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Where the snails have no name: a molecular phylogeny of Raphitomidae (Neogastropoda: Conoidea) uncovers vast unexplored diversity in the deep seas of temperate southern and eastern Australia

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Abstract :

Although raphitomid snails are a dominant component of gastropod communities in deep seas worldwide, their systematics is still largely tentative. We assembled the most complete sampling of Raphitomidae from south-eastern Australia to date. Based on morphological and molecular data from this material, we produced a robust phylogenetic framework and used it to delimit genera. For the focus area, our results show a large proportion of undescribed species- and genus-level taxa, 11 of which are formally described herein. We demonstrate that the examination of purely morphological characters rarely suffices for the purpose of accurate genus delimitation. As a result, some traditionally highly diverse raphitomid genera (such as Gymnobela) turn out to be artificial assemblages of several unrelated, mostly undescribed, genus-level lineages. Our data suggest that comparable configurations of shell and radular features, observed at the genus level, commonly do not reflect true phylogenetic relationships. However, our results are inconclusive as to whether homoplasy or conservatism are the drivers of this phenomenon. Accommodating for the inevitable sampling biases, south-eastern Australia appears as a possible hotspot for both raphitomid diversity and endemism, when compared with adjacent areas.

Keywords : comparative anatomy, convergence, endemic, mtDNA, taxonomy, shell characters

Introduction

Over a century after the expeditions of the *Challenger*, *Albatross* and *Siboga* (Watson, 1886; Dall, 1908; Schepman, 1913), deep-sea exploration remains one of the major frontiers for the discovery of marine mollusc biodiversity (Bouchet et al., 2016).

Over the last 35 years, deep-sea expeditions have been conducted across the Indo-Pacific under the *Tropical Deep-Sea Benthos* (TDSB) programme, led by the Muséum national d'Histoire naturelle (MNHN) (https://expeditions.mnhn.fr). These expeditions have revealed a significant molluscan diversity, roughly projected to be in the order of 25-30,000 species for the south Pacific (Bouchet et al., 2008). An estimated 5,000 of these comprise the group commonly referred to as turriform conoidean gastropods. Turriform Conoidea, or simply 'turrids', is a conventional name used for the heterogenous assemblage including all but two (Conidae and Terebridae) of the 18 currently recognised families in the neogastropod superfamily Conoidea Fleming, 1822 (Bouchet et al., 2009; Abdelkrim et al., 2018a). Turriform Conoidea is the most diverse group of marine molluscs, with current estimates of 354 valid Recent genera and 3776 named Recent species (Horton et al., 2019). Maximum species diversity within turrids is found in offshore and deep-sea gastropod assemblages where, however, many species exhibit low abundance (Sysoev, 1997; Kantor et al., 2008; Bouchet et al., 2009). In general, turriform conoideans are characterised by considerable morphological homoplasy, with numerous cases where distantly related taxa exhibit almost identical shell shape and sculpture (Sysoev, 1997; Kantor et al., 2008; Bouchet et al., 2009). Because of their high diversity, low abundance and morphological complexity combined, the systematics of deep-sea turriform conoideans below family level remains tentative. Genera and species are diagnosed primarily based on morphology (e.g. Bouchet & Warén, 1980; Sysoev & Kantor, 1990; Sysoev, 1996a; Sysoev, 1996b; Sysoev, 1997; Bouchet & Sysoev, 2001; Sysoev & Bouchet, 2001) and comparatively few genetic studies are available (e.g. Puillandre et al., 2009; Puillandre et al., 2010; Fedosov & Puillandre, 2012; Kantor et al. 2012; Kantor et al., 2016; Abdelkrim et al., 2018b; Kantor et al., 2018; Fassio et al. 2019; Hallan et al., 2019). However, such studies have challenged current species delimitations and highlighted pervasive genus-level paraphyly (e.g. Bouchet & Warén, 1980; Sysoev & Kantor, 1990; Sysoev, 1996a; Sysoev, 1996b; Sysoev, 1997; Bouchet & Sysoev, 2001; Sysoev & Bouchet, 2001; Puillandre et al., 2010; Kantor et al., 2018). Furthermore, a comparatively large proportion of deep-sea turriform conoideans still await description. For many areas, the number of undescribed species far outnumbers that of described species. For instance, it has been estimated that in New Caledonia, about 80% of deep-sea turriform conoideans are undescribed (Bouchet et al., 2008).

The family Raphitomidae Bellardi, 1875 (Bouchet et al., 2011), notably in the deep sea, are among the most poorly studied families of the group (Bouchet et al., 2011). The family comprises a total of 795 Recent accepted species in 65 Recent accepted genera (source WORMS, Horton et al., 2019). Nearly two-thirds of these genera (39), accounting for more than half of the overall raphitomid diversity (418 species), are found below the continental shelf. These figures are based on the notion that bathymetric preferences of turriform conoidean genera are exclusive of either deep- or shallow seas (Bouchet et al., 2009). The type species of almost half of the deep-sea raphitomid genera were described in the 19th century, with only four named after 2000. No molecular data has accompanied these descriptions, with anatomical data provided only occasionally (e.g. Sysoev & Kantor, 1986; Sysoev, 1988; Kantor & Sysoev, 1989; Sysoev & Bouchet, 2001). For the vast majority of these genera, shell features are the only source of taxonomic information accessible from their type species. In addition, descriptions of most deep-sea raphitomids species have been provided in faunistic studies, aiming primarily to present the results of sampling campaigns in a given region and not necessarily to resolve the systematics. Consequently, generic attributions have been almost exclusively based on shell features and are therefore influenced by problems with character interpretation and undetected homoplasies. This issue has resulted in the current situation whereby only three genera contain approximately half of all accepted deep-sea raphitomid species. These genera (*Pleurotomella* Verril, 1872, 100 species; *Gymnobela* Verril, 1884, 75 and *Xanthodaphne* Powell, 1942, 33) have subsequently been colloquially addressed as "dumpsters", acting as provisional containers for newly described species of problematic generic attribution. For instance, Sysoev & Bouchet (2001, p. 305) state: "we somewhat arbitrarily include the *yoshidai* complex of species in *Gymnobela*".

Among the consequences of such unresolved systematics is a tentative status of the current biogeography of deep-sea raphitomids. A search of the Global Biodiversity Information Facility (GBIF - https://www.gbif.org) for the eight most speciose genera (>10 species), reveals that they all occur outside the marine realm for which their type species was described. Most are found in several of the 30 marine realms (as delimited in Costello et al., 2017): *Pleurotomella* and *Gymnobela* occur in 18 and 19 realms respectively, *Phymorhynchus* Dall, 1908 and *Taranis* Jeffreys, 1870 occur in 15 realms, *Xanthodaphne* in 11, and *Nepotilla* Hedley, 1918 in 7.

However, without adequate phylogenetic evidence, genus monophyly cannot be assessed, thus preventing appropriate biogeographical investigation. Assumptions of wide distributions at the genus level, as currently accepted, would be upheld only in a scenario where their monophyly is confirmed. However, large distributions of single genera are currently considered rare (Sigwart, Sutton & Bennett, 2017). In the alternative scenario, any notion of wide distributions would be an artefact of genus paraphyly.

There has been no recent attempt to revise the systematics and biogeography of any deep-sea raphitomid genus. However, this is now possible for the Raphitomidae of southern and south-eastern Australia, since suitable material has become available as a result of a number of expeditions aiming to quantify slope and abyssal biodiversity of the area (Fig. 1) (MacIntosh et al. 2018; Williams, 2018; O'Hara et al., unpublished data). These surveys have yielded a considerable amount of well-preserved gastropod material from depths ranging between approximately 900 and 5000 metres. Our preliminary identification of this material has revealed a predominant raphitomid component, consisting almost exclusively of undescribed taxa.

The present study combines morphological and molecular evidence generated from this newly available material in order to construct a robust phylogenetic framework with the aim to:

a) reconstruct phylogeny of Australian deep-sea Raphitomidae, with inclusion of taxa from adjacent regions, whenever possible and appropriate;
b) delimit and describe new deep-sea raphitomid genera from southern and eastern Australia, to facilitate subsequent taxonomic revisions;
c) explore the biogeographic patterns of the raphitomid fauna in the area and (when possible) compare these with those observed in other adjacent marine regions.

Material and Methods

Sample processing

The study material was collected in a series of voyages along the Australian coast (IN2015_C01, IN2015_C02, IN2017_C01, RE_2017, Great Australian Bight; IN2017_V03, temperate east coast; IN_2018_V06, Tasmanian seamounts) (Fig. 1, Table 1). Additional comparative shallow and deep-sea material of Raphitomidae was studied from other geographic areas obtained through various expeditions: (a) SS10/2005 in southern Western Australia (McEnnulty et al., 2011), (b) several voyages of the MNHN Tropical Deep-Sea Benthos programme (Bouchet et al., 2016) (c) LAMPOS (Arntz & Brey, 2003) and ANDEEP III (Linse et al., 2007) in Antarctica, (d) AFRIDEEP in the south-western Indian Ocean (Türkay & Pätzold, 2009) (Table 1).

The material is deposited at the Australian Museum, Sydney, Australia (AMS), the Muséum national d'Histoire naturelle, Paris, France (MNHN), the South Australian Museum, Adelaide, Australia (SAMA), the Tasmanian Museum and Art Gallery, Hobart, Australia (TMAG), the Western Australian Museum, Perth, Australia (WAM) and the Bavarian State Collection of Zoology, Munich, Germany (ZSM).

Following collection, specimens were either anaesthetised with an isotonic solution of $MgCl_2$ and fixed in 96% ethanol or directly transferred into 96% ethanol. Shells were subsequently drilled to extract the retracted animal. Alternatively, for MNHN post-2012 expeditions, specimens were exposed to microwaves, bodies removed from shells and then fixed in 96% ethanol as described in Galindo et al. (2014). All shells were photographed after fixation and (when not microwaved) prior to extraction of the animal.

Taxon sampling

As a result of ongoing systematic research on the Conoidea at the AMS, over 200 (mostly unpublished) sequences of the mitochondrial gene COI have been obtained, following the protocol described below, from largely undescribed deep-sea raphitomid taxa primarily from southern and eastern Australia. In order to assist with the selection of the study material, the Automatic Barcode Gap Discovery (ABGD) methodology for primary species delimitation (Puillandre et al., 2012) was applied to a dataset containing all COI sequences. The web-based version of ABGD (http:// wwwabi.snv.jussieu.fr/public/abgd) was used with a K2P model. The relative gap width (X) was set to 1, with other parameters left to default. Resulting ABGD groups were considered species hypotheses for sample selection. Subsequently, a subset of samples was constructed that incorporated: (a) a selection of non-Australian species that represented at best the currently accepted supra-specific deep-sea raphitomid taxa (including, when possible, type species), (b) all Australian deep-sea raphitomid species as delimited by ABGD and (c) all Australian deep-sea raphitomid morphospecies for which COI data was not available. For each of the species of (a), (b) and (c), amplification of four additional genes (two mitochondrial - 16S rRNA and 12S rRNA; two nuclear - 28SrRNA and H3) was attempted. When available, additional 12S rRNA, 28SrRNA and H3 sequences were sourced from GenBank (Table 1). The ingroup (on which phylogenetic analyses are based) was assembled by selecting one sample per species of (a), (b) and (c), subject to the availability of at least three out of the total five targeted markers. When possible, specimens used for morphological study (see below) were selected among molecular vouchers to ensure an objective linkage of morphological and phylogenetic information.

From DNA extraction to sequencing

Molecular work was performed in laboratories at two institutions (AMS and MNHN). Unless otherwise stated, the two laboratories followed the same methodology.

DNA was extracted from small pieces of foot muscle by using the Bioline Isolate II Genomic DNA extraction kit for animal tissue, following the standard procedure of the manual (AMS) or using the Epmotion 5075 robot (Eppendorf), following the recommendations of the manufacturer (MNHN). A fragment of three mitochondrial genes [cytochrome oxidase subunit I (COI), rRNA 12S (12S) and rRNA 16S (16S)] and of two nuclear genes [rRNA 28S (28S) and histone H3 (H3)] were amplified using the following primer pairs: LCO1490/HCO2198 for COI (Folmer et al., 1994), 12S-I/12S-III for 12S (Simon et al., 1991), 16SH/16LC for 16S (Palumbi, 1996), C1'/D2 for 28S (Dayrat et al., 2001) and H3A/H3B for H3 (Okusu et al., 2003).

PCR reactions were performed in volumes of 25 µl, containing 3 ng DNA, 1X Qiagen CoralLoad PCR Buffer, 2.5mM $MgCl_2$, 0.25mM dNTP, 0.5mM of each primer, 0.5 µg/µl of BSA and 0.2 µl of Bioline MyTaq DNA polymerase. For COI, 12S, 16S and H3, amplification consisted of an initial denaturation step at 94°C for 4 min, followed by 37 cycles of denaturation at 94°C for 30 s, annealing at respectively 50, 57, 55 and 55°C for 30 s, followed by extension at 72°C for 1 min. The final extension was set to 72°C for 5 min.

Conditions for the 28S fragment were as above, with the exception of 30 denaturation cycles and annealing temperature set to 57°C for 45 s for the latter.

PCR products were purified and sequenced by the Macrogen (AMS) and Eurofins (MNHN) sequencing facilities. Both strands of PCR fragments were purified with ExoSAP (Affymetrix) and cycle-sequenced by use of the PCR primers. Chromatograms were manually corrected for misreads, if necessary, and forward and reverse strands were merged into one sequence file using CodonCode Aligner v. 3.6.1 (CodonCode Corporation, Dedham, MA).

Phylogenetic analyses

Sequences were manually (COI and H3) or automatically (12S, 16S and 28S) aligned using MAFFT online (Rozewicki et al., 2017) by applying the automatic selection of the alignment strategy. Where necessary, resulting alignments were refined by eye. Sequences were deposited in GenBank and BOLD (Table 1). *Turris babylonia* (Linnaeus, 1758) (Turridae), *Lienardia mighelsi* Iredale & Tomlin, 1917 (Clathurellidae) and *Citharomangelia planilabroides* (Tryon, 1884) (Mangeliidae) served as outgroups. Analyses were first performed on each gene separately to check for inconsistency between trees (results not shown). As no supported incongruences were found, all genes were concatenated in a single dataset. Phylogenetic trees were reconstructed by implementing maximum likelihood (ML) and Bayesian inference (BI) methods, using RAxML (Stamatakis, 2006) and MrBayes (Ronquist & Huelsenbeck, 2001) respectively. Both analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2), using RAxML-HPC2 on XSEDE and MrBayes v. 3.2.2 on XSEDE. In all analyses the 16S, 12S and 28S genes and the three codon positions of the COI and H3 genes were treated as independent partitions, with the substitution model set to GTR+G and GTR+G+I for the RAxML and MrBayes analyses, respectively; the parameters of the substitution model were evaluated independently for each partition during the analyses. Robustness of the nodes of the ML trees was assessed using a bootstrapping procedure with 1,000 replicates. Each of the two runs of the BI analysis consisted of six Markov chains and 10,000,000 generations, with five chains, three swaps at each generation, a sampling frequency of one tree per 1,000 generations and a chain temperature set to 0.02. Convergence of each analysis was evaluated using Tracer v. 1.4.1 (Rambaut et al., 2018) to check that all effective sample size values exceeded 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. Nodal support was assessed as posterior probability in the BI analyses.

Morphological examinations

Shell morphology and when possible, internal anatomy, including radular morphology, were studied for at least one specimen for each of the Australian species.

We describe shell morphology using the terminology established by Röckel, Korn & Kohn (1995). Descriptions are based on shells orientated in the traditional way, with the spire uppermost and with the aperture facing the viewer. Protoconchs were measured in standard position and the number of whorls counted according to Bouchet & Kantor (2004). Maximum shell length (SL) and width (SW) were measured using a digital calliper and rounded to the nearest 0.1 mm, with the number of whorls counted according to Bouchet & Kantor (2004).

When removed from ethanol, animals were briefly rehydrated in distilled water. Using standard dissection tools, the foregut organ complex, comprising the proboscis, venom gland, radula and salivary glands, was excised and the radular sac was isolated and placed on a glass slide. During the dissection process, head-foot, mantle, genital and (non-radula) foregut characters were examined where possible. After dissolution in diluted commercial bleach, clusters of hypodermic teeth where rinsed repeatedly in distilled water, then separated into individuals and ligament-connected pairs. Subsequently, the glass stub was affixed to a carbon adhesive placed on a 12 mm diameter aluminium mount. All samples were imaged at Macquarie University, Sydney, using a Phenom XL Scanning Electron Microscope.

Genus delimitation and name application

The genera were delimited according to the following criteria: (1) distinct genera form clades, (2) clades are well-supported (in terms of nodal support), (3) all species in a clade share a unique combination of morphological characters.

When sequences of the type species were not included in the analysis, genus attribution was guided by the co-occurrence in all sequenced specimens of diagnostic shell and radular (or other anatomical) features. When a combination of shell and radular characters, not previously observed in any named raphitomid genus, was shared by all species of a given clade, existing names were not considered applicable. For such clades, new genus names were introduced. When no anatomical data was available and no unequivocally typical shell traits could be observed, we refrained from introducing new genus names.

Abbreviations

12S = 12S ribosomal RNA gene; 16S = 16S ribosomal RNA gene; 28S = 28S ribosomal RNA gene; BI = Bayesian Inference; COI = Cytochrome c oxidase subunit I gene; dry = number of dry shell specimens; CMR = Australian Commonwealth Marine Reserve; GAB = Great Australian Bight; H3 = Histone H3 gene; Ht = holotype; ML = Maximum Likelihood; NSW = New South Wales; NT = Northern Territory; OD = original designation of type species; PNG = Papua New Guinea; Pt = paratype; Qld = Queensland; Tas = Tasmania; SL = shell length (mm); SW = shell width (mm); VIC = Victoria; WA = Western Australia; wet = number of ethanol-preserved (wet) specimens.

