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A multilocus molecular phylogeny of Fasciolariidae (Neogastropoda: Buccinoidea)

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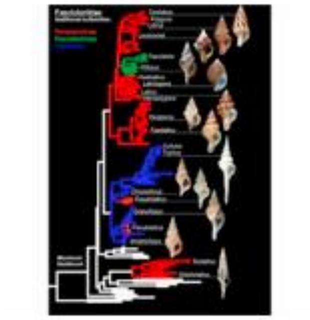
Abstract :

The neogastropod family Fasciolariidae Gray, 1853 - tulips, horse-conchs, spindles, etc., comprises important representatives of tropical and subtropical molluscan assemblages, with over 500 species in the subfamilies Fasciolariinae Gray, 1853, Fusininae Wrigley, 1927 and Peristerniinae Tryon, 1880. Fasciolariids have had a rather complicated taxonomical history, with several genus names for a long time used as waste baskets to group many unrelated species; based on shell characters, recent taxonomic revisions have, however, began to set some order in its taxonomy. The present work is the first molecular approach to the phylogeny of Fasciolariidae based on a multigene dataset, which provides support for fasciolariids, an old group with a fossil record dating back to the Cretaceous. Molecular markers used were the mitochondrial genes 16S rRNA and cytochrome c oxidase subunit I, and the nuclear genes 18S rRNA, 28S rRNA and histone H3, sequenced for up to 116 ingroup taxa and 17 outgroups. Phylogenetic analyses revealed monophyly of Dolicholatirus Bellardi, 1884 and Teralatirus Coomans, 1965, however it was not possible to discern if the group is the sister Glade to the remaining fasciolariids; the latter, on the other hand, proved monophyletic and contained highly supported groups. A first split grouped fusinines and Pseudolatirus Bellardi, 1884; a second split grouped the peristerniine genera Peristernia Morch, 1852 and Fusolatirus Kuroda and Habe, 1971, while the last group comprised fasciolariines and the remaining peristerniines. None of these clades correspond to the present-day accepted circumscription of the three recognized subfamilies.

Graphical abstract



Highlights

► A clade containing *Dolicholatirus* and *Teralatirus* is monophyletic. ► The remaining fasciolariids are monophyletic. ► Fusininae now comprises *Fusinus*, *Pseudolatirus*, and related species to these genera. ► Peristerniinae now comprises *Peristernia* and *Fusolatirus*; neither is monophyletic. ► Fasciolariinae now comprises the majority of peristerniines and fasciolariines.

Keywords : Fasciolariinae, Peristerniinae, Fusininae, Evolution, Dolicholatirus, Radula

1. Introduction

Neogastropoda, the most diverse caenogastropod mollusk clade, is supported by morphology-based phylogenetic analyses (Ponder and Lindberg, 1997; Strong, 2003) and by a Bayesian inference analysis of a combined morphological and molecular data (Ponder et al., 2008), but it has been challenged in several molecular studies (Harasewych et al., 1997; Colgan et al., 2000, 2003, 2007).. In their complete mitochondrial genome and three nuclear gene phylogeny, Osca et al. (2015) failed to recover Neogastropoda, and proposed the inclusion of Tonnoidea, or the exclusion of Cancellarioidea and possibly Volutidae from Neogastropoda. In the first case tonnoideans would have secondarily lost the traditional neogastropod synapomorphies, while in the latter these synapomorphies would be considered homoplastic, in this sense agreeing with Kantor and Fedosov (2009). The superfamily Buccinoidea includes the families Buccinidae, Belomitridae, Busyconidae, Colubrariidae, Columbellidae, Nassariidae, Melongenidae and Fasciolariidae (Bouchet and Rocroi, 2005; WoRMS, 2015). They are considered highly derived in the Neogastropoda scheme due to the absence of the accessory salivary glands and the rectal glands.

Knowledge of the phylogenetic position of Fasciolariidae and of the families included in Buccinoidea is scant, and studies that deal specifically with the taxonomic position of these taxa are few. Hayashi (2005), utilizing sequences from the complete mitochondrial 16S rRNA gene, obtained a phylogeny based on 22 buccinoid species; Kosyan et al. (2009) used 21 species of buccinoids from partial 16S rRNA sequence data; finally, Oliverio and Modica (2010), analyzed 16S rRNA data from 30 buccinoids. All these analyses failed to recover Buccinidae as monophyletic due to the intercalation of Nassariidae and/or Fasciolariidae. There are no phylogenetic hypotheses that deal specifically with the family Fasciolariidae, based either on morphological or molecular characters, and the studies that do include some fasciolariid species (e.g., Hayashi, 2005; Kosyan et al., 2009; Zou et al., 2011) lack the resolution and coverage to clarify its relationships or to test its monophyly, as the family may potentially comprise multiple paraphyletic groups (Fedosov and Kantor, 2012).

Fasciolariidae, Melongenidae, Cancellariidae and Buccinidae date back to the early Cretaceous (Valanginian, ~140 Mya) (Benton, 1993), whereas other neogastropod families appeared between the late Cretaceous to early Paleogene, suggesting that the former families represent the first offshoots of Neogastropoda (Hayashi, 2005). While Fasciolariinae appeared during the Albian (Bandel, 1993), the fossil record indicates that the family – especially Fasciolariinae and Peristerniinae (Vermeij and Snyder, 2006) – diversified extensively during the early Neogene (Aquitanian, 24 Mya).

With 540 extant species in 51 genera worldwide (WoRMS 2015), Fasciolariidae are a diverse element of the molluscan predatory fauna in shallow to deep coastal waters, especially on soft bottoms. Fasciolariids are gonochoristic with internal fertilization and, usually, direct development (Leal, 1991). They inhabit depths up to 1900 m (Callomon and Snyder, 2009) where they prey on polychaetes, bivalves and other gastropods (Rosenberg, 1992). The family is currently comprised of three subfamilies: Peristerniinae, which includes, among other genera, *Persternia* and *Latirus*; Fusininae, the spindles; and Fasciolariinae with the conspicuous and well-known tulips and horse-conchs. For a long time, the name '*Fusus'* has been used indiscriminately for numerous Cretaceous, Cenozoic and Recent spindle-shaped shells (Snyder, 2003), and likewise *Latirus*, *Fasciolaria* and *Pleuroploca* were also used for evidently heterogeneous assemblages. More recently, however, the group has undergone extensive taxonomical revision (e.g., Vermeij and Snyder, 2002, 2006; Snyder et al., 2012; Lyons and Snyder 2013), elevating several subgenera to genus rank and establishing new ones.

Sampling of multiple independently evolving genes is recommended to produce a resolved and strongly supported phylogeny avoiding issues of incongruence among single gene analyses. The use of such a multi-gene molecular approach has helped resolve problems in different molluscan clades (e.g., Puillandre et al., 2008; Aktipis et al., 2010; Tëmkin, 2010; Sharma et al., 2013). The present study aims to improve the phylogenetic understanding of the Fasciolariidae and investigate the diversification patterns of its members by conducting multi-gene phylogenetic analyses.

2. Material and methods

2.1. Taxon sampling

The present study is largely based on material vouchered in MNHN, collected during multiple expeditions conducted by MNHN and IRD, and other ad hoc fieldwork (see Acknowledgements). Before 2012, specimens were treated with an isotonic solution of magnesium chloride until relaxed (showing no response to touch), and then a tissue clip was cut. Starting from early 2012, specimens were processed using a microwave oven (Galindo et al., 2014), i.e., in most cases the entire body, or at least the last 1-1.5 whorls, were available for study. Tissue samples were preserved in 96% EtOH. Additional specimens were used from the following institutions: Academy of Natural Sciences of Philadelphia (ANSP); Florida Museum of Natural History (FMNH); Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ); Museum of Zoology, University of São Paulo (MZSP); and Santa Barbara Museum of Natural History (SBMNH). Some museum specimens were preserved in 70% EtOH. In total

116 specimens of Fasciolariidae were sequenced. The 116 ingroup taxa sampled consist of 10 Fasciolariinae, 67 Peristerniinae and 39 Fusininae. Outgroup taxa for the study consisted of 11 Buccinoidea, 2 Conoidea, 2 Muricoidea and 2 Cypraeoidea. The list of specimens, including collection voucher numbers, GenBank accession codes and collection details is found in Table 1.

2.2. Molecular methods

Total DNA was extracted from foot tissue using Qiagen's DNeasy tissue kit (Qiagen, Valencia, CA, USA). Molecular markers consisted of 2 nuclear ribosomal genes (18S rRNA and 28S rRNA), a mitochondrial ribosomal gene (16S rRNA), a mitochondrial protein-encoding gene (cytochrome *c* oxidase subunit I [COI]) and one nuclear protein-encoding gene (histone H3) Primer sequences are listed in Table 2. Purified genomic DNA was used as a template for polymerase chain reaction (PCR) amplification.

Polymerase chain reactions (PCR) were performed on a Master-cycler Pro® Eppendorf (Hamburg, Germany) in a 25µL volume reaction, and consisted of 1µL of template DNA, 1µM of each primer, 200µM of deoxynucleotide triphosphates (dNTP's; Invitrogen, Carlsbad, CA, USA), 1X PCR buffer containing 1.5mM $MgCl_2$ (Promega, Madison, WI, USA) and 1.25 units of GoTaq DNA polymerase (Promega). The fragments were amplified under the following conditions: initial denaturing at 95 °C for 15min, 40 cycles of 94°C for 30s, 43-64°C (annealing temperatures, Table 2) for 70s and 72°C for 90s, and final extension step at 72°C for 10min.

Numerous PCR additives were utilized in order to optimize DNA amplification, including BSA (Bovine serum albumin) and DMSO (Dimethyl sulfoxide). BSA was utilized with different optimal concentrations per template (0.8-5.6µg/mL). It exerts its effect through interacting with interfering substances and also stabilizing Taq DNA polymerase (Nagai et al., 1998). DMSO was used with a final concentration of 5% to reduce secondary structures that could inhibit the progress of the polymerase, being especially useful for GC-rich templates (Meyer et al., 2010).

Double-stranded PCR products were visualized by agarose gel electrophoresis (1% agarose) and purified using 2µL of diluted (1:2) ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) in a volume of 25µL PCR product and performed at 37°C for 20min followed by enzyme inactivation at 80°C for 15min. Sequencing reactions were performed in a 10µL reaction volume with Big-Dye Terminator v.3.1 (Applied Biosystems, Foster City, CA, USA) following the manufacturer's instructions. using the thermal cycler described above, with an initial denaturation step for 3 min at 94°C and 25 cycles of 94°C for 10s, 50°C for 5s and 60°C for 4min.

Sequenced products were purified using Sephadex (Amersham Biosciences) and sequenced on an ABI Prism 3730 Genetic Analyzer (Applied Biosystems). Chromatograms obtained were visualized and edited in Geneious v.8.1.2 (http://www.geneious.com, Kearse et al., 2012). All new sequences have been deposited in GenBank under accession numbers KT753546-KT754145. The 5 genes were analyzed as follows:

18S rRNA: The nearly complete gene was amplified with three overlapping markers (*a*, *b*, *c*). In the present study we include 116 ingroup specimens plus 17 outgroups, for a total of 1777-1787 bp per complete sequence. From the 116 ingroup sequences, all but 3 were complete.

28S rRNA: A 2.2 Kb fragment of the gene was amplified with three overlapping markers (*a*, *b*, *c*), as described in Giribet and Shear (2010). The dataset includes 115 ingroup specimens plus 17 outgroups, for a total of 2085-2139 bp, showing considerable length variation in 28S rRNA. Fragment *a* was sequenced for 115 ingroup taxa and 16 outgroups, fragment *b* for 116 and 17, and fragment *c* for 113 and 17.

16S rRNA: This gene was amplified for 94 ingroup and 10 outgroup terminals in a single amplicon between 505-520 bp.

COI: A 658 bp fragment of the gene was amplified for 113 ingroup and 16 outgroup terminals in a single amplicon using a combination of different primer pairs. It showed no length variation among all sampled specimens.

Histone H3: A 328 bp amplicon of this gene was amplified for 110 ingroup and 17 outgroup specimens. It was analyzed in a single fragment without variation in length among individuals sequenced.

