellopsis	
Species / sequences analyzed	8 / 65
Diagnostic nucleotide combinations	[307: 'T', 328: 'T', 349: 'A']
	[50: 'C', 307: 'T', 379: 'T']
	[95: 'C', 307: 'T', 349: 'A']
	[199: 'A', 307: 'T', 379: 'T']
	[40: 'T', 199: 'A', 379: 'T', 494: 'A']
	[50: 'C', 304: 'A', 334: 'T', 484: 'A', 520: 'A']

Table 11. New species diagnostic combinations of nucleotides in the COI alignment.

***Bathyterebra zhongshaensis* n. sp.**	
Diagnostic nucleotide combinations	[367: 'C', 499: 'C']
	[284: 'C', 487: 'C']
	[373: 'A', 502: 'G']
	[91: 'G', 581: 'C']
	[52: 'G', 85: 'C']
	[223: 'G', 328: 'G']
	[40: 'C', 322: 'G']

***Duplicaria herberti* n. sp.**	
Diagnostic nucleotide combinations	[127: 'A', 451: 'G']
	[184: 'T', 499: 'G']
	[250: 'C', 526: 'A']
	[130: 'G', 478: 'T']
	[31: 'T', 241: 'A']
	[244: 'G', 304: 'T']
	[160: 'G', 232: 'A']

***Partecosta bozzettii* n. sp.**	
Diagnostic nucleotide combinations	[121: 'G', 328: 'T']
	[85: 'A', 616: 'C']
	[271: 'A', 337: 'A']
	[301: 'G', 541: 'G']
	[347: 'C', 451: 'A']
	[82: 'G', 350: 'T']
	[13: 'C', 43: 'G']

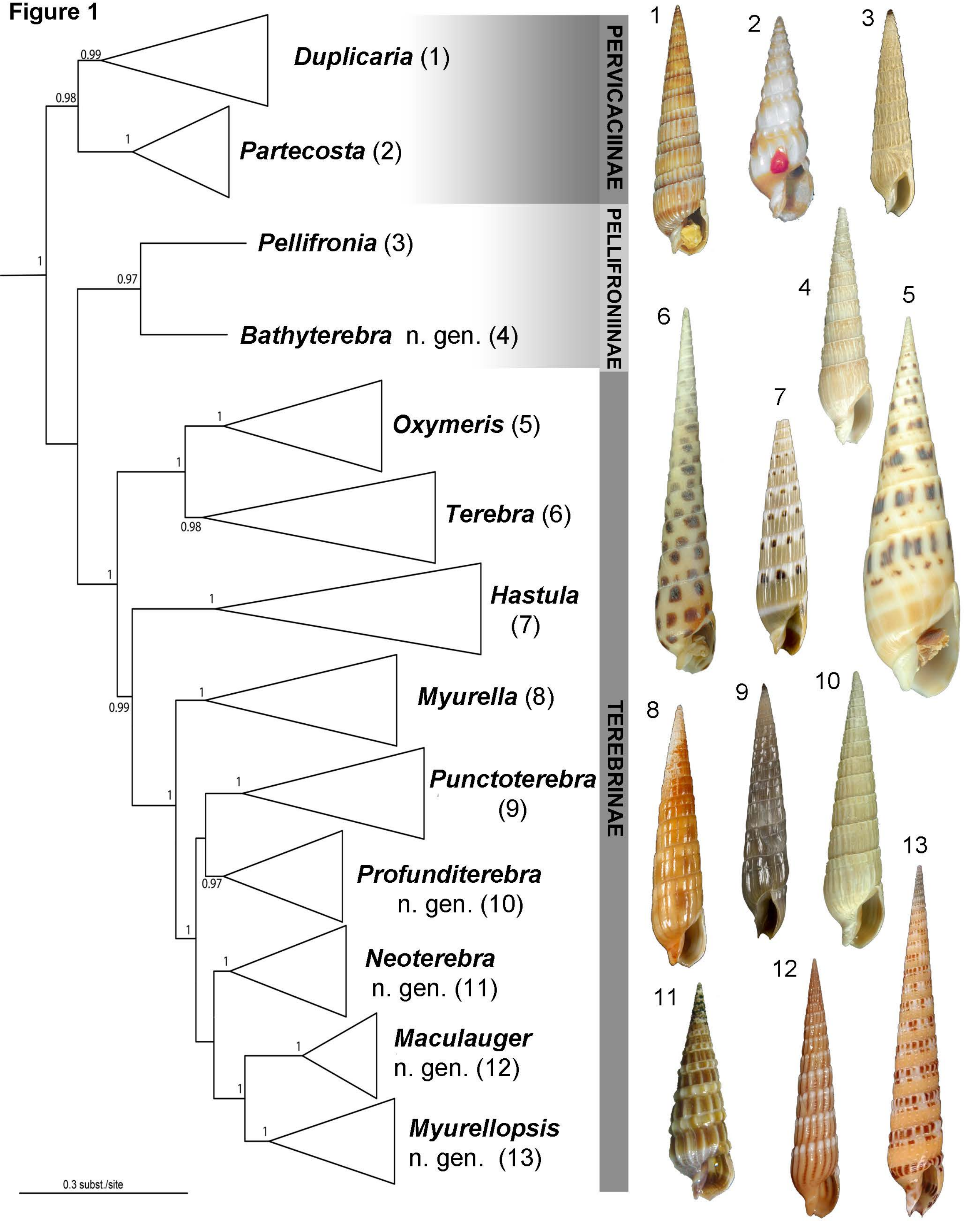
***Profunditerebra papuaprofundi* n. sp.**	
Diagnostic nucleotide combinations	[397: 'C', 457: 'C']
	[169: 'G', 601: 'C']
	[556: 'G', 658: 'C']
	[278: 'C', 343: 'G']
	[55: 'C', 487: 'G']
	[289: 'T', 622: 'C']
	[85: 'C', 355: 'G', 484: 'G']

