Macroevolution of venom apparatus innovations in auger snails (Gastropoda; Conoidea; Terebridae)

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Abstract

The Terebridae are a diverse family of tropical and subtropical marine gastropods that use a complex and modular venom apparatus to produce toxins that capture polychaete and enteropneust preys. The complexity of the terebrid venom apparatus suggests that venom apparatus development in the Terebridae could be linked to the diversification of the group and can be analyzed within a molecular phylogenetic scaffold to better understand terebrid evolution. Presented here is a molecular phylogeny of 89 terebrid species belonging to 12 of the 15 currently accepted genera, based on Bayesian inference and Maximum Likelihood analyses of amplicons of 3 mitochondrial (COI, 16S and 12S) and one nuclear (28S) genes. The evolution of the anatomy of the terebrid venom apparatus was assessed by mapping traits of six related characters: proboscis, venom gland, odontophore, accessory proboscis structure, radula, and salivary glands. A novel result concerning terebrid phylogeny was the discovery of a previously unrecognized lineage, which includes species of *Euterebra* and *Duplicaria*. The non- monophyly of most terebrid genera analyzed indicates that the current genus-level classification of the group is plagued with homoplasy and requires further taxonomic investigations. Foregut anatomy in the family Terebridae reveals an inordinate diversity of features that covers the range of variability within the entire superfamily Conoidea, and that hypodermic radulae have likely evolved independently on at least three occasions. These findings illustrate that terebrid venom apparatus evolution is not perfunctory, and involves independent and numerous changes of central features in the foregut anatomy. The multiple emergence of hypodermic marginal radular teeth in terebrids are presumably associated with variable functionalities, suggesting that terebrids have adapted to

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dietary changes that may have resulted from predator-prey relationships. The anatomical and phylogenetic results presented serve as a starting point to advance investigations about the role of predator-prey interactions in the diversification of the Terebridae and the impact on their peptide toxins, which are promising bioactive compounds for biomedical research and therapeutic drug development.

Keywords

character evolution; key innovations; predator-prey system; radula; teretoxins; toxins

1. Introduction

At the macroevolutionary level, it is hypothesized that the tempo of evolution can be viewed through the lens of key innovations (Sanderson and Donoghue, 1994). Key innovations are biological traits that promote lineage diversification (Heard and Hauser, 1995; Hodges and Arnold, 1995). The development of a venom apparatus in the marine gastropod superfamily Conoidea is a key innovation that can be used as an organizational framework to decipher the evolutionary history of this megadiverse group. Here the evolution of the venom apparatus in auger snails (Neogastropoda; Conoidea; Terebridae) is investigated using a molecular phylogenetic scaffold.

The Terebridae are a diverse family of medium to large-sized (mostly 15-150 mm) marine gastropods distributed throughout most tropical and subtropical oceans. Terebrids use their venom apparatus to capture prey, and perhaps also to defeat competitors or predators (Olivera, 1997). Similar to the peptide toxins produced by cone snails (Neogastropoda; Conoidea; Conidae), the peptide toxins produced by terebrids, teretoxins, are promising bioactive compounds for biomedical research and therapeutic drug development (Puillandre and Holford, 2010). Peptide toxins from a venom source are of increasing interest in the pharmacological industry (Chin et al., 2006; Newman and Cragg, 2007; Butler, 2008; Casewell et al., 2009; Hong, 2011). As recently demonstrated (Fry et al., 2003; Modica and Holford, 2010; Puillandre et al., 2010; Saslis-Lagoudakis et al., 2011), understanding how the organisms that produce these toxins have emerged and evolved over time, may become central in the process of drug discovery. Specifically, in the case of the Terebridae, not all species have a venom apparatus, therefore identifying the lineages that have a venom apparatus is an effective route to peptide toxin characterization. Currently, the extent of species diversification of the Terebridae is largely underestimated and the evolutionary pathways explored by the terebrid groups, especially regarding the peptide toxins they produce, remains largely unknown.

Whether used for defense or attack, the diversity of toxins developed by venomous organisms is often attributed to the process of co-evolution in predator-prey relationships (Kordis and Gubensek, 2000; Lynch, 2007; Duda, 2008; Kozminsky-Atias et al., 2008; Barlow et al., 2009). Co-evolutionary predator-prey interactions may lead to the development of specialized adaptations in the predator that are followed by counter-adaptations in the prey, which in turn can lead to further adaptations in the predator, and so on, as dictated by biotic, "Red Queen" (Van Valen, 1973) or abiotic, "Court Jester" (Barnosky, 2001) pressures. For example, numerous plants produce toxic secondary compounds that influence the behavior, growth, or survival of insects and other herbivores. In addition, herbivores have developed ways to detoxify, sequester, or render ineffective specific plant poisons (Laycock, 1978; Fowler, 1983; Zangerl et al., 2008). In snakes, it has been demonstrated that venom diversity may result by adaptation toward specific diets (Daltry et al., 1996; Wüster et al., 1999; Barlow et al., 2009). In parallel, some snake prey

have developed the ability to inhibit specific venom toxins (Heatwole and Poran, 1995; Biardi et al., 2005). By its indirect effect on fitness, the predator-prey arms race can represent a driving force of speciation and species diversification in both predators and preys populations. This is referred to as the "escalation/diversification hypothesis" (Ehrlich and Raven, 1964; but see also Berenbaum and Feeny, 1981; Berenbaum, 1983; Vermeij, 1993). Phylogenetic analyses can provide seminal evidence on rates and patterns of predation-traits evolution and species diversification (Farrell et al., 1991). However, the correlation between adaptative changes of predation- traits and species-diversification in predator-prey systems is difficult to study. Such a study requires a good understanding of the biology and the ecology of the species involved and necessitates a thorough taxonomic sampling of both predator and prey taxa. A good alternative, as attempted here with the Terebridae, is to obtain an exhaustive taxonomic sampling of one of the two taxa (predator or prey) and to study the traits or innovations that affect the ability to accomplish or avoid predation. Mapping these innovations on a phylogenetic tree then reveals patterns that may impact species diversification.

Understanding the evolutionary patterns of venom apparatus evolution in the Terebridae would significantly advance clarifying the phylogeny and systematics of the group, in addition to advancing the characterization of terebrid peptide toxins for biomedical applications. Recent molecular phylogenies (Holford et al., 2009a, 2009b; Puillandre et al., 2011) of the family Terebridae based on samples from Western and Eastern Pacific demonstrated the monophyly of terebrids relative to the other families of conoideans. Also illustrated in these phylogenetic studies is the existence of five distinctive clades, *Pellifronia, Oxymeris* [= *Acus*]*, Terebra, Hastula, and Myurella,* numbered clades A to E, respectively, with clade A, containing the recently revised *Pellifronia jungi* (Terryn and Holford, 2008), as sister species of all the other terebrids. Previous molecular analyses combined with mapping of venom apparatus morphology also indicated that the Terebridae have lost the venom apparatus at least twice during their evolution (in clades B and E). However, these phylogenies were based on a limited number of species (~ 50 for the most complete, vs the ~ 400 currently described species), and sampling was limited to the Pacific Ocean. Additionally, only the presence and absence of the venom glands were studied, overlooking other morphological and anatomical innovations potentially linked to the evolution of terebrid predatory skills and toxin diversity. In contrast, the present expanded study of the molecular phylogeny of the family Terebridae almost doubles the number of species from 50 to 89, including 12 out of the 15 accepted genera, almost triples the number of specimens, and increases the geographical area sampled by including the western Indian Ocean. The molecular phylogeny in this study is based on the three mitochondrial genes, COI, 12S, 16S, previously used in conoidean phylogenies, with the addition of one nuclear gene, 28S, shown to be useful in resolving relationships at the genus level in Conoidea and other gastropods (Williams and Ozawa, 2006; Puillandre et al., 2008). The analysis of the venom apparatus, previously reduced to the presence or absence of the venom gland, and thus underestimating the diversity of the evolutionary pathways the terebrids may have explored, is here extended to other anatomical features linked to the venom apparatus. The morphology of the radula, in particular, has been linked to prey capture, and consequently different radula types may correlate to innovations in predatory behavior, including venom evolution.

2. Material and methods

2.1. Taxon sampling

All the material studied herein was collected during several expeditions conducted by the Museum National d'Histoire Naturelle of Paris (MNHN), in partnership with Pro-Natura International (PNI), Instituto Español de Oceanografia (IOE), and Institut de Recherche pour

le Développement (IRD), the Natural History Museum of London (NHM), and the Smithsonian Tropical Research Institute (STRI) (See Table 1 and acknowledgements). Samples include 406 specimens assigned to 89 species collected off New Caledonia (4 specimens), Philippine Islands (49), Vanuatu (115), Solomon Islands (12), Australia (4), the Coral Sea (4), Panama (50), Madagascar (87), Mozambique (75), Tahiti (4), New- Zealand (1) and Fiji (1) (Fig. 1). These samples originate from depths ranging from 0 m to ~ 800 m (Table 1). In the field, all specimens were specifically fixed for molecular analysis. Living specimens were anesthetized using magnesium chloride ($MgCl_2$), a piece of tissue was cut from the head-foot, and fixed in 95% ethanol. Shells were kept intact for identification. Vouchers are deposited in MNHN. Taxonomy follows Terryn (2007), with updates in Terryn (2011) (*Cinguloterebra* synonymized with *Triplostephanus*, *Impages* with *Hastula*, and *Acus* and *Perirhoe* with *Oxymeris*). Three specimens of the family Turridae (putative sister-group of the Terebridae – Puillandre et al., 2011), Cochlespiridae (Conoidea) and Conidae (Conoidea) were used as closely related outgroups. *Harpa kajiyamai,* belonging to another neogastropod family (Harpidae), was used as a distant outgroup to root the tree.

2.2. PCR amplification and DNA sequencing

Total genomic DNA was extracted from muscle tissue using NucleoSpin[R] 96 Tissues (Macherey- Nagel) and following the manufacturer's instructions. Fragments of the mitochondrial genes Cytochrome Oxidase I (COI), 16S rRNA and 12S rRNA as well as the nuclear 28S rRNA were amplified (Table 2). PCR reactions were performed in 25 µL final volume, containing approximately 3 ng template DNA, 1.5 mM MgCl2, 0.26 mM of each nucleotide, 0.3 µM of each primer, 5% DMSO and 0.75 U of Taq Polymerase (Qbiogene). Amplification products were generated by an initial denaturation step of 4 min at 94 °C followed by 35 cycles at 94 °C for 40 s, annealing at 50°C for COI, 52°C for 28S, 51°C for 12S rRNA and 16S rRNA for 40 s and by an extension at 72°C for 1 min. PCR products were purified using ExonucleaseI and Phosphatase and sequenced using BigDye Terminator V3.1 kit (Applied biosystem) and the AB3730XL sequencer. All genes were sequenced for both directions to confirm accuracy of each sequence. Chromatograms were edited using CodonCode Aligner version 3.7.1.1. All the sequences were deposited in GenBank and BOLD (Table 1).

2.3. Datasets

Six datasets were analyzed. The first three datasets were analyzed for all taxa listed in Table 1 and consisted of three independent gene analyses performed from COI, 16S and 12S genes. The fourth dataset consisted of a combined data set of COI, 16S, and 12S and is referred to as CD1. To evaluate the robustness of the mitochondrial phylogeny, a fifth dataset corresponding to the nuclear 28S gene set was built, with one representative for most of the species. This reduced dataset was then combined with the three mitochondrial genes and is referred to as CD2.

2.4. Phylogenetic analyses

Sequences were aligned for each gene independently using MUSCLE (Edgar, 2004). The accuracy of automatic alignments was confirmed by eye using BioEdit version 7.0.0.0 (Hall, 1999). Hyper-variable regions of 12S and 16S rRNA genes were excluded from further analyses to avoid ambiguities in the homology hypotheses. Best-fit substitution models were identified for each gene separately and for each combined dataset using Modelgenerator V. 85 (Keane et al., 2006). Best-scoring Maximum Likelihood (ML) trees were estimated using RaxML (Stamatakis, 2006) from 100 independant searches each starting from distinct random trees. Robustness of the nodes were assessed using the thorough bootstrapping algorithm (Felsenstein, 1985a) with 1000 replicates. Bayesian Analyses (BA) were performed running two parallel analyses in MrBayes (Huelsenbeck and Ronquist, 2001),

consisting each of eight Markov chains of 100,000,000 generations with a sampling frequency of one tree each ten thousand generations. The number of swaps chains was set to 5, and the chain temperature at 0.02. Convergence of each analysis was evaluated using Tracer 1.4.1 (Rambaut and Drummond, 2007) to check that ESS values were all greater than 200. A consensus tree was then calculated after omitting the first 25% trees as burn-in. For the treatment of combined data using ML and BA, the data were separated into six unlinked partitions: 16S, 12S, 28S and the three codon positions of the COI gene. Analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2), using the RAxML-HPC2 on TG tool for ML and the MrBayes on TG tool for BA.

2.5. Overview of Terebridae anatomy and foregut characters

Foregut anatomy was examined by dissecting sequenced specimens. The radulae were cleaned with diluted bleach (1 part of commercially available bleach to 3-4 parts of water), rinsed several times in distilled water, mounted on clear glass cover-slips and air-dried. The cover-slips were glued to stubs, coated with gold and examined by scanning electron microscopy. Terminology previously used for description of the foregut structures in Terebridae is rather inconsistent and confusing (Miller, 1970, 1975, 1979). Here the terminology of Taylor et al. (1993), which reflects the supposed homologies within the entire Conoidea was followed. Six characters of the foregut were examined and used for tracing evolutionary pathways on the molecular tree (Table 3):

Character 1—Proboscis (PR): 0 – absent, 1 – present. PR is very variable in length, from extremely short to very long. In long proboscises, walls often form telescopic folds, while the proboscis can be coiled within the rhynchodaeum. The proboscis contains the buccal tube, i.e., the portion of the alimentrary canal extending between the buccal cavity and the true mouth, which is situated at the distal end of the proboscis (Taylor et al., 1993). The buccal tube is absent only in those species where the proboscis is lost. All examined terebrid species possess a more or less long rhynchodeal introvert (also known as labial tube – Miller, 1970). The length of the introvert correlates with the presence of the proboscis: in species without proboscis, the rhynchodeal introvert is much longer than in species with proboscis.

Character 2—Venom gland (VG): 0 – absent, 1 – present. VG, sometimes called venom duct, is an autapomorphy of Conoidea (Taylor et al., 1993); when present it always has a muscular bulb, also referred to as the venom bulb. The venom gland in Terebridae opens just posterior to the radular sac.

Character 3—Odontophore (OD): 0 – absent, 1 – present. OD, consisting of subradular cartilages and muscles, usually present in species having a radula with a strong subradular membrane. In Terebridae it can vary from being massive (*e.g., Duplicaria bernardii*) to being vestigial and hardly recognizable (*e.g., Terebra succincta*, clade E3).

Character 4—Accessory proboscis structure (APS): 0 – absent, 1 – present. APS is an extensible muscular structure that arises from the wall of the rhynchodaeum. It can be branching or club-shaped, distally papillated, or simple, stalk-shaped. A somewhat similar structure, named rhynchodeal outgrowth, is found in other Conoidea – Horaiclavidae and *Zemacies* (Borsoniidae) (Fedosov and Kantor, 2008).

Character 5—Radula (RadT): 0 – absent, 1 – consists of duplex marginal teeth, 2 – consists of solid recurved marginal teeth, 3 – consists of flat marginal teeth, 4 – consists of semi-enrolled marginal teeth, 5 – consists of hypodermic marginal teeth. Radula in Terebridae consists only of a pair of marginal teeth per transverse row. The radula was

completely lost in several lineages, but when present the marginal teeth exhibit a range of morphological types, and five major types are here recognized: (1) *Duplex teeth* (Fig. 2 A-C), consisting of a major element (limb), attached to the subradular membrane along most of its length, and an accessory limb, which is the thickened edge of the major element, usually somewhat elevated above the membrane. Here, the radula has about 20-25 rows of teeth; (2) *Solid recurved teeth* (Fig. 2 F-G) with a broad flatened base, which is attached to the relatively strong subradular membrane. In species with this type of teeth, the radula is short, with only 15-20 rows; (3) *Flat and simple teeth* (Fig. 2 D-E), attached by a narrow base to the subradular membrane. Two, not clearly delimitated, variants - *broad triangular* (Fig. 2E) and *long irregular* (Fig. 2D) - are coded as the same radular type in the analysis. The subradular membrane is usually very thin and fragile, and easily tears apart. Radulae with this type of teeth consist of 20 or more rows; (4) *Semi-enrolled teeth* with tooth edges overlapping at the base, forming a loosely enrolled tube, while closer to the tip the tooth is trough shape in section. Radulae with this type of teeth are very short, with only about 10 rows; (5) *Hypodermic hollow teeth* (Fig. 3 A-P), rather similar to the hypodermic teeth present in other Conoidea. Such teeth have a very broad basal opening of the tooth canal, with usually a reflected outward edge of the tooth, forming a collar-like structure; the apical opening can be unarmed or it can have small barb(s) or blade(s). The subradular membrane is usually very thin and vestigial. The number of rows of teeth varies from about 10 (*Terebra jenningsi*) to about 30 (*Hastula hectica* and *H. penicillata*).

Character 6—Salivary glands (SG): 0 – absent, 1 – present. SG can be paired, but are more often fused, bipartite with paired ducts. In some species, a single gland is present.

Accessory salivary gland(s) are present in different species of Terebridae, as well as in some other conoideans. They usually are very small and difficult to find by dissection, therefore not used in the analysis.