2.3. Phylogenetic analyses

Maximum likelihood (ML) and Bayesian inference (BI) analyses were conducted on static alignments using MUSCLE v.3.6 (Edgar, 2004) as implemented in the Geneious v.8.1.2 platform. In order to confirm codon position of protein encoding genes COI and histone H3, their sequences were translated into amino acids using the Geneious v.8.1.2 platform.

ML analysis was conducted using RAxML v.8.2.X (Stamatakis, 2014) on the complete dataset. For the ML searches, the General Time Reversible model with a discrete gamma distribution of site-rate heterogeneity (GTR + Γ) was specified for each individual gene. Nodal support was estimated via 1000 replicates of a rapid bootstrapping algorithm (Stamatakis et al., 2008) using the GTR-GAMMA model, via the Cyber infrastructure for Phylogenetic Research (CIPRES) portal (Miller et al., 2010). Bootstrap resampling frequencies were thereafter mapped onto the optimal tree from the independent searches.

In order to assess the monophyly of Fasciolariidae, a constrained phylogeny was generated by RAxML, and site-wise log-likelihoods were calculated for the best tree topology and for the constrained tree with fasciolariid monophyly. These values were used in CONSEL v.0.1.j (Shimodaira and Hasegawa, 2001) to calculate the probabilities according to the approximately unbiased test (AU; Shimodaira, 2002), the Kishino–Hasegawa test (KH; Kishino and Hasegawa, 1989), and the Shimodaira–Hasegawa test (SH; Shimodaira and Hasegawa, 1999).

A Bayesian inference analysis was conducted using MrBayes v.3.2.5 (Ronquist et al., 2012) with a unique model of sequence evolution with corrections for a discrete gamma distribution and/or a proportion of invariant sites (GTR + Γ + I) on each partition, as selected in jModelTest 2 v.2.1.7 (Guindon and Gascuel 2003; Darriba et al., 2012) as implemented in the CIPRES gateway (Miller et al., 2010). Default priors were used starting with random trees and three runs, each with three hot and one cold Markov chains, were conducted until the average deviation of split frequencies reached <0.01 (7,000,000 generations). Stationarity was checked using Tracer v.1.6 (Rambaut et al., 2014). After the burn-in of 25% samples was discarded, a majority-rule consensus topology was generated from the sampled trees.

3. Results

The ML analysis of the concatenated genes (133 specimens in total) resulted in a tree topology with a -*ln*L=50219.14 (Fig. 1). The BI analysis (-*ln*L=102047.8 for run1; -*ln*L=102507.2 for run2) recovered a topology highly congruent with that of the ML analysis (Fig. 2).

With the exclusion of *Dolicholatirus*/*Teralatirus*, both analyses recovered three major well-supported deep clades of Fasciolariidae, but none of these correspond to the traditional contents of the recognized subfamilies. A first split divides fasciolariids into a clade mostly corresponding to Fusininae, but also including the clearly non-monophyletic genus *Pseudolatirus* (BS=87%; PP=1.00) – traditionally classified in the Peristerniinae (BS=99%; PP=1.00). As it includes *Fusinus colus* (Linnaeus, 1758), the type species of *Fusinus* (type genus of Fusininae), we will refer to this clade as the *Fusinus colus* clade. Fasciolariinae, which appears monophyletic, is nested within a subclade of Fasciolariinae + Peristerniinae (BS=99%; PP=1.00); as it includes *Fasciolaria tulipa* (Linnaeus, 1758), the type species of *Fasciolaria* (type genus of Fasciolariinae), we will refer to it as the *Fasciolaria tulipa* clade. Finally, its sister group is a clade containing various taxa of Peristerniinae (BS=95%; PP=1.00); as it includes *Peristernia nassatula* (Lamarck, 1822), the type species of *Peristernia* (type genus of Peristerniinae), we will refer to it as the *Peristernia nassatula* clade.

The clade containing *Dolicholatirus* and *Teralatirus* was highly supported (BS=100%; PP=1.00). Its position varied in the ML and BI analyses, but in neither of them did it appeared as a sister group to, or nested within, the remaining fasciolariids. The ML analysis for the constrained tree (fasciolariid monophyly) resulted in a tree topology with a -*ln*L=50257.70, and the probability values (AU, KH and SH) calculated in CONSEL showed no significant statistical difference between the relaxed ML tree and the constrained tree.

Single ML gene trees obtained from 16S rRNA (104 sequences) displayed the same overall topology but with less resolution in the internal nodes. Gene trees from 18S rRNA (133 sequences), 28S rRNA (132 sequences) and COI (129 sequences) displayed rival topologies with many outgroup taxa nested within Fasciolariidae, and low nodal support as initially expected. Histone H3 is a conserved gene that generated a tree with short branch lengths for closely related species and low support for nodes. Individual ML trees are available in Supplementary Material Figs. S1-S5.

4. Discussion

This study presents the first comprehensive molecular phylogenetic analysis using combined sequences from nuclear and mitochondrial genes to infer the relationships of Fasciolariidae. None of the three traditionally recognized subfamilies (Fasciolariinae, Fusininae and Peristerniinae) was recovered with their currently accepted contents. The taxa currently included in Peristerniinae appeared among all three major lineages: the *Peristernia nassatula* clade (containing *Peristernia* and *Fusolatirus*); the *Fusinus colus* clade (containing *Pseudolatirus*); and a more derived *Fasciolaria tulipa* clade (containing *Polygona*, *Turrilatirus*, *Leucozonia*, *Opeatostoma*, *Lamellilatirus*, *Pustulatirus*, *Hemipolygonia*, *Nodolatirus*, *Benimakia*, and the clearly polyphyletic *Latirus*).

Our study also demonstrates the monophyly of the clade containing *Dolicholatirus* and *Teralatirus* (BS=100%; PP=1.00) (Fig. 3), although their position as the sister group to the remaining fasciolariids remains uncertain, as the tests could not statistically discriminate between the constrained and unconstrained topologies. *Dolicholatirus* and *Teralatirus* are small turriform buccinoids whose taxonomic position in Fasciolariidae has been questioned by many authors (e.g., Abbott, 1958; Vermeij and Snyder, 2006; Beu, 2011). Simone et al. (2013) pointed out the similarities between *Dolicholatirus* and *Teralatirus*, and suggested that most likely these should be better placed together, a hypothesis that we confirm as *Teralatirus* nests within *Dolicholatirus*. Based on the shape of the egg capsules and differences in radula and shell morphology, Vermeij and Snyder (2006) and Beu (2011) argued that *Dolicholatirus* likely belongs to Turbinellidae, while Simone et al. (2013) followed a conservative approach and no taxonomic changes were made.

In our current phylogeny, the two Indo-Pacific *T. noumeensis* and *D. lancea* are the sister group to the Australian *T. roboreus*, and these are the sister group to *D. cayohuesonicus*, which in turn are the sister clade to the Caribbean *D. spiceri*. The genus *Dolicholatirus* is therefore paraphyletic with respect to *Teralatirus,* which is also non-monophyletic. The similarity of the radula of *Crassicantharus norfolkensis* illustrated by Ponder (1972: figure 14) suggests that *Crassicantharus* may belong in the same clade.

Another *Dolicholatirus* sp. (Fig. 3C) from western Australia is nested in the same clade (BS=51%; PP=0.65). The radular morphology of *Dolicholatirus* sp. (Fig. 3D) is virtually identical to that of *D. cayohuesonicus* (Fig. 3E) and *T. roboreus* figured by Simone et al. (2013: Figs. 31-34). This typical radula type likely occurs within all species in this clade (A radula of *Dolicholatirus* was supposedly figured by Bandel [1984], however we suspect a misidentification as this radula does not match our own observations (bicuspidate laterals, internal cusp hook-like), and we believe Bandel's specimen to have been a buccinid instead).

At least one species of *Teralatirus, T. roboreus* has conflicting characters in favor and against its inclusion in Fasciolariidae (Simone et al., 2013). It has salivary ducts attached to the anterior esophagus, the retractor muscle of the proboscis in a single beam, and a simple stomach, which are fasciolariid-like characters; however, its radula, the lack of gland of Leiblein, and the huge esophageal gland are not. Although molecular results were unable to reliably separate *Dolicholatirus* and *Teralatirus* from the remaining fasciolariids, they are a monophyletic group with strong morphological evidence that suggest a non-fasciolariid position.

For the ML analysis, deep nodes were unresolved and/or weakly supported in all major outgroups sampled, resulting in conflicting topologies with the BI analysis. Perhaps phylogenomic analyses will be able to recover this part of the Neogastropoda tree with high support, as is usually the case with deep nodes in mollusks (Kocot et al., 2011; Smith et al., 2011; Zapata et al., 2014; Goodheart et al., 2015).

4.1. The Fasciolaria tulipa *clade*

Vermeij and Snyder (2006) considered Fasciolariinae as derived from early peristerniines and that the two groups are part of a single clade Fasciolariinae; Snyder et al. (2012) noted that the subfamilies are morphologically similar. Our analysis confirmed that fasciolariines (Fig. 4) are a clade derived from a group of Peristerniinae (BS=94%; PP=1.00). Historically, most members of this clade have been assigned to the genera *Fasciolaria* or *Pleuroploca*. However, Snyder et al. (2012), after a thorough re-examination of their taxonomy, proposed several additional genera. Species with broad axial ribs and nodose spiral sculpture appear first as several lineages among members of this clade (*Aurantilaria aurantiaca*, *Filifusus filamentosus*, *Australaria australasia*, *Triplofusus giganteus* and *Pleuroploca trapezium* – all traditionally in the genus *Pleuroploca*); while *Fasciolaria* and *Cinctura* (BS=100%; PP=1.00) represent a Caribbean lineage with obsolete axial sculpture and weakly convex spiral whorls (Fig. 4B).

Vermeij and Snyder (2002, 2006) revised the taxonomy of many *Latirus* and related genera, elevated previous subgenera to genus rank (e.g., *Polygona*, *Hemipolygona*) and described new ones (e.g., *Turrilatirus*, *Pustulatirus*). Genus-level taxonomy and phylogenetic relationships of this group have been problematic, with names such as *Latirus* and *Leucozonia* applied indiscriminately. Fasciolariinae and Peristerniinae have a long history of divergence from the Cretaceous (~140 Mya) but diversifying extensively during the Neogene (24 Mya to the present) (Vermeij and Snyder, 2006). In our study, many deep relationships within this clade received little or no support and are incongruent between the ML and BI analyses. However, all genera, with the exception of *Hemipolygona* (represented by *H. mcgintyi* and *H. armata*), are monophyletic and have high support (*Pustulatirus* [BS=99%; PP=1.00], *Benimakia* [BS=100%; PP=1.00], *Polygona* [BS=100%; PP=1.00], *Turrilatirus* [BS=100%; PP=1.00]).

A supported clade (BS=82%; PP=1.00) grouped species that were historically associated to *Latirus* (*Latirus, Benimakia*, *Pustulatirus*, *Hemipolygona*, *Nodolatirus*) (Figs. 4C-F), including notably a clade with *Latirus amplustre* and *Latirolagena smaragdula* (BS=95%; PP=0.99). *Latirolagena smaragdula* and *Latirus amplustre* grouped with *Latirus belcheri* with high support (BS=99%; PP=1.00)

The clade consisting of *Leucozonia nassa* and *L. ponderosa* was strongly supported (BS=100%; PP=1.00), but the genus was not monophyletic. *Leucozonia nassa* is a widely distributed species occurring from southeastern Brazil to North Carolina, including records from several locations in the Caribbean. Three distinct forms can be identified, which correspond to three subspecies *sensu* Abbott (1958) and Vermeij and Snyder (2002), or three species *sensu* Vermeij (1997): the typical *L. nassa nassa* which occurs in Caribbean islands and from North Carolina to Florida and the Gulf of Mexico; *L. nassa cingulifera*, found offshore NE Brazilian waters, off Bahia and the islands of Fernando de Noronha and Atol das Rocas; and *L. nassa brasiliana*, from the SE to NE Brazilian coast. Shell characters alone may be insufficient to allow unambiguous separation among the various forms (Vermeij and Snyder, 2002). Due to overlapping geographic ranges and the presence of intermediate forms, *L. nassa* is recognized as a single species (WoRMS, 2015). *Leucozonia ponderosa* was decribed by Vermeij and Snyder (1998) as endemic to Trindade Island, SE Brazil, while Vermeij and Snyder (2002) argued that it may be a local variant of the widespread *L. nassa* “with the hope that molecular investigations resolve this issue”. Couto and Pimenta (2012) examined several specimens from both *L.*

ponderosa and *L. nassa* and found no anatomical variation among them; however, they distinguished the species by their unique shell structure.