Results

Molecular analysis

In the vicinity of the barcode gap (Fig. S1), the ABGD analysis of the complete COI dataset (200+ sequences) consistently returned a partition with 55 groups of sequences (Fig. S2). Sequences of well-established and recognisable species, such as *Spergo fusiformis* (Habe, 1962), *Famelica pacifica* Sysoev & Kantor, 1987 and *Theta lyronuclea* (Clarke, 1959) were correctly grouped by ABGD (in red in Fig. S2), indicating that the inferred gap was reliable. Amplification of at least two additional target genes (among 16S, 12S, 28S and H3) was successful for (at least) one specimen of each of 50 of these species (in bold in Fig. S2). At least three of the target markers were also amplified for 8 additional morphospecies not included in the ABGD analysis due to missing COI sequences. A five-gene dataset was then generated that consisted of sequences from these 58 (50 + 8) Australian deep-sea species, with 18 additional species of Raphitomidae from outside Australia and three outgroup species from other conoidean families (Table 1). Of the total species included, 71 were from deep water and five from shallow water. Most of the Australian species (51) were undescribed. All except three could be assigned to 23 genera, 12 of which were undescribed. Formal taxonomic descriptions of the type species of these newly recognised genera are provided below. In the molecular analysis herein, type species of new genera are represented by sequences of their holotype or of paratype material. Descriptions of additional, non-type species will be presented in subsequent publications. These species are labelled with a combination of the abbreviation 'sp.' and a number (1-5).

For clarity, the following molecular and anatomical comparisons are presented with reference to existing and newly introduced taxon names. However, the underlying taxon delimitations resulted from the combined assessment of the molecular and anatomical differentiation (see Discussion) and were not foregone conclusions preceding the analyses presented in this study.

Phylogenetic analyses were based on a total of 349 sequences (281 newly produced and 68 GenBank-sourced) consisting of: 73 12S sequences (65 new + 8 from GenBank), 77 16S sequences (65 new + 12 from GenBank), 54 28S sequences (39 new + 15 from GenBank), 69 COI sequences (52 new + 17 from GenBank) and 76 H3 sequences (60 new + 16 from GenBank). The final concatenated dataset of aligned sequences had a total length of 2,853 bp (12S: 600 bp, 16S: 536 bp, 28S: 731 bp, COI: 658 bp H3: 328 bp).

While most inferred clades were well-supported by both BI (Fig. 2) and ML trees (Fig. S3), a few of the deeper nodes remained unstable and (in some cases) lacked support. In addition, the occasional presence of polytomy can be attributed to the relatively limited taxon sampling. The description of the tree topology is presented below, with emphasis given to lineages that are consistently retrieved and supported by both analyses and that are relevant to the scope of this study.

All Raphitomidae clustered into three major monophyletic groupings in both BI and ML trees. Two of these clades, A and C, contained exclusively deep-sea taxa; the third clade, B, comprised shallow-water taxa (of which no Australian representatives were included in this analysis).

The smallest of the two deep-sea clades, A, included nine species in three described genera [*Famelica* Bouchet & Warén, 1980 (3 species, 2 new), *Rimosodaphnella* Cossmann, 1916 (3 species, 2 new) and *Veprecula* Melvill, 1917 (1 known species)] and one previously undescribed genus [*Glaciotomella* n. gen n. sp. (2 species, both new)]. The latter genus was sister to a lineage comprising *Veprecula* cf. *spanionema* plus *Rimosodaphnella* spp. and

Famelica spp. All specimens in this clade were collected in temperate Australia, except for *V.* cf. *spanionema* (Philippines) and *Rimosodaphnella* sp. (New Caledonia).

Clade C contained all remaining deep-sea taxa, amounting to 62 species from 22 genera (11 known and 11 new), and 7 species not assigned to any genus. A dichotomy of C separates a small species cluster from a larger clade including the remaining samples.

The former cluster included exclusively unidentified species attributed to *Pleurotomella*, with two from Antarctica and one from SE Australia comprising one subclade, and with one from New Caledonia and one from Western Australia forming the other.

The larger clade was characterised by a basal polytomy, with four subclades containing species of more than one genus, two clades including species of a single genus [*Gladiobela* n. gen. (5 new species) and *Pagodibela* (4 new species)] and five species that did not cluster with any other sample (*Pueridaphne cirrisulcata* n. gen. n. sp., *Typhlosyrinx* sp. and three species unassigned to a genus). The first subclade contained 4 species in three new genera: *Fusobela* n. gen. (possibly 2 new species – see below), *Globodaphne pomum* n. gen. n. sp., *Trochodaphne cuprosa* n. gen. n. sp. and one species unassigned to genus; the second subclade included 10 species in three known genera: *Gymnobela* (4 new species), *Ponthiothauma* E. A. Smith, 1895 (2 new) and *Phymorhynchus* (4 species, 2 new); the third subclade comprised 2 unidentified species in 2 genera (*Mioawateria* Vella, 1954 and *Taranis* Jeffreys, 1870) and the fourth subclade contained 3 species of uncertain generic attribution and 23 species in 9 genera [*Austrotheta* n. gen. (2 new species), *Spergo* (6 species, 4 new, 1 unidentified), *Theta* (3 species, 2 new) and *Austrobela* (7 species, 6 new), *Teretiopsis* (1 unidentified) and *Tatcheria* (1 species) plus the monotypic *Biconitoma* n. gen., *Aplotoma* n. gen. and *Nodothauma* n. gen.] and].

Morphological analyses

Morphological examinations were conducted on all samples of deep-sea species from temperate Australia and form the basis for the taxonomic descriptions below. When possible and applicable, anatomical characters were assessed based on the holotype and on conspecific vouchers sequenced for mtDNA.

Shells, foregut (primarily the radula) and head-foot characters of all candidate genera were compared with features of other raphitomids where such characters are available in the literature, and by the examination of comparative material where necessary.

Of the new taxa, the shell morphology ranged from elongate-fusiform to biconical, and with sculptural elements including cancellate or with axial ribs, tubercles or spiral cords (Figs 3-4). No sculptural elaboration or varix formation/thickening of the aperture, as that seen in some other raphitomid groups such as *Hemilienardia* O. Boettger, 1895 (Fedosov et al., 2017) was observed in the deep-sea taxa. Protoconchs, where available, were largely of the typical diagonally cancellate raphitomid type (Bouchet et al., 2011) (Fig. 5), but arcuate sculpture was also observed in species of *Austrobela* and *Theta* (Fig. 5D). Clarke (1959), reported this protoconch type for *Theta lyronuclea*, which formed part of his rationale to establish the (then) subgenus *Theta.*

Observed foregut morphologies ranged from the entire foregut complex (i.e. proboscis, salivary glands, venom gland and radula) being absent, to extremely large and occupying the majority of the rhynchocoel. The radulae, exclusively of the hypodermic type, varied from simple, awl-shaped without barbs or blades, with a single dorsal blade, to double-barbed (Fig. 6). Simple, awl-shaped teeth with or without a dorsal blade were more prevalent than double-barbed teeth. The morphology of the base varied from being only slightly broader than the basal portion of the shaft (the latter herein defining the tooth length without the base), to exhibiting a distinct lateral process, to very broad and angular. The size and shape of the basal opening was generally homogenous; large, subcircular, and unrestricted [compare to, for example, the restricted, lateral and ovate opening of Strictispiridae and Bouchetispiridae (Bouchet et al., 2011; Kantor & Puillandre, 2012; Hallan et al., 2019)]. The external texture of the base ranged from very fine to very coarse (Fig. 6), whereas the length of the adapical opening, and, where present, the dorsal blade, relative to the length of the shaft ranged from short (~0.1 ratio) to extremely long (~0.5). Eyes were absent in only one taxon (*Biconitoma cretosa* n. gen. n. sp.) and observed in all remaining taxa. The majority of taxa exhibited small to minuscule eyes, whereas some possessed well-developed, large eyes.

Systematics

General remarks

If not stated otherwise, holotypes are dissected ethanol-preserved specimens and form the basis of all systematic descriptions. The number of shell whorls is approximated to one decimal unit. References to size are intended as relative to general patterns observed in the Raphitomidae (see Bouchet et al., 2011). Shell and head-foot colouration reported in descriptions are based on observations performed before fixation and may not be fully reflected in the illustrations provided (Figs 3-5). Unless otherwise stated, the authorship of the taxa described below corresponds to that of the present study.

Superfamily Conoidea Fleming, 1822

Family Raphitomidae Bellardi, 1875

Nodothauma n. gen.

Type species: *Nodothauma magnifica* n. gen. n. sp.: OD, herein.

Etymology: Derived from combination of ‘nodos’ (ancient Greek = toothless, for its lack of radula) and ‘thauma’ (for its resemblance to *Ponthiothauma*).

ZooBank registration: urn:lsid:zoobank.org:act:86B1A839-13E6-45B5-8C77-8B8F8870FBBD

Diagnosis

Shell (Fig. 3A) large, fusiform, orange-brown. Early teleoconch whorls narrow in profile, subsequent whorls somewhat broader in appearance, producing weakly concave shell outline; shoulder pronounced. Subsutural ramp wide, bearing spiral cords and weak axial riblets on its abapical portion. Siphonal canal long, tapering. Aperture large, elongate-pyriform. Columella with elongate burnt-orange stain. Anal sinus wide, u-shaped. Rhynchocoel capacious, inner walls lined with dark red epithelium. Radula and venom apparatus absent.

Nodothauma magnifica n. sp.

(Fig. 3A)

Material examined

Holotype: Australia, GAB, 1927 m, IN2015_C02_137, (-35.558, 134.083), AMS C.532707.

Paratypes: Australia, GAB, 1570 m, IN2015_C02_435, (-34.072, 130.267), 1 wet (SAMA D44139); 1912 m, IN2015_C01_054, (-35.202, 131.629), 1 wet (SAMA D44255); 1509 m, IN2015_C02_134, (-35.345, 134.045), 1 wet (AMS C.532689); 1509 m, IN2015_C02_134, (-35.345, 134.045), 1 wet (AMS C.571573); 1 wet (AMS C.571637); 1927 m, IN2015_C02_137, (-35.558, 134.083), 1 wet (AMS C.571739).

Distribution

Known only from the Great Australian Bight.

Etymology: In reference to its large shell, derived from ‘magnificus’ (Latin = majestic).

ZooBank registration: urn:lsid:zoobank.org:act:FE4DEFB1-2CB0-49DF-9C6C-9AA1042C2365

Description. Shell (Fig. 3A) large (H=71.6 mm, W=24.9 mm), elongate-fusiform, walls rather solid, opaque. Protoconch eroded. Teleoconch of about seven orange-brownish whorls;

spire outline slightly concave. Shoulder pronounced, situated slightly adapical to whorl mid-height in early whorls, and indistinct on late teleoconch whorls. Subsutural ramp wide, concave to very lightly convex; suture impressed. Spiral sculpture below subsutural ramp of well-defined cords, about 12 on penultimate whorl and in excess of 40 on last adult whorl; weaker, but distinct spirals of similar spacing present on lower half of subsutural ramp. Axial sculpture of low opisthocline riblets confined largely to penultimate and last adult whorls, unevenly spaced; elsewhere, collabral growth lines only, most prominent on subsutural ramp with slightly raised cordlets at uneven intervals, reflecting shape of anal sinus. Last adult whorl evenly convex below subsutural ramp, weakly demarcated from long, evenly tapering siphonal canal, producing slight concavity in apertural view. Aperture elongate-pyriform, approximately half of shell length; outer lip thin, unsculptured; inner lip with distinct, rather wide whitish callus; innermost part of columella marked by prominent, elongate burnt-orange vertical stain. Anal sinus wide, moderately deep, broadly u-shaped. Cephalic tentacles broad, muscular, cylindrical, of medium length, with well-developed eyes at their outer base. Rhynchostomal lips thick, with thick-walled, moderately long introvert. Rhynchocoel capacious, internal walls lined in tall, dark red epithelium; oesophagus lined with epithelium of similar appearance. Radula and venom apparatus absent.

Remarks

Nodothauma magnifica n. gen. n. sp. exhibits some similarities to *Abyssobela atoxica* Kantor & Sysoev, 1989, notably in the whorl profile, spiral sculpture, the presence of dark content inside the rhynchocoel, and the absence of a radula and venom apparatus (Kantor & Sysoev, 1989; Y. Kantor, pers comm.) However, *A. atoxica* does not possess eyes (Y. Kantor, pers. comm.), whereas in *N. magnifica* n. gen. the eyes are well-developed and rather large (see Discussion). Polychaete fragments and foraminiferae have been recovered from the intestine of specimen SAMA D44255.

Fusobela n. gen.

Type species: *Fusobela parvioculata* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of ‘fusus’ (Latin = spindle, for its fusiform shell) and ‘bela’ (indicating resemblance with *Gymnobela*).

ZooBank registration: urn:lsid:zoobank.org:act:ED9196C5-E7B8-4FA3-933C-E9BBAA914488

Diagnosis

Shell (Fig. 3B) biconical-fusiform, reddish. Protoconch multispiral. Teleoconch of at least 4 rather narrow whorls. Suture moderately impressed. Subsutural ramp wide. Scultpure of irregular spiral cords on whorl periphery and collabral growth lines. Aperture elongate, about half of shell length. Siphonal canal short, not clearly demarcated from shell base. Anal sinus moderately wide, shallowly u-shaped. Rectal gland large, black. Cephalic tentacles closely set, conical; eyes small. Venom apparatus large. Radula (Fig. 6F) of tightly rolled, slender, rather cylindrical hypodermic teeth with no distinct barbs or blades; base rather narrow, short. Ligament rather long, broad.

Fusobela parvioculata n. sp.

(Figs 3B, 5F)

Material examined

Holotype: Australia, Tasmania, Flat area south of Brians, 1414 m, IN2018_V06_169, (-44.239, 147.293), TMAG E59231.

Distribution

Known only from the type locality.

Etymology: In reference to the reduced size of its eyes, derived from ‘parvus’ (Latin = small) and ‘oculatus’ (Latin = bearing eyes), adjective of feminine gender.

ZooBank registration: urn:lsid:zoobank.org:act:54C64B09-3287-4A66-AA3E-AAB0F84BEFF1

Description. Shell (Fig. 3B) (SL=18.2, SW=8.8) biconical-fusiform, rather thin-walled, semi-translucent. Protoconch multispiral, broadly conical, of 2.7 convex whorls, eroded. Protoconch-teleoconch transition clearly defined, broadly sinuate. Teleoconch of about 4.3 whorls with reddish colouration; columellar area dark reddish; suture moderately impressed. Whorls with moderately wide subsutural ramp, straight to slightly convex throughout teleoconch. Lower portion of whorl evenly convex. Teleoconch sculpture of dense collabral growth lines, extending from subsutural ramp to lower portion of whorl; spiral sculpture of cords, more prominent on periphery and with few weaker cords on subsutural ramp. Last adult whorl weakly convex below subsutural ramp, gently tapering into short siphonal canal. Aperture elongate, approximately half of shell length; outer lip very thin, inner lip straight. Anal sinus moderately wide, shallow, u-shaped.

Anatomy (based on female). Osphradium very large; distinct, large, black rectal gland. Cephalic tentacles closely set, thick, conical; eyes small, black. Muscular bulb very large, venom gland long, convoluted, the majority situated ventral to oesophagus. Proboscis long, with folded walls. Radular sac rather large.

Radula (Fig. 6F) of hypodermic type, straight to gently curved, tightly rolled, slender, rather cylindrical, attaining 285 µm in length; no distinct barb or blade; adapical opening elongate, approaching 1/10 of shaft length; base narrow, comparatively short; external texture medium coarse. Ligament rather long, broad.

Remarks

Fusobela parvioculata n. gen. n. sp. can be differentiated from other raphitomids by the following combination of characters: a biconical-fusiform, reddish shell with short siphonal canal not clearly demarcated from the shell base; conical, broad cephalic tentacles, and long, cylindrical hypodermic teeth with no distinct barbs or blades.

An additional juvenile specimen (AMS C.571736) is here treated as *Fusobela* cf. *parvioculata*, due to the identical sculpture of the teleoconch to that of the holotype, and the close genetic relationship. Further study is required to determine whether they ought to be considered truly conspecific, or if they represent a species complex.

Aplotoma n. gen.

Type species: *Aplotoma braevitentaculata* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of ‘aplous’ (ancient Greek = simple, for its featureless shell) and ‘toma’ (in reference to the family type genus *Raphitoma*).

ZooBank registration: urn:lsid:zoobank.org:act:B4E3D8B2-912B-4654-B425-7FF464EC2E2E

Diagnosis

Shell (Fig. 3C) broadly fusiform, opaque. Teleoconch of at least 5 whitish whorls. Suture impressed. Spire whorls broad, with well-defined shoulder. Subsutural ramp wide, acclivous, with sculpture of thickened u-shaped riblets marking position of anal sinus. Whorl periphery with low, indistinct, widely set folds, intersected by closely spaced, rounded cords. Siphonal canal moderately short. Aperture about half of shell length. Anal sinus wide, u-shaped. Radular teeth (Fig. 6A) of hypodermic type, straight, somewhat loosely rolled, with long dorsal blade; adapical opening subtriangular to ovate, rather short. Base barely wider than basal portion of shaft. Ligament broad.

Aplotoma braevitentaculata n. sp.

(Figs 3C, 6A)

Material examined

Holotype: Australia, VIC, East Gippsland CMR, 2338 m, IN2017_V03_035, (-37.792, 150.382), AMS C.571635.

Distribution

Known from a single locality off East Gippsland, Victoria.

Etymology: In reference to the comparatively short cephalic tentacles, derived from 'braevis' (Latin = short) and 'tentaculatus' (Latin = bearing tentacles), adjective of feminine gender.

ZooBank registration:

urn:lsid:zoobank.org:act:119007B3-5F12-451E-BF86-C864AEFFB467

Shell (Fig. 3C) (SL=20.5, SW=10.9) broadly fusiform, rather thin-walled, opaque. Protoconch of at least 2 whorls, eroded. Protoconch-teleoconch transition clearly defined, broadly sinuate. Teleoconch of about 5.3 uniformly whitish whorls, suture impressed. Whorls rather broad, with wide subsutural ramp, straight in early teleoconch whorls and slightly concave on later ones; well-pronounced shoulder situated at approximately mid-height of whorl; lower portion of whorl subcylindrical to cylindrical. Subsutural ramp sculpture of obsolete, low and rounded cords, and evenly spaced, raised arcuate riblets. Supra-peripheral two last cords stronger and more narrowly spaced. Teleoconch axial sculpture of 20 or more rounded opisthocline ribs below subsutural ramp, roughly half to third of interspaces, becoming indistinct toward suture and obsolete toward base of last whorl. Spiral sculpture of regularly spaced cords, about eight densely placed on penultimate whorl, over 30 on last whorl alternate strong and weak, latter becoming indistinct towards whorl base. Microsculpture of indistinct collabral growth lines. Last adult whorl evenly convex below subsutural ramp, clearly demarcated from straight, moderately short siphonal canal. Aperture elongate, approximately half of shell length; outer lip thin; inner lip whitish, with thin callus, straight. Anal sinus moderately wide, shallow, u-shaped.

Cephalic tentacles very short, conical, very small eyes situated at their outer base.

