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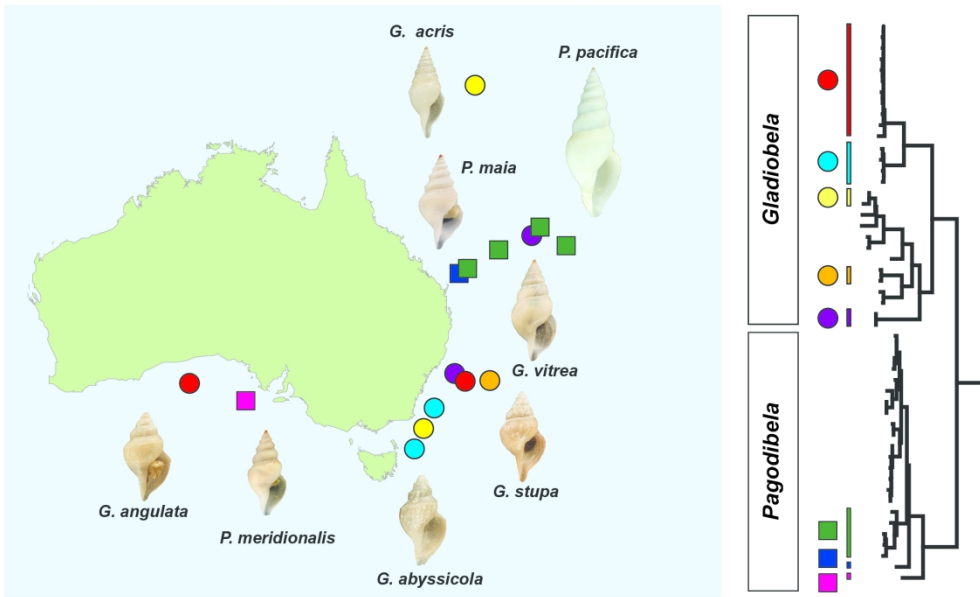
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Short summary

Distribution patterns of deep-sea benthic gastropods remain poorly known, yet such knowledge is crucial to approaching their systematics and understanding their diversity. With a focus on the raphitomid genera *Gladiobela* and *Pagodibela*, we combine genetic, shell, anatomy and distribution data to identify seven new species from Australia and beyond, which we here describe. Our findings suggest patterns of extreme rarity in some species, with others exhibiting wide Indo-Pacific distributions. We argue that wide geographic ranges in deep-sea conoidean gastropods may be more common than previously assumed, which has implications for future systematics efforts on this hyper-diverse group.

For Review Only

Few and far apart: integrative taxonomy of Australian species of *Gladiobela* and *Pagodibela* (Conoidea: Raphitomidae) reveals patterns of wide distributions and low abundance

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Running title: Molecular systematics of *Gladiobela* and *Pagodibela*

24 Abstract

25 The deep-sea malacofauna of temperate Australia remains comparatively poorly known.
26 However, a recent influx of DNA-suitable material obtained from a series of deep-sea cruises
27 facilitated integrative taxonomic study on the Conoidea (Caenogastropoda:
28 Neogastropoda). Building on a recent molecular phylogeny of the conoidean family
29 Raphitomidae, this study focussed on the genera *Gladiobela* and *Pagodibela* (both Criscione
30 et al., 2020). We subjected a comprehensive mtDNA COI dataset of deep-sea raphitomids to
31 ABGD barcode gap detection, which recognised 14 primary species hypotheses (PSHs), nine
32 of which were converted to secondary species hypotheses (SSHs). Following the additional
33 examination of the shell and hypodermic radula features, as well as consideration of
34 bathymetric and geographic data, seven of these PSHs were recognised as new to science
35 and given full species rank. Subsequently, full systematic descriptions were provided herein.
36 Of these, five were attributed to *Gladiobela* (three of which are endemic to Australia and
37 with two more widely distributed) and two were placed in *Pagodibela* (one endemic to
38 southern Australia and one widespread in the Pacific). The rarity of many ‘turrids’ reported
39 in previous studies was confirmed herein, as particularly indicated by highly disjunct
40 geographic records for two taxa. Additionally, several of the studied taxa exhibited wide
41 Indo-Pacific distributions, suggesting that wide geographic ranges in deep-sea ‘turrids’ may
42 be more common than previously assumed. Finally, impediments to deep-sea ‘turrid’
43 taxonomy in the light of such comparative rarity and unexpectedly wide distributions were
44 discussed.