2.6. Evolution of the anatomy

A reduced dataset was built for the 46 species (including the four outgroups) for which anatomical data were available. To minimize the risk of undetected cryptic species, the dissected and sequenced specimens were the same in most cases. However, for *Pellifronia jungi* and *Hastulopsis pseudopertusa* (Table 3), sequences were not obtained from the dissected specimens, and a conspecific specimen was used. Four species, *Oxymeris dimidiata*, *O. maculata*, *Terebra subulata* and *Hastula hectica*, were dissected by YK and John D. Taylor using non-sequenced material, and conspecific specimens were used for sequencing. ML analyses were performed using the method described above. The evolution of the six characters listed in Table 3, and described in the anatomy overview above, was assessed with Mesquite V2.74 (Maddison and Maddison, 2009), using the option "tracing character history" and the parsimony ancestral reconstruction method. The characters PR (proboscis), VG (venom gland), OD (odontophore), and RadT (marginal radular teeth anatomy) were treated as ordered characters (using a stepmatrix), prohibiting some of the transformation sequences, in our case from absent to present, as reapparition of these features is highly unlikely. Other characters were treated as unordered. Additionally, Bayestraits (Pagel and Meade, 2006) was used to test if the evolution of foregut characters were correlated. As Bayestraits cannot compare characters with more than two states, the character 5 (RadT) were recoded in two different characters, RadT1 and RadT2, with the states 0 "radula absent" and 1 "radula present" for RadT1, and states 0 "radula solid" and 1 "radula hypodermic" for RadT2. In the latter case, an absence of radula was coded as missing data. Independent and dependent models of Bayesdiscrete were compared. MCMC were run with default parameters, except for the number of generations, which were set to 2050000.

3. Results

3.1. Genetic diversity

Of the total of 406 samples of Terebridae used to reconstruct the molecular phylogeny of the family, 389 were sequenced for the COI gene, 400 for the 16S gene, 369 for the 12S gene and 63 for the 28S gene. For COI, 658 bp were sequenced and no indels were found. After the alignments and the removal of ambiguously aligned sites, fragments of 591, 654 and 761 bp in length were obtained for the 16S, 12S and 28S genes, respectively. For the COI gene, 218 different haplotypes were found, displaying 121 polymorphic sites and 278 parsimony informative sites. For the 16S gene, 162 different haplotypes were found, displaying 277 polymorphic sites and 235 parsimony informative sites. For the 12S gene, 164 different haplotypes were found, displaying 412 polymorphic sites and 369 parsimony informative sites. Representatives of the mitochondrial diversity were also sequenced for the 28S gene (62 specimens, including 2 outrgoups). Overall, the variability for the 28S gene was less important than for the mitochondrial genes, with 127 polymorphic sites and 94 parsimony informative sites.

3.2. Phylogenetic analyses: single-gene data sets

Modelgenerator results indicated that GTR + I + G model was the best-fit model of evolution for the four genes analyzed (COI: I = 0.47, α = 0.55; 16S: I = 0.56, α = 0.6; 12S: I = 0.3, α = 0.6 and 28S: I = 0.63, α = 0.4). Parameters of the models were estimated during the maximum likelihood and bayesian analyses for both single-gene and concatenated datasets (see below). For each gene analyzed, no supported conflict was found between the different analyses. In each of the four single gene analyses, the consensus tree showed the Terebridae to be monophyletic however, the relationships within terebrids were generally poorly resolved, with few well-supported clades (Supplementary data 1-4). Therefore only the results obtained for the combined datasets CD1 and CD2 are presented.

3.3. Phylogenetic analyses: combined data set 1 (CD1)

The best-fit model of evolution was GTR + I + G (I = 0.45, α = 0.59). Topologies derived from ML analyses of the combined data set 1 (CD1) were congruent with the topology derived from BA analyses. From these combined analyses, the Terebridae were found monophyletic, CD1, Posterior Probabilities PP = 0.99, Bootstraps B = 96% (Fig. 4). Within the Terebridae, the five major clades, *Pellifronia, Oxymeris* [= *Acus*]*, Terebra, Hastula* and *Myurella* (clades A-E, respectively) previously identified in Holford et al. (2009a) were recovered. Each were still strongly supported (PP > 0.90, B > 70%), and the topological relationships among the clades were similar, e.g., clades B-E were grouped together (PP = 0.99, B = 90%) (Fig. 4, and see Fig. 2 in Holford et al. (2009a). A sixth clade, hereafter designated as clade F, is novel in the molecular analysis and presented here for the first time. Intra-clade relationships for clades A-F are detailed in Figures 5 and 6, and some shells are illustrated for each clade in Figure 7. Clade F appeared to be the sister group to clades B-E, although the corresponding node is not supported (PP = 0.93, B = 46%). It is comprised of six newly-sampled species, four from South Madagascar, one from Australia and one from New-Zealand. The species composition of clade A remained unchanged compared to Holford et al., 2009a and 2009b, still including a single species, and appearing to be the sister group to all the other clades (althgough without statistical support). A newly-sampled species from South Mozambique was added to clade B, now totalling eight species (PP = 0.99, B = 100%). Three newly- sequenced species, one from South Madagascar, one from South Mozambique, and one from Philippines and the Solomon Islands, were added to clade C, now comprising nineteen species (PP = 0.99, B = 73%). Clade D included eleven species, of which one species, sampled in Madagascar, was new to the taxon set (PP = 1, B = 100%). Clade E contained five well-supported subclades (E1-E5), but the relationships among these

were in general poorly resolved. Clade E1 (PP = 1, B = 96%) included eleven species of which one, from Vanuatu and Australia, was new to the taxon set. Two newly-sequenced species, one from New Caledonia and one from Vanuatu and South Madagascar, were added to the thirteen species previously included in clade E2 (PP = 1, B = 97%). Clade E3 (PP = 0.97, B = 66%) included five species of which two, from the Coral Sea and Solomon Islands respectively, were new to the taxon set. Clade E4 (PP = 1, B = 75%) was new to the taxon set, with six species from Pacific Panama. Two newly-sampled species from Madagascar were added to clade E5, now comprising eight species (PP = 1, B = 94%).

Molecular analyses highlighted several incongruencies at the genus and species levels. With the exception of three genera (*Oxymeris* – clade B, *Pellifronia* – clade A and *Terenolla* – clade E1, the last two represented each by a single species), all the analyzed genera were found to be non-monophyletic. Clade B comprises eight species of the genus *Oxymeris*. As previously found (Holford et al., 2009a), clade C consists of 6 species of *Triplostephanus* and 13 of *Terebra* (*s.s.*), including *Terebra subulata*, the type species of *Terebra*. Clade D comprises eight species of *Hastula* and one *Duplicaria*. Clade E, the largest clade in terms of number of species, comprises primarily species of the genera *Myurella, Clathroterebra, Terenolla, Hastulopsis, Strioterebrum*, and the "*Terebra*" *textilis*-group (Terryn, 2007). However, as shown in Holford et al. (2009a), all these genera (except *Terenolla*) are polyphyletic, with species of each genus placed in several of the five clades E1-E5. Specifically, *Myurella* species were found in E1, E2, E3 and E5, *Clathroterebra* in E1 and E3, *Hastulopsis* in E1 and E5, *Strioterebrum* in E1 and E2, and species of *Terebra* (s.s.) are distributed in clades C, E2, E3, E4 and E5. Also, the addition of newly sampled species impacted the generic composition of clade E. For example, clade E2 now includes two species that were attributed to *Duplicaria*, *D. baileyi* and a new species *D.* sp3, and one species currently attributed to *Triplostephanus*. A newly sampled species, currently attributed to *Hastulopsis* (*H. pseudopertusa*), was included in clade E5. The new lineage, clade F, includes both *Duplicaria* and *Euterebra* species.

At species level, *plumbeum, pertusa, strigilata, succincta* and *textilis* each end up in two distinct clades, revealing cryptic species. The COI pairwise genetic distances (K2P) between the two clades were 9.6% for *plumbeum*, 9.9% for *pertusa*, 6.4% for *strigilata*, 12.47% for *succincta* and 7.73% for *textilis*. Fourteen different lineages (five in the genus *Terebra*, three in *Strioterebrum*, three in *Duplicaria*, and one each in *Myurella, Triplostephanus* and *Hastula*) were not identified to species level and may represent new species. Conversely, two specimens identified as *Triplostephanus cumingii* and *Terebra punctatostriata* (Clade C, Fig. 5) share almost identical sequences (no difference in the 16S gene and only four mutations in the 12S gene); revealing initial misidentification and/or synonymy of a species in the *T. anilis* complex.

3.4. Phylogenetic analyses: combined-gene data set 2 (CD2)

The best-fit model of evolution was GTR + I + G (I = 0.58, α = 0.55). The combined data set 2 (CD2) included 62 specimens for which at least two mitochondrial genes and the nuclear 28S gene were available. Topologies derived from both ML and BA analyses using CD2 were similar and consistent with the topology derived from analyses of the CD1 data set (Fig. 8). The family Terebridae was confirmed monophyletic (PP = 1, B = 89%). The nine clades (A-D, E1, E2, E3, E5 and F) represented in this dataset were also strongly supported, for some of them with PP and/or B superior to the supports obtained in CD1 analysis. Relationships between and within the main clades are generally similar, except for some non-supported nodes. For example, clade A is sister-group to all the other terebrids in CD1, but in CD2 its position is inverted with clade F.

3.5. Evolution of foregut characters

Reconstruction of the evolution of the proboscis (character 1) clearly demonstrates that it was lost six times in Terebridae: in clades F, B, E1 (all species), and partially in clades E2, E4, and E5 (Fig. 9A). The venom gland (character 2) was lost eight times – in clades F, B, and E1 (all species), and partially in clades E2 (twice), E4 (twice), and E5 (Fig. 9B). In many lineages the odontophore (character 3) is completely absent (including all species having hypodermic marginal radular teeth) (Fig. 9C). Reconstruction of the presence of the odontophore showed that it was lost in most of the clades independently. It is present in clades A and F, and in some species of clades D, E3 and E2. It is vestigial, and hardly discernable in *Hastula strigilata*, to the extent that its presence was revealed only on serial histological sections (J.D.Taylor, personal communication). It is possible that a rudiment of the odontophore may be present in some other species of *Hastula* as well. Reconstruction of the presence of accessory proboscis structure (character 4) showed that it appeared independently in clades E1, E2, and E4 (Fig. 9D).

Reconstruction of the presence of the radula and of the morphology of marginal radular teeth (character 5) revealed a complicated evolutionary history of radular transformations (Fig. 9E). The radula was lost several times: in the entire clades B and E1, and in some species of clades E2 and E5. The most parsimonious ancestral state for the Terebridae radular teeth is the duplex type. Duplex teeth are variable in shape: in some species (*Terebra succincta*, clade E3, and *Clathroterebra poppei* – Figs. 2 B-C) the limb also has a thickened edge, while in *Pellifronia jungi* (Fig. 2A) the limb edge is not thickened. Analysis suggests that duplex teeth are the most parsimonious ancestral state for the entire clade E and that flat teeth originated from duplex ones in clade E2. Analysis was not able to resolve a single most parsimonious state for clade D, with duplex and semi-enrolled teeth being equally parsimonious. Solid recurved teeth appeared in the single clade F. Semi-enrolled teeth were found so far in a single of the species examined here, *Hastula stylata* (Fig. 3Q). Teeth of rather similar shape were recorded in *Hastula bacillus* (Taylor and Miller, 1990). Finally, hypodermic teeth appeared independently three times – in clade C, in clade D and in the single species, *Myurella kilburni,* from clade E5. However, the structure of the hypodermic teeth is slightly different in these three lineages. In the species belonging to clade C (Fig. 3A-G), the teeth are slender, have a constriction at the base, and usually a basal spur, i.e. an anterior projection on the base of the tooth. Another important character for the hypodermic radula of clade C is that the teeth are attached to the subradular membrane at their bases. In species of clade D (*Hastula* spp.), the hypodermic teeth are conical, without constriction at the base and without spur. Contrary to the species of clade C, the teeth are attached along most of their length to the subradular membrane. Species in clade D can have a barb or blade at the tip of the tooth. In *Hastula hectica* the walls of the tooth are penetrated by numerous holes as previously described (Imperial et al., 2007) (Fig. 3J). The only species in clade E5 with hypodermic teeth (*Myurella kilburni*) has teeth with a peculiar syringe-like shape, with very narrow, attenuated distal end (slightly less than half of tooth length) and broad and probably rather flacid basal part of the tooth. As the specimen examined was badly damaged, it was not possible to examine the radula of the single species of clade E4, *Terebra elata*, that possesses a venom gland, although the presence of a venom duct was noticed (Holford, personal observation) and the presence of a radula is highly probable.

Although found in several species, such as *Triplostephanus fenestratus* and *Hastula hectica,* the presence or absence of the accessory salivary glands cannot be confirmed without histological sections and therefore the character was excluded from the analysis. Reconstruction of the presence and absence of salivary glands (character 6) suggested independent loss in one species of clade B (*Oxymeris felina*), in most species of clade E1, in one species of clade E5 (*Hastulopsis minipulchra*) and one species of clade E2 (*Duplicaria* sp. 3) (Fig. 9F).

Bayestraits analyses revealed that the evolution of several characters is strongly correlated. As shown in Table 4, the results from Bayestraits analyses indicate that the evolution of the proboscis and the venom gland, of the proboscis and the radula (presence/absence), of the venom gland and the radula (presence/absence) and of the odontophore and the radula (solid/hypodermic) are all strongly correlated with bayes factors > 10. Additionally, the evolution of the proboscis and salivary glands, of the venom gland and the salivary glands, and of the radula (presence/absence) and the salivary gland are weakly correlated with bayes factors between 5 and 10 (Table 4).

4. Discussion

A robust phylogenetic context was used to both clarify the phylogenetic relationships of the Terebridae and to provide a framework to trace the evolution of several anatomical features linked to the venom apparatus, a key innovation of the Conoidea. The molecular phylogeny of the Terebridae presented here was based on an extended dataset compared to the previous large-scale phylogeny of the group (Holford et al., 2009a, 2009b; Puillandre et al., 2011), tripling the number of specimens, doubling the number of species to include twelve out of the fifteen accepted genera, extending the sampled diversity to the West-Indian Ocean, and including an additional nuclear gene that strengthened the initial phylogeny exclusively based on mitochondrial genes. Analysis of terebrid foregut anatomy for the characters related to the presence of a venom apparatus, namely proboscis, venom gland and radula, and other characters, such as odontophore, accessory proboscis structure and salivary glands, identified unexpected evolutionary traits within the Terebridae, with implications for the whole superfamily Conoidea. Summarized below are our findings on the taxonomy, venom apparatus evolution, and predator-prey and toxin relationships in the Terebridae.

4.1. Taxonomy

The phylogenetic trees in this analysis confirmed the monophyly of the family Terebridae (Holford et al., 2009a, 2009b) and the existence of five major clades previously identified as *Pellifronia, Acus* [now *Oxymeris*], *Terebra, Hastula,* and *Myurella,* clades A-E, respectively (Holford et al., 2009a). A novel result for terebrid molecular analysis is the discovery of a new lineage, Clade F, which includes *Euterebra* and *Duplicaria* species, and appears to be the sister group to Clades B-E.

Our results suggest that taxonomic diversity of the family Terebridae is still inadequately understood. In several cases molecular data suggest the existence of at least two distinct species within what has been identified as a single morphospecies. In three cases (*S. plumbeum, H. pertusa* and *T. succincta*), the two cryptic species identified morphologically as one, were collected sympatrically, i.e. co-occuring in the same region, and sometimes syntopically, i.e. co-occuring at the same sampling station. This is the case for *H. pertusa* with includes two molecular species sampled at the same station in Santo, Vanuatu. The detection of several new cryptic lineages emphasizes that species diversity in the family Terebridae may be underestimated. Additonally, among the ca. hundred species analyzed in this study, about twenty could not be attributed to a species name according to the taxonomic literature, suggesting that they could represent new species or nominal species currently treated as synonyms.

Increasing the geographic and species diversity of Terebridae analysed in the molecular tree demonstrates that the current genus-level classification of the group is not tenable. Most of the genera recognized in the last working identification guide of the family are non-monophyletic (10 out of the 12 genera analyzed). For example, the genus *Duplicaria*, sampled for the first time in this study, represented by six species in our sampling, was found in three distinct clades (D, E2 and F). This was an unanticipated finding since

Duplicaria, which is characterized by a shell axially ribbed, and a well- marked suture doubled on the whorls by an axial sculpture on the subsutural band (Terryn, 2007), is widely accepted in the taxonomy community and was one of the unambiguous genera recognized by Bratcher and Cernhorsky (1987). Similar problems were observed for *Terebra* and *Myurella,* where species were found in five (C, E2-5) and three (E3-5) distinct clades, respectively (see also Clathroterebra, Hastulopsis, Strioterebrum, Triplostephanus – Figs. 5-6). These examples imply that shell morphology, used to describe the diversity of terebrids, can be misleading at both genus and species levels, and can lead to an incorrect classification of the family.

Despite the extensive sampling efforts deployed to complete the taxonomic coverage, our dataset is still not exhaustive. It covers less than one quarter of the species diversity of the family, with 100 analyzed species out of the ~ 400 currently accepted species (WORMS – www.marinespecies.org), representing 12 out of the 15 currently accepted genera. Further sampling is needed to obtain the missing genera *Granuliterebra*, *Microtrypetes* and *Pristiterebra*. In addition, among the genera analyzed, numerous type-species are not represented. Considering that recent studies have shown that most terebrid genera are non-monophyletic, it will also be essential to include the numerous synonymised genera. Although further taxonomic investigations are needed to stabilize the classification of the family, the phylogeny presented here provides a robust framework to analyze the evolution of several characters linked to the venom apparatus in the Terebridae.

4.2. Venom apparatus evolution

The formation of the venom gland and the appearance of the feeding mechanism of Conoidea was the initial key apomorphy of the group (Kantor and Puillandre, in press). The unique mechanism of prey envenomation is the most outstanding character of Conoidea and includes use of individual marginal radular teeth (detached from the subradular membrane) at the proboscis tip for stabbing and injecting neurotoxins into prey (Taylor et al., 1993). Teeth of very different morphologies, i.e. not only hypodermic, are used in a similar manner. This was observed directly (e.g., Kohn, 1956) and inferred from serial sectioning of different conoideans (Kantor and Taylor, 1991). Until recently, the Terebridae remained relatively poorly studied anatomically and existing data confirmed a great disparity of anatomy of the foregut, with loss of major organs, including proboscis, venom gland and radula in many species. Nevertheless, due to the absence of a robust phylogeny, the evolution of the foregut remained largely uncertain, and loss and apparition of novel features were considered ancedotal. The results from this study indicate that the evolution of the venom apparatus is not straightforward, as key features, together with the loss of various structures of the foregut anatomy, have arisen independently on at least three occasions within terebrids. These anatomical modifications appear to be the rule rather than the exception.