Oesophagus very wide; proboscis short, conical; venom gland rather short.

Radular teeth (Fig. 6A) of hypodermic type, attaining approximately 115 µm in length, straight, somewhat loosely rolled. Ventral barb absent, dorsal blade approaching 1/3 of shaft length. Adapical opening subtriangular to elongate-ovate, about 1/5-1/6 of shaft length. Base not swollen, barely wider than widest part of shaft, with medium coarse texture; lateral process present, more or less perpendicular to orientation of shaft. Basal opening large, circular. Ligament rather broad.

Remarks

See Remarks below for comparison with *Biconitoma cretosa*. Polychaete fragments were recovered from the intestine.

Biconitoma n. gen.

Type species: *Biconitoma cretosa* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of ‘biconicus’ (Latin = biconical, for its shell general shape) and ‘toma’ (in reference to the family type genus *Raphitoma* Bellardi, 1847).

ZooBank registration: urn:lsid:zoobank.org:act:8D2E3C5F-173F-40AB-95A1-BFBA222BEB04

Diagnosis

Shell (Fig. 3D) fusiform-biconical, opaque. Teleoconch of about 5 whitish whorls. Spire whorls broad, with wide subsutural ramp and rounded whorl periphery. Subsutural ramp with 3-4 equally distanced spiral threads, whorl periphery with rounded opisthocline folds and prominent spiral cords throughout height of whorl. Siphonal canal straight, tapering. Aperture elongate, >50% of shell length. Anal sinus wide, deeply u-shaped. Cephalic tentacles slightly tapering; eyes absent. Radula (Fig. 6G) of tightly rolled hypodermic teeth with sharp, relatively short blade and triangular adapical opening. Tooth base broad, with weak lateral process and coarse texture. Ligament large, broad.

Biconitoma cretosa n. sp.

(Figs 3D, 6G)

Material examined

Holotype: Australia, NSW, off Byron Bay, 2587 m, IN2017_V03_090, (-28.677, 154.203), AMS C.482313.

Paratype: Australia, NSW, off Byron Bay, 3825 m, IN2017_V03_099, (-28.371, 154.649), 1 wet (AMS C.482288).

Distribution

Known from two adjacent localities off Byron Bay, northern New South Wales.

Etymology: In reference to the somewhat chalky appearance of the shell, derived from 'cretosus' (Latin = chalky), adjective of feminine gender.

ZooBank registration: urn:lsid:zoobank.org:act:49AFD1E4-21AD-473C-A983-1504F5AAA623

Description. Shell (Fig. 3D) (SL= 24.6, SW= 12.9) fusiform-biconical, opaque. Protoconch eroded. Teleoconch of about 5 uniformly whitish, chalky whorls; suture impressed. Whorls broad, with wide, flat to lightly concave subsutural ramp and rounded to sub-cylindrical periphery. Shoulder situated slightly below half-height of whorl, severely eroded in early teleoconch whorls. Axial sculpture of 15 or more rounded opisthocline folds below subsutural ramp, roughly half to third width of their interspaces, becoming indistinct toward suture and obsolete toward base of last whorl. Spiral sculpture of fine but distinct threads on subsutural ramp, and rather prominent cords subsequently (totalling about ten on penultimate whorl, >30 on last whorl). Microsculpture of indistinct collabral growth lines.

Last adult whorl evenly convex below subsutural ramp, constricted towards stout, tapering siphonal canal. Aperture elongate, a little over half of shell length; outer lip thin, unsculptured. Inner lip whitish, rather straight, gently recurved, with distinct callus. Anal sinus wide, deep, u-shaped.

Animal uniform cream. Head broad, blunt. Cephalic tentacles of moderate length, slightly tapering toward blunt tip. Eyes absent. Penis long, slender, cylindrical, with small seminal papilla situated distally; anterior vas deferens long, undulating, visible through epidermis. Introvert rather short; rhynchostomal sphincter thick, muscular. Proboscis very long, narrow, pointed, coiled counterclockwise; venom gland of medium length; muscular bulb elongate, lustrous.

Radula (Fig. 6G) of straight, tightly rolled hypodermic teeth attaining 135 µm in length; no ventral barb; dorsal blade sharp, approximately 1/6 of length of shaft; adapical opening elongate-triangular, about 1/10 of length of shaft. Base moderately broad, with weak lateral process; exterior of base with coarse texture; basal opening large. Ligament large, broad.

Remarks

This new taxon can be differentiated from other known raphitomids by its biconical shell with distinct spiral cords; the absence of eyes; a long penis with small distal seminal papilla, and comparatively short, tightly rolled, hypodermic teeth with subtriangular adapical openings.

In terms of shell morphology, this species can be difficult to differentiate from *Aplotoma braevitentaculata* (Fig. 3C), despite their difference in radular features (Fig. 6A and 6F) and their demonstrated genetic distinctiveness. However, the latter possesses a distinctly more convex shell base, a more acutely shouldered whorl profile with narrower subsutural ramp, and its axial sculpture consists of considerably narrower ribs.

Pagodibela n. gen.

Type species: *Pagodibela maia* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of 'pagoda' (for its pagodiform shell) and 'bela' (indicating resemblance with *Gymnobela*).

ZooBank registration: urn:lsid:zoobank.org:act:94C0A331-C79B-4D25-982A-BE73432D347D

Diagnosis

Shell (Fig. 3E) fusiform-biconical, semi-translucent, with high spire. Protoconch (Fig. 5C) multispiral, cyrthoconoid, with diagonally cancellate sculpture. Teleoconch with at least 6 strongly angulated whorls; suture deep. Whorl profile pagodiform, with wide subsutural ramp terminating in prominent carina, below subsutural ramp with raised arcuate riblets and rounded spiral cords. Siphonal canal straight, tapering. Aperture elongate, almost half of shell length. Anal sinus narrow. Cephalic centacles cylindrical; eyes small. Radula (Fig. 6E) of tightly rolled hypodermic teeth with very long dorsal blade and long, narrow adapical opening. Base rather broad, with coarse external texture. Ligament small, short.

Pagodibela maia n. sp. Criscione

(Figs 3E, 5C, 6E)

Material examined

Holotype: Australia, Coral Sea CMR, 1013 m, IN2017_V03_121, (-23.587, 154.194), AMS C.571678.

Distribution

Known only from the type locality.

ZooBank registration: urn:lsid:zoobank.org:act:30D02181-94B6-45D7-9275-CEA1845F3DE6

Etymology: In honour of my adorable little explorer Maia Criscione, in recognition of the love she has always expressed for the natural world, noun in apposition.

Description. Shell (Fig. 3E) (SL=19.9, SW=9.5) fusiform-biconical, thin-walled, semi-translucent. Protoconch (Fig. 5C) orange, multispiral, broadly conical, of 2.5 gently convex to indistinctly shouldered diagonally cancellate whorls. Protoconch-teleoconch transition clearly defined, broadly sinuate. Teleoconch of 6.2 white, strongly angulated whorls; suture deeply impressed. First teleoconch whorl convex to indistinctly shouldered, succeeding whorls pagodiform, with wide, straight or slightly concave subsutural ramp concluded by gemmate carina situated about mid-height of whorl. Whorl base narrowing clearly towards lower suture. Subsutural ramp sculpture of low and rounded cords, and evenly spaced, raised arcuate riblets producing somewhat reticulate pattern. Supra-peripheral two last cords stronger and more narrowly spaced. At whorl base, regularly spaced, alternate strong and weak cords, somewhat gemmate due to weak nodules at intersections of cords with dense collabral riblets. Last adult whorl with almost triangular base, shortly constricted to and clearly demarcated from straight, tapering siphonal canal. Aperture elongate, nearly half of shell length; outer lip thin; inner lip whitish, with thin callus, straight. Anal sinus narrow.

Head wide, cephalic tentacles cylindrical; small black eyes situated at their bases. Penis small, simple. Proboscis elongate, conical, not large; venom gland short; muscular bulb large.

Radular teeth (Fig. 6E) of hypodermic type, attaining about 175 µm in length, relatively straight to slightly curved, tightly rolled; barbs absent; dorsal blade extremely long, approaching half of shaft length; adapical opening very narrow and elongate, approximately 1/3 of shaft length; base rather broad, external texture coarse, consisting of dense network of diagonal ridges, becoming obsolete toward lateral margins; lateral process very weak; basal opening large, subcircular. Ligament small, short.

Remarks

This taxon can be differentiated from other raphitomids by its pagodiform shell with a gemmate carina, sculpture of equally spaced fine spiral cords and a radula with hypodermic teeth bearing extremely long dorsal blade and adapical openings.

Austrobela n. gen.

Type species: *Austrobela rufa* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of 'auster' (Latin = south; for its discovery in the Southern Hemisphere) and 'bela' (indicating resemblance with *Gymnobela*).

ZooBank registration: urn:lsid:zoobank.org:act:C0AFB30C-6D3C-42EB-98F1-624BF9E75CC3

Diagnosis

Shell (Fig. 3F) fusiform. Protoconch (Fig. 5E) multispiral, orange. Teleoconch whorls clearly shouldered, with subcylindrical lower portion. Scultpure of axial riblets below subsutural ramp; spiral sculpture of fine, sometimes flattened cords or shallow grooves; misrosculpture of growth lines. Aperture elongate, large, about half of shell length. Siphonal canal long, straight; columella straight. Sinus wide, L-shaped. Cephalic tentacles muscular, subcylindrical; eyes large. Rhynchodeal introvert rather thin-walled, densely folded. Venom apparatus extremely large, occupying majority of rhynchocoel. Radula (Fig. 6D) of hypodermic teeth with two large, sharp distal barbs; lower portion of shaft somewhat inflated; base broad; ligament thick.

Austrobela rufa n. sp.

(Figs 3F, 5E, 6D)

Material examined

Holotype: Australia, GAB, 965 m, IN2015_C02_131, (-35.153, 134.109), AMS C.571709.

Paratypes:

Australia, GAB, 978 m, IN2015_C02_382, (-33.516, 130.265), 1 wet (AMS C.571680); 1029 m, IN2015_C01_110, (-34.629, 132.356), 1 wet (AMS C.483817); 1016 m, IN2015_C01_117, (-34.674, 132.479), 1 wet (AMS C.571681); 994 m, IN2015_C01_114, (-34.705, 132.531), 1 wet (AMS C.571679); 1350 m, IN2015_C01_108, (-34.738, 131.841), 2 wet (SAMA D44253); 2 wet (AMS C.483801); 1 wet (AMS C.483802); 2 wet (AMS C.571668); 1015 m, IN2015_C02_167, (-34.823, 132.692), 1 wet (AMS C.532677); 1509 m, IN2015_C02_134, (-35.345, 134.045), 1 wet (AMS C.532691); 1 wet (AMS C.571699). Australia, Tasmania, St

Helens flat, 1127 m, IN2018_V06_184, (-41.209, 148.797), 1 wet (AMS C.574588); 1 wet (AMS C.271201).

Distribution

Known from the Great Australian Bight, northern Tasmania and the southern coast of New South Wales.

Etymology: In reference to the colouration of its shell, derived from ‘rufus’ (Latin = red), adjective of feminine gender.

ZooBank registration: urn:lsid:zoobank.org:act:9212F7D7-D734-49A7-94AB-B24011C9BFF9

Description. Shell (Fig. 3F) (SL=35.4, SW=14.6) thin-walled, fusiform, semi-translucent to opaque. Protoconch (Fig. 5E) (based on paratype AMS C.571681) orange, cyrthoconoid, multispiral, with 4.5 whorls, first whorl with punctate sculpture (Fig. 5E), remaining whorls with fine, evenly distanced arcuate riblets (about 35 on last whorl). Protoconch-teleoconch transition sharply delineated, broadly sinuate. Teleoconch of about six whorls with broad, slightly concave subsutural ramp. Whorl lower portion with axial sculpture of strong, rather sharp opisthocline ribs, well-pronounced at shoulder of two earliest and last teleoconch whorls; whorls subcylindrical below shoulder. Third and penultimate whorls without pronounced axials. Microsculpture of dense growth lines on subsutural ramp and very fine spiral cords on whorl lower portion. Last adult whorl with about 16 axials, vanishing shortly below shoulder. Shell base evenly convex, clearly demarcated from long, slender tapering siphonal canal. Aperture elongate, about half of length of shell, rounded below shoulder and narrowing toward siphonal canal. Outer lip thin, inner lip smooth, with narrow callus on long, rather straight columella bearing vertical orange stain. Sinus wide, moderately deep, L-shaped. Shell surface glossy, early teleoconch whorls pale orange or cream, subsequent whorls of orange colour.

Anatomy (based on AMS C.27120, female, except penial characters based on AMS C.571679, male). Animal uniform whitish/cream. Cephalic tentacles large, muscular, long, subcylindrical; large eyes on outer lower base of tentacles. Rhynchostome subcircular, lined with numerous epithelial cells; very large, thin-walled introvert with numerous longitudinal folds. Oviduct large; intestine lightly curved along length of oviduct, posterior to it. Penis rather large, coiling clockwise, simple. Rectal gland greenish, filamentous/bristly in appearance, parallel to anterior intestine.

Rhynchocoel with dark red content. Venom apparatus extremely large, occupying most of rhynchoocoel; proboscis large, elongate; radular sac extremely large; venom gland very large, thick, whitish, very long and convoluted; muscular bulb lustrous, yellow, extremely large, elongate, with indentation posteriorly where pressed against oesophagus.

Radula (Fig. 6D) (based on AMS C.571679; AMS C.571709; AMS C.574588) of straight to gently curved, somewhat loosely rolled hypodermic teeth of up to 350 µm in length; lower half of shaft rather cylindrical, somewhat inflated, distal half weakly tapering toward prominent dorsal and ventral distal barbs, of which ventral barb more distal from tip; dorsal barb sharper than ventral barb. Adapical opening elongate, narrow, boundaries not clearly defined due to loosely overlapping tooth margins, up to 1/5 of shaft length. Basal third of shaft with weakly rugose texture. Base rather broad, with medium coarse texture on exterior. Basal opening large. Ligament about half width of base, solid, thick.

Remarks

This species can be differentiated from other raphitomids by the following combination of characters: a glossy shell with weakly developed sculpture, clearly pronounced, but rounded shoulder, and yellowish orange to reddish brown colouration; a hypodermic radula with two large, sharply hooked barbs; an extremely large venom apparatus occupying almost the entire rhynchocoel; a thin-walled, strongly folded introvert and the presence of well-developed, large eyes.

Although DNA sequence data for the holotype was not included in the analysis of Figure 2, a COI sequence was generated and is available on Genbank (AN MN983272).

This is a quite variable taxon based on shell morphology, with some specimens examined exhibiting shells with little to no distinct sculpture.

Based on its shell morphology, this new taxon bears considerable similarity to the north-east Atlantic *Gymnobela fulvotincta* (Dautzenberg & Fischer, 1996). However, when compared to the holotype of the latter, the following characters observed in *G. fulvocincta* distinguishes this species from *A. rufa* n. gen. n. sp.: more prominent axial ribs, producing a more angulate whorl profile; a shoulder situated lower on adult whorls; a less cylindrical whorl periphery, and a columella that is distinctly curved when observed in apertural view as opposed to the straight columella in *A. rufa* n. gen. n. sp. In terms of radular morphology, the hypodermic tooth figured in Bouchet & Warén (1980, fig. 24) shows barbs that appear distinctly less prominent in *G. fulvotincta*, and a shaft that tapers gradually as opposed to the somewhat inflated lower half of the shaft in *A. rufa* n. gen. n. sp. (Fig. 6D). When compared to the superficially similar *Gymnobela yoshidai* (Kuroda & Habe, 1961), *A. rufa* n. gen. n. sp. bears a significantly broader shell and a more sharply inclined subsutural ramp (Sysoev & Bouchet, 2001, figs 134-144).

Glaciotomella n. gen.

Type species: *Glaciotomella investigator* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of ‘glacius’ (Latin = ice, for the glossy, icy-like surface of its shell) and ‘tomella’ (indicating resemblance with *Pleurotomella*).

ZooBank registration: urn:lsid:zoobank.org:act:6FE3648B-B095-4996-B90E-C4DF4640961A

Diagnosis

Shell (Fig. 3G) with cyrtoconoid spire, chalky, semi-translucent to opaque. Teleoconch of about 5 whitish whorls; whorl profile with weakly pronounced subsutural ramp, broadly convex below. Suture deep. Scultpure below subsutural ramp of orthicline axial ribs and spiral sculpture of intermittent weak and strong cords (most prominent on immature whorls). Siphonal canal long, clearly differentiated from last adult whorl. Aperture broadly pyriform, about half of shell length. Anal sinus moderately deep, J-shaped. Cephalic tentacles small; eyes minute. Rhynchostome and rhynchostomal sphincter extremely large; rhynchocoel short. Radula of long, straight, cylindrical hypodermic teeth with no distinct barbs or blades.

Glaciotomella investigator n. gen. n. sp.

(Fig. 3G)

Material examined

Holotype: Australia, New South Wales, Hunter CMR, 2595 m, IN2017_V03_070, (-32.575, 153.162), AMS C.571621.

Distribution

Known only from the type locality.

Etymology. In reference to the Australian Government’s RV *Investigator*, on which the expedition was conducted that allowed for this species (and many other species described herein) to be collected, noun in apposition.

ZooBank registration: urn:lsid:zoobank.org:act:0B100DF6-9DEB-402B-A382-2964754D285B

Description. Shell (Fig. 3G) (SL=20.8, SW=10) with cyrthoconoid spire, relatively thin-walled, chalky, semi-translucent to opaque. Protoconch largely eroded. Teleoconch of 5 whitish whorls with slightly concave subsutural ramp, evenly and broadly convex below. Suture deep. Subsutural ramp sculpture of fine, rather regularly set axial riblets. Teleoconch sculpture below subsutural ramp of orthocline axial ribs, extending from subsutural ramp to suture, rather prominent on early teleoconch whorls, progressively weakening toward last whorl (about 18 on penultimate whorl, >20 on last whorl); numerous weak, densely set, collabral growth lines between axial ribs; spiral sculpture of regularly spaced cords with finer cordlets in their interspaces, more differentiable on early teleoconch whorls, resulting in distinctly cancellate early- to mid teleoconch whorls, and with a finer meshwork of axial and spiral elements on last adult whorl. Last adult whorl broadly convex below subsutural ramp, abruptly constricted to long siphonal canal. Boundary between last whorl and siphonal canal on left side (in apertural view) deeply concave, with siphonal canal distinctly convex. Aperture broadly pyriform, about half of shell length; outer lip very thin; inner lip with thin glossy whitish callus. Columella rather straight in apertural view, distinctly convex in lateral view. Anal sinus moderately deep, J-shaped.