45 Introduction

46 It is a well-known notion among malacologists that ‘turrids’ – members of the hyper-diverse
47 superfamily Conoidea (Caenogastropoda: Neogastropoda) not including Conidae and
48 Terebridae and historically treated as Turridae (herein referred to as ‘turrids’ to clearly
49 distinguish from Turridae *sensu stricto*) – are a particularly challenging group taxonomically.
50 Hedley (1922: p. 213) stated that ‘the marine gasteropods [sic] embraced in the family
51 Turridae (formerly Pleurotomidae) are considered by those who meddle with them to be
52 more perplexing than any other molluscan family’. The literature provides numerous
53 examples in support of that statement, such as ‘turrid pairs’, where separate species (not
54 necessarily sister taxa) have virtually indistinguishable teleoconch morphologies but
55 differing protoconchs (Powell 1942) or where even species from different families cannot be
56 readily differentiated based on shell characters (Hallan *et al.* 2020; Kantor *et al.* 2018;
57 Sysoev and Kantor 1990). Other impediments to ‘turrid’ taxonomic study include low
58 abundances in many taxa and relative difficulty in collecting due to their largely subtidal
59 habitats (Bouchet and Waren 1980; Todd and Rawlings 2014). Challenges with ‘turrid’
60 taxonomy are further exacerbated in the deep sea, where protoconchs are commonly
61 eroded or missing entirely (Criscione *et al.* 2020), and sculptural elements of the teleoconch
62 may be significantly worn owing to the dissolution of CaCO₃ (Burton 1998). Furthermore,
63 some deep-sea taxa exhibit an overall lack of indicators of terminal shell growth [such as
64 apertural thickening, formation of a varix, or similar (Bouchet and Waren 1980)]. In these
65 cases, inferences about the stage of maturity (and therefore about representative adult
66 size) are difficult, particularly where material is scarce. Paraphrasing the sentiment by
67 Marshall (1983) that material of Triphoridae ought not to be described in the absence of an
68 intact protoconch, Puillandre *et al.* (2017) emphasised that no new ‘turrids’ should be
69 described without molecular data, preferably designating a molecular voucher as a type.
70 This is particularly true for deep-sea material, given the issues raised above.
71 When conducting ‘turrid’ systematics research, notably on deep-sea taxa, there is also the
72 need to consult with taxonomic work on species that may occur far beyond conventionally
73 expected geographic limits of conspecific taxa. A study by Zaharias *et al.* (2020)
74 demonstrated that several deep-sea species of the genus *Cryptogemma* Dall, 1918
75 (Turridae) exhibit notably wide distributions. Corroborated by mitochondrial DNA evidence,
76 one species, *C. phymatias* (R. B. Watson, 1886) was shown to have a trans-oceanic

distribution, arguably providing the first molecularly confirmed such case in a benthic gastropod. Such unexpectedly wide geographic ranges may routinely escape the attention of taxonomists, notably where morphologically heterogeneous taxa are concerned; Zaharias *et al.* (2020) synonymised several species names attributable to *Cryptogemma*, suggesting that while analyses of molecular data commonly reveal unnamed taxa in the Conoidea (e.g., Fedosov and Puillandre 2012; Puillandre *et al.* 2010a), taxonomic over-splitting may also occur, arguably in part as a consequence of underestimated distribution ranges. While trans-oceanic ranges, such as that documented for *C. phymatias*, appear to be exceptionally rare based on existing evidence, wide distributions in the deep sea, particularly in the Conoidea, may not be so uncommon. Bouchet and Waren (1980) noted that among their deep-sea study material from the Western and Eastern Atlantic, there was a 34% species overlap between the two regions, suggesting that a significant portion of deep-sea ‘turrids’ may have ocean-wide distributions. Furthermore, they predicted that percentage would increase with additional study.