Terebridae were always treated as a major independent lineage of Conoidea until the recent molecular phylogeny of the Conoidea superfamily was published (Puillandre et al., 2011). The Conoidea molecular phylogeny suggests that Terebridae is a sister group of the family Turridae (*s.s.*), the component species of which can possess a venom gland, a radula with strong subradular membrane, and have duplex marginal teeth. The discovery of true duplex teeth, and flat teeth, their derivatives in Terebridae was thus quite unexpected. Prior to this study only two types of radula were known in Terebridae, solid recurved teeth and hypodermic teeth. Duplex teeth appeared to be the ancestral state for the entire family Terebridae and this is consistent with the Turridae and Terebridae being sister- groups. Clade A, represented at the moment only by *Pellifronia jungi* and likely the sister clade to all other terebrids, has similar radula to that of Turridae.

As suggested by the Bayestraits analyses, the reduction and losses of foregut characters in many lineages of the Terebridae are not casual and have a functional explanation. All species possessing a venom gland have a corresponding radula and proboscis, as the bayes factors >10 for these characters indicate (Table 4). This is explained by the peculiarities of conoidean feeding mechanism, where envenomation of the prey requires the aid of the tooth gripped at the proboscis tip and used for stabbing the prey, or channelling the toxins through the internal lumen of hypodermic teeth. Currently, feeding of radulate terebrids was observed only in different *Hastula* and *Terebra* species with hypodermic radular teeth (Marcus and Marcus, 1960; Miller, 1970, 1979; Taylor, 1990; Taylor and Miller, 1990). The observations established that these species fed in a similar manner to other conoideans, with the use of marginal teeth at the proboscis tip. The prey reported were various sedentary polychaetes, mostly spionids. A characteristic feature of terebrid feeding is the well-developed rhynchostomal introvert, which is playing an active role in capturing and engulfing the prey.

Analysis of the anatomical characters revealed that hypodermic teeth originated three times independently in Terebridae, in clades C, D, and in a single species from clade E5, *Myurella kilburni*. As detailed in the results section, the hypodermic teeth of these three groups appear to be rather different (Fig. 3). Independent apparitions of hypodermic teeth suggest increasing the effectiveness of prey envenomation. A very interesting peculiarity was found in *Hastula cinerea* and *H. hectica*, both in clade D, where in most of the specimens examined, a tooth was held at the proboscis tip even when the species was not feeding, concealed within the proboscis with its base resting on the large sphincter (Marcus and Marcus, 1960; Imperial et al., 2007). This can be explained by the presence of a relatively strong subradular membrane and tough attachment of the teeth to the membrane. In *Hastula*, because the teeth in the radular cecum are still attached to the membrane, they cannot be immediately used for stabbing prey when required. In the process of radular growth, the oldest part of the membrane, situated in the radular cecum, is permanently destroyed and the teeth are dislodged. When the tooth is separated from the membrane, it is transferred to the proboscis tip, where it is presumably held until it is used. This is also assumed for members of the other families of "turrids" that have a strong subradular membrane. In most turrid specimens examined, there was a tooth at the proboscis tip held by the sphincter(s) (Kantor and Taylor, 1991).

Although nothing is known on the feeding of species with duplex/flat teeth, it is reasonable to suppose that they are used on the proboscis tip in a manner similar to other conoideans with non- hypodermic teeth. In this respect it was interesting to find in *Terebra textilis* at the proboscis tip flat teeth very similar to those of *Terebra trismacaria* (Fig. 2D). A group of four teeth attached to the subradular membrane was found in the buccal tube somewhat posterior to the proboscis tip. It is obvious that in this case the teeth cannot be used separately for stabbing the prey, but the mechanism of transport of the teeth from radular sac to the proboscis tip persists in this species. A probable explanation in this case represents an intermediate stage of reduction of radulae and transition to feeding without use of marginal teeth at the proboscis tip.

An odontophore is present in species that have a more or less strong subradular membrane and non-hypodermic radular teeth (bayes factor >10, Table 4). It is large and powerful in species of clade F, *Duplicaria* and *Euterebra*, which lack proboscis and venom gland and therefore do not utilize teeth for stabbing and envenomation of the prey. A well-developed odontophore suggests that the radula is functioning as a whole organ only, probably for transferring the prey from rhynchodaeum to oesophagus. There is no observation on feeding of species of this clade and diet is known for only one species with similar anatomy, *Terebra nassoides*, feeding on capitellid polychaetes (Taylor, 1990). Similarly to species with

hypodermic radulae, an active role of the introvert in prey capture was also shown in *Terebra gouldi*, a species lacking venom apparatus, radula and proboscis. and that preys on the enteropneust *Ptychodera flava*, which is swallowed alive.

While reduction of the venom gland provides economy of energy that is otherwise used for producing toxins and constant formation of the radula, the rhynchostomal introvert, which is present and well-developed in all terebrids, may explain the numerous independent losses of the venom gland and associated organs. With the rhynchostomal introvert present, feeding becomes possible without stabbing and envenomation of the prey. In addition, the proboscis also becomes unnecessary, as its primary function, gripping the tooth, does not exist any more. The muscular buccal lip, which is well developed in radular-less species, serves for transferring the swallowed prey further into oesophagus. Although very little is known about diet of terebrids with such foregut anatomy, Miller (1975) suggested that they feed on different hemichordates. The family Raphitomidae is the only other taxon of Conoidea that possesses a developed rhynchostomal introvert. In that family numerous independent reductions and losses of the venom gland and radula were hypothesized (Kantor and Taylor, 2002). It was also suggested that these reductions were connected with the role of introvert in prey capture.

Bayestraits analysis revealed only weak correlations between presence of the salivary glands and proboscis, and of venom gland and presence/absence of radula (bayes factors between 6.68 and 8.38, Table 4). The low bayes factors suggest that salivary glands are not directly involved in process of envenomation of the prey. It should be noted however, that the salivary glands of cone snail species *Conus pulicarius* contained peptide toxins when analysed by transcriptome data (Biggs et al., 2008). The functions of the accessory proboscis structure remain unclear as its presence is not correlated with other foregut structures. It was suggested that it has chemosensory functions (Taylor, 1990; Taylor and Miller, 1990). The present data supports the idea that the accessory proboscis structure is not used directly in feeding processes, but may be related to detection of the prey.

4.3. Predator-prey and toxins

Numerous terebrid lineages have lost the venom apparatus, and by contrast the lineages that kept it each developed novel anatomical features, such as hypodermic marginal radular teeth. The components of the venom apparatus, radular, venom duct, venom bulb, and proboscis, were thought to be so complicated that they certainly evolved once or twice. However, the Terebridae acquired or lost similar structure several times, resulting in an anatomy sometimes convergent with that of other conoideans. In the Terebridae alone, a remarkable finding is that the hypodermic teeth, in association with reduction of the odontophore, have likely evolved on multiple and independent occasions. Additionally, the detailed anatomy demonstrates not only different origins of the teeth but also suggests differences in functional use. Analysis of radular evolution in the entire Conoidea indicate that besides terebrids, hypodermic teeth appeared only once in a major clade that unites the families Conidae, Conorbidae, Borsoniidae, Clathurellidae, Mitromorphidae, Mangeliidae and Raphitomidae (Kantor and Puillandre, in press).

The diversity of foregut anatomy in the single family Terebridae is as large as in the whole superfamily Conoidea, which includes 14 other families. For example, all major types of conoidean radular marginal teeth were recorded in the Terebridae. From prototypic duplex teeth they evolved: solid recurved teeth, which appeared independently in some Pseudomelatomidae; flat teeth, which appeared from duplex in some Drilliidae; and hypodermic teeth, which appeared independently in common ancestor of a major clade of Conoidea (Bouchet et al., 2011; Kantor and Puillandre, in press). Moreover, the flat triangular teeth of some Terebridae are unique among Conoidea. The overview of the

foregut anatomy presented in this study revealed an inordinate diversity of features in the family Terebridae. These results suggest that predator-prey relationships have played an important role in the evolutionary history of Terebridae. Indeed, repeated innovations in the foregut anatomy of terebrids suggest that they adapted to different diets (*e.g.,* deposit-feeding or carnivorous polychaetes). To date, this hypothesis remains untested as the prey of most of the analyzed terebrid species are unknown. This could be analysed by direct observation, or by indirect approaches, such as DNA-barcoding of the gut contents (Garros et al., 2008; Oliverio et al., 2009) or analysis of stable isotopes composition (Fujikura et al., 2009).

Based on the hypothesis that the diversity of foregut structures in the Terebridae is linked to the diversity of feeding types and preys, it could also be argued that the species diversity of the Terebridae could be linked to the prey diversity, and thus to foregut anatomy. However, the results also illustrate that several species may share an apparently identical foregut structure, suggesting that the diversity of the foregut and the prey are not the only factor at the origin of the species diversity in the Terebridae and other features of the prey-capture system should be investigated e.g., reduced dispersion abilities and geographical isolation (Bouchet, 1981; Duda and Palumbi, 1999; Cunha et al., 2005; Meyer et al., 2005; Cunha et al., 2008; Castelin et al., 2010), or differential selection by abiotic factors such as depth (Chase et al., 1998; Quattro et al., 2001; Zardus et al., 2006). Given the rate of evolution of conopeptides in cone snails, it can be argued that various Terebridae species evolved different toxins as an answer, or a consequence, to prey adapation. Integrative approaches will be employed to complete the phylogeny of the Terebridae, identify their respective preys, and compare their foregut anatomy and the peptide toxins they produce. An integrated approach is not only a promising way to identify the factors that led to the diversification of the Terebridae and potentially the (co-)evolution of their prey, but is also a step forward in the characterization of novel terebrid toxins with novel function and potentially new therapeutic applications. Terebrids have clearly evolved different responses to the costs and benefits of having a venom apparatus under varying conditions. Using, for example, phylogenetic independent contrasts (Felsenstein, 1985b), the large-scale phylogeny presented here could assist in analysing the potential correlation between the anatomical innovations developed by the Terebridae and various biotic and abiotic parameters.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Highlights