Mantle of single studied specimen stained with crimson, originating from distinct, well-developed rectal gland (although this staining is certainly a post-mortem feature, it may be useful to differentiate the species from conchologically similar species in other lineages).

Head with small cephalic tentacles situated on either side of rhynchostome, with extremely small eyes situated at their outer base. Rhynchostome and rhynchostomal sphincter extremely large; rhynchocoel short, with proboscis occupying most of its length. Proboscis with strongly folded walls; venom gland long, convoluted; muscular bulb large.

Radula of hypodermic teeth attaining 310 µm in length, rather straight, cylindrical. No distinct barb or blade.

Remarks

This new taxon can be differentiated from other raphitomids by the following combination of characters: a broadly fusiform shell, with strongly convex whorl profile, cancellate sculpture on early- to mid- teleoconch whorls, and a long, straight columella with a curved siphonal canal in lateral view (Fig. 3G); an extremely large rhynchostome, and long, rather straight and cylindrical hypodermic teeth with no distinct barb or blade.

Glaciotomella investigator n. sp. is similar to *Pleurotomella* (specifically, compared here to type species *P. packardii*, Verrill, 1872, and not to *Pleurotomella* in the broad sense), in that both taxa possess a shell with prominent sculpture, strongly convex whorls with an impressed suture, and a rather long siphonal canal. However, *G. investigator* differs from the latter in having a distinctly broader, more convex and less shouldered whorl profile, and a comparatively straight columella (which in *P. packardii* exhibits a prominent left-turning curve toward the anterior of the siphonal canal). Furthermore, our molecular results suggest that *Glaciotomella* and *Pleurotomella* are in fact not closely related within the Raphitomidae (Fig. 2). The radula of this species is not figured due to poor preservation state.

Austrotheta n. gen.

Type species: *Austrotheta crassidentata* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of 'auster' (Latin = south; for its discovery in the Southern Hemisphere) and 'theta' (indicating resemblance with *Theta*).

ZooBank registration:

urn:lsid:zoobank.org:act:1FCE9160-3FA0-44F9-89DE-46A6FA46ACA7

Diagnosis

Shell (Fig. 3H) fusiform, semi-translucent to opaque. Protoconch multispiral; sculpture of arcuate cordlets on upper portion of whorls and diagonally cancellate below. Teleoconch with distinctly shouldered to rounded whorls, bearing sharp opisthocline axial ribs in early to median whorls; last whorl evenly convex below narrow subsutural ramp, with undulating striae throughout its height. Siphonal canal long and straight. Aperture wide, pyriform, about half of shell length. Anal sinus rather shallow, u-shaped. Eyes minute. Radula (Fig. 6H) of very thick, cylindrical hypodermic teeth, bearing two weak distal barbs and with very short adapical opening. Base very broad, with extremely coarse external sculpture. Ligament very large.

Austrotheta crassidentata n. gen. n. sp.

(Figs 3H, 6H)

Material examined

Holotype: Australia, Tasmania, Freycinet Commonwealth Marine Reserve, 2820 m, IN2017_V03_004, (-41.731, 149.12), AMS C.519302.

Distribution

Known only from the type locality.

Etymology: In reference to its thick hypodermic tooth, derived from 'crassus' (Latin = thick) and 'dentatus' (Latin = bearing theet), adjective of feminine gender.

ZooBank registration:

urn:lsid:zoobank.org:act:4EF95055-B0D2-4151-89B1-762BD62DF8DE

Description. Shell (Fig. 3H) (SL=20.9, SW=9.6) fusiform, rather thin-walled, semi-translucent to opaque. Protoconch orange, multispiral (at least 2.5 whorls), with arcuate cordlets on adapical half to two-thirds of whorl, with diagonally cancellate sculpture below. Teleoconch of 4.4 whorls; subsutural ramp distinctly concave in early whorls, in more mature whorls less distinct and with less marked concavity. Whorl profile with prominent shoulder on early teleoconch whorls, situated at adapical third of whorl; in penultimate whorl more rounded, in last adult whorl indistinct; whorl periphery nearly cylindrical in early teleconch, more convex in mature whorls. Early teleoconch whorls with about 12 sharp, weakly opisthocline axials, vanishing well above suture, indistinct in later whorls. Spiral sculpture of dense, slightly undulating striae pronounced throughout last whorl. Microsculpture of collabral growth lines, forming distinct, raised cordlets on subsutural ramp in early whorls, weaker in more mature whorls. Last adult whorl evenly convex below subsutural ramp, with long, slender siphonal canal. Aperture wide, pyriform, about half of shell length. Inner lip with whitish callus, rather straight. Outer lip thin, unsculptured. Anal sinus rather shallow, weakly u-shaped.

Head wide, eyes very small. Muscular bulb extremely large; proboscis short, wide; radular sac thin, bearing few teeth.

Radula (Fig. 6H) of very thick, straight cylindrical hypodermic teeth exceeding 175 µm in length; two weak distal, lateral barbs; adapical opening very short, lateral (i.e., orientation of barbs and adapical opening offset to point of overlap between margins near base); base very broad, inflated, with extremely coarse external sculpture (Fig. 6H); ligament very large.

Remarks

Austrotheta crassidentata n. gen. n. sp. differs from other raphitomids in the following combined characters: a fusiform shell with sharp, weakly opisthocline axials on early teleoconch whorls and weakly sculptured late teleoconch whorls; slender siphonal canal; very thick hypodermic teeth with two weak laterally orientated barbs and a short laterally orientated adapical opening, as well as a broad base with extremely coarse external sculpture.

Based on its shell morphology, *A. crassidentata* n. gen. n. sp. resembles *Gymnobela yoshidai* (Kuroda & Habe, 1961), in which strongly shouldered subcylindrical early teleoconch whorls with sharp ribs are succeeded by evenly convex and finely striate whorls. However, the latter species has a narrower shell with a pointed spire, and a less convex, more elongated shell base, as well as a yellowish staining of the shell. A similar change in the whorl outline and sculptural pattern can be observed in *Spergo fusiformis* (based on the type series illustrated by Sysoev & Bouchet, 2001), although the latter can be readily differentiated from *A. crassidentata* n. gen. n. sp. by its larger size and narrower, rather lanceolate aperture. *A.crassidentata* n. gen. n. sp. also shows some resemblance to *Austrobela rufa* n. gen. n. sp., but can be readily differentiated by its diagonally cancellate protoconch, sharp axial ribs, a more convex shell base, and its whitish shell. When compared to *T. lyronuclea*, it differs in its more elongate shell and in its diagonally cancellate protoconch (which is arcuate in both *A. rufa* and *T. lyronuclea*).

Gladiobela n. gen.

Type species: *Gladiobela angulata* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of ‘gladius’ (Latin = sword; for the long blade of its hypodermic tooth) and ‘bela’ (indicating resemblance with *Gymnobela*).

Diagnosis

Shell (Fig. 4A) fusiform-biconical, semi-translucent. Protoconch multispiral, lower whorl portion diagonally cancellate, upper portion with arcuate sculpture only. Teleoconch with broad whorls with shoulder situated at mid-height of whorl. Anal sinus very wide, u-shaped. Animal with long, cylindrical tentacles; eyes very small. Radula (Fig. 6B) of hypodermic type, awl-shaped, with very long adapical opening; dorsal blade extremely long; base broad, angular.

ZooBank registration:

urn:lsid:zoobank.org:act:1FD74C2F-24EC-4FA6-B62F-02C380F9CAC9

Gladiobela angulata n. gen. n. sp.

(Figs 4A, 6B)

Material examined:

Holotype: Australia, New South Wales, Hunter CMR, 2595 m, IN2017_V03_070, (-32.575, 153.162), 1 wet (AMS C.571651).

Paratypes: Australia, GAB, 3350 m, IN2017_C01_197, (-34.452, 129.492), 1 wet (AMS C.571737); 1 wet (AMS C.571735); 1 wet (AMS C.571738); 1 wet (AMS C.572166); 1 wet (AMS C.572167); 1 wet (AMS C.572168); 1 wet (SAMA D49343); 3540 m, IN2017_C01_198, (-34.574, 129.572), 1 wet (SAMA D49341); 1 wet (SAMA D67750); 1 wet (SAMA D67751); 3807 m, IN2017_C01_192, (-34.589, 129.418).

Distribution

Known from the Great Australian Bight and one locality off the Hunter Commonwealth Marine Reserve, New South Wales.

Etymology: In reference to the distinct angulation at its whorl periphery, derived from 'angulata' (Latin = with angles), adjective of feminine gender.

ZooBank registration: urn:lsid:zoobank.org:act:F40216C9-F620-49A9-B91E-A91F118F7DF8

Description. Shell (Fig. 4A) (SL=18.8, SW=10.2) broadly fusiform-biconical, rather thin-walled, semi-translucent. Protoconch (based on SAMA D49341) orange, first whorl(s) strongly eroded, subsequent 1.5 whorls with diagonally cancellate sculpture on abapical third, above with arcuate sculpture only. Clear protoconch-teleoconch boundary marked by deep sinus. Teleoconch of about 4.5 uniformly honey-coloured whorls, suture impressed. Whorls broad, with very wide, slightly concave subsutural ramp; well-defined, prominent shoulder situated at approximately mid-height to just below mid-height of whorl. Axial sculpture of growth lines only, on early whorls forming slightly raised, densely set riblets. Spiral sculpture of densely set, evenly spaced sub-peripheral cords (about 8 on penultimate whorl, >30 on last whorl), few very weak cords present immediately above shoulder. Last adult whorl with slight concavity immediately below subsutural ramp, below - evenly convex, clearly demarcated from slightly tapering, long siphonal canal. Aperture elongate, approximately half of shell length; outer lip thin, unsculptured. Inner lip whitish, gently recurved. No distinct callus. Anal sinus very wide, moderately deep, u-shaped.

Anatomy (based on AMS C.571737 and AMS C.571651): Animal semi-translucent whitish. Cephalic tentacles very long, narrow, cylindrical, with extremely small eyes situated at their lower outer base. Penis rather long, narrow. Muscular bulb very long, colourless; proboscis long.

Radula (Fig. 6B) of straight to gently curved hypodermic teeth exceeding 175 µm in length; no ventral barb; dorsal blade sharp, extremely long, approximately half of shaft length; adapical opening very elongate, rather narrow, ranging between 1/4-1/2 of shaft length. Base rather broad, with distinct crescentic, slightly excavated shelf more or less perpendicular to orientation of shaft (Fig. 6B); large dorsal platform extending posteriorly, with numerous, densely arranged folds on inner surface; exterior of base with comparatively fine texture; basal opening large. Ligament broad.

Remarks

This new taxon can be differentiated from other raphitomids by its rather broad shell with a well-defined carina and a cylindrical whorl periphery with regularly spaced spiral cords, and by its hypodermic radular teeth with a very long dorsal blade extending approximately half the length of the shaft, and a prominent base forming a crescent-shaped, indented platform.

Pueridaphne n. gen.

Type species: *Pueridaphne cirrisulcata* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of ‘puer’ (Latin = child; for the similarity of its teleoconch to that of the larval shell sculpture) and ‘daphne’ (indicating resemblance with some species of *Daphnella* Hinds, 1844).

ZooBank: urn:lsid:zoobank.org:act:00258E64-8241-4207-9744-65B4BFE2C68C

Diagnosis

Shell (Fig. 4B) fusiform, opaque. Protoconch (Fig. 5D) multispiral, of 4.5 whorls of which first whorl exhibits punctate sculpture; subsequent whorls diagonally cancellate. Teleoconch of at least 4.5 uniformly white whorls. Suture impressed. Teleoconch whorls with wide subsutural ramp and well-defined shoulder in immature whorls, lower whorl portion and shell base with fine cancellate sculpture. Siphonal canal long, straight. Anal sinus wide, deeply u-shaped. Animal reddish brown. Cephalic tentacles (Fig. S4A) very long, cylindrical, exhibiting longitudinal groove throughout; eyes very small. Venom apparatus (Fig. S4B) large. Radula (Fig. 6C) of straight, tightly rolled hypodermic teeth with sharp, very long blade and long adapical opening. Base broad, with lateral process and extremely coarse external texture. Ligament broad.

Pueridaphne cirrisulcata n. gen. n. sp.

(Figs 4B, 5D, 6C, 9)

Material examined:

Holotype: Australia, GAB, 3350 m, IN2017_C01_197, (-34.452, 129.492), AMS C.572165.

Paratypes: Australia, New South Wales, Hunter CMR, 4031 m, IN2017_V03_079, (-32.131, 152.527), 1 wet (AMS C.563160); Jervis CMR, 2667 m, IN2017_V03_055, (-35.335, 151.259), 1 wet (AMS C.563103); VIC, East Gippsland CMR, 3850 m, IN2017_V03_032, (-38.479, 150.185), 1 wet (AMS C.571609); GAB, 3350 m, IN2017_C01_197, (-34.452, 129.492), 1 wet (AMS C.571631); 3540 m, IN2017_C01_198, (-34.574, 129.572), 1 wet (SAMA D49340a).

Distribution

Known to occur from the Great Australian Bight, via East Gippsland, Victoria, northward along the southeast Australian coast to the Hunter Commonwealth Marine Reserve, New South Wales.

Etymology: In reference to the groove present along the cephalic tentacles, derived from ‘cirrus’ (Latin = tentacle) and ‘sulcatus’ (Latin = bearing a groove), adjective of feminine gender.

ZooBank registration: urn:lsid:zoobank.org:act:0F0DD864-FF79-4C78-8A06-F99431B19039

Description. Shell (Fig. 4B) (SL=15, SW=7.4) fusiform, rather thin-walled, opaque. Protoconch (based on paratype AMS C.563103) orange, broadly conical, multispiral, with 4.5 whorls, first whorl with punctate sculpture, subsequent whorls diagonally cancellate (Fig. 5D). Protoconch-teleoconch transition clearly defined, broadly sinuate. Teleoconch of 4.6 uniformly whitish whorls, suture impressed. Whorls rather broad, with wide subsutural ramp, steep in early teleoconch whorls and progressively more concave in later whorls; well-pronounced shoulder situated at approximately mid-height of whorl. Subsutural ramp sculpture of raised, dense growth lines. Lower whorl portion with axial sculpture of numerous (> 100 on last whorl), dense, raised growth lines, intersecting rounded, evenly spaced (>20 on last whorl) spiral cords to form distinctly diagonally cancellate pattern; sculpture weaker on last whorl. Last adult whorl evenly convex below subsutural ramp; siphonal canal slender, moderately long, slightly curved. Aperture elongate, approximately half of shell length; outer lip thin, unsculptured. Inner lip whitish, gently recurved toward left with spiral sculpture extending uninterrupted from base, with very thin callus. Anal sinus wide, deep, u-shaped.

Anatomy (based on SAMA D49340a; AMS C.572165; AMS C.571609). Animal reddish brown, with epidermis of very fine textile-like appearance; head short, rather blunt. Penis large, very long, coiled clockwise, subcylindrical, tip blunt (Fig. S4A). Cephalic tentacles very long, cylindrical, bearing densely set latitudinal folds; distinct longitudinal groove present along their full length (Fig. S4A). Eyes very small, situated at outer lower base of cephalic tentacles. Prostate (Fig. S4A) gland large, yellowish, clearly visible beneath thin epidermis; anterior vas deferens undulating.

Introvert large, thick-walled, cup-shaped with expanding rim, whitish; rhynchostomal sphincter bluish grey, encircling introvert periphery, surrounded on both sides by dense white epithelial cells. Proboscis reddish brown, extremely large, long, pointed, coiled clockwise in rhyncocoel, outer walls bearing dense, very strong latitudinal folds (Fig. S4B); radular sac large; venom gland long and convoluted, colourless, situated posterior right of proboscis; muscular bulb ovate, lustrous pink, with micro-fibrous surface (Fig. S4B). Radula (Fig. 6C) (based on SAMA D49340a; AMS C.572165; AMS C.571609) of hypodermic teeth, straight, tightly rolled, attaining 150 µm in length, rather broad; slight constriction at approximately lower-third mark of shaft; no ventral barb; dorsal blade sharp, extending about 1/3 of shaft length; adapical opening elongate-ovate, approximately 1/5 to 1/6 shaft length, seen as marked indentation in lateral profile; base broad, angular, with distinct lateral process; basal texture extremely coarse, with dense network of weakly triangular to subcircular tubercles, larger on base proper than (immediate) basal portion of shaft; basal opening broad. Ligament broad.

Remarks

This new taxon can readily be distinguished from other raphitomids by the following combination of characters: a densely cancellate teleoconch; dark red pigmentation of the external animal; very long, strongly folded cephalic tentacles with a longitudinal groove or furrow extending across their full length; an extremely long, strongly folded proboscis; radular teeth with a long blade, a slight constriction of the shaft at its abapical third, and an extremely coarse texture on the base exterior.

Globodaphne n. gen.

Type species: *Globodaphne pomum* n. gen. n. sp.; OD, herein.

Etymology: Derived from combination of ‘globus’ (Latin = globe, for its sub-globose shell) and ‘daphne’ (indicating resemblance to *Xanthodaphne*).

ZooBank registration: urn:lsid:zoobank.org:act:369D1B2A-EDCA-48E2-83AD-C6215BD46D28

Diagnosis

Shell (Fig. 4C) sub-globose, thin-walled, semi-translucent. Protoconch (Fig. 5B) multispiral, with dense diagonally cancellate sculpture. Teleoconch of few, pale whorls. Suture impressed. Whorl profile very broad, strongly convex. Sculpture throughout whorl of dense, weakly arcuate riblets and dense, irregularly set spiral cordlets. Siphonal canal straight, short. Aperture wide, ovate, about 2/3 of shell length. Anal sinus very shallow. Cephalic tentacles long, cylindrical; eyes extremely small. Venom apparatus and radula absent.

Globodaphne pomum n. gen. n. sp.

(Figs 4C, 5B)

Material examined

Holotype: Australia, New South Wales, Hunter CMR, 2595 m, IN2017_V03_070, (-32.575, 153.162), AMS C.482283.

Distribution

Known only from the type locality.

Etymology: In reference to the somewhat globose shape of its shell, derived from ‘pomum’ (Latin = apple), noun in apposition.