***Profunditerebra macclesfieldensis* n. sp.**	
Diagnostic nucleotide combinations	[61: 'C', 343: 'A']
	[169: 'G', 400: 'C']
	[445: 'C', 485: 'T']
	[457: 'C', 655: 'G']
	[367: 'C', 487: 'G']
	[58: 'C', 475: 'A']
	[91: 'T', 556: 'A']

***Neoterebra guadeloupensis* n. sp.**	
Diagnostic nucleotide combinations	[40: 'G', 97: 'C']
	[550: 'G', 628: 'A']
	[127: 'G', 439: 'T']
	[484: 'G', 493: 'A']
	[112: 'A', 604: 'C']
	[313: 'C', 625: 'G']
	[526: 'G', 619: 'T']

***Maculauger sudchinensis* n. sp.**	
Diagnostic nucleotide combinations	[238: 'G', 241: 'C']
	[487: 'A', 514: 'T']
	[169: 'A', 256: 'A']
	[163: 'G', 646: 'C']
	[313: 'G', 625: 'G']
	[85: 'C', 409: 'C']
	[217: 'G', 541: 'G']

Figure 1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Duplicaria (1)
Partecosta (2)
Pellifronia (3)
Bathyterebra n. gen. (4)
Oxymeris (5)
Terebra (6)
Hastula (7)
Myurella (8)
Punctoterebra (9)
Profunditerebra n. gen. (10)
Neoterebra n. gen. (11)
Maculauger n. gen. (12)
Myurellopsis n. gen. (13)
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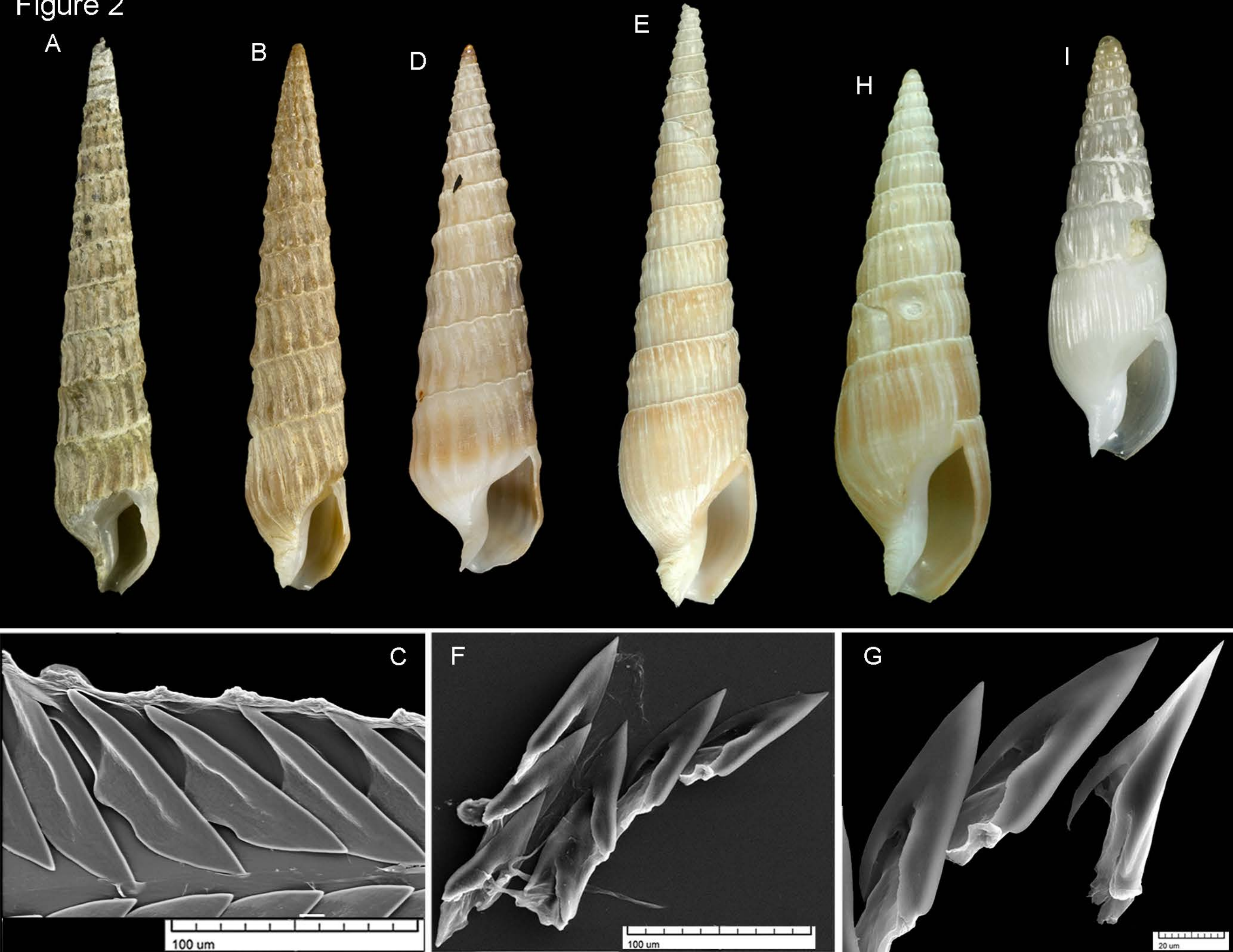
Figure 2