An expanded molecular phylogeny of venomous marine snails Terebridae is presented. > Six characters associated with the venom apparatus are used to map terebrid evolution. > Hypodermic teeth and other innovations have likely evolved on multiple occasions. > Multiple radular origins may reflect variable functionalities associated to feeding. > Terebrids may have adapted to dietary changes following predator-prey relationships.
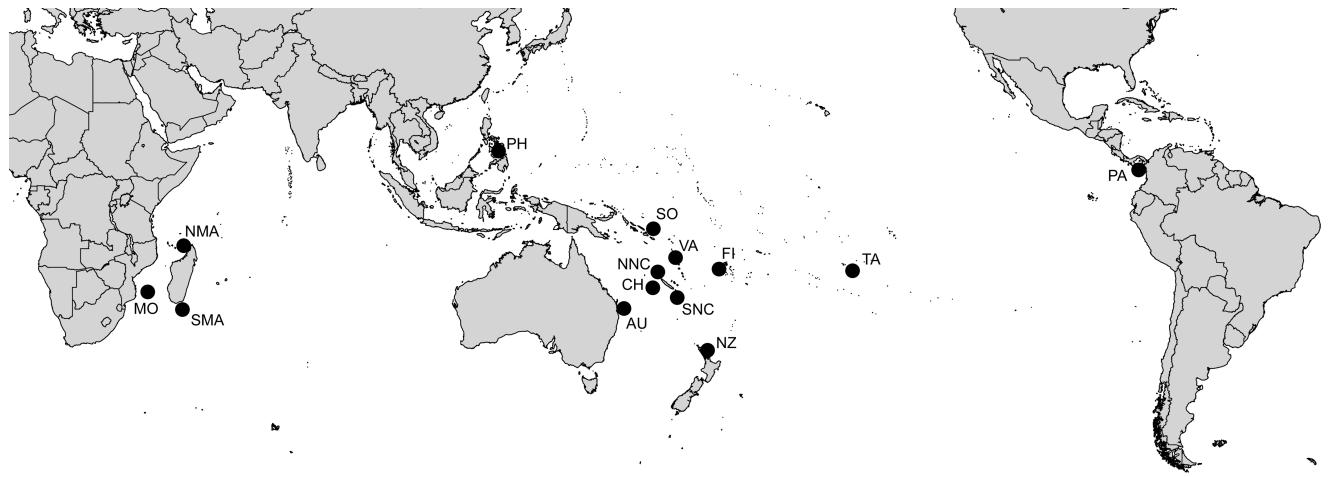
Figure 1.
Map showing localities sampled for Terebridae study. AU, Queensland, Australia; CH, Coral Sea; FI, Fiji; SMA, South Madagascar; MO, Mozambique; NMA, North Madagascar; NNC, North New Caledonia; PA, Pacific Panama; PH, Philippines; SNC, South New Caledonia; SO, Solomon Islands; TA, Tahiti; VA, Vanuatu.
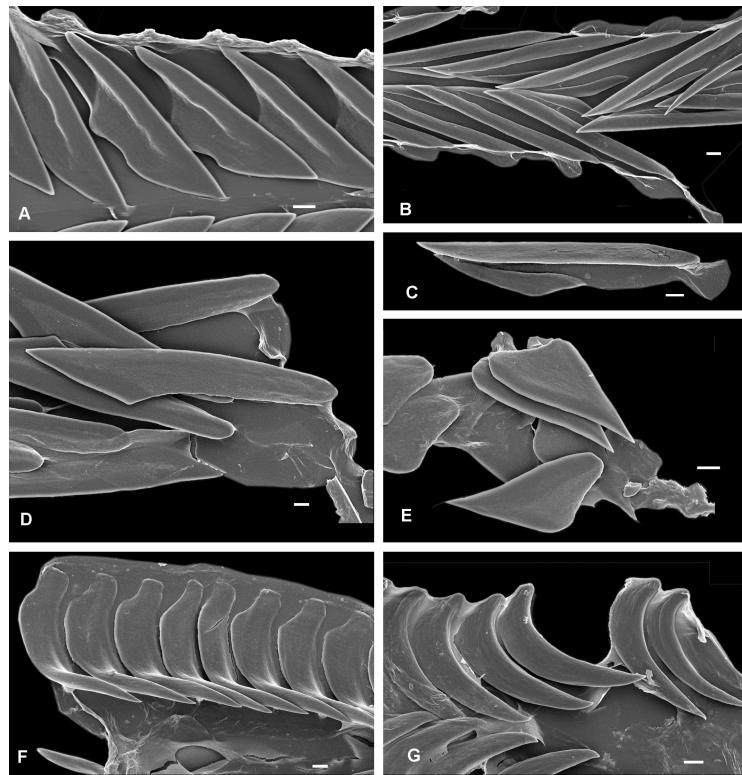
Figure 2.
Flat (A-E) and solid recurved (F-G) teeth of Terebridae. A – *Pellifronia jungi*
(IM_2007_30591), ventral view of radular membrane, only half shown; B – *Clathroterebra poppei* (IM_2007_30546), ventral view of radular membrane; C – *Terebra succincta*
(IM_2007_30582), separate marginal tooth; D – *Terebra trismacaria* (IM_2007_30579),
ventral vies of radular membrane; E – *Myurella lineaperlata* (IM_2007_30635), group of
teeth attached to the subradular membrane; F – *Euterebra fuscolutea* (IM_2009_10133),
ventral view of radular membrane, only half shown; G – *Duplicaria* sp. 2 (IM_2009_10164),
ventral view of radular membrane, only half shown. Scale bars – 10 µm.
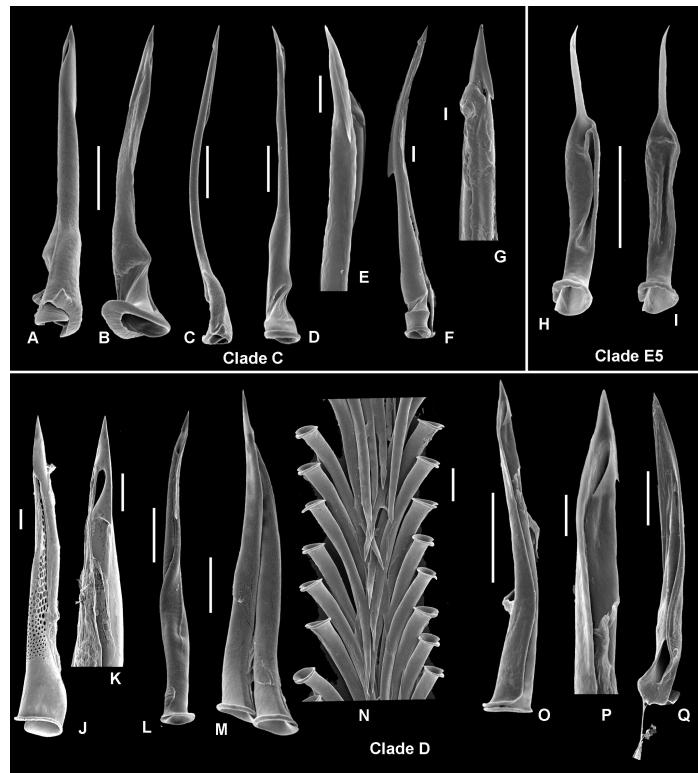
Figure 3.
Hypodermic (A-O) and semienrolled (Q) teeth in Terebridae. **Clade C** (A-G): A, B –
Terebra cingulifera (IM_2007_30382); C – *Triplostephanus fenestratus* (IM_2007_30418);
D-E – *Triplostephanus triseriatus* (IM_2007_30404); F-G – *Terebra guttata*
(IM_2007_30376);. Clade E5 (H-I) – *Myurella kilburni* (IM_2007_30461); **Clade D** (J-P):
J- K – *Hastula hectica,* Philippines, Panglao Island; L – *Hastula lanceata* (IM_2007_30535);
M-N – *Hastula penicillata* (IM_2007_30540), N – central part of the radular membrane; O-P
– *Hastula strigilata* (IM_2007_30607); Q – *Hastula stylata* (IM_2009_10106). Scale bars: 50
µm (except E, G, P – 10 µm).
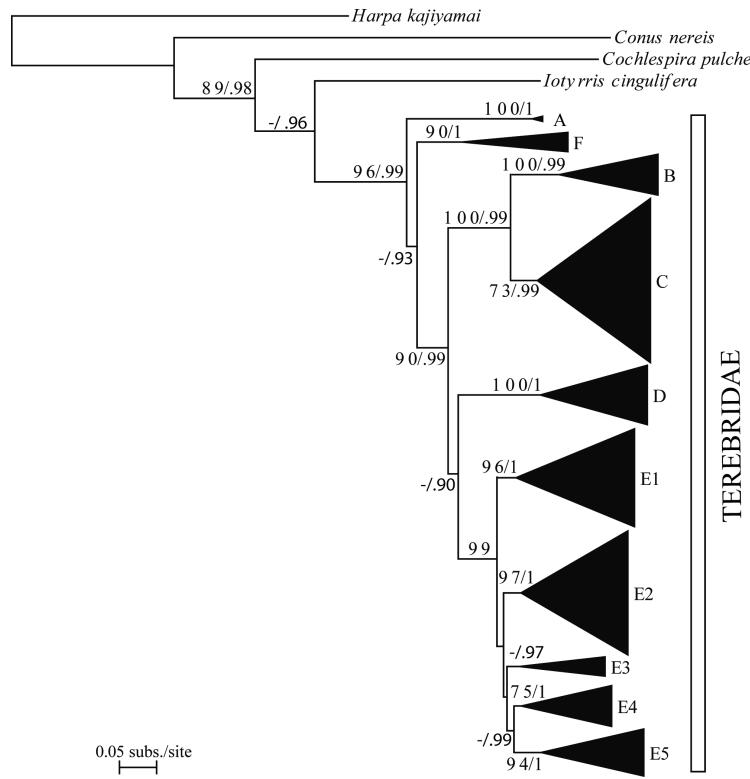
Figure 4.
Likelihood phylogenetic tree obtained with 410 specimen sequences for the COI, 12S and 16S genes. Boostraps and Posterior Probabilities are indicated for each node (when > B = 70% and > PP = 0.90 respectively). The ten collapsed clades of Terebridae (A, B, C, D, E1, E2, E3, E4, E5 and F) are detailed on Figures 2-5.
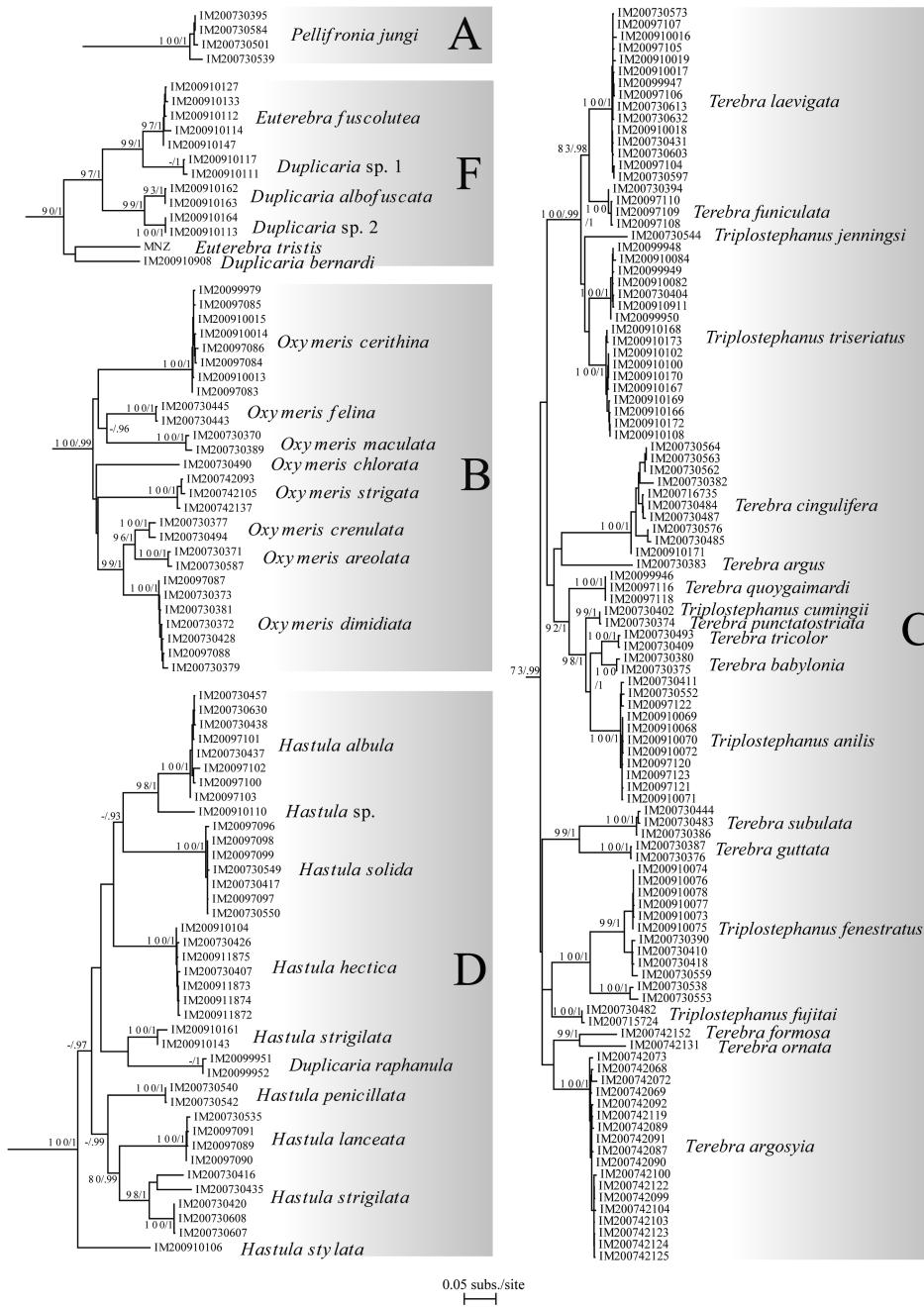
Figure 5.
Likelihood phylogenetic tree for clades A, B, C, D, F. Boostraps and Posterior Probabilities are indicated for each node (when > 70 and > 0.90 respectively). For clarity purposes, intraspecific support values are not shown.
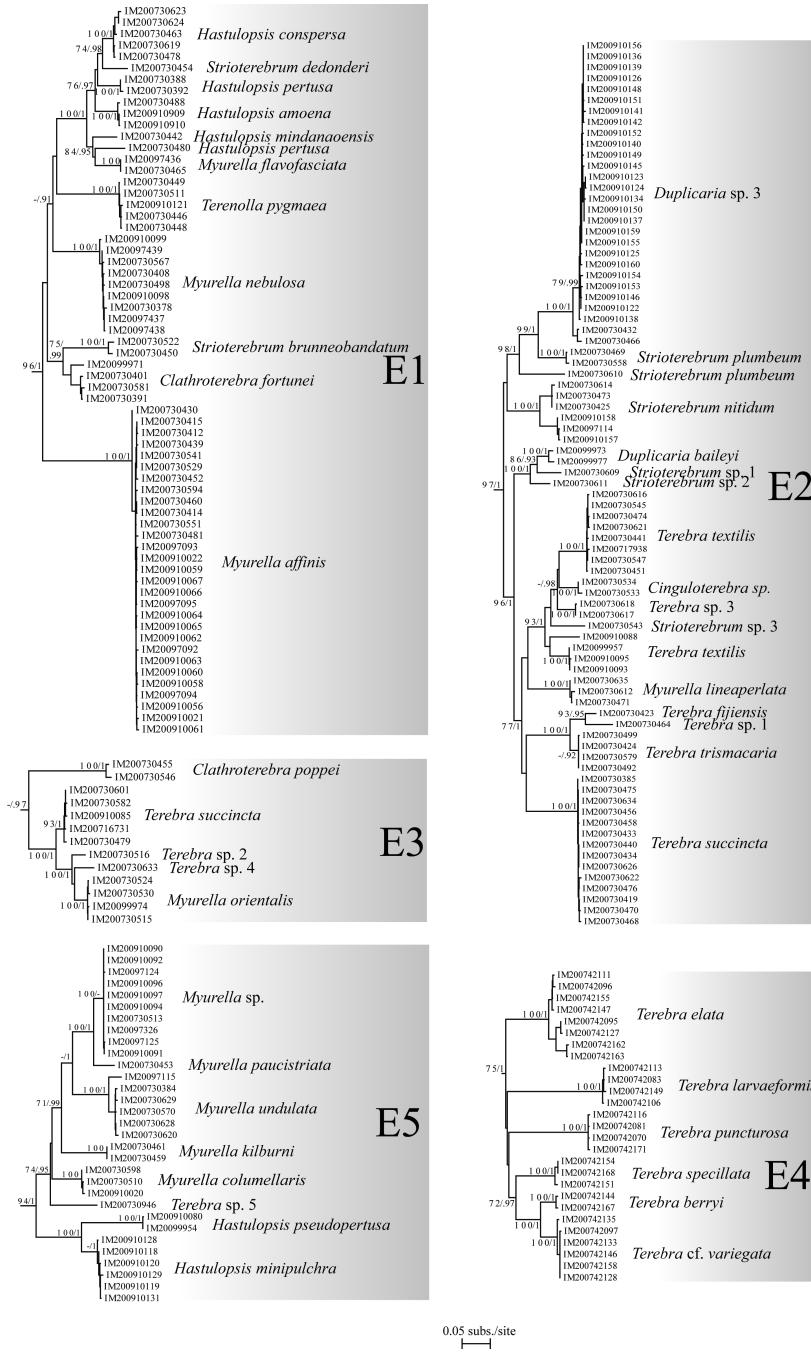
Figure 6.
Likelihood phylogenetic tree for the clades E1-E5. Boostraps and Posterior Probabilities are indicated for each node (when B > 70% and PP > 0.90 respectively). For clarity purposes, intraspecific support values are not shown.
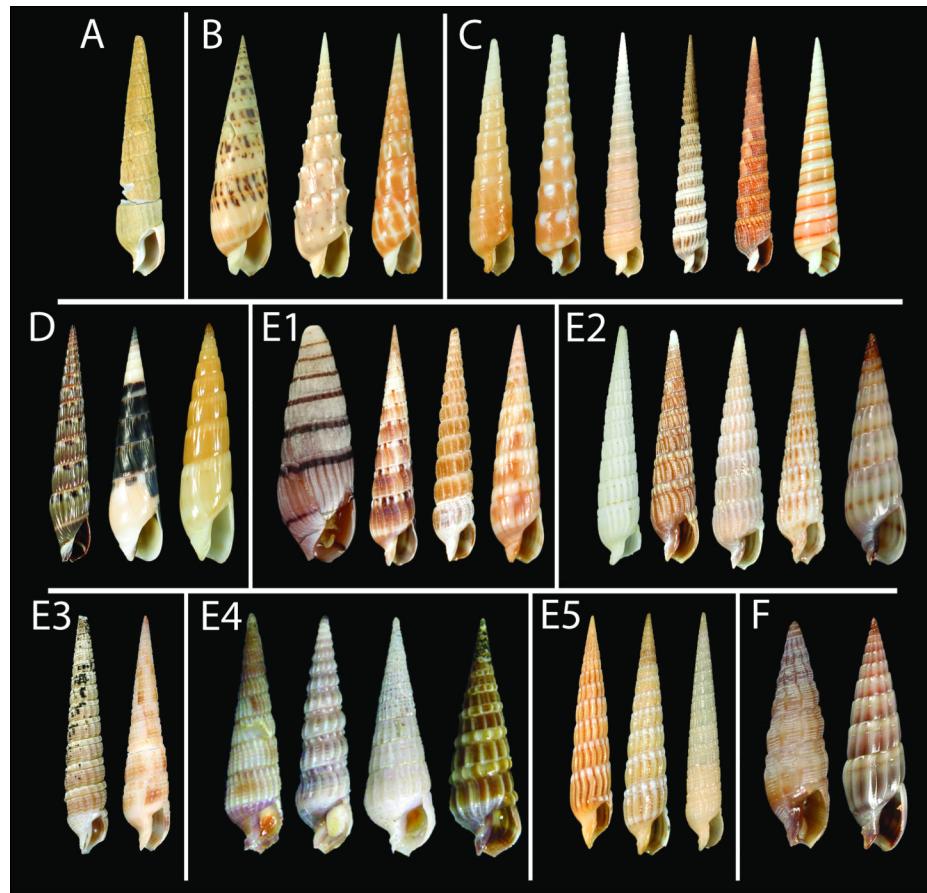
Figure 7.
Illustration of some specimens in each clade. From left to right: **Clade A**: *Pellifronia jungi*
IM_2007_30539; **Clade B**: *Oxymeris maculata* IM_2007_30370, *Oxymeris crenulata*
IM_2007_30377, *Oxymeris dimidiata* IM_2007_30379; **Clade C**: *Terebra argus*
IM_2007_30383, *Terebra guttata* IM_2007_30387, *Terebra funiculata* IM_2007_30394,
Triplostephanus fujitai IM_2007_30482, *Terebra cingulifera* IM_2007_30485, *Terebra*
tricolor IM_2007_30493; **Clade D**: *Hastula strigilata* IM_2007_30416, *Hastula hectica*
IM_2007_30426, *Hastula albula* IM_2007_30437; **Clade E1**: *Terenolla pygmaea*
IM_2009_10121, *Hastulopsis pertusa* IM_2007_30388, *Clathroterebra fortunei*
IM_2007_30391, *Myurella affinis* IM_2007_30415; **Clade E2**: *Terebra fijiensis*
IM_2007_30423, *Terebra succincta* IM_2007_30433, *Terebra textilis* IM_2007_30451,
Myurella lineaperlata IM_2007_30471, *Duplicaria* sp. 3 IM_2009_10151; **Clade E3**:
Terebra succincta IM_2007_16731, *Myurella orientalis* IM_2007_30515; **Clade E4**:
Terebra elata IM_2007_42111, *Terebra larvaeformis* IM_2007_42113, *Terebra puncturosa*
IM_2007_42116, *Terebra berryi* IM_2007_42144; **Clade E5**: *Myurella undulata*
IM_2007_30384, *Myurella paucistriata* IM_2007_30453, *Terebra* sp. 5 IM_2007_30946;
Clade F: *Euterebra fuscolutea* IM_2009_10112, *Duplicaria albofuscata* IM_2009_10162
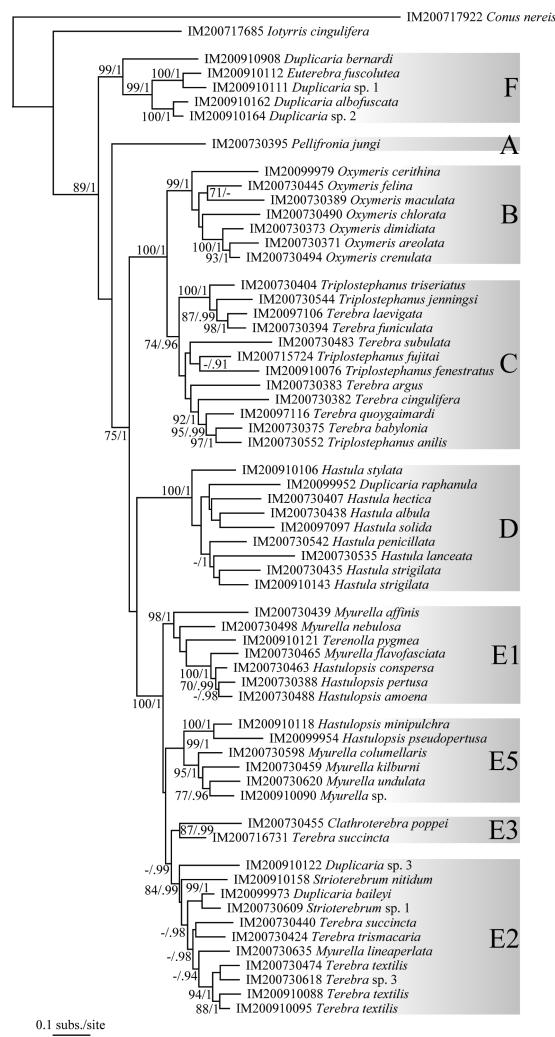
Figure 8.
Likelihood phylogenetic tree obtained with 63 specimens sequences for the COI, 12S, 16S and 28S genes.
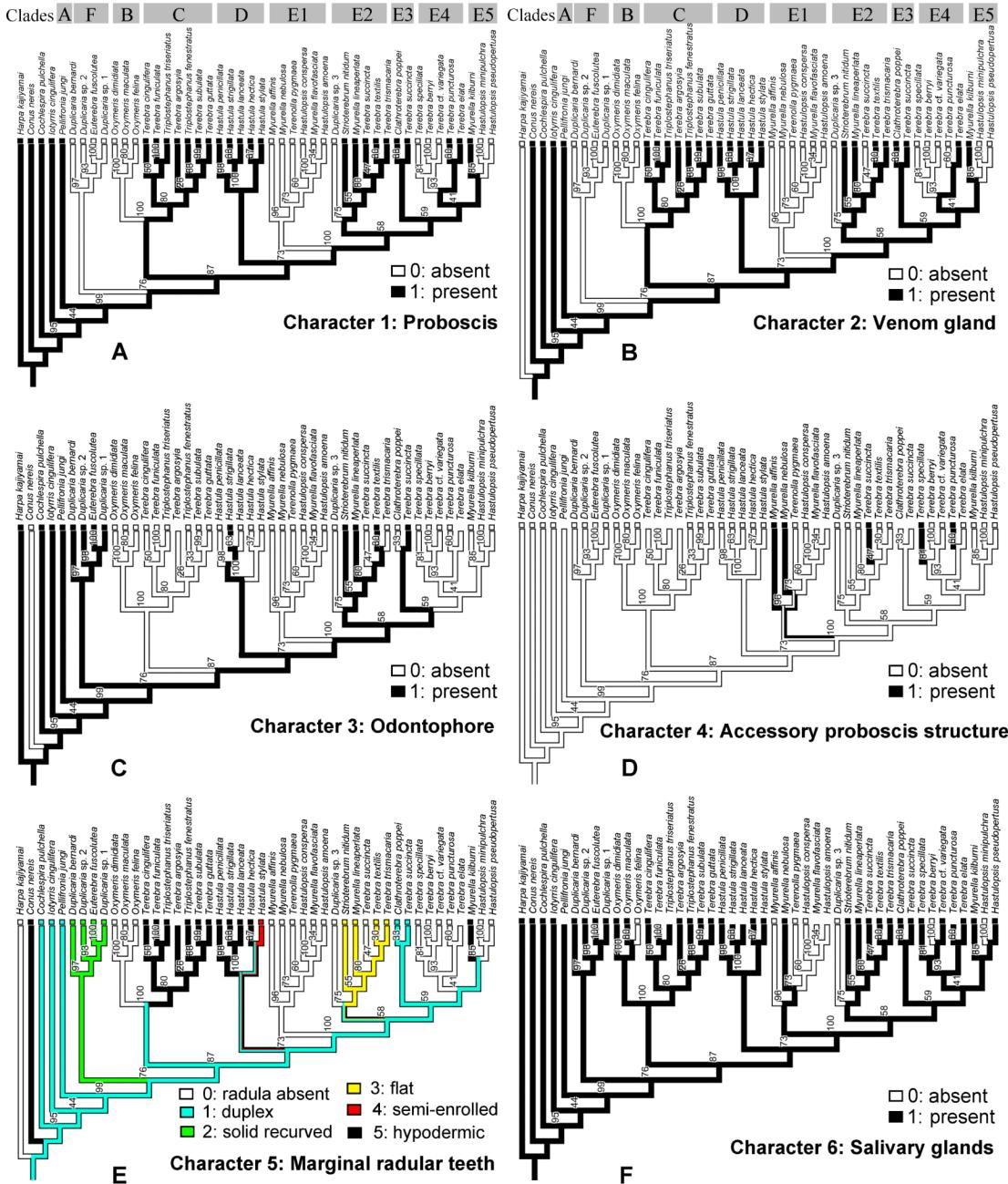
Figure 9.
Character mapping of the six characters presented in the Table 2. Bootstraps are shown for each node.