ZooBank registration: urn:lsid:zoobank.org:act:F590311C-2E22-41BA-B3E1-558F746AA2BD

Description. Shell (Fig. 4C) (SL=14.1, SW=10) sub-globose, rather thin-walled, semi-translucent. Protoconch (Fig. 5B) multispiral, broadly cyrthoconoid, orange, of about 3 convex whorls; protoconch sculpture of numerous (about 60 on last whorl) thin opisthocline riblets, about half width of interspaces, and (9 on last whorl) weak spiral cordlets, becoming more conspicuous toward transition to teleoconch. Protoconch-teleoconch transition rather gradual, demarcated by colour transition. Teleoconch of about 2.7 pale orange whorls, suture impressed. Whorls very broad, with wide, poorly defined subsutural ramp. Lower portion of whorl evenly convex. Teleoconch sculpture of dense, thin, regularly spaced, moderately arcuate riblets (50 on last whorl) and dense, low, irregularly spaced cordlets (about 90 on last whorl). Riblets extending to suture on first 2 whorls and becoming somewhat inconspicuous towards base of last adult whorl. Microsculpture of very dense, barely detectable collabral growth lines. Last adult whorl evenly convex below subsutural ramp, clearly demarcated from straight, short siphonal canal. Aperture wide, ovate, approximately two-thirds of shell length; outer lip very thin, inner lip cream-orange, with thin callus, straight. Anal sinus very shallow.

Cephalic tentacles long, cylindrical; eyes extremely small. Very large introvert, occupying most of rynchocoel volume. Venom apparatus and radula absent.

Remarks

This taxon exhibits some superficial resemblance in shell morphology to *T. cuprosa* n. gen. n. sp., described below, which also possesses a sub-globose shell. In terms of differences in shell morphology, *G. pomum* n. gen. n. sp. can be distinguished from the latter by its less steep subsutural whorl portion, deeper suture, and more delicate spiral sculpture. When compared to *Lusitanops* F. Nordsieck, 1968 [type species *L. lusitanicus* (Sykes, 1906)] and *Xanthodaphne* (type species *X. membranacea*), *G. pomum* exhibits a distinctly more globose shell. Additionally, it can readily be differentiated from *Lusitanops* by its clearly delineated siphonal canal, and from *Xanthodaphne* by its comparatively shallow anal sinus.

Trochodaphne n. gen.

Type species: *Trochodaphne cuprosa* n. gen. n. sp.; OD, herein.

Etymology: Derived from a combination of 'trochus' (Latin = spinning top, for its shell shape) and 'daphne' (indicating resemblance with *Xanthodaphne*).

GenBank registration: urn:lsid:zoobank.org:act:7C58D631-5865-4B7A-913C-0CBAFC72522A

Diagnosis

Shell (Fig. 4D) sub-globose, semi-translucent. Protoconch (Fig. 5A) multispiral, with diagonally cancellate sculpture. Teleoconch of few copper-hued whorls. Suture moderately impressed. Whorl profile broad, convex, no distinct subsutural ramp. Teleoconch sculpture of alternating strong and weak spiral cords. Aperture wide, ovate, >2/3 of shell length. Anal sinus indistinct.

Trochodaphne cuprosa n. gen. n. sp.

(Figs 4D, 5A)

Material examined

Holotype: Australia, New South Wales, Jervis CMR, 2650 m, IN2017_V03_056, (-35.333, 151.258), 1 wet (AMS C.571611).

Distribution

Known only from the type locality.

Etymology: In reference to the colouration of its shell, derived from ‘cuprosus’ (Latin = coppery), adjective of feminine gender.

ZooBank registration: urn:lsid:zoobank.org:act:169E6E79-B8C7-4169-A321-2EF87AE84C71

Description. Shell (Fig. 4D) (SL=12.6, SW=9) sub-globose, thin-walled, semi-translucent. Protoconch (Fig. 5A) multispiral, broadly conical, orange, of about 3 evenly convex whorls; protoconch sculpture diagonally cancellate. Protoconch-teleoconch transition clearly defined, weakly sinuate. Teleoconch of about 2.7 copper-hued whorls, suture moderately impressed. Teleoconch whorls broad, strongly convex in outline, with no clearly defined subsutural ramp. Teleoconch sculpture of dense, low, regularly spaced cords alternate strong and weak (about 40 each on last whorl), latter becoming indistinct towards base of last adult whorl. Microsculpture of very dense, barely detectable collabral growth lines. Siphonal canal clearly demarcated from shell base, straight, sculptured with low longitudinal cords. Aperture wide, ovate, more than two thirds of shell length; outer lip very thin. Anal sinus indistinct.

Anatomy unknown.

Remarks

See below for comparison with *G. pomum* n. gen. n. sp.

Trochodaphne cuprosa n. gen. n. sp., in terms of its shell morphology, bears some similarity to the genus *Lusitanops* in its overall convex whorl outline, sculpture dominated by spiral elements, and shallow anal sinus, particularly when compared to *Lusitanops dictyota* Sysoev, 1997. The latter, however, has notably broader whorls than the type species. We are, however, reluctant to consider this new taxon as *Lusitanops*, as neither the type species *L. lusitanicus* nor *L. dictyota* possess such a distinctly globose shell as that of *T. cuprosa* n. gen. n. sp., which in that regard more resembles *G. pomum* n. gen. n. sp. described herein than *Lusitanops*. Sysoev (1997) noted that *L. dictyota* does not possess a radula, however, no anatomical data is available for *T. cuprosa*. Furthermore, with the exception of *L. dictyota* (whose placement in the genus is based solely on shell characters), species of *Lusitanops* bear a weak and short siphonal canal (Bouchet & Warén, 1980), whereas in *T. cuprosa* n. gen. n. sp. the canal is of moderate length, and very clearly demarcated from the last adult whorl as seen on its left side (when observed in apertural view, see Fig. 4D). *T. cuprosa* n. gen. n. sp. is also similar to some species of *Teretiopsis* (e.g. *T. abyssalis* Kantor & Sysoev, 1989), however, the latter has a narrower shell with clearly angulated whorls. Some species in the genus *Phymorhynchus* (for example, *P. major* Bouchet & Warén, 2001 or *P. ovatus* Bouchet & Warén, 2001) also possess (sub)globose shells, with strongly convex whorls and closely set rounded cords, but both of these species are notably larger, with thick, chalky white shells. *T. cuprosa* n. gen. n. sp. may also superficially resemble *Xanthodaphne* Powell, 1942 in that the latter also exhibits somewhat inflated whorls with distinct spiral elements; however, the type species *X. membranacea* has a well-developed anal sinus, a more distinctly shouldered, less convex whorl profile, less prominent spiral sculpture, and is also far less globose than *Trochodaphne* n. gen.

Discussion

Genus-level systematics

In order to apply genus names to the study material, the integrative approach described above was followed. The evidence forming the basis for our genus-level attributions is provided below.

The examination of shell features was deemed sufficient to enable genus placement for four clades, namely *Teretiopsis* Kantor & Sysoev, 1989, *Mioawateria*, *Famelica* and *Rimosodaphnella*. Although the radula is absent in *Teretiopsis* (Kantor & Sysoev, 1989) and has not been studied in the latter three genera, each of these genera is characterised by a distinctive combination of shell features not reported for any other raphitomid genus (Bouchet & Warén, 1980; Sysoev & Kantor, 1987 for *Famelica*; Morassi & Bonfitto, 2010 for *Mioawateria*; Bonfitto & Morassi, 2013 for *Rimosodaphnella*).

The attribution to *Phymorhynchus* of one clade (retrieved in the BI analysis only) was also supported by shell features. Although there is no published account on the radula of the type species, *P. castaneus* (Dall, 1895), species of *Phymorhynchus* possess large shells with strongly convex whorls bearing prominent spiral sculpture and with a very wide aperture lacking a subsutural sinus (Warén & Bouchet, 2009). This unique combination of features was shared by all studied Australian samples in the clade.

However, most clades retrieved by our analysis could only be preliminarily associated with genera that are not well-defined conchologically. In such cases, an assessment of combined morpho-anatomical features formed the basis for our genus attribution.

Species of three clades (forming the ‘*Bathybela*-like’ group in Fig. 7) exhibited large shells with a shallow anal sinus and comparatively weak sculpture. This combination of characters is found in at least three genera, namely *Bathybela, Spergo* and *Pontiothauma*. Given this non-exclusive character combination, the need of taxonomic revision has been invoked for all three (Bouchet & Warén, 1980; Sysoev & Bouchet, 2001). Radular details have been published for type material of the type species of *Spergo* (Dall, 1895, pl. 24, fig 1h) and *Ponthiotauma* (Page, 1903, pl. 42, figs 5-9, 14), while the radula of the type species of *Bathybela*, *B. nudator* (Locard, 1897), is figured by Bouchet & Warén (1980 p. 10, fig. 16). *Nodothauma magnifica* n. gen. n. sp. lacks venom apparatus and radula, and could therefore not convincingly be assigned to any of the above genera. While neither of the remaining two clades showed a radula referable to *Bathybela*, these did exhibit radulae typical of *Spergo* and *Pontiothauma* respectively, leading to the attribution to these two genera.

Samples of five clades (corresponding to *Gymnobela s.l.* of Fig. 7) exhibited shells that, according to the current taxonomic treatment (see Sysoev & Ivanov, 1985; Sysoev, 1990; Sysoev, 1996b; Sysoev & Bouchet, 2001), were attributable to the genus *Gymnobela*. The description of the type species *G. engonia* Verril, 1884 contains no account of the radula, but the hypodermic tooth is illustrated in Bouchet & Warén (1980, p. 12, fig. 31). All clades in the *Gymnobela s.l.* group varied considerably in the radula of their constituent samples, with only one containing specimens with radular features resembling those of *G. engonia*. Consequently, this latter clade is attributed to *Gymnobela* s.s., and new generic names, *Fusobela*, *Gladiobela*, *Pagodibela* and *Austrobela* are here introduced for the taxa represented by the remaining four clades.

Similarly, samples of two clades (corresponding to *Pleurotomella s.l.*, Fig. 7) had shell features corresponding to those of *Pleurotomella* (see Bouchet & Warén, 1980). The radula of the type species *P. packardii* is known only from an illustration in Bouchet & Warén (1980, p. 11, fig. 26). Species of the two clades possessed different radulae, but only one clade exhibited a radular morphology similar to that of *P. packardii.* From this clade, we examined the radula of *Pleurotomella* sp. 1 and for a further specimen (AMS C.487456), conspecific with *Pleurotomella* sp. 2 (WAM S32236) (Fig S2). Both radulae appear very similar to that figured in Bouchet & Warén (1980) for *P. packardii*, hence this clade is attributed to *Pleurotomella*. A new genus name, *Glaciotomella* n. gen., is proposed for species of the other clade, exhibiting a *Pleurotomella*-like shell albeit with a rather divergent radula from that of *P. packardii*. In our molecular analysis (Fig. 2), species of *Pleurotomella* show a degree of divergence comparable to that of the nodes separating different genera in the same analysis. This indication of comparatively distant relationships suggests the need for further taxonomic investigation, which cannot be conducted based on our limited data.

One clade contained a specimen (AMS C.482290) exhibiting a nearly identical shell to the holotype of *Theta lyronuclea* (type species of *Theta*), both in its teleoconch and protoconch morphology. Furthermore, its radula was very similar to that figured for that species by Bouchet & Warén (1980, p. 9, fig. 13). In spite of the considerable geographic distance of its collecting site (off E Australia) from the type locality of *T. lyronuclea* (off Bermuda), AMS C.482290 was considered as belonging to this species. Consequently, the clade in which it forms a part was assigned to *Theta*. Known examples of conoidean species with global, transoceanic distributions are rare. However, the phenomenon has been reported for the turrid *Cryptogemma benthima* (Dall, 1908) (Zaharias et al., 2020).

One clade contained two species sharing a fusiform shell with cylindrical whorl periphery, as well as very thick, double-barbed hypodermic teeth with a large, coarse base. As this character combinaton is unique within the Raphitomidae, the clade was assigned to a new genus, *Austrotheta* n. gen.

One sample (AMS C.519335) not clustering with any other sample could be readily assigned to *Typhlosyrinx* due to its large, very elongate shell with an ovate last adult whorl and a very short siphonal canal, and in its large, double-barbed hypodermic teeth (Bouchet & Sysoev, 2001)

Two unrelated species (AMS C.482283 and AMS C.571611) shared a nearly globose shell, with a high whorl expansion rate (sensu Raup, 1961) and sculpture of densely set, weak cordlets. Not observed in any known genus of the Raphitomidae, these combined characters here prompted the establishment of two new genera; *Globodaphne* n. gen. and *Trochodaphne* n. gen.

Two additional unrelated samples, that did not cluster with any of the other clades within this analysis (AMS C.519362 and AMS C.571734), shared a relatively large, subglobose, thin-walled shell with weakly developed sculpture. These combined features are referable to *Xanthodaphne*. These two unrelated taxa, however, exhibit rather different hypodermic teeth (not shown). The type species of *Xanthodaphne*, *X. membranacea* (Watson, 1886), was described for the deep sea of New Zealand based on an empty shell, and for which no radular data is available. Bouchet & Warén (1980; p. 8, fig. 9) figured the radula (but not the shell) of a specimen from "the bathyal of New Zealand", albeit with no repository detail provided. The radula figured therein exhibits a single-bladed tooth, which differs from the tooth of both AMS C.519362 (with two weak barbs, one serrated) and AMS C.571734 (with two distinct barbs). Pending thorough taxonomic definition of *Xanthodaphne*, we therefore refrain from attributing these two clades to this or any other genus.

An additional specimen that did not cluster within any of the other clades (AMS C.571643) exhibited a conical, unsculptured shell resembling that of *Abyssothauma* Sysoev, 1996 and some species of *Eubela* Dall, 1889. Unfortunately, the radula preparation was unsuccessful and genus attribution was therefore not attempted.

Deep-sea raphitomid species have been assigned to genera based on morphology only (Bouchet & Warén, 1980; Sysoev & Ivanov, 1985; Sysoev & Kantor, 1987; Sysoev, 1996a; Sysoev, 1996b; Sysoev, 1997; Sysoev & Bouchet, 2001; Figueeira & Absalao, 2012). These attributions appear as largely driven by shell morphology, despite, in some cases, substantial differentiation in radular morphology can be observed in these taxonomic groups. The present work confirms that (arguably) homogenous shell characters in deep-sea raphitomids are of limited taxonomic utility as conchologically similar clusters vary considerably in their radular anatomy. Within the Conoidea, there are numerous examples of taxa with very similar shells differing significantly in their radular morphology (Kantor et al., 2008), such as for the two deep-sea raphitomid genera *Typhlosyrinx* and *Leiosyrinx* Bouchet & Sysoev, 2001 (Bouchet & Sysoev, 2001). The suitability of the radula as a diagnostic character compared to that of the shell was molecularly tested for some turriform conoideans (Kantor et al., 2018). There, the variation in radular morphology and considerable genetic differentiation between highly convergent shell morphotypes was regarded as an indication of shell-wise cryptic genus-level diversity. Our study demonstrates that, to some extent, this applies also to several deep-sea genera of the Raphitomidae. Conversely, two species of the shallow-water raphitomid genus *Hemilienardia* possess a remarkably divergent radula from that of their congeners and other raphitomids (Fedosov et al., 2017). We therefore emphasise the importance of an integrative approach, combining morphological and molecular data, when studying the taxonomy of turriform conoideans.

Our results also suggest that maintaining the integrity of some of the traditionally highly speciose genus concepts (such as *Gymnobela s.l.* or *Pleurotomella s.l.*) is untenable unless a number of well-established and morphologically highly distinct genera are synonymised. Such a decision is in accordance with studies on other conoidean groups (Puillandre et al., 2015; Fedosov et al., 2020). Therefore, twelve new genera are introduced herein in order to avoid synonymising well-established genus names.

Patterns in morphological characters

Shell

Three broad shell morphological 'types' can be recognised: (a) large fusiform, with relatively weak sculpture, (b) a fusiform-biconical, and (c), with comparatively prominent sculpture, convex whorls with deeply impressed suture, and a sharply delineated siphonal canal. These types are rather conserved morphologies distributed in non-related lineages across the phylogenetic tree (Fig. 7). Other, less prevalent types (e.g. the globose *Trochodaphne* n. gen./*Globodaphne* n. gen. and biconical *Biconitoma* n. gen./*Aplotoma* n. gen.) also occur in unrelated lineages (Fig. 7). Such a non-monophyletic distribution of similar shell morphologies is not unexpected; shell convergence within the Conoidea is widely acknowledged, and reported for several families (e.g. Bouchet et al., 2011; Kantor et al., 2018; Hallan et al., 2019).

Several shallow-water raphitomids, such as *Hemilienardia* and *Kermia* Oliver, 1915 (Fedosov & Puillandre, 2012) possess thick, elaborate sculpture, commonly with reinforcement of the aperture. Very few such shell-strengthening strategies have been encountered in the deep-sea taxa studied herein (Figs 3, 6). While sculptural elements are generally seen, reinforcement by means of thickening or sculptural elaboration of the aperture is absent in all deep-sea taxa studied here.

Radula

Three configurations of the hypodermic tooth were encountered: double-barbed, awl-shaped with dorsal blade, and awl-shaped with no distinct blade. These are distributed across the tree irrespective of supra-specific phylogenetic relationships. For instance, the unrelated *Austrobela, Pontiothauma* and *Typhlosyrinx* all have double-barbed teeth (Fig. 7). However, genus-level synapomorphies can be identified in most genera by considering a combination of characters, such as morphology and size of barbs and blades, the relative length of the adapical opening, and base morphology and texture. Whether such conserved morphology reflects true phylogenetic signal and/or identical prey type, or both, remains to be established. While polychaete fragments have been encountered in some taxa (see Systematics), the identification of such fragments is inadequate in order to infer dietary patterns among these taxa.

A number of examined species have lost the venom apparatus (Fig. 7), the loss of which is known to occur in distantly related clades in the Raphitomidae and in Conoidea more broadly (Kantor & Sysoev, 1986; Kantor & Sysoev, 1989; Taylor, 1990; Kantor & Taylor, 2002; Medinskaya & Sysoev, 2003; Castelin et al., 2012). Kantor and Sysoev (1989) argued that in conoideans where rhynchostomal lips and the rhynchodeal introvert develop and become more significant for prey capture, the necessity of the radula decreases, potentially resulting in the subsequent loss of the radula and venom apparatus. Members of another conoidean family, Terebridae, where radula, venom gland and proboscis have been repeatedly lost also typically possess a rhynchodeal introvert (Castelin et al., 2012; Fedosov et al., 2020). Ball et al. (1997) suggested that the reduction or absence of the proboscis in raphitomids were indicative of paedomorphic states (see Ponder & Lindberg, 1997 for discussion on potential heterochrony in gastropods) and Kantor & Taylor (2002) proposed that the loss of radula and venom apparatus may also be linked to paedomorphosis. Ball (pers. comm. as provided in Kantor & Taylor, 2002) reported that the venom gland is among the last of the major foregut organs to develop during ontogeny. Many of the new taxa herein possess thick rhynchostomes and well-developed introverts, such as *Glaciotomella investigator* n. gen. n. sp., *Nodothauma magnifica* n. gen. n. sp., *B. cretosa* n. gen. n. sp., *G. pomum* n. gen. n. sp. and *P. cirricsulcata* n. gen. n. sp. Nevertheless, there is no clear correlation between the presence of a rhynchodeal introvert and the reduction or loss of radula and venom apparatus – the venom apparatus and radula are lost in *G. pomum* n. gen. n. sp. and *N. magnifica* n. gen. n. sp., but are well-developed in *P. cirrisulcata* n. gen. n. sp. and *B. cretosa*, n. gen. n. sp. and all four taxa possess a a well-developed introvert.