The deep-sea Australian malacofauna has, until recently, remained among the most poorly known in the Indo-Pacific region owing to a lack of study material, particularly that suitable for molecular analysis (Criscione *et al.* 2020). However, recent deep-sea expeditions in southern and eastern Australia, notably aboard the research vessel *Investigator*, have delivered a wealth of material from several major groups of the Mollusca (see MacIntosh *et al.* 2018; O'Hara 2019). The extremely diverse superfamily Conoidea is prevalent in these samples, and now subject to ongoing collaborative study between the Australian Museum, Sydney (AM) and the Muséum National d'Histoire Naturelle, Paris (MNHN) (Criscione *et al.* 2020; Hallan *et al.* 2020; Zaharias *et al.* 2020). The ‘turrid’ family Raphitomidae is particularly well-represented among this conoidean material (O'Hara 2019). A recent molecular phylogeny by Criscione *et al.* (2020) revealed a considerable diversity of previously unknown deep-sea raphitomid lineages and included the description of twelve new genera. Building on the classification framework set out by this latter study, two of the genera described therein are further treated here: *Gladiobela* Criscione *et al.*, 2020 and *Pagodibela* Criscione *et al.*, 2020. *Gladiobela angulata* Criscione *et al.*, 2020, type species of its genus, is known from bathyal depths (3350–3807 m) of the Great Australian Bight (henceforth GAB), and from a single locality off the NSW Central Coast (~2600 m). This study describes five additional species of *Gladiobela*, three of which are possibly endemic to

109 temperate Australia, and two potentially widespread in the eastern Indo-Pacific, with all
110 members of the genus occurring from bathyal to abyssal depths (~500-4850 m). *Pagodibela*
111 *maia* Criscione, 2020, type species of its genus, is known only from a single record from the
112 Coral Sea (~1000 m). Two additional species of *Pagodibela*, one from the GAB and the other
113 from north Queensland to the Society Islands, are also described herein. Generic diagnoses
114 are provided for both genera, as well as details of the shell and venom apparatus.
115 Furthermore, morphological characters, as well as patterns of bathymetry and biogeography
116 are presented. Finally, impediments to future 'turrid' systematics given their comparative
117 scarcity (in terms of number of individuals) and unusually wide distributions at the species-
118 level are discussed.

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Materials and methods

Taxon sampling

The samples studied herein were selected from among all deep-sea Raphitomidae ethanol-preserved material from the malacological collections of the Australian Museum, Sydney (AMS), the South Australian Museum, Adelaide (SAMA) and the Muséum national d'Histoire naturelle, Paris (MNHN). As a result of ongoing systematic research on the Conoidea at the AMS and MNHN, several hundreds sequences of the mitochondrial gene cytochrome c oxidase subunit 1 (COI) were obtained from a few hundreds largely undescribed representative raphitomid taxa. In order to assist with the selection of the study material, a pilot analysis was performed on a dataset including all raphitomid COI sequences, using the neighbour-joining method (NJ) (Saitou and Nei 1987) implemented in MEGA 7 (Kumar *et al.* 2016). The dataset encompassed sequences of the type species of many deep-sea raphitomid genera, including the holotypes of *G. angulata* (MN983180) and *P. maia* (MN983188). A subset of sequences was generated which included all COI sequences that in the resulting tree (not shown) were more closely related to the sequences of either of the two holotypes than to any type species of any other raphitomid genus in the dataset. The dataset thus obtained (henceforth referred to as 'ingroup') forms the basis for the molecular analysis described below. Additional material relevant to this study, but for which attempts of amplifying COI failed, was selected based on the results of a NJ analysis (see below) of a dataset comprising all 12S sequences available for raphitomids. This dataset, albeit much smaller than the COI one (about 200 sequences), included sequences of the holotypes of type species of *Gladiobela* (MN985672) and *Pagodibela* (MN985684). A subset of 12S sequences was formed with these and other sequences that in the resulting tree (not shown) were more closely related to them than to any type species of any other raphitomid genus in the dataset.

Among the ingroup specimens, morphological examination was only conducted on those collected in Australian waters and some of those collected outside Australia (see Results). Geographic and bathymetric data were available for all ingroup specimens. Geographic distributions were assessed with reference to marine biogeographic realms as delimited in Costello *et al.* (2017). According to Bouchet *et al.* (2008), when inferring species distributions from sampling depth intervals, only shallower depth values were considered, as there is no evidence that the species collected occurs beyond that value.