Table 1

List of specimens analysed

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2007_30391	*Clathroterebra*	*fortunei*	Solomon Islands	7°59′S, 157°33′E; 260	E1	CONO381-08	EU685535	EU685384	EU685675	
IM_2007_30401	*Clathroterebra*	*fortunei*	Philippines	9°39′N, 123°48′E; 255-268	E1	CONO284-08	EU685526	EU685371	EU685663	
IM_2007_30581	*Clathroterebra*	*fortunei*	Philippines	9°39′N, 123°48′E; 255-268	E1	XXX	XXX	XXX	XXX	
IM_2009_9971	*Clathroterebra*	*fortunei*	Mozambique	25°33′S, 33°13′E; 253-262	E1	XXX	XXX	XXX	XXX	
IM_2007_30455	*Clathroterebra*	*poppei*	Philippines	9°36.4′N, 123°53.8′E; 60-62	E3	CONO266-08	EU685523	EU685368	EU685660	XXX
IM_2007_30546	*Clathroterebra*	*poppei*	Vanuatu	15°36′S, 167°03′E; 86-118	E3	CONO482-08	EU685596	EU685455	EU685748	XXX
IM_2009_10162	*Duplicaria*	*albofuscata*	South Madagascar	25°03.7-8′S, 46°57.7′E; 3-4	F	XXX	XXX	XXX	XXX	XXX
IM_2009_10163	*Duplicaria*	*albofuscata*	South Madagascar	25°03.7-8′S, 46°57.7′E; 3-4	F	XXX	XXX		XXX	XXX
IM_2009_9973	*Duplicaria*	*baileyi*	South New-Caledonia	22°06′S, 167°03′E; 190-200	E2	XXX	XXX	XXX	XXX	XXX
IM_2009_9977	*Duplicaria*	*baileyi*	South New-Caledonia	22°06′S, 167°03′E; 190-200	E2	XXX	XXX	XXX	XXX	
IM_2009_10908	*Duplicaria*	*bernardi*	Australia	26°56′607″S, 153°23′8.13″E; 40	F	XXX	XXX		XXX	XXX
IM_2009_9951	*Duplicaria*	*raphanula*	North Madagascar	14°31′S, 47°25′E; 50-107	D	XXX	XXX	XXX	XXX	
IM_2009_9952	*Duplicaria*	*raphanula*	North Madagascar	14°31′S, 47°25′E; 50-107	D	XXX	XXX	XXX	XXX	XXX
IM_2009_10111	*Duplicaria*	sp. 1	South Madagascar	25°04.4-7′S, 46°55.3-56.3′E; 19-26	F	XXX	XXX		XXX	XXX
IM_2009_10117	*Duplicaria*	sp. 1	South Madagascar	25°04.4-7′S, 46°55.3-56.3′E; 19-26	F	XXX	XXX		XXX	
IM_2009_10113	*Duplicaria*	sp. 2	South Madagascar	25°03.7-8′S, 46°57.6-7′E; 2-7	F	XXX	XXX		XXX	
IM_2009_10164	*Duplicaria*	sp. 2	South Madagascar	25°03.7-8′S, 46°57.6-7′E; 2-7	F	XXX	XXX		XXX	XXX
IM_2007_30432	*Duplicaria*	sp. 3	Vanuatu	15°35.4′S, 166°58.7′E; 3-8	E2	XXX	XXX	XXX	XXX	
IM_2007_30466	*Duplicaria*	sp. 3	Vanuatu	15°35.4′S, 166°58.7′E; 3-8	E2	XXX	XXX	XXX		
IM_2009_10122	*Duplicaria*	sp. 3	South Madagascar	25°26.1-4′S, 44°55.2-6′E; 17-20	E2	XXX	XXX	XXX	XXX	XXX
IM_2009_10123	*Duplicaria*	sp. 3	South Madagascar	25°25.80-8′S, 44°55.7-8′E; 11-13	E2	XXX	XXX	XXX	XXX	
IM_2009_10124	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2′S, 44°51.1-7′E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10125	*Duplicaria*	sp. 3	South Madagascar	25°26.1-4′S, 44°55.2-6′E; 17-20	E2	XXX	XXX	XXX	XXX	
IM_2009_10126	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2′S, 44°51.1-7′E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10134	*Duplicaria*	sp. 3	South Madagascar	25°25.9′S, 44°55.1-2′E; 18-20	E2	XXX	XXX	XXX	XXX	
IM_2009_10136	*Duplicaria*	sp. 3	South Madagascar	25°26.1-4′S, 44°55.2-6′E; 17-20	E2	XXX	XXX	XXX	XXX	
IM_2009_10137	*Duplicaria*	sp. 3	South Madagascar	25°25.80-8′S, 44°55.7-8′E; 11-13	E2	XXX	XXX	XXX	XXX	

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2009_10138	*Duplicaria*	sp. 3	South Madagascar	25°23.1-2´S, 44°51.4-6´E; 20-23	E2	XXX	XXX	XXX	XXXe	
IM_2009_10139	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2´S, 44°51.1-7´E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10140	*Duplicaria*	sp. 3	South Madagascar	25°23.6-7´S, 44°53.3-5´E; 10-12	E2	XXX	XXX	XXX	XXX	
IM_2009_10141	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2´S, 44°51.1-7´E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10142	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2´S, 44°51.1-7´E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10145	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2´S, 44°51.1-7´E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10146	*Duplicaria*	sp. 3	South Madagascar	25°26.1-4´S, 44°55.2-6´E; 17-20	E2	XXX	XXX	XXX	XXX	
IM_2009_10148	*Duplicaria*	sp. 3	South Madagascar	25°26.7´S, 44°55.8´E; 15	E2	XXX	XXX	XXX	XXX	
IM_2009_10149	*Duplicaria*	sp. 3	South Madagascar	25°26.7´S, 44°55.8´E; 15	E2	XXX	XXX	XXX	XXX	
IM_2009_10150	*Duplicaria*	sp. 3	South Madagascar	25°26.7´S, 44°55.8´E; 15	E2	XXX	XXX	XXX	XXX	
IM_2009_10151	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2´S, 44°51.1-7´E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10152	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2´S, 44°51.1-7´E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10153	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2´S, 44°51.1-7´E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10154	*Duplicaria*	sp. 3	South Madagascar	25°24.1-2´S, 44°51.1-7´E; 24-26	E2	XXX	XXX	XXX	XXX	
IM_2009_10155	*Duplicaria*	sp. 3	South Madagascar	25°25.80-8´S, 44°55.7-8´E; 11-13	E2	XXX	XXX	XXX	XXX	
IM_2009_10156	*Duplicaria*	sp. 3	South Madagascar	25°25.80-8´S, 44°55.7-8´E; 11-13	E2	XXX	XXX	XXX	XXX	
IM_2009_10159	*Duplicaria*	sp. 3	South Madagascar	25°25.80-8´S, 44°55.7-8´E; 11-13	E2	XXX	XXX	XXX	XXX	
IM_2009_10160	*Duplicaria*	sp. 3	South Madagascar	25°26.1-4´S, 44°55.2-6´E; 17-20	E2	XXX	XXX	XXX	XXX	
IM_2009_10112	*Euterebra*	*fuscolutea*	South Madagascar	25°04.4-7´S, 46°55.3-56.3´E; 19-26	F	XXX	XXX	XXX	XXX	XXX
IM_2009_10114	*Euterebra*	*fuscolutea*	South Madagascar	25°03.7´S, 46°57.8´E; 7	F	XXX	XXX		XXX	
IM_2009_10127	*Euterebra*	*fuscolutea*	South Madagascar	25°26.0-1´S, 44°54.2-9´E; 21-24	F	XXX	XXX		XXX	
IM_2009_10133	*Euterebra*	*fuscolutea*	South Madagascar	25°26.8´S, 44°54.9´E; 27	F	XXX	XXX		XXX	
IM_2009_10147	*Euterebra*	*fuscolutea*	South Madagascar	25°25.9´S, 44°55.1-2´E; 18-20	F	XXX	XXX		XXX	
Museum of New Zealand	*Euterebra*	*tristis*	New-Zealand	35°13.20´S, 174°14.30´E, 2-8	F	XXX		HQ401611	HQ401677	
IM_2007_30437	*Hastula*	*albula*	Vanuatu	15°26.6´S, 167°15.2´E;	D	CONO477-08	EU685592	EU685451	EU685743	
IM_2007_30438	*Hastula*	*albula*	Vanuatu	15°26.6´S, 167°15.2´E;	D	CONO478-08	EU685593	EU685471	EU685744	XXX
IM_2007_30457	*Hastula*	*albula*	Vanuatu	15°22.6´S, 167°11.6´E;	D	CONO501-08	EU685612	EU685471	EU685764	
IM_2007_30630	*Hastula*	*albula*	Vanuatu	15°35.7´S, 166°59.3´E; 12	D	CONO511-08	EU685620	EU685480	EU685773	
IM_2009_7100	*Hastula*	*albula*	Mozambique	25°59.0´S, 32°54.5´E; 0	D	XXX	XXX	XXX	XXX	
IM_2009_7101	*Hastula*	*albula*	Mozambique	25°59.0´S, 32°54.5´E; 0	D	XXX	XXX	XXX	XXX	

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2009_7102	Hastula	albula	Mozambique	25°59.0′S, 32°54.5′E; 0	D	XXX	XXX	XXX		
IM_2009_7103	Hastula	albula	Mozambique	25°59.0′S, 32°54.5′E; 0	D	XXX	XXX	XXX	EU685655	XXX
IM_2007_30407	Hastula	hectica	Philippines	07°38.5′N, 008°25.1′W; 883	D	CONO260-08	EU685518	EU685363		
IM_2007_30426	Hastula	hectica	Vanuatu	15°35.4′S, 166°58.7′E; 3-8	D	CONO498-08	EU685610	EU685469	EU685762	XXX
IM_2009_10104	Hastula	hectica	South Madagascar	25°08.9′S, 46°45.4′E; 0-1	D	XXX	XXX	XXX	XXX	
IM_2009_11872	Hastula	hectica	Tahiti	17°30′28.28″S, 149°27′0.14″W; 0	D	XXX	XXX		XXX	
IM_2009_11873	Hastula	hectica	Tahiti	17°30′28.28″S, 149°27′0.14″W; 0	D	XXX	XXX		XXX	
IM_2009_11874	Hastula	hectica	Tahiti	17°30′28.28″S, 149°27′0.14″W; 0	D	XXX	XXX		XXX	
IM_2009_11875	Hastula	hectica	Tahiti	17°30′28.28″S, 149°27′0.14″W; 0	D	XXX	XXX		XXX	
IM_2007_30535	Hastula	lanceata	Philippines	9°33.0′N, 123°46.5′E; 8-14	D	CONO203-08	EU685495		EU685631	XXX
IM_2009_7089	Hastula	lanceata	Mozambique	25°59.0′S, 32°54.5′E; 0	D	XXX	XXX	XXX	XXX	
IM_2009_7090	Hastula	lanceata	Mozambique	25°59.0′S, 32°54.5′E; 0	D	XXX	XXX	XXX	XXX	
IM_2009_7091	Hastula	lanceata	Mozambique	25°59.0′S, 32°54.5′E; 0	D	XXX	XXX	XXX	XXX	
IM_2007_30540	Hastula	penicillata	Vanuatu	15°22.6′S, 167°11.6′E;	D	CONO503-08	EU685614	EU685473	EU685766	
IM_2007_30542	Hastula	penicillata	Vanuatu	15°22.6′S, 167°11.6′E;	D	CONO502-08	EU685613	EU685472	EU685765	XXX
IM_2007_30417	Hastula	solida	Vanuatu	15°26.6′S, 167°15.2′E;	D	XXX	XXX	EU685450	EU685742	
IM_2007_30549	Hastula	solida	Vanuatu	15°26.6′S, 167°15.2′E;	D	XXX		EU685449	EU685741	
IM_2007_30550	Hastula	solida	Vanuatu	15°26.6′S, 167°15.2′E;	D	CONO476-08	EU685591	EU685448	EU685740	
IM_2009_7096	Hastula	solida	Mozambique	25°59.0′S, 32°54.5′E; 0	D	XXX	XXX	XXX	XXX	
IM_2009_7097	Hastula	solida	Mozambique	25°59.0′S, 32°54.5′E; 0	D	XXX	XXX	XXX	XXX	XXX
IM_2009_7098	Hastula	solida	Mozambique	25°59.0′S, 32°54.5′E; 0	D	XXX	XXX	XXX	XXX	
IM_2009_7099	Hastula	solida	Mozambique	25°59.0′S, 32°54.5′E; 0	D	XXX		XXX	XXX	
IM_2009_10110	Hastula	sp.	South Madagascar	25°03.7′S, 46°57.8′E; 7	D	XXX	XXX	XXX	XXX	
IM_2007_30416	Hastula	strigilata	Vanuatu	15°35.2′S, 167°59.4′E;	D	XXX	XXX	EU685435	EU685727	
IM_2007_30420	Hastula	strigilata	Vanuatu	15°35.2′S, 167°59.4′E;	D	XXX	XXX	EU685434	EU685726	
IM_2007_30435	Hastula	strigilata	Vanuatu	15°33.4′S, 167°12.4′E; 2-6	D	CONO466-08	EU685581	XXX	XXX	XXX
IM_2007_30607	Hastula	strigilata	Vanuatu	15°35.2′S, 167°59.4′E;	D	XXX	XXX	EU685433	EU685725	
IM_2007_30608	Hastula	strigilata	Vanuatu	15°35.2′S, 167°59.4′E;	D	CONO465-08	EU685580		EU685724	
IM_2009_10143	Hastula	strigilata	South Madagascar	25°23.6-7′S, 44°53.3-5′E; 10-12	D	XXX	XXX	XXX	XXX	XXX
IM_2009_10161	Hastula	strigilata	South Madagascar	25°08.9′S, 46°45.4′E; 0-1	D	XXX	XXX	XXX	XXX	XXX
IM_2009_10106	Hastula	stylata	South Madagascar	24°47.1′S, 47°11.9′E; 0-1	D	XXX	XXX	XXX	XXX	XXX