In our study, we had representatives of all three geographical subspecies of *Leucozonia nassa*, and they grouped as a single well supported clade (BS=100%; PP=1.00). *Leucozonia ponderosa* appeared as sister to *L. nassa cingulifera* from the Fernando de Noronha Archipelago, NE Brazil. These insular species grouped with the coastal SE Brazilian *L. nassa brasiliana*, a clade that is sister group to the three Caribbean specimens corresponding to *L. nassa*. The Caribbean clade was highly supported in both ML and BI analysis (BS=95%; PP=1.00), albeit the other nodes within this group received weak support and conflicting topologies among analyses.

Opeatostoma pseudodon is the sister group to the western Atlantic *Leucozonia nassa* complex clade with high support (BS=92%; PP=1.00) (Figs. 4G-H).The radula of *Opeatostoma pseudodon* has similar lateral tooth morphology to other *Leucozonia* species. Bullock (1974) called attention to the fact that the shell of the Indo-Pacific *Latirus gibbulus*, the type of the genus, has features – notably its radula – that suggest affinity with species now classified in *Leucozonia*, rather than with the other species of *Latirus*. The radula of the species of *Latirus* and related genera (e.g., *Polygona*, *Turrilatirus*) has a small denticle on the inner side of the laterals, but this is reduced or absent in species of *Leucozonia* and *Opeatostoma*.

Latirus gibbulus (Fig. 4I) is grouped with *L. pictus* (BS=100%; PP=1.00), and *Leucozonia ocellata* with *L. cerata* (BS=100%; PP=1.00). However, deeper nodes are incongruent and have little support for their position among the other major lineages. Like the clade of *Leucozonia* + *Opeatostoma*, their radulae are similar because *L. nassa* and *O. pseudodon* lack the small denticle on the inner side of the lateral teeth.

Lyons (1991) suggested that, if *L. gibbulus* proves to be allied with *Leucozonia*, *Leucozonia* will become a junior synonym of *Latirus* and many species classified in *Latirus* will have to be re-classified. While *L. gibbulus* is in fact allied to *Polygona* and *Turrilatirus* (BS=85%; PP=0.75), *Leucozonia* is not monophyletic so *L. ocellata* and *L. cerata* must be placed in a different genus. On the same note, *Latirus* proved to be polyphyletic, comprising three distinct lineages: 1): *Latirus gibbulus* + *L. pictus*, 2): *L. amplustre* + *L. belcheri* + *Latirolagena smaragdulus* (BS=98%; PP=1.00) and 3): *Latirus polygonus* + *L. vischii* (BS=100%; PP=1.00).

Latirus gibbulus + *L. pictus* received support with (*Polygona* + *Turrilatirus*) in the ML tree (BS=85%) (Figs. 4J-K). Several authors have recognized informal groups within *Polygona* (Lyons, 1991; Vermeij and Snyder, 2006); Vermeij and Snyder (2006) also grouped species of *Polygona* into two groups but opted against giving them formal status in view of the "absence of more definitive molecular evidence". The first group with *Polygona infundibulum* and the second with *P. angulata*. In our analyses, *Polygona infundibulum* grouped with *P. bernadensis* (BS=100%; PP=1.00), while this clade is sister group to *P. angulata*; although a more thorough sampling of *Polygona* species is desirable, these groups concur with those recognized by Vermeij and Snyder (2006) and may indeed justify formal separation, possibly as subgenera.

4.2. The Peristernia nassatula *clade*

The genera *Peristernia* and *Fusolatirus* have strong support, both in the ML and BI analysis (BP=95%; PP=1.00) (Fig. 5) and in radular features, confirming the distinctiveness of the subfamily Peristerniinae.

Peristernia nassatula (type species of the genus) forms a well-supported clade with *P. forskalii*, *P. reincarnata* and *P. gemmata* (BS=100%; PP=1.00) (Figs. 5A-C); *Peristernia marquesana* clustered with several related and possibly new species with high support (BS=97%; PP=1.00), and this clade is sister to some species of *Fusolatirus* (BS=100%; PP=1.00). Because *Peristernia* is paraphyletic, the species in the clade of *P. marquesana* will have to be classified in a new genus. Vermeij (2001) assigned *P. marquesana* to the genus *Benimakia*; however *B. fastigium* and *B. lanceolata* cluster in the *Fasciolaria tulipa* clade.

The clade including *Peristernia marquesana* and its closest relatives is supported in both analysis (Figs. 5D-F), and it likely includes species related to *P. ustulata* (https://science.mnhn.fr/institution/mnhn/collection/im/item/2000-6506) and *P. lyrata* (see Poppe [2008: 108-109] for the illustration of several forms). All four sequenced specimens in this clade have a dark spot in the siphonal canal and a pseudo-umbilicus, as well as varying degree of coloration of the spire. The genus *Peristernia* and its allies have not been the subject of taxonomical revisions, and several species (e.g., Figs. 5E-F) are most likely new to science.

The genus *Fusolatirus* (Figs. 5G-H) appeared diphyletic. *Fusolatirus rikae* is the sister taxon to *Peristernia* and all other *Fusolatirus* species (BS=100%; PP=1.00), and a clade nested within *Peristernia* comprises *Fusolatirus pearsoni*, *F. pachyus* and *F. bruijnii* (BP=95%; PP=1.00). Snyder and Bouchet (2006) considered *Fusolatirus* a valid genus of peristerniine fasciolariids with long siphonal canal, imbricated subsutural spiral ridge and *Peristernia*-like radula. In fact all radulae of *Peristernia* and *Fusolatirus* figured in the literature (e.g., Bandel, 1984; Taylor and Lewis, 1995; Kosyan et al., 2009 [*Peristernia*]; Snyder and Bouchet, 2006 [*Fusolatirus*]) have *Peristernia*-like radula, with the lateral teeth with alternating smaller and larger cusps, while in other Fasciolariidae the lateral teeth have regular cusp sizes.

4.3 The Fusinus colus *clade*

The clade containing all members of Fusininae is monophyletic and highly supported (BS=87%; PP=1.00) (Fig. 6), with five major groups corresponding roughly to the five genera *Fusinus* (BS=99%; PP=1.00), *Amiantofusus* (BS=100%; PP=1.00), *Granulifusus* (BS=50%; PP=1.00), *Chryseofusus* (BS=100%; PP=1.00) and *Angulofusus* (monotypic). The genus *Pseudolatirus*, previously assigned to Peristerniinae, is polyphyletic and nested in two of these groups. However, due to the low support and incongruence of deeper nodes, the relationships among them are not well resolved. Vermeij and Snyder (2002) suggested that fusinines are a stem-group distinguished from the other subfamilies by the absence of columellar folds. Shells of fusinine generalized morphology extend back to the early Cretaceous and probably represent the plesiomorphic shell type of Neogastropoda (Harasewych, 1990; Riedel, 2000).

The central Pacific species *Cyrtulus serotinus* is endemic to the Marquesas Archipelago in French Polynesia, being the only species of the genus. The shape of its shell is unique within fusinines, with a last whorl embracing the earlier whorls, accompanied by a loss of ornamentation. Grabau (1907), in his article about ontogenetic variation, noted that "no one can distinguish the young of *Cyrtulus serotinus* from that of any member of the *Fusus* series (…). Nevertheless, it remains true that *Cyrtulus serotinus* is a derivation of modern *Fusus*." It is clear that this species is a *Fusinus* (*Fusus*, *sensu* Grabau [1907]) if one takes a look at a growth series (Figs. 6A-B). This species, nested within *Fusinus*, is sister to the Philippine *Fusinus longissimus* (BS=100%; PP=1.00). We thus agree with Grabau (1907) and consider *Cyrtulus serotinus* as part of the genus *Fusinus*, albeit highly derived.

Amiantofusus (Fig. 6E) was described to accommodate deep-water species that possess shells that are strikingly similar to Buccinidae, but with unique protoconch morphology and fasciolariid-like radula and soft-part morphology (Fraussen et al., 2007). In our analyses, the genus was strongly supported in both analyses (BS=100%; PP=1.00), but the relationship with other Fusinininae proved controversial. In the BI analysis, *Amiantofusus* is sister group to *Fusinus* (PP=0.97) and this clade is in turn sister group to *Chryseofusus* + *Pseudolatirus* (PP=0.98); (*Amiantofusus* + *Fusinus* + *Chryseofusus* + *Pseudolatirus*) is sister group to *Granulifusus* + *Pseudolatirus* (PP=0.57); and *Angulofusus* is a basal group to all the remaining fusinines (PP=0.57). In the ML analysis, *Amiantofusus* is the sister genus to (*Granulifusus* + *Pseudolatirus* + *Angulofusus*), albeit unsupported (BS=33%), while this group is sister group to the remaining fusinines (BS=44%).

In our phylogeny, *Chryseofusus* (Fig. 6F), is monophyletic and highly supported (BS=100%; PP=1.00), forming a clade with the *Pseudolatirus pallidus* complex in both analyses (BS=96%; PP=1.00).

The genus *Pseudolatirus* is currently classified in Peristerniinae (Snyder, 2003), however, Stahlschmidt and Fraussen (2012) noted that the type species is conchologically more similar to those of the subfamily Fusininae rather than to Peristerniinae, which is confirmed in the present study. *Pseudolatirus* proved non-monophyletic in our analysis, as it forms two main clades nested within the Fusininae. The lineage of *Pseudolatirus* that is sister group to *Chryseofusus* comprises a species complex of *Pseudolatirus pallidus* (Figs. 6G-I); Callomon and Snyder (2009) pointed that many shells of this species differ somewhat among them (e.g., having finer and more broadly spaced axial sculpture, more slender profile), suggesting that this species, as well as others in the genus, require additional attention. Both *P. pallidus* and *P.* aff. *pallidus* have a different placement of the axial sculpture as noted by Callomon and Snyder (2009), and both appear together with an undescribed species (Fig. 6I). Since grouping with *Chryseofusus* seems an unlikely choice based on conchological characters alone, one must assume that the

Pseudolatirus shell morphology is plesiomorphic, which is corroborated by the fact that this form is present in two independent clades (see below). *Pseudolatirus* also appears as a grade of two lineages that are basal to *Granulifusus* (BS=98%; PP=1.00) (Figs. 6J-K). *Pseudolatirus discrepans* is closest to *Granulifusus*, although this clade is poorly supported in the ML analysis (BS=51%; PP=0.92). This species has been considered a *Granulifusus* by several authors (e.g., Okutani, 2000; Poppe, 2008), and based on our tree topology and on the sculpture of the initial whorls (which closely resembles that of many *Granulifusus*), we agree with the placement of *Pseudolatirus discrepans* in *Granulifusus*.

In the clade of *Granulifusus* + *Pseudolatirus*, a first split separates *Pseudolatirus kuroseanus* + *P. kurodai* from the rest, and while they share some similarities, there are very few resemblances between them and a *Granulifusus*-like shell. A more conservative approach is taken here, as taking any taxonomic actions herein requires additional research, including the investigation of type specimens and synonymies; however we consider *Pseudolatirus* to be a heterogeneous assemblage in the subfamily Fusininae.

Granulifusus is an Indo-Pacific genus, being one of the Indo-Pacific elements occurring in Japanese warm waters (Shuto, 1958). The genus was revised by Hadorn and Fraussen (2005), who described several new species (e.g., *G. bacciballus*, *G. benjamini*) and transferred several others to it. In our phylogeny, *Granulifusus* is monophyletic (BS=51%, PP=0.92), a first split separates *G. discrepans* from of the remaining *Granulifusus* (BS=50%, PP=0.92). A second split separates *Granulifusus staminatus* from the rest (BS=82%; PP=1.00), including an undescribed species (Fig. 6L) with a canaliculated suture and reduced granulated surface; this new species is sister to *G. kiranus* (BS=100%; PP=1.00).