Eyes

Bouchet & Warén (1980) noted an unexpectedly high proportion of abyssal turriform conoidean species that possess eyes in their study of the North Atlantic fauna, which is consistent with our results. Some taxa, such as *Austrobela* and *Spergo* have comparatively large and well-developed eyes in all species studied here, suggesting that this feature may be diagnostic for these genera. In the majority of lineages, such as *Gymnobela, Pontiothauma, Gladiobela* n. gen., *Pueridaphne* n. gen., *Rimosodaphnella* and *Glaciotomella* n. gen., the eyes are very small to minuscule. For only one taxon, *Biconitoma* n. gen., no eyes were observed. Juvenile specimens of *N. magnifica* n. gen. n. sp. possess large eyes whereas in adults the eyes are in part covered by epidermis. Juveniles with eyes and blind conspecific adults have been reported for deep-sea species of turriform conoideans by Bouchet & Warén (1994).

Bathymetric distribution

Our data (Fig. 8) show that, in the deep waters of SE Australia, genera of Raphitomidae occur on a bathymetrical range spanning from the mid-bathyal to the lower abyssal (as delimited in Lalli & Parsons, 1997). While most genera exhibit a distribution that is either typically bathyal or abyssal, some occur in both zones. With a bathymetrical range of about 4000 m, *Theta*, *Spergo* and *Gladiobela* n. gen. are present from the mid-bathyal to the lower abyssal. The range of *Famelica* (3000 m) extends from the upper bathyal to the upper abyssal, while the occurrence of *Austrobela* n. gen. and *Fusobela* n. gen. (2000 m) stretch from the bathyal to lower abyssal. A similar wide range is observed for *Gymnobela* and *Phymorhynchus*, which are, however, restricted to abyssal depths. Comparably wide bathymetrical distributions have been reported for several conoidean genera in the Antarctic region (Kantor et al., 2016).

Faunal and biogeographical implications

Patterns of diversity

Deep-sea expeditions retain their pioneering nature, due to their high cost and challenging logistics. Often, due to great distances and technical difficulties, only a relatively limited number of samples can be obtained in a single voyage. Even when characterisation of the benthic fauna is the primary aim, adapting the sampling methodology to target a specific taxonomic group is often impractical. Such limitations have affected deep-sea surveys also in SE Australia, that are the main source of material for this study. In the gastropod material collected, in particular, there was a bias towards large forms. As small snails are a significant portion of the overall turriform conoidean diversity (Bouchet et al., 2009), it is possible that our study material represents a taxonomically impoverished portion of the total raphitomid fauna. As a consequence, the taxonomical and geographical coverage discussed below cannot be exhaustive.

Prior to this study, the distribution of deep-sea raphitomid genera in Australia was primarily known from museum specimen data. Only scattered records for eight genera were available: *Gymnobela* (Torres Strait to S Tas), *Nepotilla* Hedley, 1918 (Central Qld to SW WA), *Pleurotomella* (Torres Strait to GAB), *Taranis* (NT to Eyre Peninsula), *Thatcheria* Angas, 1877 (N WA), *Veprecula* (Central WA to N Tas), *Xanthodaphne* (S NSW) and *Spergo* (WA) (source ALA, http://www.ala.org.au). However, many of these records occur outside our target area (southern and eastern coast) and/or are based on material not examined in this study. Furthermore, this material was identified based on shell morphology and is therefore possibly of unreliable identification, given issues with shell homoplasy raised previously. For these reasons, these records are here ignored, with the discussion of diversity and distribution of SE Australian deep-sea raphitomids below based exclusively on our study material.

One of the most apparent outcomes of this study is the high level of previously unrecognised diversity in the deep-sea raphitomid fauna of SE Australia. More than half of the genera and most of the species (87%) present in the area are undescribed, which is consistent with reported estimates of unnamed turriform conoideans of the tropical Indo-Pacific (Bouchet et al., 2008).

Our data further indicate that the raphitomid fauna of the study area includes 58 species from at least 24 genera. These figures, amounting to over one-third of the overall accepted raphitomid genera and more than 7% of the named species, indicate that the diversity of Raphitomidae in temperate SE Australia is significantly greater than previously understood.

Biogeographic overlap with adjacent basins

Assessing the extent and composition of raphitomid diversity in the study area compared with those of other deep-sea regions is challenging, due to geographical and methodological biases. Firstly, the faunistic coverage on Raphitomidae in the deep sea is incomplete, with comparable data available only for some regions of the tropical SW Pacific (Bouchet et al., 2009), Atlantic (Bouchet & Warén, 1980; Figueeira & Absalao, 2012) and Antarctica (Kantor et al., 2016). Secondly, these reports refer to areas of varying geographic extent and with different bathymetrical ranges (e.g. Barnard, 1963; Sysoev & Ivanov, 1985; Sysoev, 1988; Sysoev, 1990; Sysoev, 1996b) and are thus of problematic comparison. Lastly, in most available studies, taxonomic treatments rest exclusively on morphological evidence and with no supporting molecular data. The comparisons below are therefore: (a) limited to the deep sea of relatively well-studied neighbouring basins, (b) restricted to genus-level and (c) exploratory in nature, pending further collecting as well as taxonomic investigations.

Our findings show minimal overlap with the raphitomid fauna of one directly adjacent basin, the Southern Ocean. Only one genus (*Pleurotomella*) and none of the 17 raphitomid species occurring in Antarctica (reviewed in Kantor et al., 2016) have been recorded in SE Australia. Interpretation of published data on shells and radulae of deep-sea raphitomids from the Cape Point region in South Africa (Barnard, 1963; Sysoev, 1996b), suggests that these areas share four genera with SE Australia (*Famelica* n. gen., *Gymnobela*, *Pontiothauma* and *Theta*). A similar comparison is more difficult with the fauna of the Nasca and Sala-y-Gomez ridges (SE Pacific; Sysoev & Ivanov, 1985; Sysoev, 1990) for which only shell data is available. However, the evidence suggests that this area shares *Pleurotomella* and possibly *Gymnobela* and *Austrobela* n. gen. with SE Australia, although these conclusions remain untested, pending the availability of material suitable for molecular study from the relevant areas.

Nevertheless, where preliminary molecular data do exist (this, and other studies in preparation), they suggest, in combination with morphology, that some of the newly recognised genera (*Austrobela* n. gen., *Pagodibela* and *Gladiobela* n. gen.), as well as some other genera (e.g. *Famelica*, *Spergo* and *Theta*), have ranges extending well into the tropical Indo-Pacific. No evidence is available to date for *Glaciotomella* n. gen., *Austrotheta* n. gen. or any of the monotypic genera described herein to suggest that these may occur outside the study area.

Range size and endemism

The number (seven) and proportion (one third) of putative endemic genera found in this study are greater than those recorded for other realms. Five genera are endemic to the south Australian realm and two are unique to the Coral Sea realm (sensu Costello et al., 2017). To date, only seven deep-sea raphitomid genera are known to be endemic to one single marine realm, namely *Buccinaria* Kittl, 1887, *Rocroithys* Sysoev & Bouchet, 2001, *Leiosyrinx* (Bouchet & Sysoev, 2001) for the Indo-Pacific realm; *Abyssobela* (Sysoev & Kantor, 1986) and *Vitjazinella* for the Offshore W Pacific; *Tuskaroia* (Sysoev, 1988) for the N Pacific and *Abyssothauma* Sysoev, 1996 for South Africa. No endemic genera are found in the SE Pacific ridges mentioned above (Sysoev & Ivanov, 1985; Sysoev, 1990) or in Antarctica (Kantor et al., 2016).

The extension of the distribution range of deep-sea turriform conoideans is thought to depend on two alternative larval developmental strategies. Taxa with planktotrophic larvae are usually considered more effective dispersers than direct developers (with lecitotrophic larvae) and have greater ranges (Bouchet & Warén, 1994). Planktotrophy can be assessed by the presence of a multispiral protoconch, while lecitotrophy is associated with a paucispiral protoconch (Thorson, 1950). Species, for which examination of the protoconch was possible in this study, exhibited a multispiral protoconch, except those attributed to *Pontiothauma*. This is in accordance with the notion that planktotrophy is the dominant mode of development in deep-sea turriform conoideans (Bouchet & Warén, 1994). While higher dispersal potential could in theory explain the wide ranges observed here for some genera, it does not provide sufficient justification for the potentially much more restricted ranges reported for other genera. It has been speculated that the larvae of many deep-sea turriform conoideans may undergo (total or partial) demersal development (Shimek, 1986; Bouchet & Warén, 1994), known to purportedly reduce dispersal ability of some deep-sea invertebrates (Young et al., 2017). There is no evidence of demersal larval life in any of the genera studied here, and further ecological investigation is required to assess whether such a strategy can be linked to more restricted distribution ranges. The purported wide range of *Ponthiothauma* despite its lecitotrophic larva is also in disagreement with the general rule. However, it has been suggested that lecitotrophic larvae of some deep-sea gastropods are capable of spending longer periods as demersal, drifting, nonfeeding larvae and thus have a greater dispersal ability than commonly thought (Bouchet & Warén, 1994).Environmental factors may also influence distribution patterns of raphitomid genera. Species of *Buccinaria* Kittl, 1887 are endemic to the Indo/Indo-Pacific realm, where they occur on reducing sediment at bathyal depths. It has been hypothesised that the absence of this genus from the neighbouring deep waters off NW Australia and the Arabian Sea may be due to the lack of such preferential substrate (Bouchet & Sysoev, 1997).

Our preliminary observations suggest that distribution patterns of deep-sea raphitomid genera can be highly heterogenous. While some genera seem to possess very wide ranges, others appear strictly endemic. However, further molecular and ecological data on

Raphitomidae worldwide are required to assess the real taxonomic diversity, and observed distribution patterns presented herein, as well as to further elucidate their underlying mechanisms.

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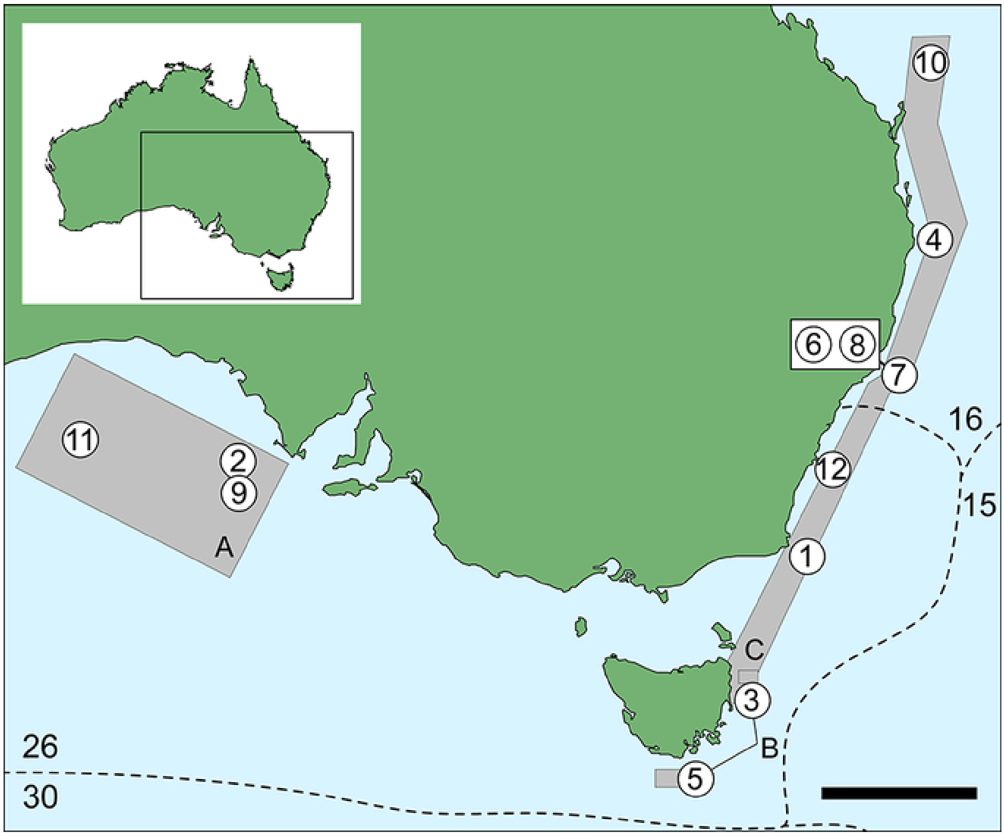

Figure 1. Distribution of deep-sea Raphitomidae in southern and eastern Australia. Numbers in circles mark type localities of species described herein, namely (1) Aplotoma braevitentaculata n. gen. n. sp. (2), Austrobela rufa n. gen. n. sp. (3); Austrotheta crassidentata n. gen. n. sp.; (4) Biconitoma cretosa n. gen. n. sp. (5), Fusobela parvioculata n. gen. n. sp. (6), Glaciotomella investigator n. gen. n. sp. (7), Gladiobela angulata n. gen. n. sp. (8), Globodaphne pomum n. gen. n. sp. (9), Nodothauma magnifica n. gen. n. sp. (10), Pagodibela maia n. gen. n. sp. (11), Pueridaphne cirrisulcata n. gen. n. sp. (12), Trochodaphne cuprosa n. gen. n. sp. Shades correspond to areas targeted by sampling: A. the GAB, B. the east coast, C. Tasmanian seamounts (see text). Dashed lines mark limits among marine realms (numbered as in Costello et al., 2017).

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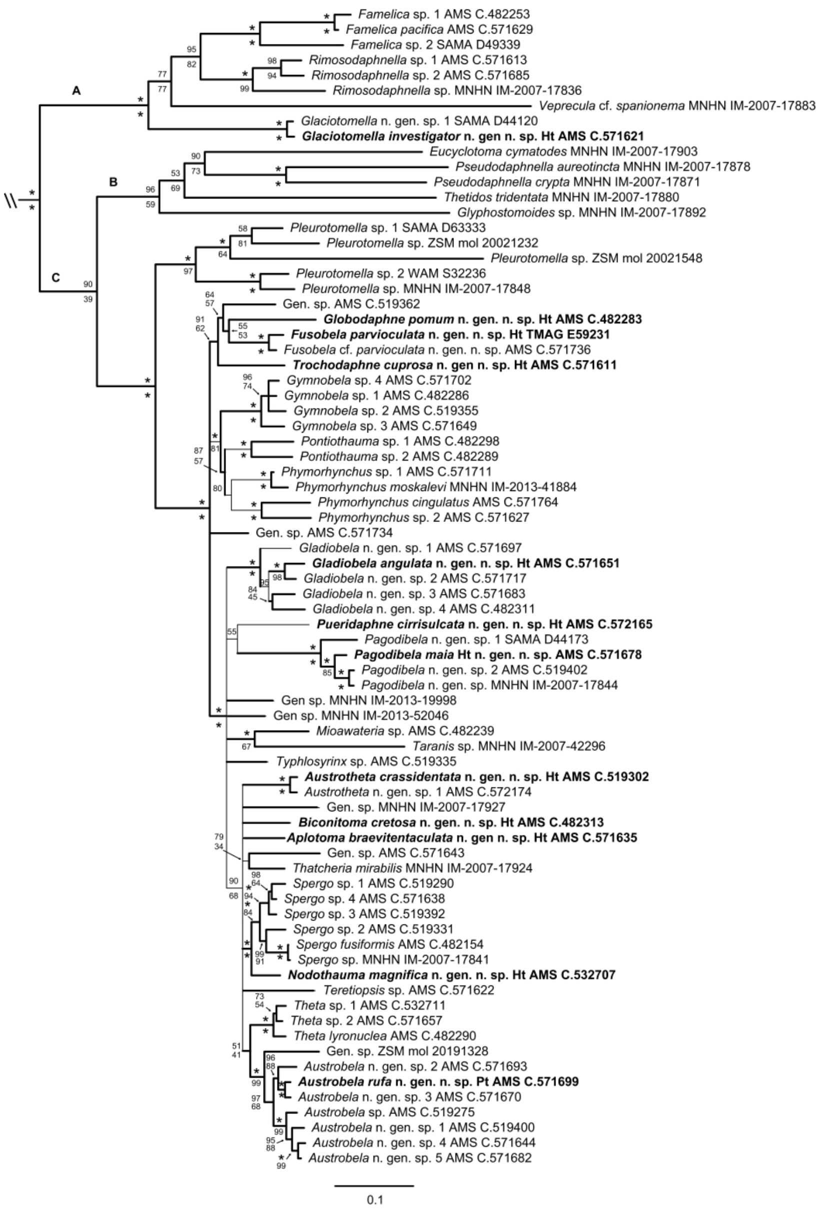

Figure 2. Bayesian consensus phylogram based on analyses of the concatenated COI, 16S, 12S, 28S and H3 sequences. Thick lines mark branches consistent with the topology of the ML tree. Numbers above branches indicate nodal support (%) by Bayesian posterior probabilities (BPP). Numbers below branches indicate nodal support (%) by ML bootstrap (BTSP). BPP and BTSP values of 100% are both represented by asterisks. Outgroup taxa are not shown. Names of species described herein are in bold.