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2007_30488	*Hastulopsis*	*amoena*	Vanuatu	15°31.7′S, 167°09.4′E; 9-13	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10909	*Hastulopsis*	*amoena*	Australia	26°56′607″S, 153°23′813″E; 40	E1	XXX	XXX	XXX	XXX	
IM_2009_10910	*Hastulopsis*	*amoena*	Australia	26°56′607″S, 153°23′813″E; 40	E1	XXX	XXX	XXX	XXX	XXX
IM_2007_30463	*Hastulopsis*	*conspersa*	Vanuatu		E1	CONO445-08	EU685560	EU685411	EU685702	
IM_2007_30478	*Hastulopsis*	*conspersa*	Vanuatu		E1	CONO446-08	EU685561	EU685412	EU685703	
IM_2007_30619	*Hastulopsis*	*conspersa*	Vanuatu	15°33.1′S, 167°12.2′E; 3-40	E1	CONO437-08	EU685552	EU685403	EU685694	
IM_2007_30623	*Hastulopsis*	*conspersa*	Vanuatu		E1	CONO443-08	EU685558	EU685409	EU685700	
IM_2007_30624	*Hastulopsis*	*conspersa*	Vanuatu	15°33.4′S, 167°12.4′E; 2-6	E1	CONO518-08	EU685623	EU685483	EU685776	
IM_2007_30442	*Hastulopsis*	*mindanaoensis*	Philippines		E1	CONO207-08	EU685499	EU685344	EU685635	
IM_2009_10118	*Hastulopsis*	*minipulchra*	South Madagascar	25°30.2′S, 45°46.3′E; 41-42	E5	XXX	XXX	XXX	XXX	XXX
IM_2009_10119	*Hastulopsis*	*minipulchra*	South Madagascar	25°28.6′S, 44°56.8′E; 12	E5	XXX	XXX	XXX	XXX	
IM_2009_10120	*Hastulopsis*	*minipulchra*	South Madagascar	25°22.8-23.7′S, 44°51.1′E; 18-21	E5	XXX	XXX	XXX	XXX	
IM_2009_10128	*Hastulopsis*	*minipulchra*	South Madagascar	25°22.8-23.7′S, 44°51.1′E; 18-21	E5	XXX	XXX	XXX	XXX	
IM_2009_10129	*Hastulopsis*	*minipulchra*	South Madagascar	25°28.6′S, 44°56.8′E; 12	E5	XXX	XXX	XXX	XXX	
IM_2009_10131	*Hastulopsis*	*minipulchra*	South Madagascar	25°22.8-23.7′S, 44°51.1′E; 18-21	E5	XXX	XXX	XXX	XXX	
IM_2007_30388	*Hastulopsis*	*pertusa*	Vanuatu	13°25′S, 47°57′E; 71-158	E1	CONO447-08	EU685562	EU685413	EU685704	XXX
IM_2007_30392	*Hastulopsis*	*pertusa*	Vanuatu		E1	CONO448-08	EU685563	EU685414	EU685705	
IM_2007_30480	*Hastulopsis*	*pertusa*	Vanuatu		E1	CONO444-08	EU685559	EU685410	EU685701	
IM_2009_10080	*Hastulopsis*	*pseudopertusa*	North Madagascar	13°25′S, 47°57′E; 71-158	E5	XXX	XXX		XXX	
IM_2009_9954	*Hastulopsis*	*pseudopertusa*	North Madagascar		E5	XXX	XXX	XXX	XXX	XXX
IM_2007_30412	*Myurella*	*affinis*	Vanuatu	15°26.6′S, 167°15.2′E;	E1	CONO468-08	EU685583	EU685437	EU685729	
IM_2007_30414	*Myurella*	*affinis*	Vanuatu	15°26.6′S, 167°15.2′E;	E1	CONO467-08	EU685582	EU685436	EU685728	
IM_2007_30415	*Myurella*	*affinis*	Vanuatu	9°32.8′N, 123°45.9′E; 2	E1	XXX	XXX	XXX	XXX	
IM_2007_30430	*Myurella*	*affinis*	Philippines	9°37.4′N, 123°54.5′E; 6-8	E1	CONO214-08	EU685506	EU685351	EU685642	XXX
IM_2007_30439	*Myurella*	*affinis*	Philippines	08°36.7′N, 079°00′W; 28	E1	CONO218-08	EU685508	EU685353	EU685644	
IM_2007_30452	*Myurella*	*affinis*	Philippines	9°37.4′N, 123°54.5′E; 6-8	E1	CONO215-08	EU685507	EU685352	EU685643	
IM_2007_30460	*Myurella*	*affinis*	Philippines	9°35.7′N, 123°44.4′E; 0-2	E1	CONO239-08	EU685512	EU685356	EU685648	
IM_2007_30481	*Myurella*	*affinis*	Philippines	9°35.7′N, 123°44.4′E; 0-2	E1	CONO283-08	EU685525	EU685370	EU685662	
IM_2007_30529	*Myurella*	*affinis*	Philippines	08°36.7′N, 079°00′W; 28	E1	XXX	XXX	XXX		
IM_2007_30541	*Myurella*	*affinis*	Vanuatu	15°36.8′S, 167°08.5′E; 1-42	E1	CONO485-08	EU685599	EU685458	EU685751	
IM_2007_30551	*Myurella*	*affinis*	Vanuatu	9°32.8′N, 123°45.9′E; 2	E1	XXX	XXX	XXX	XXX	

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2007_30594	*Myurella*	*affinis*	Vanuatu	9°32.8′N, 123°45.9′E; 2	E1	CONO475-08	EU685590	EU685447	EU685739	
IM_2009_10021	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10022	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10056	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10058	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10059	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10060	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10061	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10062	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10063	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10064	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10065	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_10066	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX		XXX	XXX
IM_2009_10067	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_7092	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_7093	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_7094	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2009_7095	*Myurella*	*affinis*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	XXX
IM_2007_30510	*Myurella*	*columellaris*	Philippines	9°35.7′N, 123°44.4′E; 0-2	E5	CONO237-08	EU685510		EU685646	
IM_2007_30598	*Myurella*	*columellaris*	Vanuatu	15°26.6′S, 167°15.2′E;	E5	CONO469-08	EU685584	EU685438	EU685730	XXX
IM_2009_10020	*Myurella*	*columellaris*	Mozambique	25°59.0′S, 32°54.5′E; 0	E5	XXX	XXX	XXX	XXX	
IM_2007_30465	*Myurella*	*flavofasciata*	Philippines	9°29.4′N, 123°56.0′E; 15-20	E1	CONO247-08	EU685515	EU685360	EU685652	XXX
IM_2009_7436	*Myurella*	*flavofasciata*	Mozambique	25°59.0′S, 32°54.5′E; 0	E1	XXX	XXX	XXX	XXX	
IM_2007_30459	*Myurella*	*kilburni*	Philippines	9°35.7′N, 123°44.4′E; 0-2	E5	CONO238-08	EU685511	EU685355	EU685647	XXX
IM_2007_30461	*Myurella*	*kilburni*	Vanuatu	15°42.7′S, 167°15.1′E; 2-3	E5	CONO491-08	EU685604	EU685463	EU685756	
IM_2007_30471	*Myurella*	*lineaperlata*	Vanuatu	15°29′S, 167°14.9′E; 2-4	E2	CONO461-08	EU685576	EU685429	EU685720	
IM_2007_30612	*Myurella*	*lineaperlata*	Vanuatu	15°29′S, 167°14.9′E; 2-4	E2	CONO460-08	EU685575	EU685428	EU685719	
IM_2007_30635	*Myurella*	*lineaperlata*	Vanuatu	15°33.4′S, 167°12.4′E; 2-6	E2	CONO519-08	EU685624	EU685484	EU685777	XXX
IM_2007_30378	*Myurella*	*nebulosa*	Vanuatu	15°33.1′S, 167°12.2′E; 3-40	E1	CONO407-08		EU685392	EU685683	
IM_2007_30408	*Myurella*	*nebulosa*	Philippines	9°29.4′N, 123°56.0′E; 15-20	E1	CONO248-08	EU685516	EU685361	EU685653	
IM_2007_30498	*Myurella*	*nebulosa*	Vanuatu	15°27.6′S, 167°14.3′E; 6-35	E1	CONO479-08	EU685594	EU685453	EU685746	XXX

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2007_30567	*Myurella*	*nebulosa*	Vanuatu	15°34.7′ S, 167°13.8′ E; 14-25	E1	CONO459-08	EU685574	EU685426	EU685717	
IM_2009_10098	*Myurella*	*nebulosa*	Mozambique	26°12′ S, 35°03′ E; 87-90	E1	XXX	XXX	XXX	XXX	
IM_2009_10099	*Myurella*	*nebulosa*	Mozambique	26°12′ S, 35°03′ E; 87-90	E1	XXX	XXX	XXX	XXX	
IM_2009_7437	*Myurella*	*nebulosa*	Mozambique	26°12′ S, 35°03′ E; 87-90	E1	XXX	XXX	XXX	XXX	
IM_2009_7438	*Myurella*	*nebulosa*	Mozambique	26°12′ S, 35°03′ E; 87-90	E1	XXX	XXX	XXX	XXX	
IM_2009_7439	*Myurella*	*nebulosa*	Mozambique	26°12′ S, 35°03′ E; 87-90	E1	XXX	XXX	XXX	XXX	
IM_2007_30515	*Myurella*	*orientalis*	Chesterfield Islands	20°06′ S, 160°23′ E; 280-304	E3	CONO202-08	EU685494	EU685340	EU685630	
IM_2007_30524	*Myurella*	*orientalis*	Solomon Islands	9°07′ S, 158°21′ E; 267-329	E3	XXX	XXX	XXX	XXX	XXX
IM_2007_30530	*Myurella*	*orientalis*	Chesterfield Islands	20°29′ S, 158°42′ E; 197-230	E3	CONO201-08	EU685493	EU685339	EU685629	
IM_2009_9974	*Myurella*	*orientalis*	North New-Caledonia	18°02′ S, 163°04′ E; 320-337	E3	XXX	XXX	XXX	XXX	
IM_2007_30453	*Myurella*	*paucistriata*	Vanuatu	15°29.6′ S, 167°14.9′ E; 2-5	E5	CONO480-08	EU685595	EU685454	EU685747	
IM_2007_30513	*Myurella*	sp.	Philippines	9°36.4′ N, 123°53.8′ E; 60-62	E5	CONO265-08	EU685522	EU685367	EU685659	
IM_2009_10090	*Myurella*	sp.	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	E5	XXX	XXX	XXX	XXX	XXX
IM_2009_10091	*Myurella*	sp.	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	E5	XXX	XXX	XXX	XXX	
IM_2009_10092	*Myurella*	sp.	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	E5	XXX	XXX	XXX	XXX	
IM_2009_10094	*Myurella*	sp.	North Madagascar	15° 30,15′ S, 46° 4,3′ E; 29-36	E5	XXX	XXX	XXX	XXX	
IM_2009_10096	*Myurella*	sp.	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	E5	XXX	XXX	XXX	XXX	
IM_2009_10097	*Myurella*	sp.	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	E5	XXX	XXX	XXX	XXX	
IM_2009_7124	*Myurella*	sp.	Mozambique	25°59.0′ S, 32°54.5′ E; 0	E5	XXX	XXX	XXX	XXX	
IM_2009_7125	*Myurella*	sp.	Mozambique	25°59.0′ S, 32°54.5′ E; 0	E5	XXX	XXX	XXX	XXX	
IM_2009_7326	*Myurella*	sp.	Mozambique	25°59.0′ S, 32°54.5′ E; 0	E5	XXX		XXX	XXX	
IM_2007_30384	*Myurella*	*undulata*	Vanuatu	15°26.6′ S, 167°15.2′ E;	E5	CONO472-08	EU685587	EU685441	EU685733	
IM_2007_30570	*Myurella*	*undulata*	Vanuatu	15°38.1′ S, 167°05.9′ E;	E5	CONO494-08	EU685606	EU685465	EU685758	
IM_2007_30620	*Myurella*	*undulata*	Vanuatu	15°31.3′ S, 167°10.4′ E; 3-18	E5	CONO440-08	EU685555	EU685406	EU685697	XXX
IM_2007_30628	*Myurella*	*undulata*	Vanuatu	15°33.1′ S, 167°12.2′ E; 3-40	E5	CONO409-08	EU685543	EU685394	EU685685	
IM_2007_30629	*Myurella*	*undulata*	Vanuatu	15°33.1′ S, 167°12.2′ E; 3-40	E5	CONO408-08	EU685542	EU685393	EU685684	
IM_2009_7115	*Myurella*	*undulata*	Mozambique	25°59.0′ S, 32°54.5′ E; 0	E5	XXX	XXX	XXX	XXX	
IM_2007_30371	*Oxymeris*	*areolata*	Vanuatu	15°28.7′ S, 167°15.2′ E; 19	B	CONO406-08	JN589001	HQ401637	HQ401700	XXX
IM_2007_30587	*Oxymeris*	*areolata*	Philippines	9°37.4′ N, 123°46.9′ E; 3-20	B	CONO241-08	EU685513	EU685357	EU685649	
IM_2009_10013	*Oxymeris*	*cerithina*	Mozambique	25°59.0′ S, 32°54.5′ E; 0	B	XXX	XXX	XXX	XXX	
IM_2009_10014	*Oxymeris*	*cerithina*	Mozambique	25°59.0′ S, 32°54.5′ E; 0	B	XXX	XXX	XXX	XXX	

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2009_10015	*Oxymeris*	*cerithina*	Mozambique	25°59.0′S, 32°54.5′E; 0	B	XXX	XXX	XXX	XXX	
IM_2009_7083	*Oxymeris*	*cerithina*	Mozambique	25°59.0′S, 32°54.5′E; 0	B	XXX	XXX	XXX	XXX	
IM_2009_7084	*Oxymeris*	*cerithina*	Mozambique	25°59.0′S, 32°54.5′E; 0	B	XXX	XXX	XXX	XXX	
IM_2009_7085	*Oxymeris*	*cerithina*	Mozambique	25°59.0′S, 32°54.5′E; 0	B	XXX	XXX	XXX		
IM_2009_7086	*Oxymeris*	*cerithina*	Mozambique	25°59.0′S, 32°54.5′E; 0	B	XXX	XXX	XXX	XXX	
IM_2009_9979	*Oxymeris*	*cerithina*	Mozambique	25°59.0′S, 32°54.5′E; 0	B	XXX	XXX	XXX	XXX	XXX
IM_2007_30490	*Oxymeris*	*chlorata*	Vanuatu	15°22.6′S, 167°11.6′E;	B	CONO504-08	EU685615	EU685474	EU685767	XXX
IM_2007_30377	*Oxymeris*	*crenulata*	Vanuatu	15°34.4′S, 167°13.1′E; 9	B	CONO442-08	EU685557	EU685408	EU685699	
IM_2007_30494	*Oxymeris*	*crenulata*	Vanuatu	15°34.4′S, 167°13.1′E; 9	B	CONO441-08	EU685556	EU685407	EU685698	XXX
IM_2007_30372	*Oxymeris*	*dimidiata*	Vanuatu	15°32.5′S, 167°10.5′E; 5-10	B	CONO487-08	EU685601	EU685460	EU685753	
IM_2007_30373	*Oxymeris*	*dimidiata*	Vanuatu		B	CONO449-08	EU685564	EU685415	EU685706	XXX
IM_2007_30379	*Oxymeris*	*dimidiata*	Vanuatu	15°32.5′S, 167°10.5′E; 5-10	B	CONO486-08	EU685600	EU685459	EU685752	
IM_2007_30381	*Oxymeris*	*dimidiata*	Vanuatu	15°35.4′S, 166°59.7′E; 3-37	B	CONO510-08	EU685619	EU685479	EU685772	
IM_2007_30428	*Oxymeris*	*dimidiata*	Vanuatu	15°38.1′S, 167°05.9′E;	B	CONO495-08	EU685607	EU685466	EU685759	
IM_2009_7087	*Oxymeris*	*dimidiata*	Mozambique	25°59.0′S, 32°54.5′E; 0	B	XXX	XXX	XXX	XXX	
IM_2009_7088	*Oxymeris*	*dimidiata*	Mozambique	25°59.0′S, 32°54.5′E; 0	B	XXX	XXX	XXX	XXX	
IM_2007_30443	*Oxymeris*	*felina*	Philippines	9°37.4′N, 123°54.5′E; 6-8	B	CONO208-08	EU685500	EU685345	EU685636	
IM_2007_30445	*Oxymeris*	*felina*	Philippines	9°37.4′N, 123°54.5′E; 6-8	B	CONO210-08	EU685502	EU685347	EU685638	XXX
IM_2007_30370	*Oxymeris*	*maculata*	Philippines	9°37.4′N, 123°46.9′E; 3-20	B	CONO204-08	EU685496	EU685341	EU685632	
IM_2007_30389	*Oxymeris*	*maculata*	Vanuatu	15°28.7′S, 167°15.2′E; 19	B	CONO405-08	EU685541	EU685391	EU685682	XXX
IM_2007_42093	*Oxymeris*	*strigata*	Panama	08°11.8′N, 078°57.1′W; 24	B	CONO974-09	FJ707455.1	FJ707388.1	FJ707422.1	
IM_2007_42105	*Oxymeris*	*strigata*	Panama	08°11.8′N, 078°57.5′W; 22	B	CONO979-09	FJ707460.1	FJ707393.1	FJ707428.1	
IM_2007_42137	*Oxymeris*	*strigata*	Panama	08°14.7′N, 079°05.6′W; 18	B	CONO990-09	FJ707471.1	FJ707404.1	FJ707439.1	
IM_2007_30395	*Pellifronia*	*jungi*	Philippines	9°38′N, 123°40′E; 606-631	A	CONO292-08	EU685530	EU685375	EU685666	XXX
IM_2007_30501	*Pellifronia*	*jungi*	Solomon Islands	8°26′S, 159°26′E; 543-593	A	XXX	XXX	EU685385	EU685676	
IM_2007_30539	*Pellifronia*	*jungi*	Vanuatu	15°44′S, 167°03′E; 618-722	A	XXX	XXX	XXX	XXX	
IM_2007_30584	*Pellifronia*	*jungi*	Philippines	9°34′N, 123°38′E; 729-733	A	CONO347-08	EU685532	EU685380	EU685671	
IM_2007_30450	*Strioterebrum*	*brunneobandatum*	Philippines	9°43′N, 123°49′E; 123-135	E1	CONO256-08	EU685517	EU685362	EU685654	
IM_2007_30522	*Strioterebrum*	*brunneobandatum*	Solomon Islands	8°38′S, 157°22′E; 195-197	E1	XXX	XXX	XXX		
IM_2007_30454	*Strioterebrum*	*dedonderi*	Philippines	9°36.4′N, 123°53.8′E; 60-62	E1	CONO263-08	EU685521	EU685366	EU685658	
IM_2007_30425	*Strioterebrum*	*nitidum*	Vanuatu	15°35.4′S, 166°58.7′E; 3-8	E2	CONO506-08	EU685616	EU685475	EU685768	