In the original description of *Angulofusus nedae*, the only representative of the genus *Angulofusus*, a superficial conchological resemblance to some Conoidea was noted by its authors

(Fedosov and Kantor, 2012), notably the distinctive anal sinus. However its anatomy and radular structure placed it unambiguously in the family Fasciolariidae and Fedosov and Kantor (2012) noted that the radula, soft-part coloration and internal anatomy of *Angulofusus nedae* are very similar to those of species in the genus *Amiantofusus*; however, upon examination of its COI sequence through BLAST scores in the NCBI database, a closer relationship to *Granulifusus* was proposed. Indeed, in our multi-gene ML analysis, *Angulofusus nedae* is grouped with the (*Granulifusus* + *Pseudolatirus*) clade, albeit weakly supported (BS=66%).

By using a dense taxon sampling and a multigene analysis of the putative members of the Fasciolariidae we were able to test the monophyly of the family and its main subclades. While the current molecular data are not able to conclude unambiguously whether the family includes or not the *Dolicholatirus*/*Teralatirus* clade, it showed reliable structure and three clades, each including the type species of the type genus of the three currently recognized subfamilies. These clades do not strictly correspond to the currently accepted taxonomy, as only Fasciolariinae is monophyletic but deeply nested within a clade of taxa hitherto classified as peristerniines. The type species of the type genus of Peristerniinae is present in another, Peristerniinae-only, clade. And, finally, Fusininae includes also members of the hitherto peristerniine genus *Pseudolatirus*. Our phylogenetic hypothesis thus provides a compelling new classification of the Fasciolariidae where the three current subfamilies are maintained, albeit with completely revised taxonomic extensions.

5. Conclusions

The clade consisting of *Dolicholatirus*/*Teralatirus* is monophyletic; however, topology tests do not support or reject its relationship to the remaining fasciolariids. The remaining fasciolariids are monophyletic and strongly supported, and fall into three main clades that correspond to the three currently recognized subfamilies, but with their taxonomic extension considerably revised:

1) *Fusinus colus* clade, containing all the Fusininae, consisting of five major lineages corresponding to the genera *Amiantofusus*, *Angulofusus*, *Chryseofusus*, *Fusinus* and *Granulifusus*, and also including the non-monophyletic *Pseudolatirus*;
2) *Peristernia nassatula* clade, consisting of the non-monophyletic *Peristernia* and *Fusolatirus*; the name Peristerniinae can be retained for this clade;
3) *Fasciolaria tulipa* clade, consisting of a monophyletic *Fasciolaria-Pleuroploca* clade and many other genera currently classified as peristerniines, among which the genera *Latirus*, *Leucozonia*, and *Hemipolygona* appeared non-monophyletic; deep nodes within this clade were unresolved or poorly supported. The taxonomic extension of the subfamily Fasciolariinae can be revised to encompass this third clade.

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References

Abbott, R.T., 1958. The marine mollusks of Grand Cayman Island, British West Indies. Monogr. Acad. Nat. Sci. Philadelphia 11, 1–138.

Aktipis, S.H., Boehm, E., Giribet, G., 2011. Another step towards understanding the slit-limpets (Fissurellidae, Fissurelloidea, Vetigastropoda, Gastropoda): a combined five-gene molecular phylogeny. Zool. Scr. 40, 238–259.

Auwera, G.V, Chapelle, S., De Wächter, R., 1994. Structure of the large ribosomal subunit RNA of *Phytophthora megasperma*, and phylogeny of the Oomycetes. FEBS Lett. 338, 133–136.

Bandel, K., 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda. Zool. Verh. 214, 1–188.

Bandel, K., 1993. Caenogastropoda during Mesozoic times. Scr. Geol. Special vol. 2, 7–56.

Benton, M.J., 1993. The Fossil Record 2, in: Benton, M.J. (Ed.), Chapman and Hall, London, pp. 845 (http://www.fossilrecord.net/fossilrecord/).

Beu, A., 2011. Marine Mollusca of isotope stages of the last 2 million years in New Zealand. Part 4. Gastropoda (Ptenoglossa, Neogastropoda, Heterobranchia). J. R. Soc. N.Z. 41, 11–53.

Bouchet, P., Rocroi, J.P. 2005. Classification and nomenclator of gastropod families. Malacologia 47, 1–397.

Bullock, R.C., 1974. A contribution to the systematics of some West Indian *Latirus* (Gastropoda: Fasciolariidae). Nautilus 88, 69–79.

Callomon, P., Snyder, M.A., 2009. On the genus *Fusinus* in Japan. V: Further species, an unnamed form and discussion. Venus 67(3-4), 1–14.

Carpenter, J.M., Wheeler, W.C., 1999. Towards simultaneous analysis of morphological and molecular data in Hymenoptera. Zool. Scr. 28, 251–260.

Colgan, D., Ponder, W.F., Eggler, P.E., 2000. Gastropod evolutionary rates and phylogenetic relationships assessed using partial 28S rDNA and histone H3 sequences. Zool. Scr. 29, 29–63.

Colgan, D.J., McLauchlan, A., Wislon, G.D.F., Livingston, S., Edgecombe, G.D., Macaranas, J., Cassis, G., Gray, M.R., 1998. Molecular phylogenetics of the Arthropoda: relationships based on histone H3 and U2 snRNA DNA sequences. Aust. J. Zool. 46, 419–37.

Colgan, D.J., Ponder, W.F., Beacham, E., Macaranas, J.M., 2003. Molecular phylogenetic studies of Gastropoda based on six gene segments representing coding or non-coding and mitochondrial or nuclear DNA. Moll. Res. 23, 123–148.

Colgan, D.J., Ponder W.F., Beacham, E. Macaranas, J., 2007. Molecular phylogenetics of Caenogastropoda (Gastropoda: Mollusca). Mol. Phylogenet. Evol. 42, 717–737.

Couto, D.R., Pimenta, A.D., 2012. Comparative morphology of *Leucozonia* from Brazil (Neogastropoda: Buccinoidea: Fasciolariidae). Am. Malacol. Bul. 30, 103–116.

Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. Nat. Meth. 9, 772.

Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucl. Acids Res. 32, 1792–1797.

Edgecombe, G.D., Giribet, G., 2006. A century later – a total evidence re-evaluation of the phylogeny of scutigeromorph centipedes (Myriapoda: Chilopoda). Invertebr. Syst. 20, 503–525.

Fedosov, A.E., Kantor. Y.I., 2012. A new species and genus of enigmatic turriform Fasciolariidae from the Central Indo-Pacific (Gastropoda: Neogastropoda). Arch. Molluskenkunde 141, 137–144.

Folmer, O., Black, M., Hoeh, W., Lutz, R. Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotechnol. 3, 294–299.

Fraussen, K., Kantor, Y. Hadorn, R., 2007. *Amiantofusus* gen. nov. for *Fusus amiantus* Dall, 1889 (Mollusca: Gastropoda: Fasciolariidae) with description of a new and extensive Indo-West Pacific radiation. Novapex 8, 79–101.

Galindo, L.A., Puillandre, N., Strong, E.E. Bouchet, P., 2014. Using microwaves to prepare gastropod for DNA barcoding. Mol. Ecol. Res. 14, 700–705.

Geller, J., Meyer, C., Parker, M., Hawk, H., 2013. Redesign of PCR primers for mitochondrial cytochrome *c* oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. Mol. Ecol. Resour. 13, 851–861.

Giribet, G., Carranza, S., Baguñà, J., Riutort, M., Ribera, C., 1996. First molecular evidence for the existence of a Tardigrada + Arthropoda clade. Mol. Biol. Evol. 13, 76–84.

Giribet, G., Shear, W.A., 2010. The genus *Siro* Latreille, 1796 (Opiliones, Cyphophthalmi, Sironidae), in North America with a phylogenetic analysis based on molecular data and the description of four new species. Bull. Mus. Comp. Zool. 160, 1–33.

Goodheart, J., Camacho-García, Y., Padula, V., Schrödl, M., Cervera, J. L., Gosliner, T. M., Valdés, Á. 2015. Systematics and biogeography of *Pleurobranchus* Cuvier, 1804, sea slugs (Heterobranchia: Nudipleura: Pleurobranchidae). Zool. J. Linn. Soc. 174, 322–362.

Grabau, A.W., 1907. Studies of Gastropoda III. On orthogenetic variation in Gastropoda. Am. Nat. 607–651.

Guindon, S., Gascuel, O., 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Syst. Biol. 52, 696–704.

Harasewych, M.G., 1990. Studies on bathyal and abyssal Buccinidae (Gastropoda: Neogastropoda): 1. *Metula fusiformis* Clench and Aguayo, 1941. Nautilus 104, 120–130.

Harasewych, M.G., Adamkewicz, S.L., Blake, J.A., Saudek, D., Spriggs, T. Bult C.J., 1997. Neogastropod phylogeny: A molecular perspective. J. Moll. Stud. 63, 327–351.

Hayashi, S., 2005. The molecular phylogeny of the Buccinidae (Caenogastropoda: Neogastropoda) as inferred from the complete mitochondrial 16S rRNA gene sequences of selected representatives. Moll. Res. 25, 85–98.

Kantor, Y.I., Fedosov. A., 2009. Morphology and development of the valve of Leiblein: possible evidence for paraphyly of the Neogastropoda. Nautilus 123, 1–73.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Stones-Havas, S., Duran, C., Thierer, S., Ashton, B., Meintjes, P. Drummond, A., 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28, 1647–1649.

Kishino, H., Hasegawa, M., 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. J. Mol. Evol. 29, 170–179.

Kocot, K.M., Cannon, J.T., Todt, C., Citarella, M.R., Kohn, A.B., Meyer, A., Santos, S.R., Schander, C., Moroz, L.L. Lieb, A. Halanych, K.M., 2011. Phylogenomics reveals deep molluscan relationships. Nature 477, 452–456.

Kosyan, A.R., Modica, M.V., Oliverio, M., 2009. The anatomy and relationships of *Troschelia* (Neogastropoda, Buccinidae): New evidence for a closer fasciolariid-buccinid relationship? Nautilus, 123, 95–105.

Kuroda, T., Habe, T., 1952. Check list and bibliography of the recent marine Mollusca of Japan. Tokyo, pp. 210.

Kuroda, T., Habe, T., 1954. On some Japanese Mollusca described by A. Adams, whose specimens are deposited in the Redpath Museum of Canada (No. 1). Venus 18, 1–16.

Leal, J.H., 1991. Marine prosobranch gastropods from oceanic islands off Brazil: species composition and biogeography. Universal Book Services/W. Backhuys. pp. 418.

Lyons, W.G., 1991. Post-Miocene species of *Latirus* Montfort, 1810 (Mollusca: Fasciolariidae) of southern Florida, with a review of regional marine biostratigraphy. Bull. Fla. Mus. Nat. Hist. (Biol. Sci.) 34, 131–208.

Lyons, W.G., Snyder, M.A., 2013. The genus *Pustulatirus* Vermeij and Snyder, 2006 (Gastropoda: Fasciolariidae: Peristerniinae) in the western Atlantic, with descriptions of three new species. Zootaxa 3636, 35–58.

Meyer, A., Todt, C., Mikkelsen, N. Lieb, B., 2010. Fast evolving 18S rRNA sequences from Solenogastres (Mollusca) resist standard PCR amplification and give new insights into mollusk substitution rate heterogeneity. BMC Evol. Biol. 10, 70.

Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Gateway Computing Environments Workshop (GCE), pp. 1–8.

Nagai, M., Yoshida, A. Sato, N., 1998. Additive effects of bovine serum albumin, dithiothreitol and glycerolon PCR. Int. Union Biochem. Mol. Biol. Life 44, 157–163.

Oliverio, M., Modica, M.V., 2010. Relationships of the haematophagous marine snail *Colubraria* (Rachiglossa: Colubrariidae), within the neogastropod phylogenetic framework. Zool. J. Linn. Soc. 158, 779–800.

Osca, D., Templado, J. Zardoya, R., 2015. Caenogastropod mitogenomics. Mol. Phylogenet. Evol. 98, 118–128.

Palumbi, S.R. 1996. Nucleic acids II: the polymerase chain reaction. Mol. Syst. 2, 205–247.