151

152 Molecular methods

153 Molecular work was performed in laboratories at two different Institutions (AMS and
154 MNHN). Unless otherwise stated, the same methodology was followed by both laboratories.

155 DNA extraction was performed on at least one specimen per morphospecies per collecting
156 site. DNA was extracted from small pieces of foot muscle by use of a Bioline Isolate II
157 Genomic DNA extraction kit for animal tissue, following the standard procedure of the
158 manual (AM) or using the Epmotion 5075 robot (Eppendorf), following the
159 recommendations by the manufacturer (MNHN). Fragments of the two mitochondrial genes
160 COI and 12S were amplified using the primer pairs LCO1490/HCO2198 (Folmer *et al.* 1994)
161 and 12S-I/12S-III for 12S (Simon *et al.* 1991). PCR reactions were performed in volumes of 25
162 μ l, containing 3 ng DNA, 1X Qiagen CoralLoad PCR Buffer, 2.5mM $MgCl_2$, 0.25mM dNTP,
163 0.5mM of each primer, 0.5 μ g/ μ l of BSA and 0.2 μ l of Bioline MyTaq DNA polymerase.
164 Amplification consisted of an initial denaturation step at 94°C for 4 min, followed by 37
165 cycles of denaturation at 94°C for 30 s, annealing at 50°C (COI) or 57°C (12S) for 30 s,
166 followed by extension at 72°C for 1 min. The final extension was conducted at 72°C for 5
167 min.

168 PCR products were purified and sequenced by the Macrogen (AMS) and Eurofins (MNHN)
169 sequencing facilities. When necessary, chromatograms were manually corrected for
170 misreads and forward and reverse strands were merged into one sequence file using
171 CodonCode Aligner v. 9.0.1 (CodonCode Corporation, Dedham, MA). COI sequences did not
172 require alignment as these had identical lengths of 658 bp after trimming of the primer
173 sites. Alignments of 12S sequences were generated using MUSCLE as implemented in
174 MEGA7 (Kumar *et al.* 2016).

175 Phylogenetic analyses were conducted on the COI dataset, using Maximum Likelihood (ML)
176 and Bayesian inference (BI) methods. All sequences used deposited in GenBank (Table S1).
177 Sequences of thirteen deep-sea raphitomid genera were added to serve as outgroups (Table
178 S1). Their selection was based on a multi-gene (mitochondrial and nuclear) phylogeny
179 containing many southern and south-eastern Australian Raphitomidae (Criscione *et al.*
180 2020). ML was performed using the program MEGA7 with Nearest-Neighbour-Interchange
181 (NNI) as heuristic method and automatic generation of the initial tree. One thousand
182 bootstrap replicates (BS) were performed to assess the topology support. The BI analysis

was performed in MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) and included 2 runs of 10^7 generations, with 4 chains each and a sampling frequency of one tree per 1,000 generations. Other parameters were set to default. A consensus tree was then calculated after checking for chain convergence and discarding the first 25% trees as burn-in. Prior to the model-based ML phylogenetic analyses, TN93+G+I was identified as best-fit model of nucleotide substitution by means of the Bayesian Information Criterion as implemented in MEGA 7 (Kumar *et al.* 2016). According to MrBayes manual (p. 94), a priori model testing was not performed, and the GTR+G+I model was applied to the BI analysis. Nodal support was assessed by values of Bayesian posterior clade probabilities (BPP).

Due to the smaller number of sequences selected to form the 12S dataset, a NJ analysis only was deemed sufficient to represent the phylogenetic relationships based on this gene. This analysis was performed in MEGA 7 (Kumar *et al.* 2016). Uncorrected pairwise genetic distances were calculated using MEGA7 with the option 'pair-wise deletion of gaps'.