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2007_30473	*Strioterebrum*	*nitidum*	Vanuatu	15°35.4′ S, 166°58.7′E; 3-8	E2	CONO507-08	EU685617	EU685476	EU685769	
IM_2007_30614	*Strioterebrum*	*nitidum*	Vanuatu	15°31.7′ S, 167°09.4′ E; 9-13	E2	XXX		EU685424	EU685715	
IM_2009_10157	*Strioterebrum*	*nitidum*	South Madagascar	25°26.1-4′ S, 44°55.2-6′ E; 17-20	E2	XXX	XXX	XXX	XXX	
IM_2009_10158	*Strioterebrum*	*nitidum*	South Madagascar	25°24.1-2′ S, 44°51.1-7′E; 24-26	E2	XXX	XXX	XXX	XXX	XXX
IM_2009_7114	*Strioterebrum*	*nitidum*	Mozambique	25°59.0′ S, 32°54.5′ E; 0	E2	XXX	XXX		XXX	
IM_2007_30610	*Strioterebrum*	*plumbeum*	Vanuatu	15°35.2′ S, 167°59.4′ E;	E2	CONO463-08	EU685578	EU685431	EU685722	
IM_2007_30469	*Strioterebrum*	*plumbeum*	Vanuatu	15°31.7′ S, 167°09.4′ E; 9-13	E2	CONO456-08	EU685571	EU685422	EU685713	
IM_2007_30558	*Strioterebrum*	*plumbeum*	Vanuatu	15°31.7′ S, 167°09.4′ E; 9-13	E2	CONO455-08	EU685570	EU685421	EU685712	
IM_2007_30609	*Strioterebrum*	sp. 1	Vanuatu	15°35.2′ S, 167°59.4′ E;	E2	CONO464-08	EU685579	EU685432	EU685723	XXX
IM_2007_30611	*Strioterebrum*	sp. 2	Vanuatu	15°35.2′ S, 167°59.4′ E;	E2	CONO462-08	EU685577	EU685430	EU685721	
IM_2007_30543	*Strioterebrum*	sp. 3	Vanuatu	15°35.4′ S, 166°58.7′E; 3-8	E2	CONO499-08	EU685611	EU685470	EU685763	
IM_2007_42068	*Terebra*	*argosyia*	Panama	08°37.2′N, 079°01.1′W; 25	C	CONO962-09	FJ707443.1	FJ707376.1	FJ707408.1	
IM_2007_42069	*Terebra*	*argosyia*	Panama	08°37.2′N, 079°01.1′W; 25	C	CONO963-09	FJ707444.1	FJ707377.1	FJ707409.1	
IM_2007_42072	*Terebra*	*argosyia*	Panama	08°15.6′N, 078°51.6′W; 24	C	CONO964-09	FJ707445.1	FJ707378.1	FJ707411.1	
IM_2007_42073	*Terebra*	*argosyia*	Panama	08°15.6′N, 078°51.6′W; 24	C	CONO965-09	FJ707446.1	FJ707379.1	FJ707412.1	
IM_2007_42087	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.1′W; 21	C	CONO969-09	FJ707450.1	FJ707383.1	FJ707417.1	
IM_2007_42089	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.1′W; 21	C	CONO970-09	FJ707451.1	FJ707384.1	FJ707418.1	
IM_2007_42090	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.1′W; 21	C	CONO971-09	FJ707452.1	FJ707385.1	FJ707419.1	
IM_2007_42091	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.1′W; 21	C	CONO972-09	FJ707453.1	FJ707386.1	FJ707420.1	
IM_2007_42092	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.1′W; 21	C	CONO973-09	FJ707454.1	FJ707387.1	FJ707421.1	
IM_2007_42099	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.5′W; 24	C	CONO975-09	FJ707456.1	FJ707389.1	FJ707423.1	
IM_2007_42100	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.5′W; 24	C	CONO976-09	FJ707457.1	FJ707390.1	FJ707424.1	
IM_2007_42103	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.5′W; 22	C	CONO977-09	FJ707458.1	FJ707391.1	FJ707426.1	
IM_2007_42104	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.5′W; 22	C	CONO978-09	FJ707459.1	FJ707392.1	FJ707427.1	
IM_2007_42119	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.5′W; 22	C	CONO981-09	FJ707462.1	FJ707395.1	FJ707430.1	
IM_2007_42122	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.5′W; 22	C	CONO984-09	FJ707465.1	FJ707398.1	FJ707433.1	
IM_2007_42123	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.5′W; 22	C	CONO985-09	FJ707466.1	FJ707399.1	FJ707434.1	
IM_2007_42124	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.5′W; 22	C	CONO986-09	FJ707467.1	FJ707400.1	FJ707435.1	
IM_2007_42125	*Terebra*	*argosyia*	Panama	08°11.8′N, 078°57.5′W; 22	C	CONO987-09	FJ707468.1	FJ707401.1	FJ707436.1	
IM_2007_30383	*Terebra*	*argus*	Vanuatu	15°26.6′ S, 167°15.2′E;	C	XXX	XXX	EU685442	EU685734	XXX
IM_2007_30375	*Terebra*	*babylonia*	Vanuatu	9°32.8′N, 123°45.9′E; 2	C	XXX	XXX	EU685445	EU685737	XXX

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2007_30380	*Terebra*	*babylonia*	Vanuatu	9°32.8′N, 123°45.9′E; 2	C	CONO474-08	EU685589	EU685446	EU685738	
IM_2007_42144	*Terebra*	*berryi*	Panama	08°14.7′N, 079°05.6′W; 18	E4	XXX	XXX	XXX	XXX	
IM_2007_42167	*Terebra*	*berryi*	Panama	08°33′N, 079°04′W; 19	E4	XXX	XXX	XXX	XXX	
IM_2007_42097	*Terebra*	*cf. variegata*	Panama	08°11.8′N, 078°57.1′W; 26	E4	XXX	XXX	XXX	XXX	
IM_2007_42128	*Terebra*	*cf. variegata*	Panama	08°14.9′N, 079°05.7′W; 14	E4	XXX	XXX	XXX	XXX	
IM_2007_42133	*Terebra*	*cf. variegata*	Panama	08°14.8′N, 079°05.9′W; 13	E4	XXX	XXX	XXX	XXX	
IM_2007_42135	*Terebra*	*cf. variegata*	Panama	08°14.8′N, 079°05.9′W; 13	E4	XXX	XXX	XXX	XXX	
IM_2007_42146	*Terebra*	*cf. variegata*	Panama	08°14.7′N, 079°05.6′W; 18	E4	XXX	XXX	XXX	XXX	
IM_2007_42158	*Terebra*	*cf. variegata*	Panama	08°24.5′N, 079°04.7′W; 18	E4	XXX	XXX	XXX	XXX	
IM_2007_16735	*Terebra*	*cingulifera*	Philippines	9°36′N, 123°44′E; 382-434	C	CONO340-08	EU015735	EU685379	EU685670	EU015620
IM_2007_30382	*Terebra*	*cingulifera*	Vanuatu	15°26.6′S, 167°15.2′E;	C	XXX	XXX	EU685443	EU685735	XXX
IM_2007_30484	*Terebra*	*cingulifera*	Solomon Islands	8°38′S, 157°22′E; 195-197	C	XXX	XXX	XXX	XXX	
IM_2007_30485	*Terebra*	*cingulifera*	Vanuatu	15°32.5′S, 167°10.5′E; 5-10	C	CONO490-08	EU685603	EU685462	EU685755	
IM_2007_30487	*Terebra*	*cingulifera*	Solomon Islands	8°40′S, 157°23′E; 214-243	C	CONO382-08	EU685536	EU685386	EU685677	
IM_2007_30562	*Terebra*	*cingulifera*	Philippines	16°04′N, 121°57′E; 98-107	C	XXX	XXX		XXX	
IM_2007_30563	*Terebra*	*cingulifera*	Philippines	16°05.85′N, 121°58.85′E; 83	C	XXX	XXX		XXX	
IM_2007_30564	*Terebra*	*cingulifera*	Philippines	15°54′N, 121°42′E; 125-198	C	XXX	XXX		XXX	
IM_2007_30576	*Terebra*	*cingulifera*	Vanuatu	15°36.8′S, 167°08.7′E; 3-36	C	XXX	XXX		XXX	
IM_2009_10171	*Terebra*	*cingulifera*	South Madagascar	25°04.7′S, 47°03.4′E; 64-65	C	XXX	XXX	XXX	XXX	
IM_2007_42095	*Terebra*	*elata*	Panama	08°11.8′N, 078°57.1′W; 26	E4	XXX	XXX	XXX	XXX	
IM_2007_42096	*Terebra*	*elata*	Panama	08°11.8′N, 078°57.1′W; 26	E4	XXX	XXX	XXX	XXX	
IM_2007_42111	*Terebra*	*elata*	Panama	08°11.8′N, 078°57.5′W; 22	E4	XXX	XXX	XXX	XXX	
IM_2007_42127	*Terebra*	*elata*	Panama	08°11.8′N, 078°57.5′W; 22	E4	XXX	XXX	XXX	XXX	
IM_2007_42147	*Terebra*	*elata*	Panama	08°14.7′N, 079°05.4′W; 18	E4	XXX	XXX	XXX	XXX	
IM_2007_42155	*Terebra*	*elata*	Panama	08°24.5′N, 079°04.7′W; 18	E4	XXX	XXX	XXX	XXX	
IM_2007_42162	*Terebra*	*elata*	Panama	08°31.2′N, 079°06.8′W; 32	E4	XXX	XXX	XXX	XXX	
IM_2007_42163	*Terebra*	*elata*	Panama	08°31.2′N, 079°06.8′W; 32	E4	XXX	XXX	XXX	XXX	
IM_2007_30423	*Terebra*	*fijiensis*	Vanuatu	15°33′S, 167°16.7′E; 92	E2	CONO520-08	EU685625	EU685485	EU685778	
IM_2007_42152	*Terebra*	*formosa*	Panama	08°16.9′N, 079°02.7′W; 39	C	CONO991-09	FJ707472.1	FJ707405.1	FJ707440.1	
IM_2007_30394	*Terebra*	*funiculata*	Vanuatu		C	CONO450-08	EU685565	EU685416	EU685707	
IM_2009_7108	*Terebra*	*funiculata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	XXX

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MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2009_7109	*Terebra*	*funiculata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_7110	*Terebra*	*funiculata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2007_30376	*Terebra*	*guttata*	Vanuatu	15°33.1′S, 167°12.2′E; 3-40	C	CONO439-08	EU685554	EU685405	EU685696	
IM_2007_30387	*Terebra*	*guttata*	Vanuatu	15°33.1′S, 167°12.2′E; 3-40	C	CONO438-08	EU685553	EU685404	EU685695	
IM_2007_30431	*Terebra*	*laevigata*	Philippines	9°36.8′N, 123°52.2′E;	C	CONO262-08	EU685520	EU685365	EU685657	
IM_2007_30573	*Terebra*	*laevigata*	Vanuatu	15°29.6′S, 167°14.9′E; 2-5	C	XXX	XXX	XXX	XXX	
IM_2007_30597	*Terebra*	*laevigata*	Vanuatu	15°26.6′S, 167°15.2′E;	C	CONO471-08	EU685586	EU685440	EU685732	
IM_2007_30603	*Terebra*	*laevigata*	Vanuatu	15°43.4′S, 167°15.0′E; 6	C	CONO484-08	EU685598	EU685457	EU685750	
IM_2007_30613	*Terebra*	*laevigata*	Vanuatu	15°31.7′S, 167°09.4′E; 9-13	C	CONO458-08	EU685573	EU685425	EU685716	
IM_2007_30632	*Terebra*	*laevigata*	Vanuatu	15°31.7′S, 167°09.4′E; 9-13	C	CONO457-08	EU685572	EU685423	EU685714	
IM_2009_10016	*Terebra*	*laevigata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_10017	*Terebra*	*laevigata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_10018	*Terebra*	*laevigata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_10019	*Terebra*	*laevigata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_7104	*Terebra*	*laevigata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_7105	*Terebra*	*laevigata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_7106	*Terebra*	*laevigata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	XXX
IM_2009_7107	*Terebra*	*laevigata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_9947	*Terebra*	*laevigata*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2007_42083	*Terebra*	*larvaeformis*	Panama	08°11.8′N, 078°57.1′W; 21	E4	XXX	XXX	XXX	XXX	
IM_2007_42106	*Terebra*	*larvaeformis*	Panama	08°11.8′N, 078°57.5′W; 22	E4	XXX	XXX	XXX	XXX	
IM_2007_42113	*Terebra*	*larvaeformis*	Panama	08°11.8′N, 078°57.5′W; 22	E4	XXX	XXX	XXX	XXX	
IM_2007_42149	*Terebra*	*larvaeformis*	Panama	08°14.7′N, 079°05.4′W; 18	E4	XXX	XXX	XXX	XXX	
IM_2007_42131	*Terebra*	*ornata*	Panama	08°16.9′N, 079°02.7′W; 39	C	CONO988-09	FJ707469.1	FJ707402.1	FJ707437.1	
IM_2007_30374	*Terebra*	*punctatostriata*	Vanuatu	15°31.4′S, 167°09.7′E; 4-18	C	XXX		EU685427	EU685718	
IM_2007_42070	*Terebra*	*puncturosa*	Panama	08°15.6′N, 078°51.6′W; 24	E4	XXX	XXX	XXX	XXX	
IM_2007_42081	*Terebra*	*puncturosa*	Panama	08°11.8′N, 078°57.1′W; 21	E4	XXX	XXX	XXX	XXX	
IM_2007_42116	*Terebra*	*puncturosa*	Panama	08°11.8′N, 078°57.5′W; 22	E4	XXX	XXX	XXX	XXX	
IM_2007_42171	*Terebra*	*puncturosa*	Panama	08°33′N, 079°04′W; 19	E4	XXX	XXX	XXX	XXX	
IM_2009_7116	*Terebra*	*quoygaimardi*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_7118	*Terebra*	*quoygaimardi*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	XXX

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2009_9946	*Terebra*	*quoygaimardi*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2007_30464	*Terebra*	sp. 1	Philippines	9°35.3′N, 123°52.2′E; 84-87	E2	CONO206-08	EU685498	EU685343	EU685634	
IM_2007_30516	*Terebra*	sp. 2	Chesterfield Islands	24°46′S, 159°43′E; 400-418	E3	XXX	XXX	XXX	XXX	
IM_2007_30617	*Terebra*	sp. 3	Vanuatu	15°31.7′S, 167°09.7′E; 18-21	E2	CONO430-08	EU685549	EU685400	EU685691	
IM_2007_30618	*Terebra*	sp. 3	Vanuatu	15°31.7′S, 167°09.7′E; 18-21	E2	CONO431-08	EU685550	EU685401	EU685692	XXX
IM_2007_30633	*Terebra*	sp. 4	Solomon Islands	9°07′ S, 158°21′ E; 267-329	E3	XXX	XXX	XXX	XXX	
IM_2007_30946	*Terebra*	sp. 5	Chesterfield Islands	20°21′S, 158°46′E; 345-351	E5	XXX		XXX	XXX	
IM_2007_42151	*Terebra*	*specillata*	Panama	08°16.9′N, 079°02.7′W; 39	E4	XXX	XXX	XXX	XXX	
IM_2007_42154	*Terebra*	*specillata*	Panama	08°24.5′N, 079°04.7′W; 18	E4	XXX	XXX	XXX	XXX	
IM_2007_42168	*Terebra*	*specillata*	Panama	08°33′N, 079°04′W; 19	E4	XXX	XXX	XXX	XXX	
IM_2007_30386	*Terebra*	*subulata*	Vanuatu	15°36.6′S, 167°10.1′E; 8-20	C	CONO436-08	EU685551	EU685402	EU685693	
IM_2007_30444	*Terebra*	*subulata*	Philippines	9°37.4′N, 123°54.5′E; 6-8	C	CONO209-08	EU685501	EU685346	EU685637	
IM_2007_30483	*Terebra*	*subulata*	Philippines		C	CONO277-08	EU685524	EU685369	EU685661	XXX
IM_2007_16731	*Terebra*	*succincta*	Philippines	9°30′N, 123°42′ E; 356-396	E3	CONO331-08	EU015732	EU685378	EU685669	EU015617
IM_2007_30385	*Terebra*	*succincta*	Vanuatu	15°26.6′S, 167°15.2′E;	E2	CONO470-08	EU685585	EU685439	EU685731	
IM_2007_30419	*Terebra*	*succincta*	Vanuatu	15°35.4′S, 166°58.7′E; 3-8	E2	XXX	XXX	XXX	XXX	
IM_2007_30433	*Terebra*	*succincta*	Vanuatu	15°33.4′S, 167°12.4′E; 2-6	E2	CONO516-08	EU685621	EU685481	EU685774	
IM_2007_30434	*Terebra*	*succincta*	Vanuatu	15°33.4′S, 167°12.4′E; 2-6	E2	CONO517-08	EU685622	EU685482	EU685775	
IM_2007_30440	*Terebra*	*succincta*	Vanuatu	15°31.7′S, 167°09.7′E; 18-21	E2	CONO426-08	EU685545	EU685396	EU685687	XXX
IM_2007_30456	*Terebra*	*succincta*	Vanuatu	15°31.7′S, 167°09.7′E; 18-21	E2	CONO427-08	EU685546	EU685397	EU685688	
IM_2007_30458	*Terebra*	*succincta*	Vanuatu	15°31.7′S, 167°09.7′E; 18-21	E2	CONO428-08	EU685547	EU685398	EU685689	
IM_2007_30468	*Terebra*	*succincta*	Vanuatu	15°35.4′S, 166°58.7′E; 3-8	E2	XXX	XXX	XXX	XXX	
IM_2007_30470	*Terebra*	*succincta*	Vanuatu	15°35.4′S, 166°58.7′E; 3-8	E2	XXX	XXX	XXX	XXX	
IM_2007_30475	*Terebra*	*succincta*	Vanuatu		E2	CONO451-08	EU685566	EU685417	EU685708	
IM_2007_30476	*Terebra*	*succincta*	Vanuatu		E2	CONO452-08	EU685567	EU685418	EU685709	
IM_2007_30479	*Terebra*	*succincta*	Solomon Islands	7°14′ S, 158°29′ E; 286-423	E3	CONO379-08	EU685534	EU685381	EU685672	
IM_2007_30582	*Terebra*	*succincta*	Philippines	9°39′N, 123°48′E; 255-268	E3	CONO285-08	EU685527	EU685372		
IM_2007_30601	*Terebra*	*succincta*	Vanuatu	15°41′S, 167°00′E; 517-614	E3	CONO492-08	EU685605	EU685464	EU685757	
IM_2007_30622	*Terebra*	*succincta*	Vanuatu		E2	XXX	XXX	XXX	XXX	
IM_2007_30626	*Terebra*	*succincta*	Vanuatu	15°31.7′S, 167°09.7′E; 18-21	E2	CONO425-08	EU685544	EU685395	EU685686	
IM_2007_30634	*Terebra*	*succincta*	Vanuatu	15°31.7′S, 167°09.7′E; 18-21	E2	CONO429-08	EU685548	EU685399	EU685690	