Ponder, W.F., Colgan, D.J., Healy, J.M., Nützel, A., Simone, L.R.L., Strong, E.E., 2008. Caenogastropoda in: Ponder, W.F., Lindberg, D.R. (Eds.), Phylogeny and evolution of the Mollusca. Univ. Calif. Press. pp. 331–383.

Ponder, W.F., 1972. Notes on some Australian species and genera of the family Buccinidae (Neogastropoda). J. Malacol. Soc. Aust. 2, 249–265.

Ponder, W.F., Lindberg D.R., 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. Zool. J. L. Soc. 119, 83–265.

Poppe, G.T., 2008. Philippine marine mollusks: Gastropoda, Pt. 2. ConchBooks. pp. 848.

Puillandre, N., Kantor, Y.I., Sysoev, A., Couloux, A., Meyer, C., Rawlings, T., Todd, J.A. Bouchet, P., 2011. The dragon tamed? A molecular phylogeny of the Conoidea (Gastropoda). J. Moll. Stud. 77, 259–272.

Rambaut, A., Suchard, M.A., Xie, D., Drummond, A.J., 2014. Tracer v1. 6. Computer program and documentation distributed by the author, website http://beast. bio. ed. ac. uk/Tracer [accessed 27 July 2014].

Riedel, F., 2000 Ursprung und evolution der "höheren" Caenogastropoda. Berl. Geowiss. Abhhandl. Reihe E Paläobiol. 32, 1–240.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61, 539–542.

Rosenberg, G. 1992. The Encyclopedia of Seashells. Dorset Press, New York. 224 pp.

Schwendinger, P.J., Giribet, G., 2005. The systematics of the south-east Asian genus *Fangensis* Rambla (Opiliones : Cyphophthalmi : Stylocellidae). Inv. Syst. 19, 297–323.

Sharma, P.P., Zardus J.D., Boyle, E.E., González, V.L. Jennings, R.M., McIntyre, E., Wheeler, W.C., Etter, R.J. Giribet, G., 2013. Into the deep: a phylogenetic approach to the bivalve subclass Protobranchia. Mol. Phylogenet. Evol. 69, 188–204.

Shimodaira, H., 2002. An approximately unbiased test of phylogenetic tree selection. Syst. Biol. 51, 492–508.

Shimodaira, H., Hasegawa, M., 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Mol. Biol. Evol. 16, 1114–1116.

Shimodaira, H., Hasegawa, M., 2001. CONSEL: for assessing the confidence of phylogenetic tree selection. Bioinformatics 17, 1246–1247.

Shuto, T., 1958. *Granulifusus* from the Miyazaki Group. Trans. Proc. Palaeont. Soc. Japan NS 31, 253–264.

Simone, L.R.L., Cavallari, D.C., Abbate, D., 2013. Revision of the genus *Teralatirus* Coomans 1965 in the Western Atlantic, with an anatomical description of *T. roboreus* (Reeve 1845) (Gastropoda: Neogastropoda: Fasciolariidae). Arch. Molluskenkunde 142, 215–226.

Smith, S.A., Wilson, N.G., Goetz, F.E., Feehery, C., Andrade, S.C., Rouse, G.W., Giribet, G. Dunn, C.W., 2011. Resolving the evolutionary relationships of molluscs with phylogenomic tools. Nature 480, 364–367.

Snyder, M.A. Callomon, P., 2005. On some *Fusolatirus* from Japan and the Philippines, with description of a new species (Gastropoda: Fasciolariidae). Venus 63, 109–119.

Snyder, M.A., 2003. Catalogue of the marine gastropod family Fasciolariidae. Acad. Nat. Sci. Philadelphia. 431 pp.

Snyder, M.A., P. Bouchet, P., 2006. New species and new records of deep-water *Fusolatirus* (Neogastropoda: Fasciolariidae) from the West Pacific. J. Conchol. 39, 1–12.

Snyder, M.A., Vermeij, G.J., Lyons, W.G., 2012. The genera and biogeography of Fasciolariinae (Gastropoda, Neogastropoda, Fasciolariidae). Basteria 76, 31–70.

Stahlschmidt, P., Fraussen, K., 2012. *Crassibougia*, a new genus for *Fusus clausicaudatus* Hinds, 1844, from South Africa, with description of a new species (Gastropoda: Fasciolariidae). Misc. Malacol. 5, 85–93.

Stamatakis, A., 2014. RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. Bioinformatics 31, 1–2.

Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML web servers. Syst. Biol. 57, 758–771.

Strong, E.E., 2003. Refining molluscan characters: morphology, character coding and a phylogeny of the Caenogastropoda. Zool. J. Linn. Soc. 137, 447–554.

Taylor, J.D., Lewis, A., 1995. Diet and radular morphology of *Peristernia* and *Latirolagena* (Gastropoda: Fasciolariidae) from Indo-Pacific coral reefs. J. Nat. Hist. 29, 1143–1154.

Tëmkin, I., 2010. Molecular phylogeny of pearl oysters and their relatives (Mollusca, Bivalvia, Pterioidea). BMC Evol. Biol. 10, 342.

Vermeij, G.J., 1997. The genus *Leucozonia* (Gastropoda: Fasciolariidae) in the Neogene of tropical America. Tulane Stud. Geol. Paleont. 29, 129–134.

Vermeij, G.J., 2001. Innovation and evolution at the edge: origins and fates of gastropods with a labral tooth. Biol. J. Linn. Soc. 72, 461–508.

Vermeij, G.J., Snyder, M.A., 1998. *Leucozonia ponderosa*, a new fasciolariid gastropod from Brazil. Nautilus 112, 117–119.

Vermeij, G.J., Snyder, M.A., 2002. *Leucozonia* and related genera of fasciolariid gastropods: shell-based taxonomy and relationships. Proc. Acad. Nat. Sci. Philadelphia 152, 23–44.

Vermeij, G.J., Snyder, M.A., 2006. Shell characters and taxonomy of *Latirus* and related fasciolariid groups. J. Moll. Stud. 72, 413–424.

Whiting, M.F., Carpenter, J.C., Wheeler, Q.D., Wheeler, W.C., 1997. The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. Syst. Biol. 46, 1–68.

WoRMS, 2015. World Register of Marine Species, http://www.marinespecies.org/ Last accessed 27 October 2015.

Zapata, F., Wilson, N.G., Howison, M., Andrade, S.C., Jörger, K.M., Schrödl, M., Goetz, F.E., Giribet, G., Dunn, C.W., 2014. Phylogenomic analyses of deep gastropod relationships reject Orthogastropoda. Proc. R. Soc. Lond. B Biol. Sci. 281, 1–9.

Zou, S., Li, Q., Kong, L. 2011. Additional gene data and increased sampling give new insights into the phylogenetic relationships of Neogastropoda, within the caenogastropod phylogenetic framework. Mol. Phylogenet. Evol. 61, 425–435.

Table 1

Table 1
List of species sampled and gene fragments included in phylogenetic analyses with GenBank accession numbers. Outgroup species appear in bold.