Morphological examinations

All studied samples consisted of soft parts and shells, which had been separated following the methodology (drilling or microwaving) mentioned in Criscione *et al.* (2020). We studied shell morphology and (when possible) internal anatomy, including radular morphology. Shells were affixed to plasticine and positioned with their vertical axis parallel to the observation plane. Each shell was then photographed from above using a Canon EOS 6D digital SLR camera. Maximum shell length (SL) and width (SW) were measured on digitised images using the calibrated ruler tool in Adobe Photoshop CC v.20.0.6 and measurements rounded to the nearest 0.1 mm. The number of shell whorls was counted under a Leica MZ8 stereomicroscope, according to Bouchet and Kantor (2004). While it was possible to obtain the number of teleoconch whorls (Wt) for all studied specimens, protoconch whorls could only be counted occasionally due to widespread erosion of the apex. In order to capture the shell proportions regardless of their size, the ratios SL/SW, SL/Wt and SW/Wt were generated. Ideally, to prevent the effects of allometry, only shells at terminal growth could be used in the morphometric analysis of this study. However, terminal growth could not be assessed for the samples of this study (see above). As an approximation, shells of a given PSHs were assumed to have reached terminal growth when their Wt were within one unit of

the maximum Wt value observed for that given PSHs. Based on the data obtained, descriptive statistics and plots were produced in SYSTAT v.13.1 (Systat Software, Inc., 2009). Anatomical studies were conducted on animals removed from ethanol and briefly rehydrated in distilled water. Using standard dissection tools, the venom apparatus was excised and the radular sac isolated and placed on a glass slide; during this 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 were rinsed repeatedly in distilled water, then separated into individuals and ligament-connected pairs/smaller clusters. 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.

Species delimitation

The Automatic Barcode Gap Discovery (ABGD) (Puillandre *et al.* 2012b) was applied for primary species delimitation to the dataset containing all COI ingroup sequences. The web-based version of ABGD (<https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html>) was used with a p-distance model. The relative gap width (X) was set to 1 and other parameters left to default. Resulting ABGD groups were considered primary species hypotheses, henceforth referred to as PSHs. Following Puillandre *et al.* (2012c), conversion of PSHs to secondary species hypotheses (SSHs) was conducted through comparative examination of morphological characters as well as through evaluation of geographic and bathymetric data. In particular, for each PSH examined, the co-occurrence of the following conditions was considered evidence supporting such conversion: (i) the PSH is a highly supported clade (BPP>98% and BS > 90%), (ii) the PSH shows lower values of intra-PSH genetic p-distance in COI when compared with values of inter-PSH distances measured with the most closely related PSH, (iii) all its constituent specimens share at least one distinctive morphological feature deemed not to be polymorphic or ecophenotypic, and without exhibiting intermediate forms. When the above criteria were met, the presence of genetic or morphological divergence and/or bathymetrical partitioning in sympatry was considered additional evidence supporting species delimitation. Clearly, when PSHs are represented by one sequence only, criteria (i) and (ii) cannot be assessed. In those cases, the decision was guided by presence of additional bathymetrical and morphological evidence as well as

comparisons with intra-generic patterns of genetic distance. When available, species names were assigned to SSHs based on the current taxonomy. New species names were introduced when no names were available, and formal descriptions for these taxa are given in the systematic section below.

Abbreviations

CMR=Commonwealth Marine Reserve; Ht=holotype; NSW=New South Wales; PNG= Papua New Guinea; Pt=paratype; QLD=Queensland, SA=South Australia, TAS=Tasmania; VIC=Victoria; wet=number of ethanol-preserved (wet) specimens.

Results

Molecular studies

Molecular analyses were based on a total of 75 COI sequences (42 newly produced and 33 GenBank-sourced) generated from specimens collected off Australia during the expeditions IN2015_C01, IN2015_C02 (GAB) and IN2017_V03 (Tasman and Coral Seas) and other localities of the tropical and temperate Indian and Pacific Oceans, during a number of voyages that formed part of the Tropical Deep-sea Benthos programme of MNHN (Fig. 1, Table S1). The dataset analysed included 51 ingroup sequences and 24 sequences representing 24 deep-water raphitomid species of 13 different genera that were used as outgroups

Except for extremely low and high prior values, the ABGD analysis of the COI ingroup dataset consistently returned a partition with 14 groups of sequences (PSHs). Among all PSHs (Fig. 2), five (G1, G2, G4, P2 and P3) contain exclusively Australian samples, three (G3, G5 and P1) include samples from Australian seas and beyond, while the remaining six (GA-GE and PA) encompass sequences from outside Australian waters.