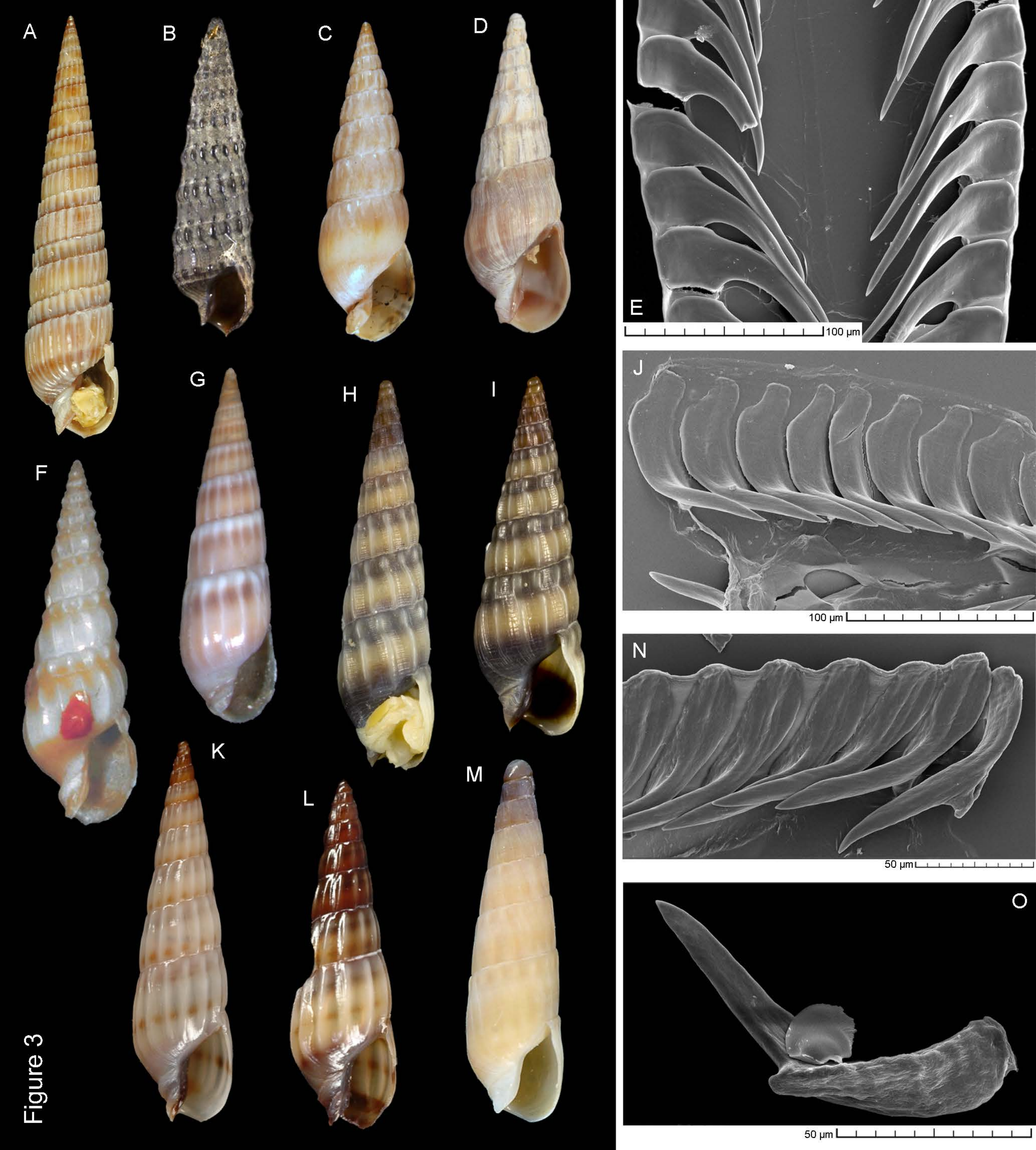


Figure 3

Figure 4