Taxon			Voucher #	Locality	18S rRNA	28S rRNA	16S rRNA	COI	H3
Amiantofusus candoris	Bu	f	MNHN IM-2013-19759	Bismarck Sea	KT753546	KT753679	KT753807	KT753912	KT754043
Amiantofusus pacificus	Bu	f	MNHN IM-2009-13533	New Caledonia	KT753552	KT753685	KT753812	KT753918	KT754049
Amiantofusus pacificus	Bu	f	MNHN IM-2013-44400	Taiwan	KT753581	KT753714	KT753837	KT753947	KT754078
Amiantofusus sebalis	Bu	f	MNHN IM-2007-32837	Solomon Islands	KT753545	KT753678	–	KT753911	KT754042
Amiantofusus sebalis	Bu	f	MNHN IM-2013-44196	Taiwan	KT753592	KT753725	KT753846	KT753958	KT754089
Angulofusus nedae	Bu	f	MNHN IM-2007-32574	Vanuatu	KT753618	KT753751	–	KT753984	KT754114
Aurantilaria aurantiaca	Bu	f	MZSP 101904	northeast Brazil	KT753649	KT753782	KT753888	KT754013	KT754143
Australaria australasia	Bu	f	MNHN IM-2013-42516	Western Australia	KT753624	KT753757	KT753875	KT753990	KT754120
Benimakia fastigium	Bu	f	FMNH UF-369083	Vanuatu	KT753645	KT753778	–	KT754010	KT754139
Benimakia lanceolata	Bu	f	MNHN IM-2013-11873	Papua New Guinea	KT753593	KT753726	KT753847	KT753959	KT754090
Chryseofusus acherusius	Bu	f	MNHN IM-2013-44302	Taiwan	KT753590	KT753723	KT753844	KT753956	KT754087
Chryseofusus bradneri	Bu	f	MNHN IM-2007-32977	New Caledonia	KT753577	KT753710	KT753833	KT753943	KT754074
Chryseofusus graciliformis	Bu	f	MNHN IM-2007-32797	Solomon Islands	KT753582	KT753715	KT753838	KT753948	KT754079
Chryseofusus graciliformis	Bu	f	MNHN IM-2013-19938	Solomon Sea	KT753597	KT753730	KT753851	KT753963	KT754094
Cinctura hunteria	Bu	f	MCZ 382637	Florida	KT753646	KT753779	KT753887	KT754011	KT754140
Cyrtulus serotinus	Bu	f	MNHN IM-2013-42532	Marquesas Islands	KT753603	KT753736	KT753857	KT753969	KT754099
Dolicholatirus aff. *cayohuesonicus*	Bu	f	MNHN IM-2013-7917	Guadeloupe	KT753540	KT753673	KT753802	KT753907	KT754037
Dolicholatirus aff. *cayohuesonicus*	Bu	f	MNHN IM-2013-20291	Guadeloupe	KT753550	KT753683	KT753810	KT753916	KT754047
Dolicholatirus aff. *spiceri*	Bu	f	MNHN IM-2013-42519	Western Australia	KT753564	KT753697	–	KT753930	KT754061
Dolicholatirus lancea	Bu	f	MNHN IM-2013-16640	Papua New Guinea	KT753572	KT753705	KT753828	KT753938	KT754069
Dolicholatirus sp.	Bu	f	MNHN IM-2009-29739	Western Australia	KT753541	KT753674	KT753803	–	KT754038
Dolicholatirus spiceri	Bu	f	MNHN IM-2013-42515	Western Australia	KT753570	KT753703	KT753826	KT753936	KT754067
Fasciolaria bullisi	Bu	f	FMNH UF-351146	Florida	KT753622	KT753755	KT753874	KT753988	KT754118
Fasciolaria sp.	Bu	f	MNHN IM-2013-55965	French Guiana	KT753626	KT753759	KT753876	KT753992	KT754122
Fasciolaria tulipa	Bu	f	MNHN IM-2013-19559	Guadeloupe	KT753588	KT753721	KT753842	KT753954	KT754085
Filifusus filamentosus	Bu	f	MNHN IM-2013-13107	Papua New Guinea	KT753543	KT753676	KT753805	KT753909	KT754040
Fusinus agatha	Bu	f	MZSP 53680	northeast Brazil	KT753627	KT753760	–	KT753993	–
Fusinus australis	Bu	f	MNHN IM-2013-42512	Western Australia	KT753557	KT753690	KT753816	KT753923	KT754054
Fusinus brasiliensis	Bu	f	MZSP 117595	southeast Brazil	KT753620	KT753753	KT753872	KT753986	KT754116
Fusinus brasiliensis	Bu	f	MZSP 108889	southeast Brazil	KT753640	KT753773	KT753882	KT754005	KT754134
Fusinus colus	Bu	f	MNHN IM-2007-32560	New Caledonia	KT753533	KT753666	KT753796	KT753901	KT754030
Fusinus crassiplicatus	Bu	f	MNHN IM-2007-34663	New Caledonia	KT753551	KT753684	KT753811	KT753917	KT754048
Fusinus excavatus	Bu	f	ANSP A21957	Barbados	KT753634	KT753767	KT753879	KT754000	KT754129
Fusinus filosus	Bu	f	MNHN IM-2013-42523	Congo	KT753553	KT753686	–	KT753919	KT754050
Fusinus forceps	Bu	f	MNHN IM-2007-38235	Madagascar	KT753574	KT753707	KT753830	KT753940	KT754071
Fusinus gracillimus	Bu	f	MNHN IM-2013-42521	Mozambique	KT753558	KT753691	KT753817	KT753924	KT754055
Fusinus longissimus	Bu	f	MNHN IM-2007-32535	Philippines	KT753534	KT753667	–	–	KT754031
Fusinus mauiensis	Bu	f	FMNH 413989	Hawaii	KT753621	KT753754	KT753873	KT753987	KT754117
Fusinus pulchellus	Bu	f	MCZ 378473	France	KT753630	KT753763	–	KT753996	KT754125
Fusinus salisburyi	Bu	f	MNHN IM-2007-32588	New Caledonia	KT753609	KT753742	KT753863	KT753975	KT754105
Fusinus sandvichensis	Bu	f	FMNH UF-414048	Hawaii	KT753637	KT753770	–	KT754002	KT754131
Fusinus sandvichensis	Bu	f	FMNH 414020	Hawaii	KT753644	KT753777	KT753886	KT754009	KT754138
Fusinus similis	Bu	f	ANSP A20012/411168	Japan	KT753652	KT753785	KT753890	KT754016	KT754146
Fusinus syracusanus	Bu	f	MNHN IM-2013-32440	Tunisia	KT753602	KT753735	KT753856	KT753968	KT754098
Fusinus virginiae	Bu	f	MNHN IM-2007-36654	Madagascar	KT753578	KT753711	KT753834	KT753944	KT754075
Fusolatirus bruijnii	Bu	f	MNHN IM-2013-16671	Papua New Guinea	KT753538	KT753671	KT753800	KT753905	KT754035
Fusolatirus bruijnii	Bu	f	MNHN IM-2013-18013	Papua New Guinea	KT753613	KT753746	KT753867	KT753979	KT754109
Fusolatirus pachyus	Bu	f	MNHN IM-2007-35084	New Caledonia	KT753595	KT753728	KT753849	KT753961	KT754092
Fusolatirus pearsoni	Bu	f	MNHN IM-2007-32495	Vanuatu	KT753555	KT753688	KT753814	KT753921	KT754052
Fusolatirus rikae	Bu	f	MNHN IM-2007-32498	Vanuatu	KT753610	KT753743	KT753864	KT753976	KT754106
Fusolatirus sp.	Bu	f	MNHN IM-2007-38359	Madagascar	KT753573	KT753706	KT753829	KT753939	KT754070
Fusolatirus sp.	Bu	f	MNHN IM-2007-32508	Vanuatu	KT753616	KT753749	KT753870	KT753982	KT754112
Granulifusus aff. *kiranus*	Bu	f	MNHN IM-2013-19037	Bismarck Sea	KT753600	KT753733	KT753854	KT753966	KT754096
Granulifusus aff. *niponicus*	Bu	f	MNHN IM-2007-32823	New Caledonia	KT753584	KT753717	–	KT753950	KT754081
Granulifusus bacciballus	Bu	f	MNHN IM-2007-35089	New Caledonia	KT753563	KT753696	KT753822	KT753929	KT754060
Granulifusus benjamini	Bu	f	MNHN IM-2007-32816	New Caledonia	KT753566	KT753699	–	KT753932	KT754063
Granulifusus hayashi	Bu	f	MNHN IM-2013-19210	Bismarck Sea	KT753589	KT753722	KT753843	KT753955	KT754086
Granulifusus niponicus	Bu	f	MNHN IM-2013-19903	Solomon Sea	KT753569	KT753702	–	KT753935	KT754066
Granulifusus sp.	Bu	f	MNHN IM-2013-19724	Bismarck Sea	KT753556	KT753689	KT753815	KT753922	KT754053
Granulifusus sp.	Bu	f	MNHN IM-2009-6658	Solomon Islands	KT753561	KT753694	KT753820	KT753927	KT754058
Granulifusus staminatus	Bu	f	MNHN IM-2007-32750	Philippines	KT753607	KT753740	KT753861	KT753973	KT754103
Hemipolygona armata	Bu	f	MNHN IM-2013-42511	Senegal	KT753608	KT753741	KT753862	KT753974	KT754104
Hemipolygona mcgintyi	Bu	f	MZSP 36166	Florida USA	KT753659	KT753792	–	KT754023	KT754152
Lamellilatirus lamyi	Bu	f	MNHN IM-2013-56511	French Guiana	KT753642	KT753775	KT753884	KT754007	KT754136
Latirolagena smaragdulus	Bu	f	MNHN IM-2007-32547	Vanuatu	KT753598	KT753731	KT753852	KT753964	–
Latirus amplustre	Bu	f	FMNH UF-410623	Kiribati	KT753657	KT753790	KT753894	KT754021	KT754150
Latirus belcheri	Bu	f	MNHN IM-2007-32490	Vanuatu	KT753587	KT753720	–	KT753953	KT754084
Latirus gibbulus	Bu	f	MNHN IM-2007-32544	Philippines	KT753542	KT753675	KT753804	KT753908	KT754039
Latirus pictus	Bu	f	MNHN IM-2013-10540	Papua New Guinea	KT753601	KT753734	KT753855	KT753967	KT754097
Latirus polygonus	Bu	f	MZSP 99782	Djibouti	KT753629	KT753762	KT753878	KT753995	KT754124
Latirus vischii	Bu	f	MNHN IM-2009-15038	south Madagascar	KT753547	KT753680	KT753808	KT753913	KT754044
Leucozonia cerata	Bu	f	MZSP 63825	Ecuador	KT753643	KT753776	KT753885	KT754008	KT754137
Leucozonia nassa brasiliana	Bu	f	MZSP 117596	southeast Brazil	KT753628	KT753761	KT753877	KT753994	KT754123
Leucozonia nassa brasiliana	Bu	f	MZSP 103954	southeast Brazil	KT753648	KT753781	–	KT754012	KT754142

(*continued on next page*)

Table 1 (*continued*)

Taxon			Voucher #	Locality	18S rRNA	28S rRNA	16S rRNA	COI	H3
Leucozonia nassa cingulifera	Bu	f	MZSP 112955	offshore northeast Brazil	KT753655	KT753788	KT753892	KT754019	KT754148
Leucozonia nassa nassa	Bu	f	MNHN IM-2013-20181	Guadeloupe	KT753535	KT753668	KT753797	KT753902	KT754032
Leucozonia nassa nassa	Bu	f	MNHN IM-2007-9388	Guadeloupe	KT753568	KT753701	KT753825	KT753934	KT754065
Leucozonia nassa nassa	Bu	f	MZSP 69365	Dominican Republic	KT753636	KT753769	–	–	–
Leucozonia ocellata	Bu	f	MNHN IM-2013-20444	Guadeloupe	KT753612	KT753745	KT753866	KT753978	KT754108
Leucozonia ponderosa	Bu	f	MZSP 115436	southeast Brazil	KT753654	KT753787	KT753891	KT754018	–
Nodolatirus rapanus	Bu	f	MNHN IM-2013-42534	Austral Islands	KT753539	KT753672	KT753801	KT753906	KT754036
Opeatostoma pseudodon	Bu	f	MZSP 68483	Ecuador	KT753661	–	KT753897	KT754025	–
Peristernia forskalii	Bu	f	MNHN IM-2013-42522	Mozambique	KT753537	KT753670	KT753799	KT753904	KT754034
Peristernia gemmata	Bu	f	MNHN IM-2013-42528	Marquesas Islands	KT753614	KT753747	KT753868	KT753980	KT754110
Peristernia marquesana	Bu	f	MNHN IM-2013-15306	Papua New Guinea	KT753548	KT753681	–	KT753914	KT754045
Peristernia marquesana	Bu	f	MNHN IM-2007-32486	Vanuatu	KT753567	KT753700	KT753824	KT753933	KT754064
Peristernia nassatula	Bu	f	MNHN IM-2007-32487	Vanuatu	KT753579	KT753712	KT753835	KT753945	KT754076
Peristernia nassatula	Bu	f	MNHN IM-2013-18061	Papua New Guinea	KT753591	KT753724	KT753845	KT753957	KT754088
Peristernia reincarnata	Bu	f	MNHN IM-2007-32482	Vanuatu	KT753575	KT753708	KT753831	KT753941	KT754072
Peristernia sp.	Bu	f	MNHN IM-2013-17660	Papua New Guinea	KT753560	KT753693	KT753819	KT753926	KT754057
Peristernia sp.	Bu	f	MNHN IM-2013-10337	Papua New Guinea	KT753580	KT753713	KT753836	KT753946	KT754077
Peristernia sp.	Bu	f	MNHN IM-2013-10336	Papua New Guinea	KT753599	KT753732	KT753853	KT753965	KT754095
Peristernia sp.	Bu	f	MNHN IM-2013-12522	Papua New Guinea	KT753604	KT753737	KT753858	KT753970	KT754100
Peristernia sp.	Bu	f	MNHN IM-2013-13553	Papua New Guinea	KT753611	KT753744	KT753865	KT753977	KT754107
Peristernia sp.	Bu	f	FMNH 457386	Guam	KT753656	KT753789	KT753893	KT754020	KT754149
Pleuroploca trapezium	Bu	f	MNHN IM-2009-15358	south Madagascar	KT753576	KT753709	KT753832	KT753942	KT754073
Pleuroploca trapezium	Bu	f	MNHN IM-2007-32591	Vanuatu	KT753596	KT753729	KT753850	KT753962	KT754093
Polygona angulata	Bu	f	MZSP 112907	northeast Brazil	KT753619	KT753752	KT753871	KT753985	KT754115
Polygona bernadensis	Bu	f	MNHN IM-2013-56077	French Guiana	KT753635	KT753768	–	KT754001	KT754130
Polygona infundibulum	Bu	f	MNHN IM-2013-19591	Guadeloupe	KT753585	KT753718	KT753840	KT753951	KT754082
Pseudolatirus aff. *pallidus*	Bu	f	MNHN IM-2007-32913	Philippines	KT753586	KT753719	KT753841	KT753952	KT754083
Pseudolatirus discrepans	Bu	f	MNHN IM-2007-34604	Philippines	KT753562	KT753695	KT753821	KT753928	KT754059
Pseudolatirus discrepans	Bu	f	MNHN IM-2007-32791	Solomon Islands	KT753594	KT753727	KT753848	KT753960	KT754091
Pseudolatirus kurodai	Bu	f	MNHN IM-2013-42520	New Caledonia	KT753531	KT753664	–	KT753899	KT754028
Pseudolatirus kuroseanus	Bu	f	MNHN IM-2013-14709	Papua New Guinea	KT753571	KT753704	KT753827	KT753937	KT754068
Pseudolatirus pallidus	Bu	f	MNHN IM-2007-32537	Solomon Islands	KT753544	KT753677	KT753806	KT753910	KT754041
Pseudolatirus sp.	Bu	f	MNHN IM-2007-32510	New Caledonia	KT753565	KT753698	KT753823	KT753931	KT754062
Pustulatirus ogum	Bu	f	MZSP 69481	southeast Brazil	KT753653	KT753786	–	KT754017	KT754147
Pustulatirus praestantior	Bu	f	FMNH UF-359664	west Panama	KT753650	KT753783	–	KT754014	KT754144
Teralatirus noumeensis	Bu	f	MNHN IM-2013-42526	Austral Islands	KT753549	KT753682	KT753809	KT753915	KT754046
Teralatirus noumeensis	Bu	f	MNHN IM-2013-4032	Papua New Guinea	KT753632	KT753765	–	KT753998	KT754127
Teralatirus roboreus	Bu	f	MZSP 108682	Grenada	KT753660	KT753793	KT753896	KT754024	–
Triplofusus giganteus	Bu	f	MCZ 382636	Florida	KT753638	KT753771	KT753880	KT754003	KT754132
Turrilatirus craticulatus	Bu	f	MNHN IM-2007-32504	Vanuatu	KT753554	KT753687	KT753813	KT753920	KT754051
Turrilatirus turritus	Bu	f	MNHN IM-2007-32516	Vanuatu	KT753532	KT753665	–	KT753900	KT754029
Turrilatirus turritus	Bu	f	MNHN IM-2013-17100	Papua New Guinea	KT753615	KT753748	KT753869	KT753981	KT754111
Buccinum undatum	**Bu**	**b**	**MCZ 378265**	**Sweden**	**KT753631**	**KT753764**	**–**	**KT753997**	**KT754126**
Busycon africanus	**Bu**	**b**	**MNHN IM-2013-42510**	**Senegal**	**KT753536**	**KT753669**	**KT753798**	**KT753903**	**KT754033**
Euthria cumulata	**Bu**	**b**	**MNHN IM-2007-34931**	**New Caledonia**	**KT753583**	**KT753716**	**KT753839**	**KT753949**	**KT754080**
***Euthria* sp.**	**Bu**	**b**	**MNHN IM-2007-34934**	**New Caledonia**	**KT753559**	**KT753692**	**KT753818**	**KT753925**	**KT754056**
***Manaria* sp.**	**Bu**	**b**	**MNHN IM-2007-36855**	**Madagascar**	**KT753605**	**KT753738**	**KT753859**	**KT753971**	**KT754101**
Neptunea antiqua	**Bu**	**b**	**MCZ 378610**	**Sweden**	**KT753623**	**KT753756**	**–**	**KT753989**	**KT754119**
***Prodotia* sp.**	**Bu**	**b**	**MNHN IM-2007-34675**	**New Caledonia**	**KT753606**	**KT753739**	**KT753860**	**KT753972**	**KT754102**
Columbella aureomexicana	**Bu**	**c**	**MCZ 378333**	**Baja California, Mexico**	**KT753633**	**KT753766**	**–**	**KT753999**	**KT754128**
Mitrella scripta	**Bu**	**c**	**MCZ 378586**	**southeast France**	**KT753658**	**KT753791**	**KT753895**	**KT754022**	**KT754151**
Nassarius glans	**Bu**	**n**	**MCZ 378603**	**east Australia**	**KT753641**	**KT753774**	**KT753883**	**KT754006**	**KT754135**
Nassarius reticulatus	**Bu**	**n**	**MCZ 378509**	**Sweden**	**KT753617**	**KT753750**	**–**	**KT753983**	**KT754113**
Conus angasi	**Co**	**c**	**MCZ 382632**	**East Australia**	**KT753663**	**KT753795**	**KT753898**	**KT754027**	**KT754154**
***Phymorhynchus* sp.**	**Co**	**r**	**MCZ 378670**	**Unkown**	**KT753662**	**KT753794**	**–**	**KT754026**	**KT754153**
Thais nodosa	**Mu**	**m**	**MCZ 378809**	**Cameroon**	**KT753639**	**KT753772**	**KT753881**	**KT754004**	**KT754133**
Thais speciosa	**Mu**	**m**	**MCZ 378767**	**Baja California, Mexico**	**KT753647**	**KT753780**	**–**	**–**	**KT754141**
Erosaria erosa	**Cy**	**c**	**MCZ 378355**	**east Australia**	**KT753625**	**KT753758**	**–**	**KT753991**	**KT754121**
Monetaria annulus	**Cy**	**c**	**MCZ 378587**	**east Australia**	**KT753651**	**KT753784**	**KT753889**	**KT754015**	**KT754145**