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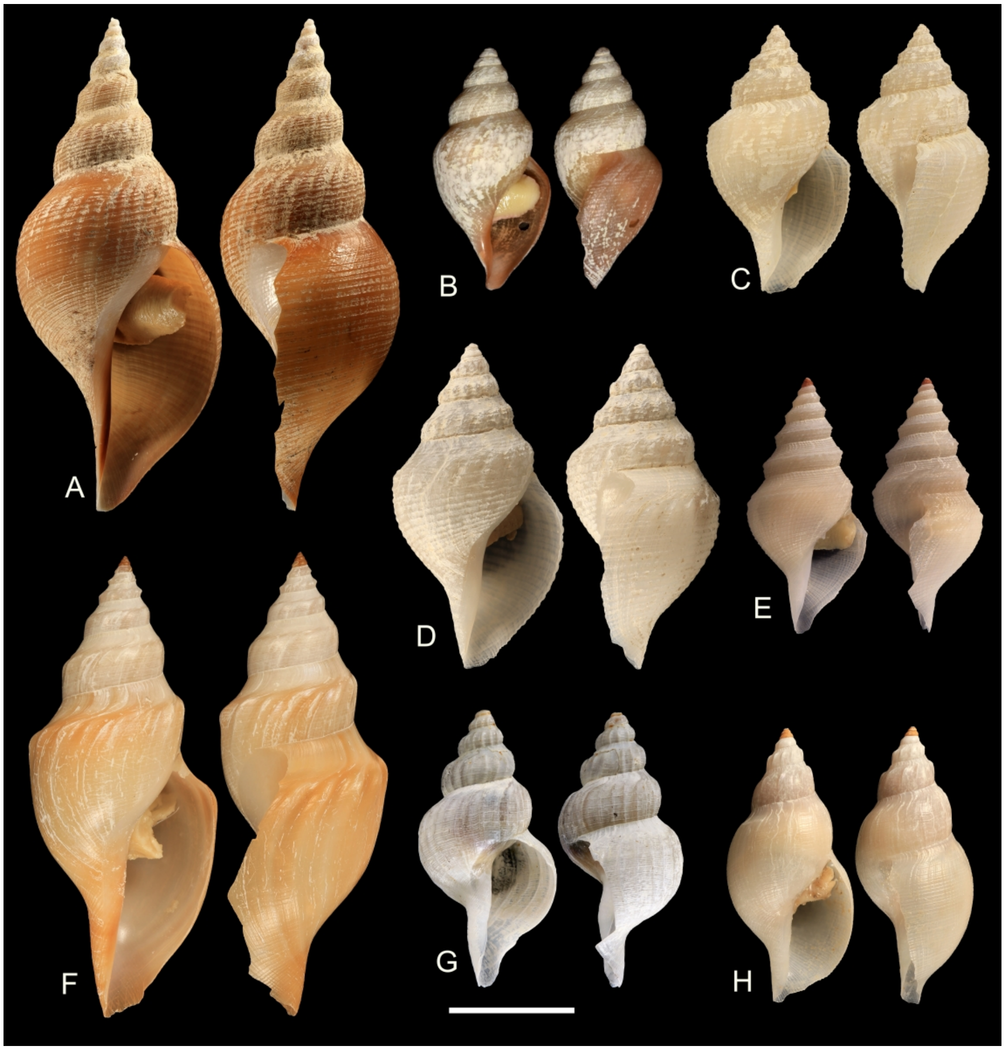

Figure 3. Shells of species described herein. A, Notothauma magnifica n. gen. n. sp., holotype AMS C.532707; B, Fusobela parvioculata n. gen. n. sp., holotype TMAG E59231; C, Aplotoma braevitentaculata n. gen. n. sp., holotype AMS C.571635; D, Biconitoma cretosa n. gen. n. sp., holotype AMS C.482313. E, Pagodibela maia n. gen. n. sp., holotype AMS C.571678; F, Austrobela rufa n. gen. n. sp., holotype AMS C.571709; G, Glaciotomella investigator n. gen. n. sp., holotype AMS C.571621; H, Austrotheta crassidentata n. gen. n. sp., holotype AMS C.519302. Scale bar 20 mm (A), 10 mm (B-H).

168x175mm (600 x 600 DPI)

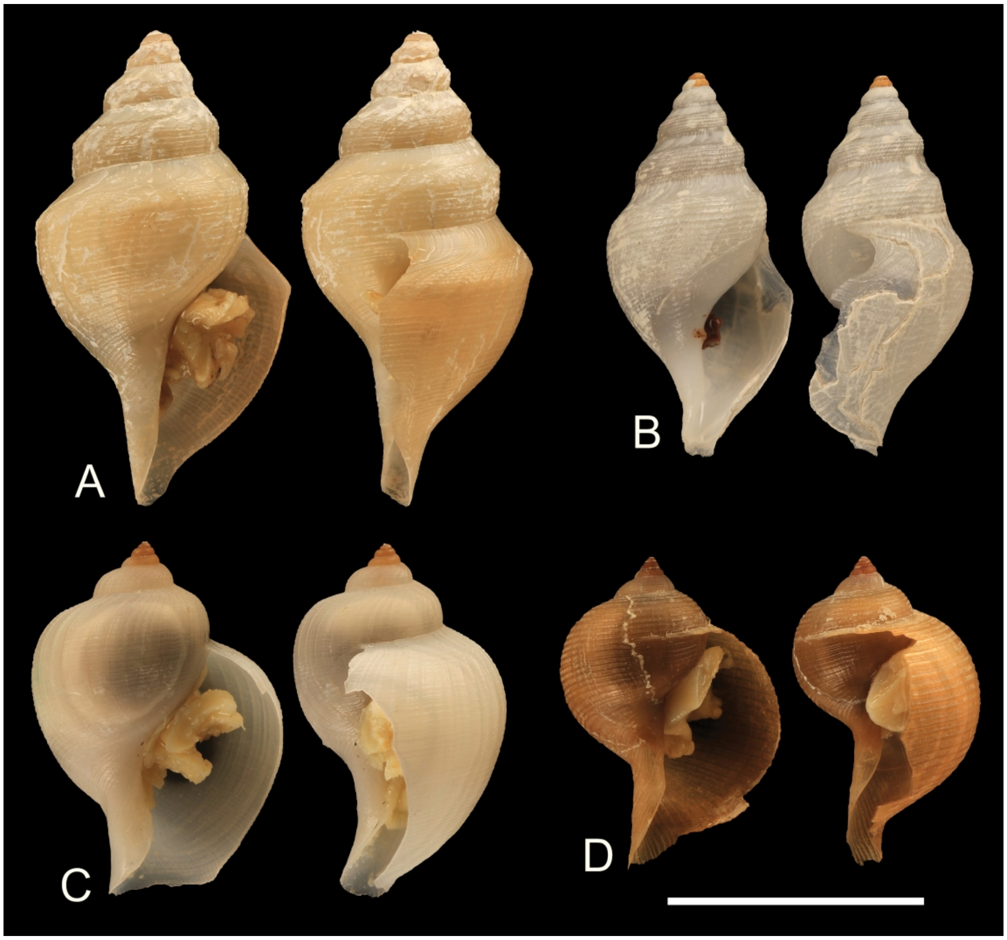

Figure 4. Shells of species described herein. A, Gladiobela angulata n. gen. n. sp., holotype AMS C.571651; B, Pueridaphne cirrisulcata n. gen. n. sp., holotype AMS C.572165; C, Globodaphne pomum n. gen. n. sp., holotype AMS C.482283; D, Trochodaphne cuprosa n. gen. n. sp., holotype AMS C.571611. Scale bar 10 mm.

167x156mm (600 x 600 DPI)

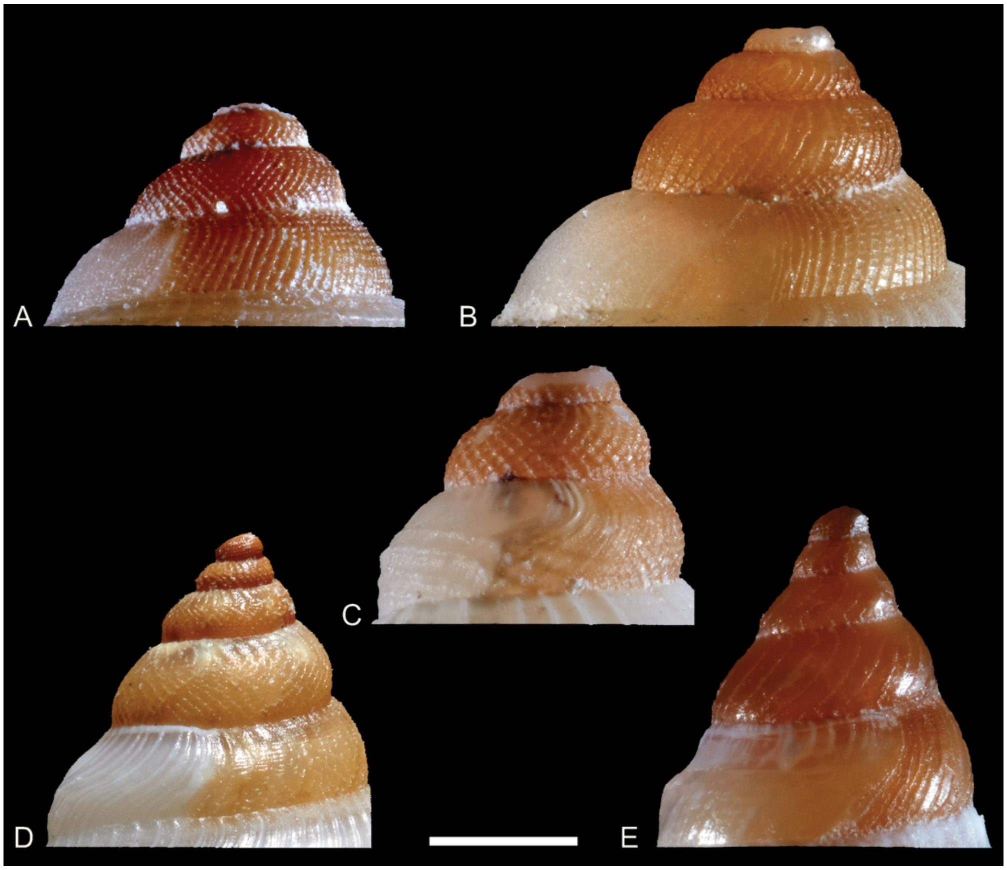

Figure 5. Larval shells of species described herein. A, Trochodaphne cuprosa n. gen. n. sp., holotype AMS C.571611; B, Globodaphne pomum n. gen. n. sp., holotype AMS C.482283; C, Pagodibela maia n. gen. n. sp., holotype AMS C.571678; D, Pueridaphne cirrisulcata n. gen. n. sp., paratype AMS C.563103; E, Austrobela rufa n. gen. n. sp., paratype AMS C. 571681. Scale bar = 500 µm.

83x72mm (600 x 600 DPI)

Figure 6. Hypodermic teeth of species described herein. A, Aplotoma braevitentaculata n. gen. n. sp., holotype AMS C.571635; C, Pueridaphne cirrisulcata n. gen. n. sp., paratype AMS C.571609; D: Austrobela rufa n. gen. n. sp.: holotype AMS C.571709 (left), paratype AMS C.571679 (right); B, Gladiobela angulata n. gen. n. sp., paratype AMS C.571737; E, Pagodibela maia n. gen. n. sp., holotype AMS C.571678; F, Fusobela parvioculata n. gen. n. sp., holotype TMAG E59231; G, Biconitoma cretosa n. gen. n. sp., holotype AMS C.482313; H, Austrotheta crassidentata n. gen. n. sp., holotype AMS C.519302. Scale bar = 50 μm.

168x150mm (600 x 600 DPI)

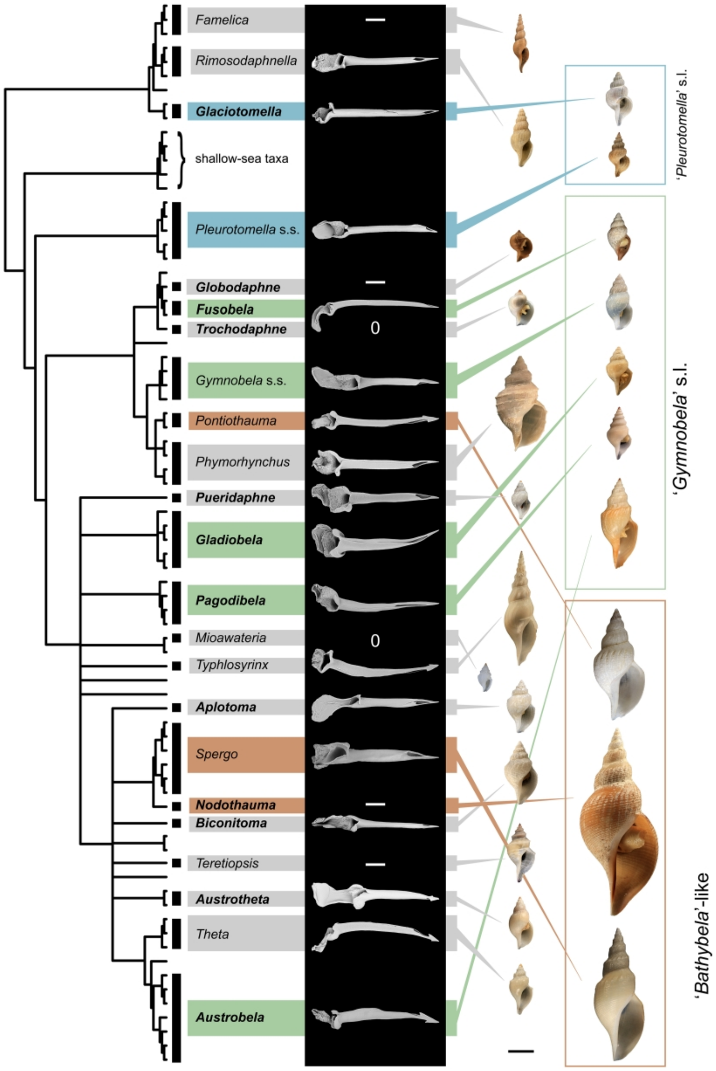

Figure 7. Shell (scalebar = 10 mm) and radula (not in scale) of deep-sea raphitomids mapped on genus-level clades (black boxes) of the strict consensus cladogram for the ML and BI analyses. For most clades attributed to newly described genera, images of the genus type specimen are shown (see Systematics). The radula of Glaciotomella n. gen. sp. 1 (SAMA D44120) is shown instead of that of the type species. For clades assigned to named genera, shell and radula are shown from specimens present in the analysis of Fig. 2 or from congeneric vouchers of the following species: Pleurotomella sp. 2 (WAM S32236, shell; AMS C.487456, radula); Famelica sp. 1 (AMS C.482253); Rimosodaphnella sp. 1 (AMS C.571613); Pontiothauma sp. 2 (AMS C.571641, shell; AMS C.519398, radula); Phymorhynchus cingulatus (Dall, 1890) (AMS C.571764, shell; AMS C.571665, radula); Gymnobela n. sp. 4 (AMS C.571666, shell; AMS C.482314, radula); Typhlosyrinx sp. (AMS C.519335); Mioawateria sp. (MNHN IM-2013-68769); Teretiopsis sp. (AMS C.571622); Austrotheta crassidentata n. gen n. sp. (AMS C.519302); Spergo sp. 1 (AMS C.519290); Theta lyronuclea (Clarke, 1959) (AMS C572169, shell; AMS C.571733, radula). Note that two separate clades are attributed to Phymorhynchus (see Discussion). Images are not shown for clades of uncertain generic attribution and not containing Australian samples. Shell images of conchologically cryptic genera groups (see Discussions) are

grouped in boxes. Dashes represent radula absence for the genus and zeros indicate missing data.

167x224mm (600 x 600 DPI)

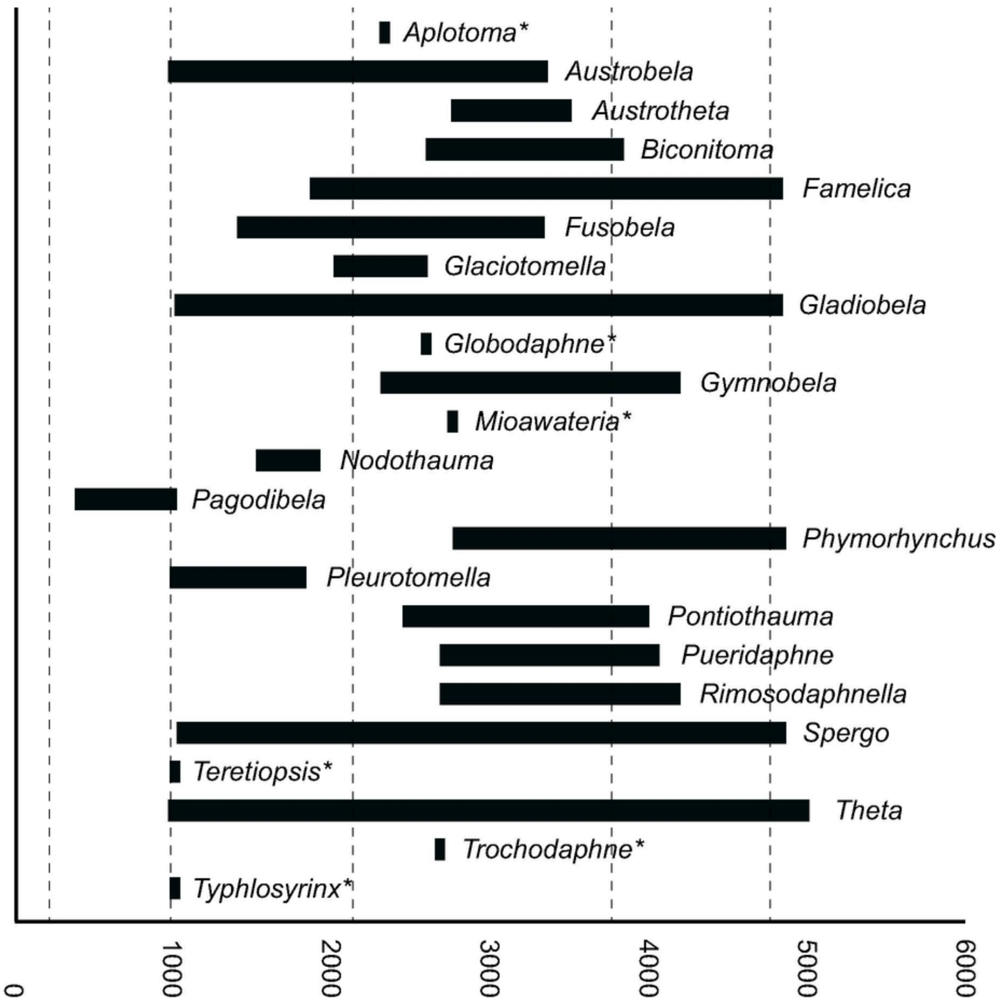

Figure 8. Bathymetric ranges of genera of Raphitomidae in SE temperate Australian waters. A, Continental shelf; B, upper continental slope; C, lower continental slope; D, continental rise; E, abyssal plain; F, hadal depths. Asterisks mark genera known from one sample only.