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2009_10085	*Terebra*	*succincta*	North New-Caledonia	20°17′ S, 163°50′E; 590-809	E3	XXX	XXX	XXX	XXX	
IM_2007_17938	*Terebra*	*textilis*	Vanuatu	15°35.4′ S, 166°58.7′E; 3-8	E2	CONO509-08	EU015750	EU685478	EU685771	EU015635
IM_2007_30441	*Terebra*	*textilis*	Vanuatu	15°33.4′ S, 167°12.4′E; 2-6	E2	XXX	XXX	EU685364	EU685656	
IM_2007_30451	*Terebra*	*textilis*	Philippines	9°36.8′N, 123°52.2′E;	E2	CONO261-08	EU685519	EU685477	EU685770	XXX
IM_2007_30474	*Terebra*	*textilis*	Vanuatu	15°35.4′ S, 166°58.7′E; 3-8	E2	CONO508-08	EU685618	EU685468	EU685761	
IM_2007_30545	*Terebra*	*textilis*	Vanuatu	15°31.3′ S, 167°09.9′E; 1-6	E2	CONO497-08	EU685609	EU685467	EU685760	
IM_2007_30547	*Terebra*	*textilis*	Vanuatu	15°31.3′ S, 167°09.9′E; 1-6	E2	CONO496-08	EU685608	EU685420	EU685711	
IM_2007_30616	*Terebra*	*textilis*	Vanuatu		E2	CONO454-08	EU685569	EU685419	EU685710	
IM_2007_30621	*Terebra*	*textilis*	Vanuatu		E2	CONO453-08	EU685568			
IM_2009_10088	*Terebra*	*textilis*	North Madagascar	14° 31,9′ S, 47° 26,54′ E; 46-54	E2	XXX	XXX		XXX	XXX
IM_2009_10093	*Terebra*	*textilis*	North Madagascar	15° 30,15′ S, 46° 4,3′ E; 29-36	E2	XXX	XXX		XXX	XXX
IM_2009_10095	*Terebra*	*textilis*	North Madagascar	15° 30,15′ S, 46° 4,3′ E; 29-36	E2	XXX	XXX		XXX	XXX
IM_2009_9957	*Terebra*	*textilis*	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	E2	XXX	XXX		XXX	
IM_2007_30409	*Terebra*	*tricolor*	Vanuatu	15°33,1′ S, 167°17.8′E; 15-25	C	CONO404-08	EU685540	EU685390	EU685681	
IM_2007_30493	*Terebra*	*tricolor*	Vanuatu	15°38.5′S, 167°15.1′E; 13	C	CONO488-08	EU685602	EU685461	EU685754	
IM_2007_30424	*Terebra*	*trismacaria*	Solomon Islands	8°37′ S, 157°21′ E; 150-160	E2	CONO380-08		EU685383	EU685674	
IM_2007_30492	*Terebra*	*trismacaria*	Solomon Islands	8°40′ S, 157°23′ E; 214-243	E2	CONO384-08	EU685538	EU685388	EU685679	
IM_2007_30499	*Terebra*	*trismacaria*	Solomon Islands	8°40′ S, 157°23′ E; 214-243	E2	CONO385-08	EU685539	EU685389	EU685680	
IM_2007_30579	*Terebra*	*trismacaria*	Solomon Islands	8°40′ S, 157°23′ E; 214-243	E2	CONO383-08	EU685537	EU685387	EU685678	
IM_2007_30446	*Terenolla*	*pygmaea*	Philippines	9°37.4′N, 123°54.5′E; 4-5	E1	CONO211-08	EU685503	EU685348	EU685639	
IM_2007_30448	*Terenolla*	*pygmaea*	Philippines	9°37.4′N, 123°54.5′E; 4-5	E1	CONO212-08	EU685504	EU685349	EU685640	
IM_2007_30449	*Terenolla*	*pygmaea*	Philippines	9°37.4′N, 123°54.5′E; 4-5	E1	CONO213-08	EU685505	EU685350	EU685641	
IM_2007_30511	*Terenolla*	*pygmaea*	Philippines	9°35.7′N, 123°44.4′E; 0-2	E1	CONO236-08	EU685509	EU685354	EU685645	
IM_2009_10121	*Terenolla*	*pygmaea*	South Madagascar		E1	XXX	XXX	XXX	XXX	XXX
IM_2007_30411	*Triplostephanus*	*anilis*	Vanuatu	15°35.4′N, 166°58.7′E; 3-8	C	CONO493-08	XXX	XXX	XXX	XXX
IM_2007_30552	*Triplostephanus*	*anilis*	Vanuatu	15°35.2′ S, 167°59.4′E;	C	CONO473-08	EU685588	EU685444	EU685736	XXX
IM_2009_10068	*Triplostephanus*	*anilis*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_10069	*Triplostephanus*	*anilis*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_10070	*Triplostephanus*	*anilis*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_10071	*Triplostephanus*	*anilis*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_10072	*Triplostephanus*	*anilis*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2009_7120	*Triplostephanus*	*anilis*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_7121	*Triplostephanus*	*anilis*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_7122	*Triplostephanus*	*anilis*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2009_7123	*Triplostephanus*	*anilis*	Mozambique	25°59.0′S, 32°54.5′E; 0	C	XXX	XXX	XXX	XXX	
IM_2007_30402	*Triplostephanus*	*cumingii*	Fiji	18°26.4′S, 178°02.4′E; 50-51	C	XXX		EU685487	EU685779	
IM_2007_30390	*Triplostephanus*	*fenestratus*	Philippines	9°29′N, 123°44′E; 271-318	C	CONO305-08	EU685531	EU685376	EU685667	
IM_2007_30410	*Triplostephanus*	*fenestratus*	Philippines	9°39′N, 123°48′E; 255-268	C	CONO287-08	EU685529	EU685374	EU685665	
IM_2007_30418	*Triplostephanus*	*fenestratus*	Philippines	9°39′N, 123°48′E; 255-268	C	CONO286-08	EU685528	EU685373	EU685664	
IM_2007_30538	*Triplostephanus*	*fenestratus*	Philippines	9°39′N, 123°48′E; 255-268	C	XXX	XXX	XXX		
IM_2007_30553	*Triplostephanus*	*fenestratus*	Vanuatu	15°42′S, 167°02′E; 268-445	C	XXX	XXX	XXX	XXX	
IM_2007_30559	*Triplostephanus*	*fenestratus*	Philippines	9°39′N, 123°48′E; 255-268	C	XXX	XXX	XXX	XXX	
IM_2009_10073	*Triplostephanus*	*fenestratus*	North Madagascar	14°30′S, 47°27′E; 274-325	C	XXX	XXX	XXX	XXX	
IM_2009_10074	*Triplostephanus*	*fenestratus*	North Madagascar	14°30′S, 47°27′E; 274-325	C	XXX	XXX	XXX	XXX	
IM_2009_10075	*Triplostephanus*	*fenestratus*	North Madagascar	14°30′S, 47°27′E; 274-325	C	XXX	XXX	XXX	XXX	
IM_2009_10076	*Triplostephanus*	*fenestratus*	North Madagascar	14°30′S, 47°27′E; 274-325	C	XXX	XXX	XXX	XXX	XXX
IM_2009_10077	*Triplostephanus*	*fenestratus*	North Madagascar	14°30′S, 47°27′E; 274-325	C	XXX	XXX	XXX	XXX	
IM_2009_10078	*Triplostephanus*	*fenestratus*	North Madagascar	14°30′S, 47°27′E; 274-325	C	XXX	XXX	XXX	XXX	
IM_2007_15724	*Triplostephanus*	*fujitai*	Philippines	9°27′N, 123°49′E; 273-356	C	CONO306-08	EU015725	EU685377	EU685668	EU015610
IM_2007_30482	*Triplostephanus*	*fujitai*	Vanuatu	15°42′S, 167°02′E; 268-445	C	CONO181-08	EU685492	XXX	EU685628	
IM_2007_30544	*Triplostephanus*	*jenningsi*	Vanuatu	15°28.6′S, 167°15.1′E; 3-31	C	CONO483-08	EU685597	EU685456	EU685749	XXX
IM_2007_30533	*Triplostephanus*	sp.	Philippines	9°42.1′N, 123°51.4′E; 3-4	E2	XXX	XXX	XXX	XXX	
IM_2007_30534	*Triplostephanus*	sp.	Philippines	9°42.1′N, 123°51.4′E; 3-4	E2	CONO243-08	EU685514	EU685359	EU685651	
IM_2007_30404	*Triplostephanus*	*triseriatus*	Philippines	9°35.3′N, 123°52.2′E; 84-87	C	CONO205-08	EU685497	EU685342	EU685633	XXX
IM_2009_10082	*Triplostephanus*	*triseriatus*	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	C	XXX	XXX	XXX	XXX	
IM_2009_10084	*Triplostephanus*	*triseriatus*	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	C	XXX	XXX	XXX	XXX	
IM_2009_10100	*Triplostephanus*	*triseriatus*	South Madagascar	25°22.4′S, 47°02.8′E; 89-95	C	XXX	XXX	XXX	XXX	
IM_2009_10102	*Triplostephanus*	*triseriatus*	South Madagascar	25°02.4-5′S, 47°03.2-6′E; 54-56	C	XXX	XXX	XXX	XXX	
IM_2009_10108	*Triplostephanus*	*triseriatus*	South Madagascar	25°22.4′S, 47°02.8′E; 89-95	C	XXX	XXX	XXX	XXX	
IM_2009_10166	*Triplostephanus*	*triseriatus*	South Madagascar	25°04.7′S, 47°03.4′E; 64-65	C	XXX	XXX	XXX	XXX	
IM_2009_10167	*Triplostephanus*	*triseriatus*	South Madagascar	25°04.7′S, 47°03.4′E; 64-65	C	XXX	XXX	XXX	XXX	
IM_2009_10168	*Triplostephanus*	*triseriatus*	South Madagascar	25°04.7′S, 47°03.4′E; 64-65	C	XXX	XXX	XXX	XXX	

MNHN Ids	Genus	species	Country	Coordinates; depth (m)	Clade	BOLD ID	Genbank COI	GenBank 12S	GenBank 16S	GenBank 28S
IM_2009_10169	*Triplostephanus*	*triseriatus*	South Madagascar	25°04.7′ S, 47°03.4′ E; 64-65	C	XXX	XXX	XXX	XXX	
IM_2009_10170	*Triplostephanus*	*triseriatus*	South Madagascar	25°04.7′ S, 47°03.4′ E; 64-65	C	XXX	XXX	XXX	XXX	
IM_2009_10172	*Triplostephanus*	*triseriatus*	South Madagascar	25°04.7′ S, 47°03.4′ E; 64-65	C	XXX	XXX	XXX	XXX	
IM_2009_10173	*Triplostephanus*	*triseriatus*	South Madagascar	25°04.7′ S, 47°03.4′ E; 64-65	C	XXX	XXX	XXX	XXX	
IM_2009_10911	*Triplostephanus*	*triseriatus*	Australia	27°02′069″S, 153°19′00″E; 3,5-7,8	C	XXX	XXX		XXX	
IM_2009_9948	*Triplostephanus*	*triseriatus*	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	C	XXX	XXX	XXX	XXX	
IM_2009_9949	*Triplostephanus*	*triseriatus*	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	C	XXX	XXX	XXX	XXX	
IM_2009_9950	*Triplostephanus*	*triseriatus*	North Madagascar	12° 35,92′ S, 48° 35,22′ E; 50-52	C	XXX	XXX	XXX	XXX	
IM_2007_40568	*Cochlespira*	*pulchella*			Outgroup	FRANZ2207-08	EU685627	EU685488	EU685781	
IM_2007_17922	*Conus*	*nereis*			Outgroup	CONO339-08	EU015734	EU685489	EU685782	EU015619
IM_2007_40569	*Harpa*	*kajiyamai*			Outgroup		EU685626	EU685491	EU685783	
IM_2007_17685	*Iotyrris*	*cingulifera*			Outgroup	CONO515-08	EU127881	EU685490	EU685780	EU127890

Table 2

Primers used for gene amplification and sequencing. PCG = Protein Coding Gene

Gene	Primer name	Primer Sequences (5′-3′)	Sens	Tm	References	Length of Amplification	Gene type
COI	LCOI1490	GGT CAA CAA ATC ATA AAG ATA TTG G	F	48/50	Folmer et al., 1994	660	mtDNA PCG
COI	HCOI2198	TAA ACT TCA GGG TGA CCA AAA AAT CA	R	48/50	Folmer et al. 1994		
16S	16Sa-L	CGC CTG TTT ATC AAA AAC AT	F	51	Palumbi, 1996	460	mtDNA rRNA
16S	16Sb-H2	CTC CGG TTT GAA CTC AGA TCA	R	51	Palumbi 1996		
12S	12SA	AAA CTG GGA TTA GAT ACC CCA CTA T	F	51	Palumbi 1996	370	mtDNA rRNA
12S	12SB	GAG GGT GAC GGG CGG TGT GT	R	51	Palumbi 1996		
28S	C1′	ACC CGC TGA ATT TAA GCA T	F	56	Jovelin and Justine, 2001	830	nDNA rRNA
28S	D2	TCC GTG TTT CAA GAC GGG	R	56	Jovelin and Justine, 2001		

Table 3

Matrix of the anatomical characters used for the character mapping. Numbers in parentheses in the column "MNHN vouchers" correspond to specimens used to reconstruct the phylogenetic tree when the dissected specimen was not available or when its sequencing failed. JDT and YK: species dissected by John D. Taylor and Yuri Kantor.

1. Proboscis (PR): 0 – absent, 1 – present
2. Venom gland (VG): 0 – absent, 1 – present
3. Odontophore (OD): 0 – absent, 1 – present
4. Accessory proboscis structure (APS): 0 – absent, 1 – present
5. Marginal radular teeth (RadT): 0 – radula absent, 1 – duplex, 2 – solid recurved, 3 – flat, 4 – semienrolled, 5 – hypodermic
6. Salivary gland(s) (SG): 0 – absent, 1 – present

Species	MNHN vouchers	clade	PR	VG	OD	APS	RadT	SG
Clathroterebra poppei	IM_2007_30546	E3	1	1	0	?	1	1
Duplicaria bernardi	IM_2009_10908	F	0	0	1	0	2	1
Duplicaria sp. 1	IM_2009_10111	F	0	0	1	0	2	1
Duplicaria sp. 2	IM_2009_10164	F	0	0	1	0	2	1
Duplicaria sp. 3	IM_2009_10134	E2	0	0	0	0	0	0
Euterebra fuscolutea	IM_2009_10127	F	0	0	1	0	2	1
Hastula hectica	YK (IM_2009_10104)	D	1	1	0	0	5	1
Hastula lanceata	IM_2007_30535	D	1	1	0	0	5	?
Hastula penicillata	IM_2007_30540	D	1	1	0	0	5	1
Hastula strigillata	IM_2007_30607	D	?	1	1	0	5	?
Hastula stylata	IM_2009_10106	D	1	1	0	0	4	1
Hastulopsis amoena	IM_2009_10909	E1	0	0	0	?	0	?
Hastulopsis conspersa	IM_2007_30619	E1	0	0	0	0	0	0
Hastulopsis minipulchra	IM_2009_10129	E5	0	0	0	0	0	0
Hastulopsis pseudopertusa	IM_2009_9953 (9954)	E5	0	0	0	0	0	1
Myurella affinis	IM_2007_30439	E1	0	0	0	1	0	0
Myurella flavofasciata	IM_2007_30465	E1	0	0	0	?	0	?
Myurella kilburni	IM_2007_30461	E5	1	1	0	0	5	1
Myurella lineaperlata	IM_2007_30635	E2	1	1	1	0	3	1
Myurella nebulosa	IM_2007_30408	E1	0	0	0	1	0	1
Oxymeris dimidiata	JDT (IM_2007_30373)	B	0	0	0	0	0	1
Oxymeris felina	IM_2007_30443	B	0	0	0	0	0	0

Species	MNHN vouchers	clade	PR	VG	OD	APS	RadT	SG
Oxymeris maculata	JDT (IM_2007_30389)	B	0	0	0	0	0	1
Pellifronia jungi	IM_2007_30591 (30395)	A	1	1	1	?	1	?
Strioterebrum nitidum	IM_2009_7114	E2	1	1	1	0	3	1
Terebra argosyia	IM_2007_42087	C	?	1	?	?	?	1
Terebra berryi	IM_2007_42167	E4	0	0	0	0	0	0
Terebra cf. variegata	IM_2007_42128	E4	0	0	0	0	0	1
Terebra cingulifera	IM_2007_30382	C	1	1	0	?	5	1
Terebra elata	IM_2007_42095	E4	1	1	?	0	?	1
Terebra funiculata	IM_2007_30394	C	?	1	0	?	5	?
Terebra guttata	IM_2007_30376	C	1	1	0	0	5	1
Terebra puncturosa	IM_2007_42171	E4	1	0	0	1	0	?
Terebra specillata	IM_2007_42168	E4	0	0	0	0	0	1
Terebra subulata	JDT (IM_2007_30444)	C	1	1	0	0	5	1
Terebra succincta	IM_2007_30385	E2	1	0	0	1	0	1
Terebra succincta	IM_2007_30582	E3	1	1	1	?	1	1
Terebra textilis	IM_2007_30547	E2	1	1	1	0	3	1
Terebra trismacaria	IM_2007_30579	E2	1	1	0	0	3	1
Terenolla pygmaea	IM_2007_30449	E1	0	0	0	0	0	0
Triplostephanus fenestratus	IM_2007_30418	C	1	1	0	0	5	1
Triplostephanus triseriatus	IM_2007_30404	C	1	1	0	?	5	?
Cochlespira pulchella	IM_2007_40568	Out	1	1	1	0	1	1
Conus nereis	IM_2007_17922	Out	1	1	0	0	5	1
Harpa kajiyamai	IM_2007_40569	Out	1	0	1	0	0	1
Iotyrris cingulifera	IM_2007_17685	Out	1	1	1	0	1	1

Table 4

Bayesfactor obtained with bayestraits from comparing the posterior probabilities of the independent and dependent models for seven discrete characters (PR = Proboscis, VG = venom gland, OD = Odontophore, APS = Accessory proboscis Structure, RadT1 and 2 = Marginal radular Teeth – see text for details, SG = Salivary glands).

	PR	VG	OD	APS	RadT1	RadT2	SG
PR							
VG	35.16						
OD	−4	−0.82					
APS	−2.48	1.16	−7.6				
RadT1	14.9	27.48	4.14	4.3			
RadT2	1.58	0.04	11.56	−2.72	−0.38		
SG	8.38	6.68	−0.12	−1.38	7.54	−2.64	