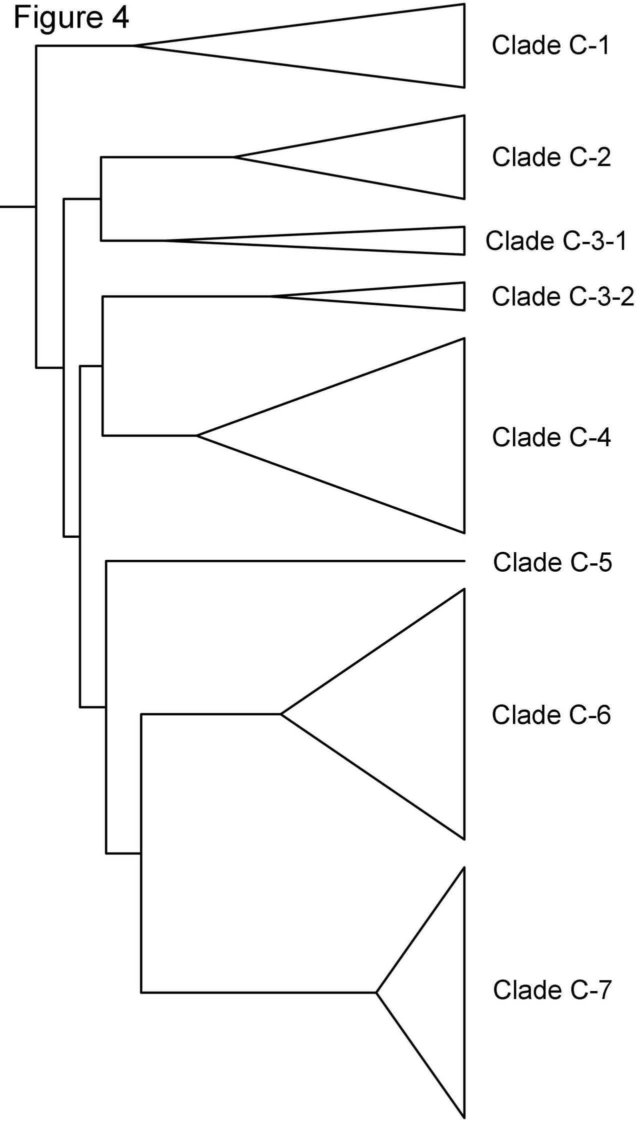
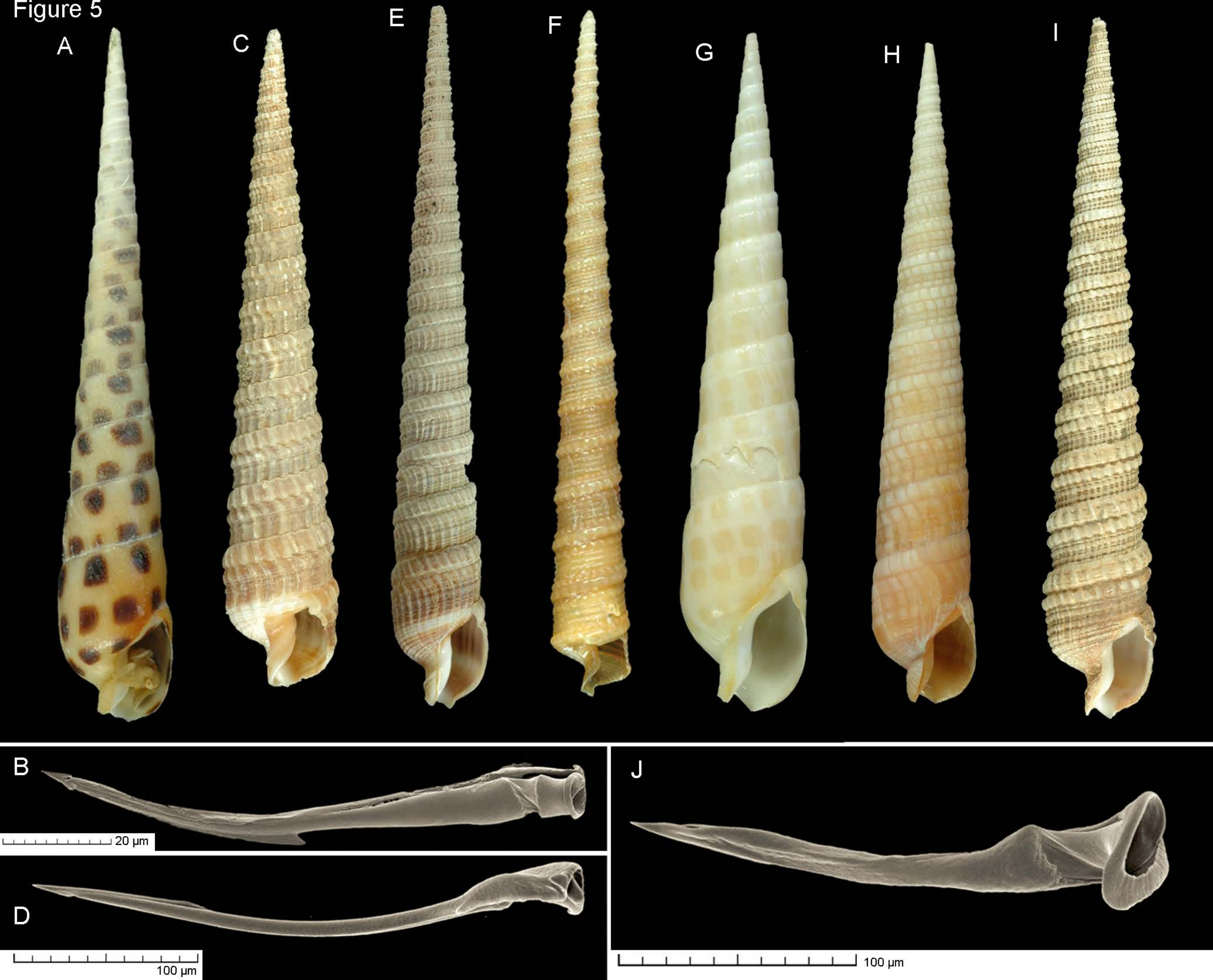