78x77mm (300 x 300 DPI)

Family	Taxon	Museum	Registration no.	voucher	Locality/Expedition	BOLD id	COI	16S	12S	H3	28S
Turridae	*Turris babylonia* (Linnaeus, 1758)	MNHN	IM-2007-17754		Philippines, (9.618, 123.877), 8-22 m, Panglao 2004, R42.	CONO226-08	EU015677	HQ401715	HQ401652	EU015786	EU015562
Mangeliidae	*Citharomangelia planilabroides* (Tryon, 1884)	MNHN	IM-2007-17896		Philippines, (9.56, 123.725), 0-3 m, Panglao 2004, D5.	CONO219-08	EU015670	MN320420	MN322387	EU015779	EU015555
	Lienardia cf. *mighelsi* Iredale & Tomlin, 1917	MNHN	IM-2007-17897		Philippines, (9.618, 123.768), 3 m, Panglao 2004, B8.	CONO220-08	EU015671	MN942688	MN942694	EU015780	EU015556
Raphitomidae	***Aplotoma braevitentaculata* n. gen. n. sp.**	AMS	C.571635	Ht	Australia, VIC, East Gippsland CMR, (-37.792, 150.382), 2338 m, IN2017_V03.	-	MN983163	MN985714	MN985653	MN971739	-
	Austrobela n. gen. sp.	AMS	C.519275		Australia, NSW, Coral Sea CMR, (-23.587, 154.194), 1013 m, IN2017_V03	-	MN983164	MN985715	MN985654	MN971740	MN985775
	Austrobela n. gen. sp. 1	AMS	C.519400		Australia, Qld, Coral Sea CMR, (-23.631, 154.66), 1770 m, IN2017_V03.	-	-	MN985716	MN985655	MN971741	MN985776
	Austrobela n. gen. sp. 2	AMS	C.571693		Australia, GAB, (-34.074, 129.182), 2649 m, IN2015_C01.	-	MN983165	MN985717	MN985656	MN971742	MN985777
	Austrobela n. gen. sp. 3	AMS	C.571670		Australia, GAB, (-34.823, 132.692), 1015 m, IN2015_C02.	-	MN983166	MN985718	MN985657	MN971743	MN985778
	Austrobela n. gen. sp. 4	AMS	C.571644		Australia, NSW, Hunter CMR, (-32.575, 153.162), 2595 m, IN2017_V03.	-	MN983167	MN985719	MN985658	MN971744	-
	Austrobela n. gen. sp. 5	AMS	C.571682		Australia, NSW, off Byron Bay, (-28.677, 154.203), 2587 m, IN2017_V03.	-	-	MN985720	MN985659	MN971745	-
	***Austrobela rufa* n. gen. n. sp.**	AMS	C.571699	Pt	Australia, GAB, (-35.345, 134.045), 1509 m, IN2015_C02.	-	MN983168	MN985721	MN985660	MN971746	MN985779
	***Austrotheta crassidentata* n. gen n. sp.**	AMS	C.519302	Ht	Australia, TAS, Freycinet CMR, (-41.731, 149.12), 2820 m, IN2017_V03.	-	MT260886	MN985768	MN985707	MN971792	MN985812
	Austrotheta n. gen. sp. 1	AMS	C.572174		Australia, GAB, (-34.574, 129.572), 3540 m, IN2015_C01.	-	MN983208	MN985765	MN985704	MN971789	MN985809
	***Biconitoma cretosa* n. sp.**	AMS	C.482313	Ht	Australia, NSW, off Byron Bay, (-28.677, 154.203), 2587 m, IN2017_V03.	-	MN983169	MN985722	MN985661	MN971747	MN985780
	Eucyclotoma cymatodes (Hervier, 1897)	MNHN	IM-2007-17903		Philippines, (9.49, 123.933), 6-8 m, Panglao 2004, S12.	CONO227-08	EU015678	HQ401676	HQ401610	EU015787	EU015563
	Famelica sp. 1	AMS	C.482253		Australia, Qld, off Moreton Bay, (-26.946, 153.945), 2520 m, IN2017_V03.	-	MN983170	MN985723	MN985662	MN971748	-
	Famelica sp. 2	SAMA	D49339		Australia, GAB, (-34.768, 130.713), 1873 m, IN2015_C01.	-	MN983171	MN985724	MN985663	MN971749	MN985781
	Famelica pacifica Sysoev & Kantor, 1987	AMS	C.571629		Australia, TAS, Flinders CMR, (-40.473, 149.397), 4114 m, IN2017_V03.	-	MN983172	MN985725	MN985664	MN971750	MN985782
	Fusobela cf. *parvioculata* n. gen. n. sp.	AMS	C.571736	Pt	Australia, GAB, (-34.452, 129.492), 3350 m, IN2015_C01.	-	-	MN985726	MN985665	MN971751	-
	***Fusobela parvioculata* n. gen. n. sp.**	TMAG	E59231	Ht	Australia, Tasmania, Flat area S of Brians, (-44.239, 147.293), 1414 m, IN2018_V06.	-	MN983173	MN985727	MN985666	MN971752	-
	***Glaciotomella investigator* n. sp.**	AMS	C.571621	Ht	Australia, NSW, Hunter CMR, (-32.575, 153.162), 2595 m, IN2017_V03.	-	MN983178	MN985731	MN985670	-	MN985784
	Glaciotomella sp. 1 n. gen. n. sp.	SAMA	D44120		Australia, GAB, (-34.625, 130.28), 2007 m, IN2015_C02.	-	MN983179	MN985732	MN985671	MN971756	MN985785
	***Gladiobela angulata* n. gen. n. sp.**	AMS	C.571651	Ht	Australia, NSW, Hunter CMR, (-32.575, 153.162), 2595 m, IN2017_V03.	-	MN983180	MN985733	MN985672	MN971757	-
	Gladiobela n. gen. sp. 1	AMS	C.571697		Australia, VIC, East Gippsland CMR, (-38.479, 150.185), 3850 m, IN2017_V03.	-	MN983181	MN985734	MN985673	MN971758	MN985786
	Gladiobela n. gen. sp. 2	AMS	C.571717		Australia, NSW, off Bermagui, (-36.351, 150.914), 4747 m, IN2017_V03.	-	MN983182	MN985735	MN985674	MN971759	MN985787
	Gladiobela n. gen. sp. 3	AMS	C.571683		Australia, NSW, Hunter CMR, (-32.138, 153.527), 3980 m, IN2017_V03.	-	MN983183	MN985736	MN985675	MN971760	MN985788
	Gladiobela n. gen. sp. 4	AMS	C.482311		Australia, NSW, Hunter CMR, (-32.479, 152.994), 1006 m, IN2017_V03.	-	MN983184	MN985737	MN985676	MN971761	-
	***Globodaphne pomum* n. gen. n. sp.**	AMS	C.482283	Ht	Australia, NSW, Hunter CMR, (-32.575, 153.162), 2595 m, IN2017_V03.	-	MN983185	MN985738	MN985677	MN971762	MN985789
	Glyphostomoides sp.	MNHN	IM-2007-17892		Philippines, (9.5, 123.833), 100-138 m, Panglao 2004, T39.	CONO281-08	EU015715	HQ401681	-	EU015824	EU015600
	Gymnobela sp. 1	AMS	C.482286		Australia, NSW, Jervis CMR, (-35.114, 151.469), 3952 m, IN2017_V03.	-	-	MN985739	MN985678	MN971763	MN985790
	Gymnobela sp. 2	AMS	C.519355		Australia, NSW, Jervis CMR, (-35.333, 151.258), 2650 m, IN2017_V03.	-	-	MN985740	MN985679	MN971764	-
	Gymnobela sp. 3	AMS	C.571649		Australia, TAS, Bass Strait, (-39.552, 149.553), 4197 m, IN2017_V03.	-	-	MN985741	MN985680	MN971765	MN985791
	Gymnobela sp. 4	AMS	C.571702		Australia, NSW, Jervis CMR, (-35.333, 151.258), 2650 m, IN2017_V03.	-	-	MN985742	MN985681	MN971766	MN985792
	Mioawateria sp. 1	AMS	C.482239		Australia, VIC, East Gippsland CMR, (-37.815, 150.373), 2746 m, IN2017_V03.	-	MN983186	MN985743	MN985682	MN971767	MN985793
	***Nodothauma magnifica* n. gen. n. sp.**	AMS	C.532707	Ht	Australia, GAB, (-35.558, 134.083), 1927 m, IN2015_C01	-	MN983187	MN985744	MN985683	MN971768	-
	***Pagodibela maia* n. gen. n. sp.**	AMS	C.571678	Ht	Australia, Qld, Coral Sea CMR, (-23.587, 154.194), 1013 m, IN2017_V03.	-	MN983188	MN985745	MN985684	MN971769	-
	Pagodibela n. gen. sp. 1	SAMA	D44173		Australia, GAB, (-35.043, 134.079), 367 m, IN2015_C01.	-	MN983189	MN985746	MN985685	MN971770	MN985794
	Pagodibela n. gen. sp. 2	AMS	C.519402		Australia, Qld, Coral Sea CMR, (-23.587, 154.194), 1013 m, IN2017_V03.	-	MN983190	MN985747	MN985686	MN971771	MN985795
	Pagodibela n. gen. sp.	MNHN	IM-2007-17844		New Caledonia, (-20.967, 160.967), 641-652 m, EBISCO, CP2645.	CONO186-08	EU015652	MN942687	MN942693	EU015760	EU015536
	Phymorhynchus cingulatus (Dall, 1890)	AMS	C.571764		Australia, TAS, Bass Strait, (-39.552, 149.553), 4133 m, IN2017_V03.	-	-	MN985748	MN985687	MN971772	MN985796
	Phymorhynchus moskalevi Sysoev & Kantor, 1995	MNHN	IM-2013-41884		North Atlantic Ocean, (23.367, -44.95), 3466 m, BICOSE, PL568_NAS.	CONO2814-19	MN942683	MN942686	MN942692	MN942935	-
	Phymorhynchus sp. 1	AMS	C.571711		Australia, VIC, East Gippsland CMR, (-38.479, 150.185), 3850 m, IN2017_V03.	-	MN983191	MN985749	MN985688	MN971773	MN985797
	Phymorhynchus sp. 2	AMS	C.571627		Australia, NSW, off Bermagui, (-36.351, 150.914), 4851 m, IN2017_V03.	-	MN983192	MN985750	MN985689	MN971774	MN985798
	Pleurotomella sp. 1	SAMA	D63333		Australia, GAB, (-34.738, 131.841), 1350 m, IN2015_C01.	-	MN983193	MN985751	MN985690	MN971775	-
	Pleurotomella sp. 2	WAM	S32236		Australia, WA, Off Houtman Abrolhos Islands, (-29.061, 113.636), 1000 m, SS1005.	-	MN983194	MN985752	MN985691	MN971776	-
	Pleurotomella sp.	MNHN	IM-2007-17848		New Caledonia, (-20.083, 160.333), 627-741 m, EBISCO, DW2625.	CONO191-08	EU015657	HQ401701	HQ401640	EU015765	EU015541

Ponthiothauma sp. 1	AMS	C.482298		Australia, NSW, Central Eastern CMR, (-30.264, 153.87), 4481 m, IN2017_V03.	-	MN983196	MN985753	MN985692	MN971777	MN985799
Ponthiothauma sp. 2	AMS	C.482289		Australia, NSW, Central Eastern CMR, (-30.098, 153.899), 2429 m, IN2017_V03.	-	MN983197	MN985754	MN985693	MN971778	MN985800
Pseudodaphnella aureotincta (Hervier, 1897)	MNHN	IM-2007-17878		Philippines, (9.49, 123.935), 16 m, Panglao 2004, B25.	CONO259-08	EU015700	HQ401688	HQ401624	EU015809	EU015585
Pseudodaphnella crypta Fedosov & Puillandre, 2012	MNHN	IM-2007-17871		Philippines, (9.692, 123.85), 21 m, Panglao 2004, S25.	CONO251-08	EU015693	-	MN942691	EU015802	EU015578
Pueridaphne cirrisulcata **n. gen. n. sp.**	AMS	C.572165	Ht	Australia, GAB, (-34.452, 129.492), 3350 m, IN2015_C01.	-	MN983198	MN985755	MN985694	MN971779	-
Rimosodaphnella sp. 1	AMS	C.571613		Australia, NSW, Jervis CMR, (-35.333, 151.258), 2650 m, IN2017_V03.	-	MN983199	MN985756	MN985695	MN971780	MN985801
Rimosodaphnella sp. 2	AMS	C.571685		Australia, TAS, Bass Strait, (-39.552, 149.553), 4197 m, IN2017_V03.	-	MN983200	MN985757	MN985696	MN971781	MN985802
Rimosodaphnella sp.	MNHN	IM-2007-17836		Vanuatu, off Epi, (-16.633, 167.950), 618-641m, BOA1, CP 2462.	CONO150-08	EU015645	HQ401704	-	EU015754	EU015529
Spergo fusiformis (Habe, 1962)	AMS	C.482154		Australia, NSW, Coral Sea CMR, (-23.587, 154.194), 1013 m, IN2017_V03.	-	MN983201	MN985758	MN985697	MN971782	MN985803
Spergo sp. 1	AMS	C.519290		Australia, TAS, Freycinet CMR, (-41.731, 149.12), 2820 m, IN2017_V03.	-	MN983202	MN985759	MN985698	MN971783	MN985804
Spergo sp. 2	AMS	C.519331		Australia, TAS, Bass Strait, (-39.552, 149.553), 4197 m, IN2017_V03.	-	MN983203	MN985760	MN985699	MN971784	MN985805
Spergo sp. 3	AMS	C.519392		Australia, TAS, Flinders CMR, (-40.473, 149.397), 4114 m, IN2017_V03.	-	MN983204	MN985761	MN985700	MN971785	MN985806
Spergo sp. 4	AMS	C.571638		Australia, NSW, Hunter CMR, (-32.575, 153.162), 2595 m, IN2017_V03.	-	MN983205	MN985762	MN985701	MN971786	MN985807
Spergo sp.	MNHN	IM-2007-17841		New Caledonia, (-21.533, 162.5), 458-750 m, EBISCO, CP2648.	CONO184-08	EU015650	HQ401682	-	EU015759	EU015534
Taranis sp.	MNHN	IM-2007-42296		Philippines, Aurora, off Dipaculao, (15.95, 121.833), 473 m, AURORA 2007, CP2749.	CONO561-08	HQ401584	HQ401707	HQ401645	-	MN868947
Teretiopsis sp.	AMS	C.571622		Australia, Qld, Coral Sea CMR, (-23.587, 154.194), 1013 m, IN2017_V03.	-	MN983206	MN985763	MN985702	MN971787	-
Thatcheria mirabilis Angas, 1877	MNHN	IM-2007-17924		Solomon Islands, (-8.283, 160), 464-523 m, SALOMON 2, CP2184.	CONO349-08	EU015736	FJ868138	FJ868124	EU015843	EU015621
Theta lyronuclea (A. H. Clarke, 1959)	AMS	C.482290		Australia, NSW, Jervis CMR, (-35.114, 151.469), 3952 m, IN2017_V03.	-	MN983207	MN985764	MN985703	MN971788	MN985808
Theta sp. 2	AMS	C.532711		Australia, GAB, (-35.818, 134.109), 2852 m, IN2015_C02.	-	MN983209	MN985766	MN985705	MN971790	MN985810
Theta sp. 3	AMS	C.571657		Australia, NSW, Hunter CMR, (-32.575, 153.162), 2595 m, IN2017_V03.	-	MN983210	MN985767	MN985706	MN971791	MN985811
Thetidos tridentata Fedosov & Puillandre, 2012	MNHN	IM-2007-17880		Philippines, (9.515, 123.687), 90-110 m, Panglao 2004, L46.	CONO267-08	EU015702	-	MN942690	EU015811	EU015587
Trochodaphne cuprosa **n. gen. n. sp.**	AMS	C.571611	Ht	Australia, NSW, Jervis CMR, (-35.333, 151.258), 2650 m, IN2017_V03.	-	MN983211	MN985770	MN985709	MN971794	MN985813
Typhlosyrinx sp.	AMS	C.519335		Australia, NSW, off Byron Bay, (-28.054, 154.083), 999 m, IN2017.	-	MN983212	MN985771	MN985710	MN971795	-
Unassigned genus and species	AMS	C.571643		Australia, VIC, East Gippsland CMR, (-38.479, 150.185), 3850 m, IN2017_V03.	-	MN983175	MN985728	MN985667	MN971796	MN985783
Unassigned genus and species	AMS	C.519362		Australia, NSW, off Bermagui, (-36.355, 150.644), 2821 m, IN2017_V03.	-	MN983174	MN985729	MN985668	MN971755	-
Unassigned genus and species	AMS	C.571734		Australia, GAB, (-34.452, 129.492), 3350 m, IN2015_C01.	-	MN983176	MN985730	MN985669	MN971754	-
Unassigned genus and species	MNHN	IM-2007-17927		Solomon Islands, (-8.067, 156.917), 399-427 m, SALOMON 2, CP2260.	CONO360-08	EU015740	HQ401674	HQ401607	EU015847	EU015625
Unassigned genus and species	MNHN	IM-2013-19998		Papua New Guinea, (-5.5, 146.15), 400 m, PAPUA NIUGINI, CP4020.	CONO2813-19	-	MN942689	-	MN942936	MN868946
Unassigned genus and species	MNHN	IM-2013-52046		Papua New Guinea, (-3.317, 143.45), 422-425 m, PAPUA NIUGINI, CP4049.	MITRI080-15	KR087296	KR088045	KR087382	KR088123	
Unassigned genus and species	ZSM	mol_20021232		Antarctica, (-54.023, -62.022), 272 m, LAMPOS, ANT XIX-5.	-	-	MN985774	MN985713	MN971797	EU015562
Unassigned genus and species	ZSM	mol_20191328		Antarctica, (-54.023, -62.022), 272 m, LAMPOS, ANT XIX-5.	-	MN983177	MN985773	MN985712	MN971753	EU015529
Unassigned genus and species	ZSM	mol_20021548		Antarctica, Drake-Strasse (-54.504, -56.137), 286.3 m, LAMPOS, ANT XIX.	-	MN983195	MN985772	MN985711	-	EU015534
Veprecula cf. *spanionema*	MNHN	IM-2007-17883		Philippines, (9.515, 123.687), 90-110 m, Panglao 2004, L46.	CONO270-08	EU015705	HQ401717	-	EU015814	EU015590