Bu = Buccinoidea. f = Fasciolariidae. b = Buccinidae. c = Columbellidae. n = Nassariidae. Co = Conoidea. c = Conidae. r = Raphitomidae. Mu = Muricoidea. m = Muricidae. Cy = Cypraeoidea. c = Cypraeidae.

Table 2

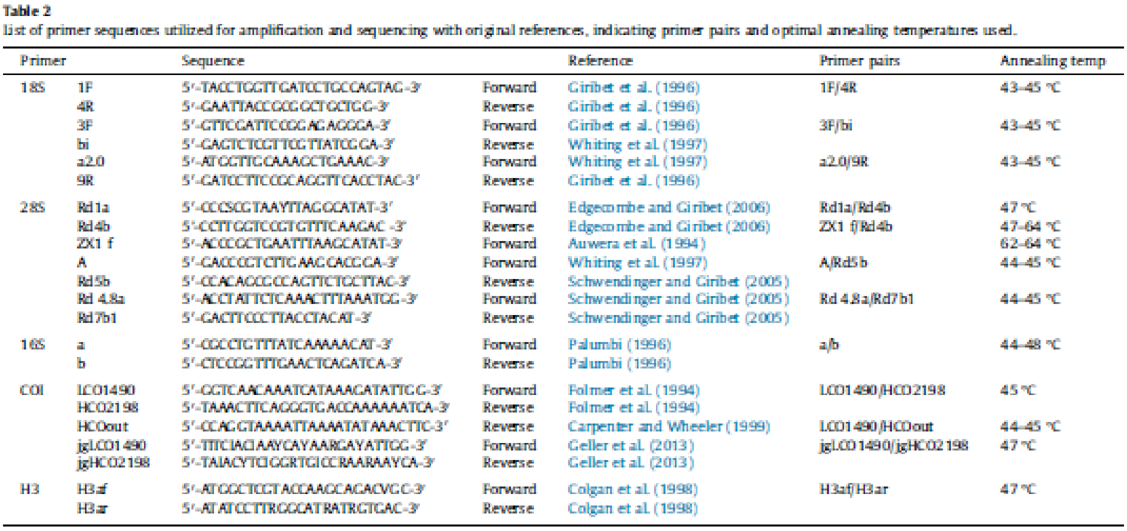

Table 2

List of primer sequences utilized for amplification and sequencing with original references, indicating primer pairs and optimal annealing temperatures used.

Primer		Sequence		Reference	Primer pairs	Annealing temp
18S	1F	5′-TACCTGGTTGATCCTGCCAGTAG-3′	Forward	Giribet et al. (1996)	1F/4R	43–45 °C
	4R	5′-GAATTACCGCGGCTGCTGG-3′	Reverse	Giribet et al. (1996)		
	3F	5′-GTTCGATTCCGGAGAGGGA-3′	Forward	Giribet et al. (1996)	3F/bi	43–45 °C
	bi	5′-GAGTCTCGTTCGTTATCGGA-3′	Reverse	Whiting et al. (1997)		
	a2.0	5′-ATGGTTGCAAAGCTGAAAC-3′	Forward	Whiting et al. (1997)	a2.0/9R	43–45 °C
	9R	5′-GATCCTTCCGCAGGTTCACCTAC-3′	Reverse	Giribet et al. (1996)		
28S	Rd1a	5′-CCCSCGTAAYTTAGGCATAT-3′	Forward	Edgecombe and Giribet (2006)	Rd1a/Rd4b	47 °C
	Rd4b	5′-CCTTGGTCCGTGTTTCAAGAC -3′	Reverse	Edgecombe and Giribet (2006)	ZX1 f/Rd4b	47–64 °C
	ZX1 f	5′-ACCCGCTGAATTTAAGCATAT-3′	Forward	Auwera et al. (1994)		62–64 °C
	A	5′-GACCCGTCTTGAAGCACGCA-3′	Forward	Whiting et al. (1997)	A/Rd5b	44–45 °C
	Rd5b	5′-CCACAGCGCCAGTTCTGCTTAC-3′	Reverse	Schwendinger and Giribet (2005)		
	Rd 4.8a	5′-ACCTATTCTCAAACTTTAAATGG-3′	Forward	Schwendinger and Giribet (2005)	Rd 4.8a/Rd7b1	44–45 °C
	Rd7b1	5′-GACTTCCCTTACCTACAT-3′	Reverse	Schwendinger and Giribet (2005)		
16S	a	5′-CGCCTGTTTATCAAAAACAT-3′	Forward	Palumbi (1996)	a/b	44–48 °C
	b	5′-CTCCGGTTTGAACTCAGATCA-3′	Reverse	Palumbi (1996)		
COI	LCO1490	5′-GGTCAACAAATCATAAAGATATTGG-3′	Forward	Folmer et al. (1994)	LCO1490/HCO2198	45 °C
	HCO2198	5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	Reverse	Folmer et al. (1994)		
	HCOout	5′-CCAGGTAAAATTAAAATATAAACTTC-3′	Reverse	Carpenter and Wheeler (1999)	LCO1490/HCOout	44–45 °C
	jgLCO1490	5′-TITCIACIAAYCAYAARGAYATTGG-3′	Forward	Geller et al. (2013)	jgLCO1490/jgHCO2198	47 °C
	jgHCO2198	5′-TAIACYTCIGGRTGICCRAARAAYCA-3′	Reverse	Geller et al. (2013)		
H3	H3af	5′-ATGGCTCGTACCAAGCAGACVGC-3′	Forward	Colgan et al. (1998)	H3af/H3ar	47 °C
	H3ar	5′-ATATCCTTRGGCATRATRGTGAC-3′	Reverse	Colgan et al. (1998)		

Figure 1

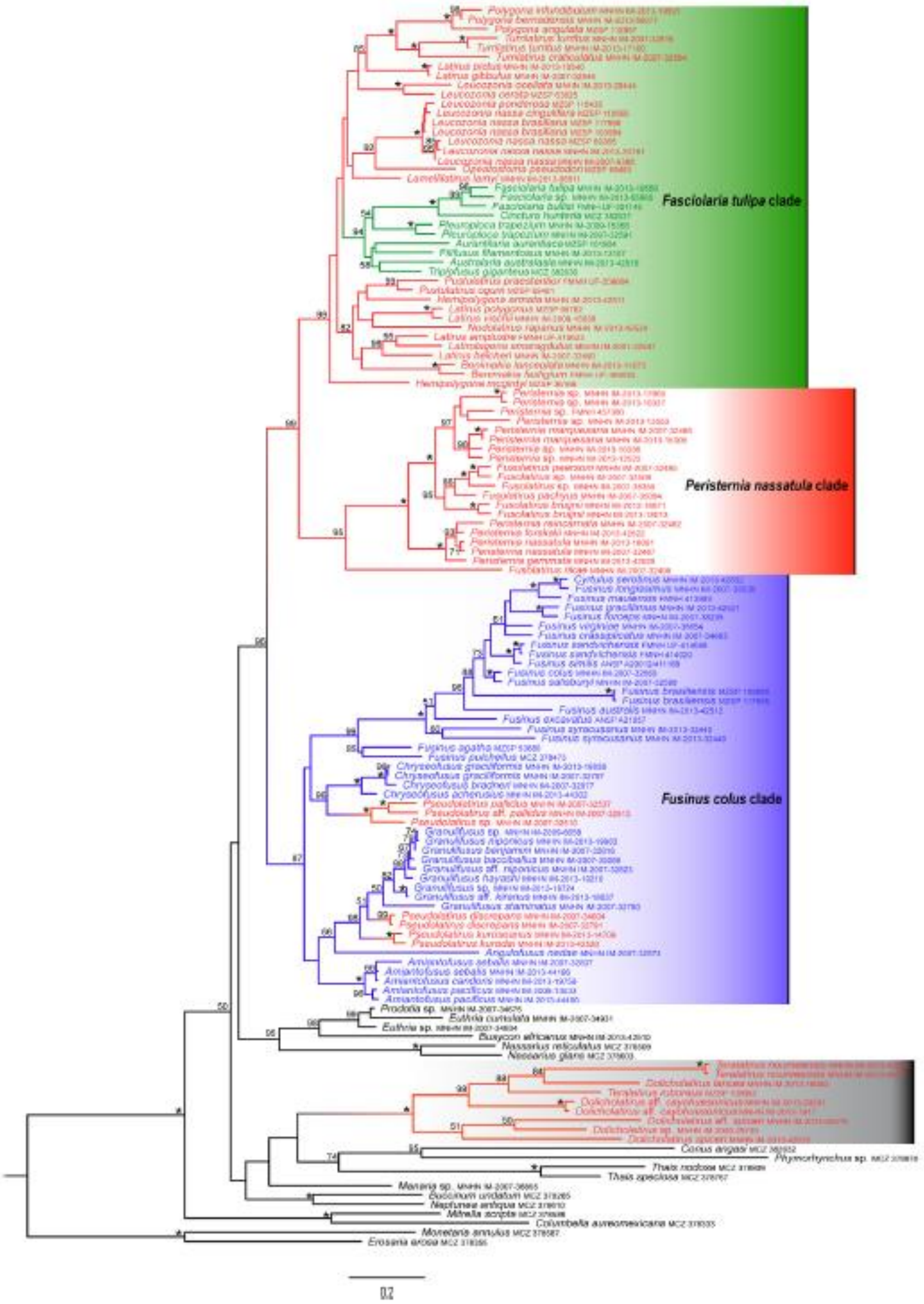

Fig. 1. Phylogenetic relationships of Fasciolariidae based on maximum likelihood analysis of five genes (–ln *L* = 50219.139606). Numbers on nodes indicate bootstrap resampling, only bootstraps over 50 are shown, * indicate BS = 100%. Color of taxon names indicates traditional subfamily placement (green: Fasciolariinae; blue: Fusininae; red: Peristerniinae). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Figure 2