Clade C-1
Clade C-2
Clade C-3-1
Clade C-3-2
Clade C-4
Clade C-5
Clade C-6
Clade C-7

Figure 5



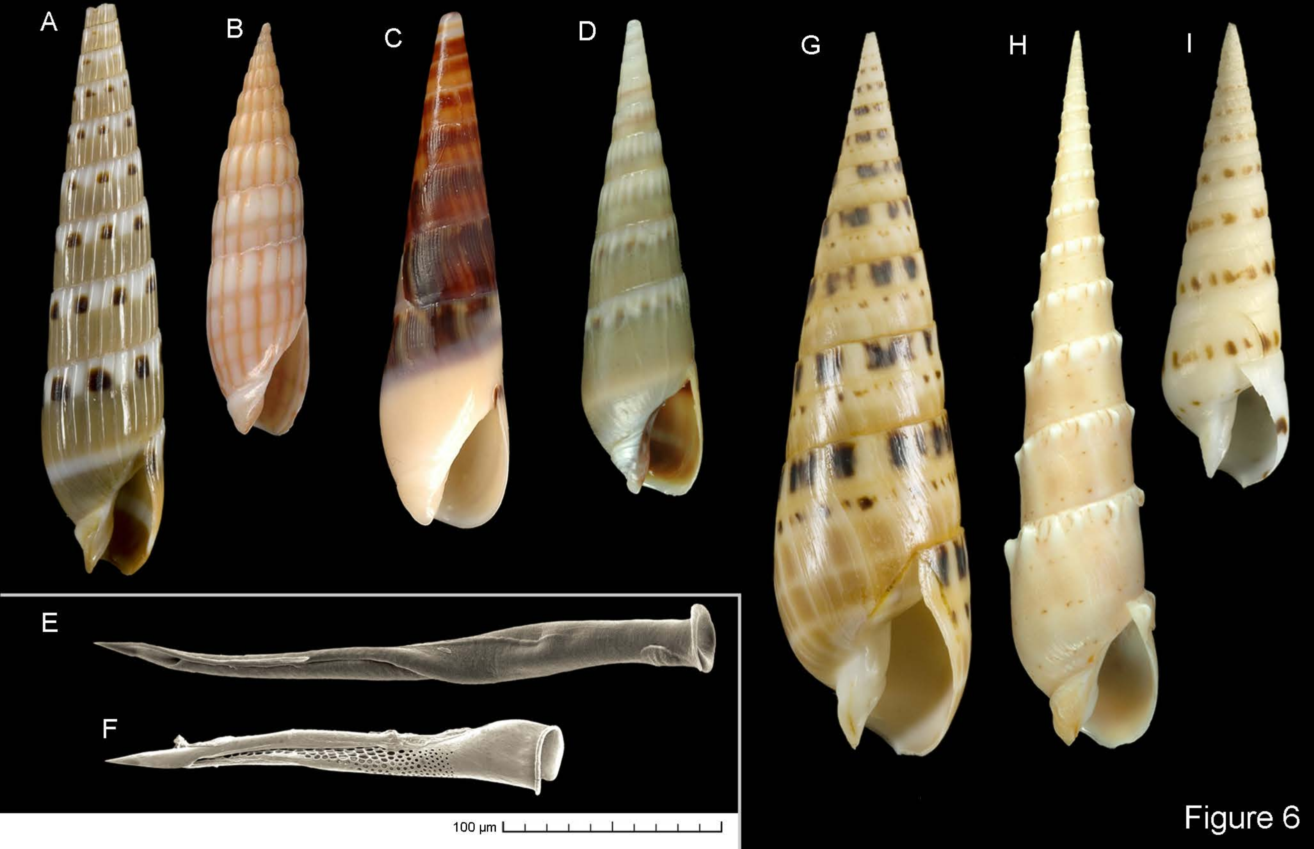
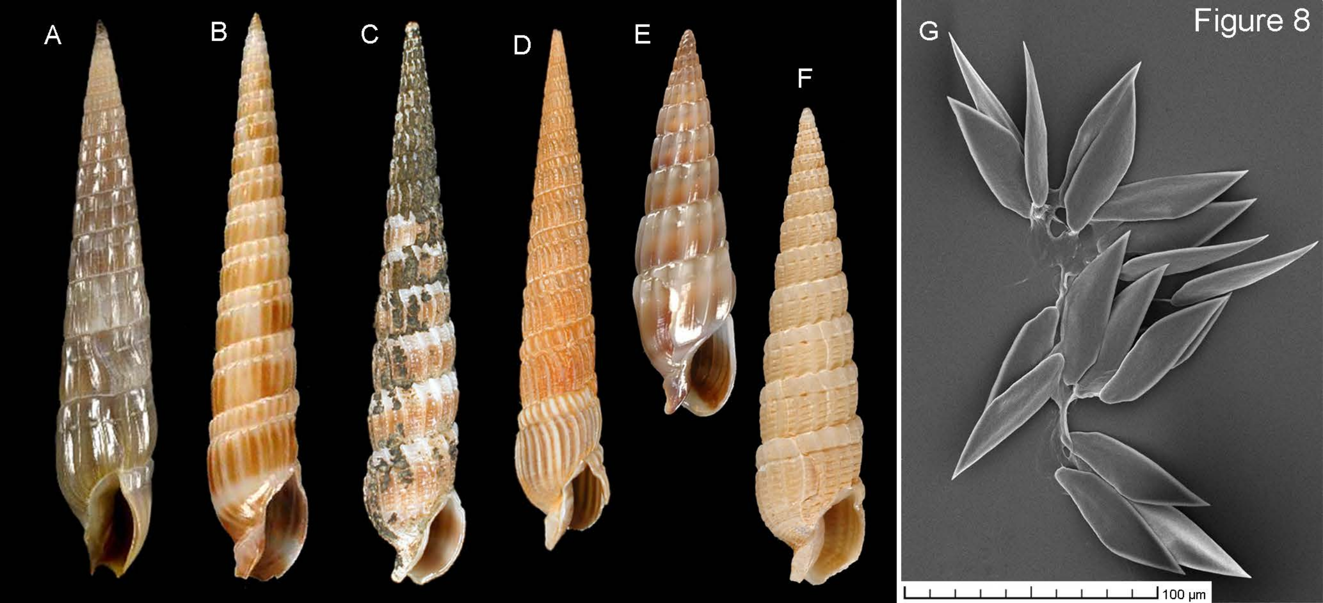


Figure 6

Figure 7

Figure 8



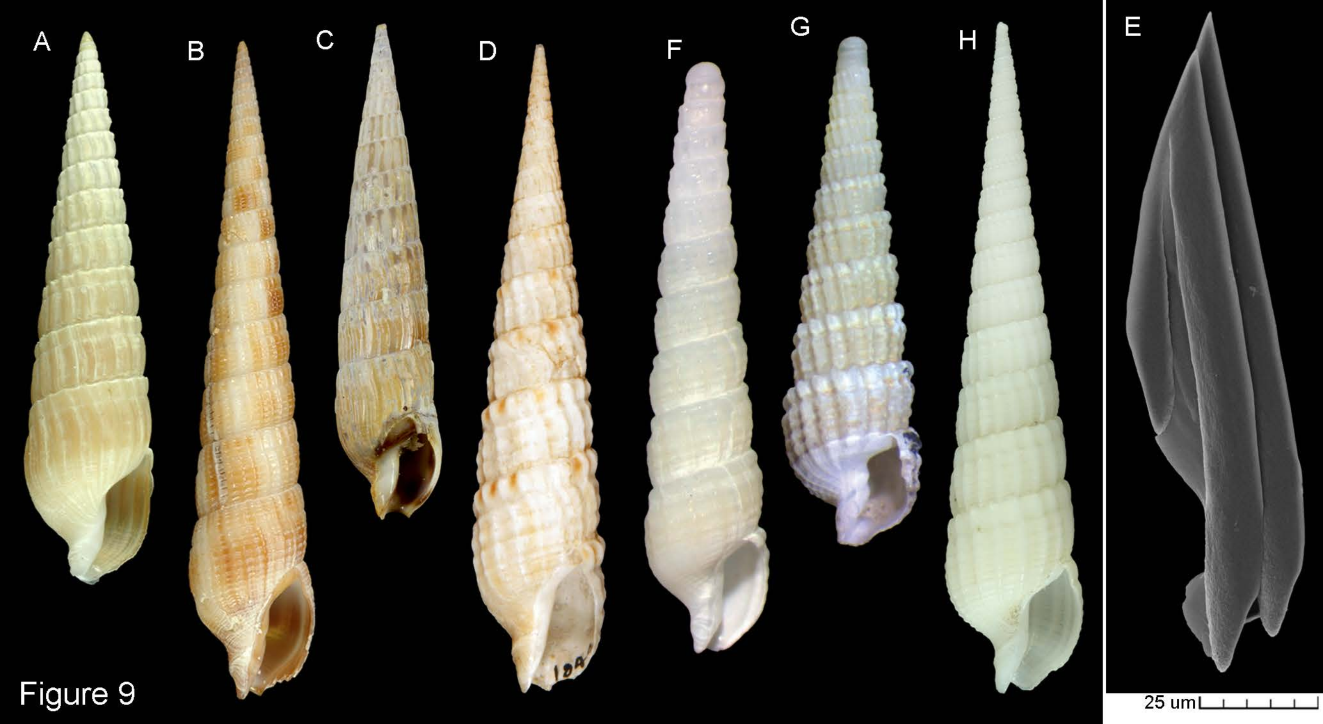


Figure 9