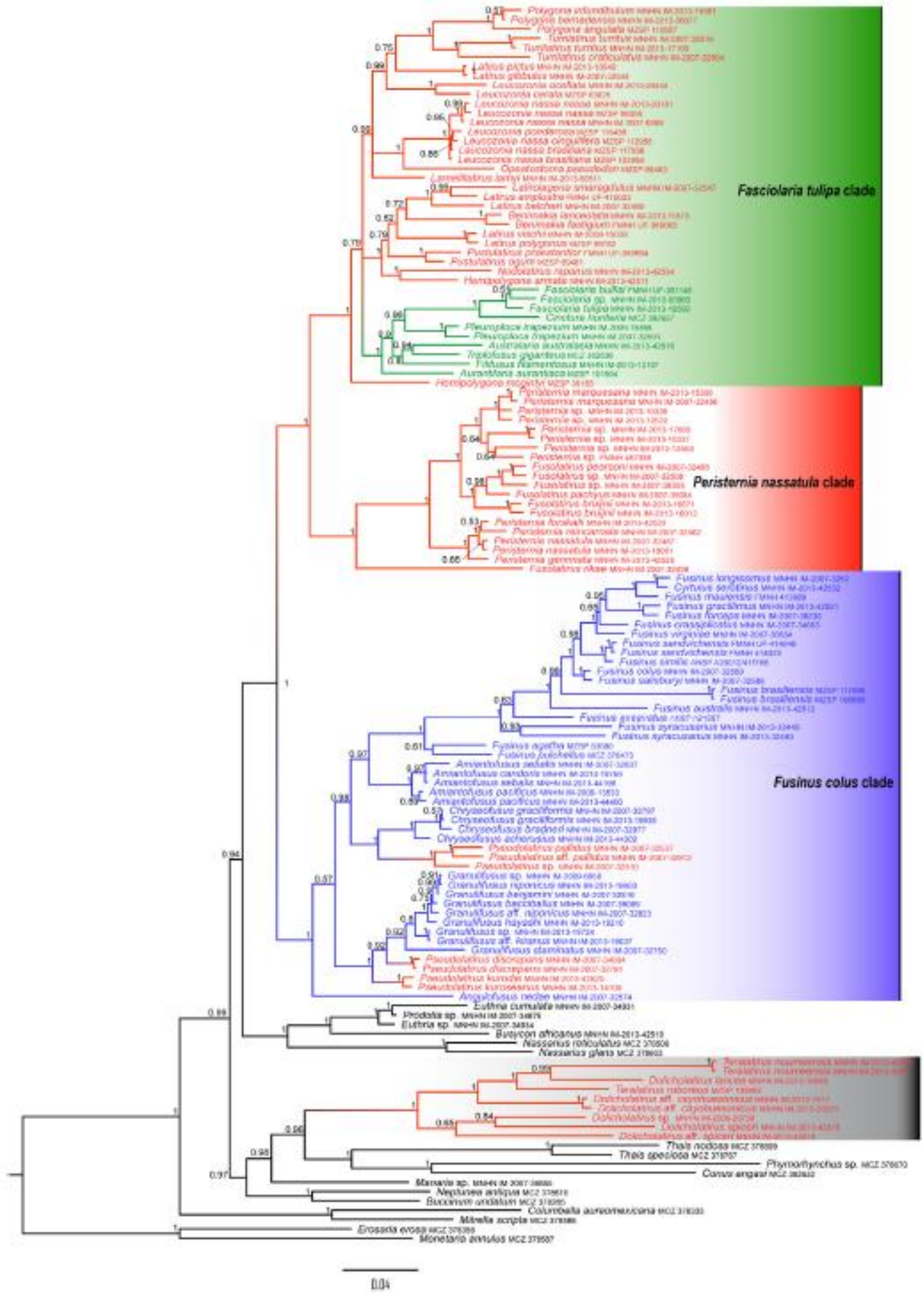

Fig. 2. Phylogenetic relationships of Fasciolariidae based on Bayesian inference analysis of five genes. Numbers on nodes indicate posterior probabilities, only posterior probabilities over 0.5 are shown. Color of taxon names indicates traditional subfamily placement (green: Fasciolariinae; blue: Fusininae; red: Peristerniinae). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Figure 3

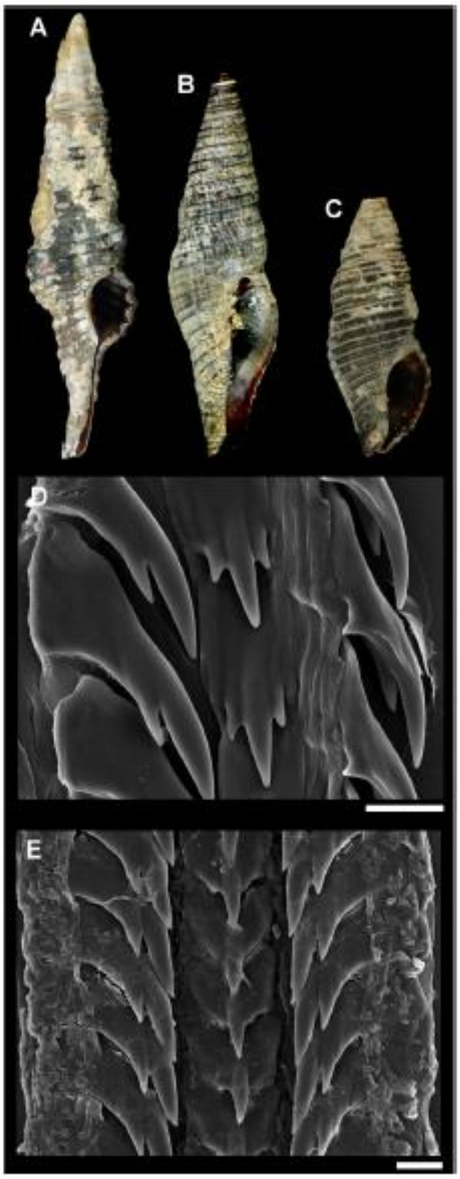

Fig. 3. Vouchers of sequenced non-Fasciolariidae specimens and radulae: A: *Dolicholatirus lancea*, MNHN IM-2013-16640, Papua New Guinea; B: *Dolicholatirus spiceri*, MNHN IM-2013-42515, Western Australia; C: *Dolicholatirus* sp., MNHN IM-2009-29739, Western Australia; D: radula of *Dolicholatirus cayohuesonicus*, MNHN IM-2013-20291, Guadeloupe; E: radula of *Dolicholatirus* sp., MNHN IM-2009-29739, Western Australia. Scale bars = 10 µl.

Figure 4

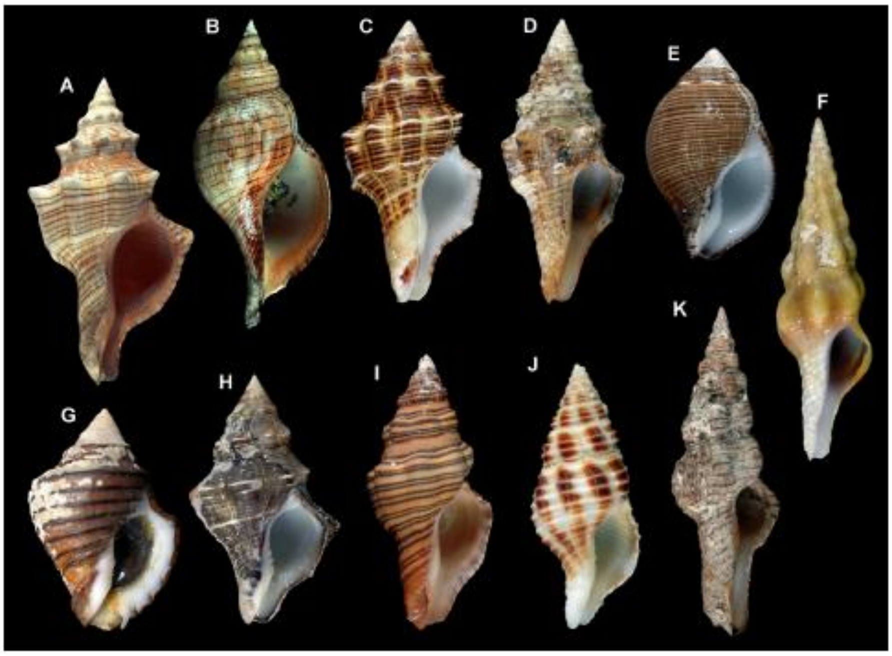

Fig. 4. Vouchers of sequenced specimens of Fasciolariidae: A: *Pleuroploca trapezium*, MNHN IM-2007-32591, Vanuatu; B: *Fasciolaria tulipa*, MNHN IM-2013-19559, Guadeloupe; C: *Latirus vischii*, MNHN IM-2009-15038, south Madagascar; D: *Latirus belcheri*, MNHN IM-2007-32490, Vanuatu; E: *Latirolagena smaragdulus*, MNHN IM-2007-32547, Vanuatu; F: *Benimakia lanceolata*, MNHN IM-2013-11873, Papua New Guinea; G: *Opeatostoma pseudodon*, MZSP 68483, Ecuador; H: *Leucozonia nassa nassa*, MNHN IM-2013-20181, Guadeloupe; I: *Latirus gibbulus*, MNHN IM-2007-32544, Philippines; J: *Turrilatirus craticulatus*, MNHN IM-2007-32504, Vanuatu; K: *Polygona infundibulum*, MNHN IM-2013-19591, Guadeloupe.

Figure 5

Fig. 5. Vouchers of sequenced specimens of Fasciolariidae: *Peristernia nassatula* clade. A: *Peristernia nassatula*, MNHN IM-2007-32487, Vanuatu; B: *Peristernia reincarnata*, MNHN IM-2007-32482, Vanuatu; C: *Peristernia gemmata*, MNHN IM-2013-42528, Marquesas Islands; D: *Peristernia marquesana*, MNHN IM-2007-32486, Vanuatu; E: *Peristernia* sp., MNHN IM-2013-12522, Papua New Guinea; F: *Peristernia* sp., MNHN IM-2013-10337, Papua New Guinea; G: *Fusolatirus bruijnii*, MNHN IM-2013-18013, Papua New Guinea; H: *Fusolatirus pachyus*, MNHN IM-2007-35084, New Caledonia.

Figure 6

Fig. 6. Vouchers of sequenced specimens of Fasciolariidae: *Fusinus colus* clade. A–C: *Cyrtulus serotinus* growth series, Marquesas Islands: A: MNHN IM-2013-42530; B: MNHN IM-2013-4251; C: MNHN IM-2013-42532; D: *Fusinus colus*, MNHN IM-2007-32560, New Caledonia; E: *Amiantofusus sebalis*, MNHN IM-2007-32837, Solomon Islands. F: *Chryseofusus graciliformis*, MNHN IM-2007-32797, Solomon Islands; G: *Pseudolatirus pallidus*, MNHN IM-2007-32537, Solomon Islands; H: *Pseudolatirus* aff. *pallidus*, MNHN IM-2007-32913, Philippines; I: *Pseudolatirus* sp., MNHN IM-2007-32510, New Caledonia; J: *Pseudolatirus kurodai*, MNHN IM-2013-42520, New Caledonia; K: *Pseudolatirus discrepans*, MNHN IM-2007-34604, Philippines; L: *Granulifusus* sp., MNHN IM-2013-19724, Bismarck Sea.