Figure 10

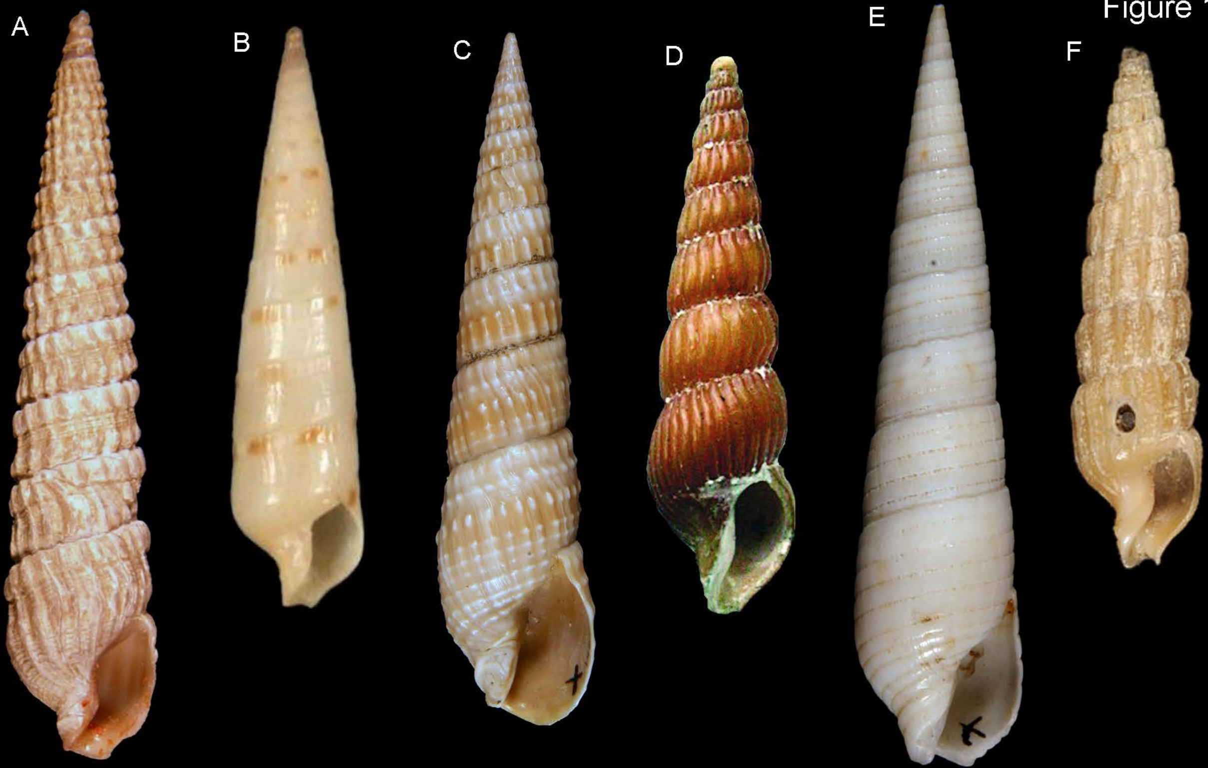


Figure 11

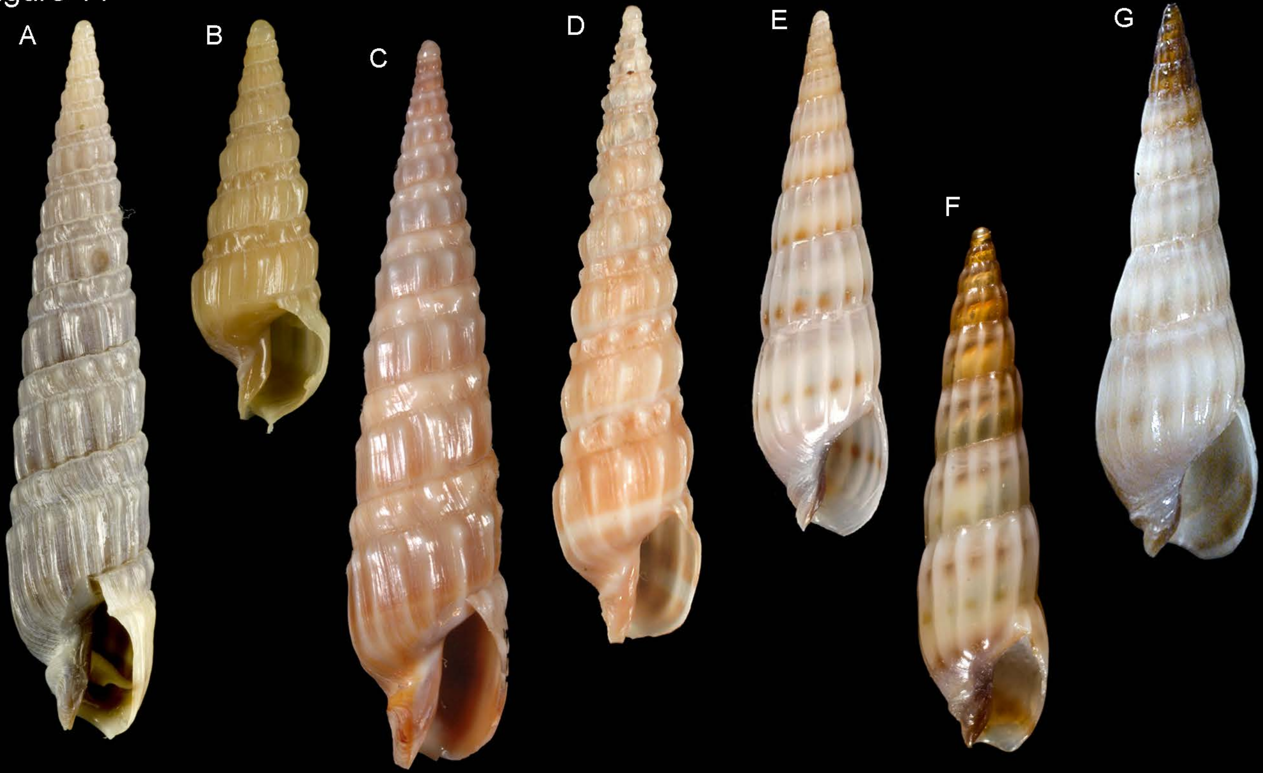


Figure 12

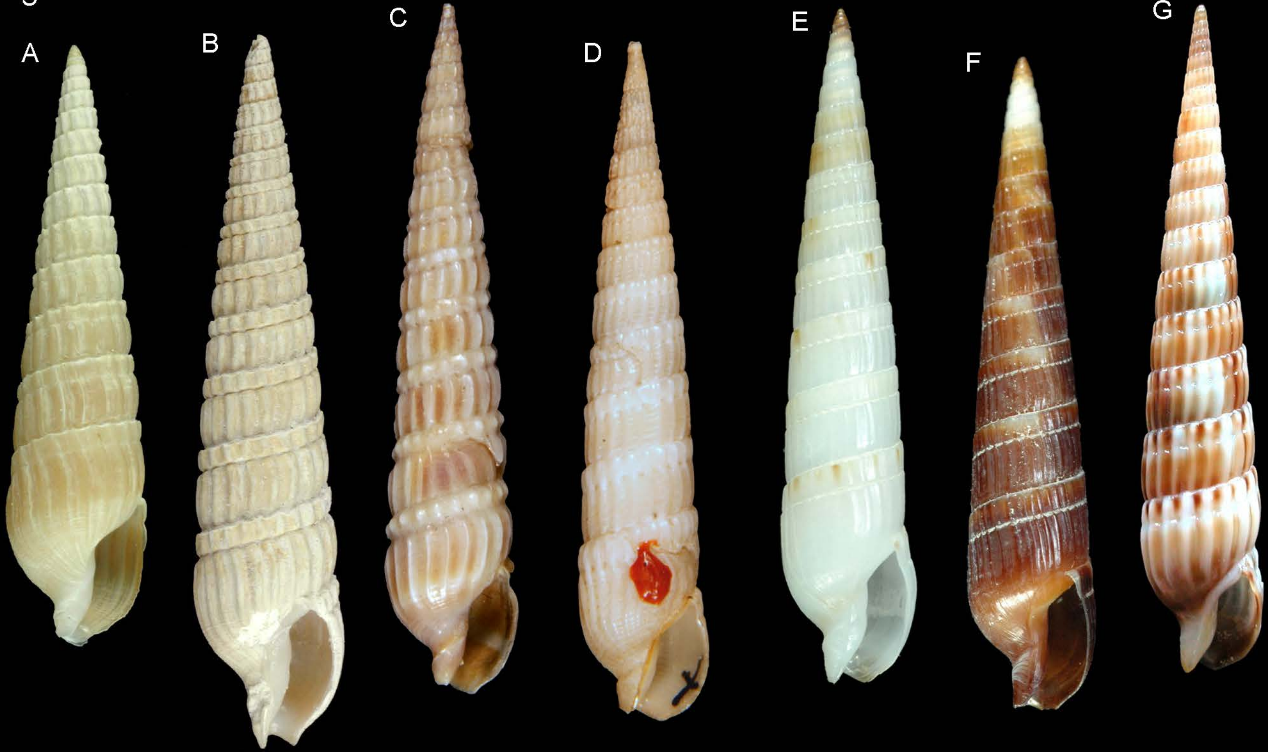


Figure 13