The BI and ML analyses generated trees with nearly identical topologies, showing only minor differences in the relative position of individual sequences within some of the PSH clades (Fig. 2). Clades representing PSH-level relationships and above were generally well-supported, with very few exceptions. In both analyses, two major genus-level clades were retrieved, namely *Gladiobela* (BPP=100%, BS=93%) and *Pagodibela* (BPP and BS=100%).

These two clades included ten and four PSHs respectively, all forming well-supported (in

terms of nodal support: BPP>98%; BS>90%) and well-differentiated (in terms of branch lengths) PSH clades.

Within the two genus-level clades, there was no overlap between intra- and inter-PSH distances. In the *Gladiobela* clade, the intra-PSH pairwise distances in COI ranged from 0 to 1.1 % (average=0.5 %) with inter-PSH distances ranging from 4.0 to 11.7 % (average=8.2 %) (Table 1). The lowest inter-PSH distances were observed between GD and GE and the highest intra-PSH distances were found within G3. In the *Pagodibela* clade, the intra-PSH pairwise distances were between 1.8 and 1.9%, whereas inter-PSH distances ranged from 4.4 to 7.1 % (average=5.6 %) (Table 2). The lowest inter-PSH distances were observed between P2 and PA and the highest intra-PSH distances were found within P1.

The NJ tree obtained analysing the 12S dataset contained four sequences in a cluster, each obtained from samples of four distinct *Gladiobela* PSHs (G1, G3, G4, G5 - as delimited above). One additional sequence (MT081495), from sample AMS C.571625, was the sister group of this former cluster and exhibited values of p-distances (5.1-6.6%; Table S2) with its members that were within the range of those measured for COI between *Gladiobela* PSHs. Additionally, its genetic similarity (in terms of p-distance values) with G1, G3, G4, G5 was greater than that measured with sequences of samples of *Pagodibela* or of any other genus in the analysis (data not shown), suggesting its attribution to *Gladiobela*. Given that 12S largely shares patterns of inheritance with COI, this sample was considered an additional *Gladiobela* PSH (G6) to undergo further testing for conversion to SSH.

Morphological studies

Shell morphology was examined for all sequenced material and internal anatomy, including radular morphology (when possible) for at least two sequenced specimens per PSH. The *Gladiobela* clade contains three PSHs (G1, G2 and G4) exhibiting a gross shell morphology, whorl profile and sculptural elements that are comparatively similar (Fig. 3A, B, D), whereas the remaining taxa possess heterogeneous shell morphologies, including high-spined and broad fusiform shells with varying sculpture (Fig. 3).

Due to the limited amount of material available (and specifically of shells at a stage equivalent terminal growth), the sample size was too small to permit inclusion of all PSHs in a statistically rigorous morphometric analysis at this time. A scatterplot of SW/Wt and SH/Wt for *Gladiobela* (Fig. 4) revealed that G1 and G2 can be differentiated by shell size

(with the latter exhibiting larger values of both length and width) and proportions (with the latter showing a larger SH/SW ratio). The plot shows that G3 has the smallest and most slender shell of all congeners, while G6 has the largest and broadest shell.

As protoconchs were largely eroded (an intact protoconch could not be observed for all species), this character will not be given much emphasis herein. However, all larval shells that could be examined were multispiral and exhibited the typical raphitomid diagonally cancellate sculpture (Fig. 5).

All members of *Gladiobela* shared hypodermic, somewhat tightly rolled teeth with a very long dorsal blade (Fig. 6A), elongate adapical opening and moderately broad to very broad base (Fig. 6). The sister taxa G1, G2 and G3 can be characterised by teeth with extremely long dorsal blades and a very broad, angular base with a crescent-shaped indentation around the perimeter of the lower shaft and an elongate posterior extension (Fig. 7); G4 is a notable outlier with an extremely long tooth compared to its congeners (Fig. 6F), whereas G5 and G6 possess teeth with a narrower, less angular base (Fig. 6B, D). All members exhibit moderate to long, tapering to cylindrical cephalic tentacles with very small eyespots at their lower outer bases.

Pagodibela PSHs vary notably in shell morphology, from strongly pagodiform with prominent sculpture, to subconical and comparatively smooth (Fig. 3G-J). Their radulae consist of hypodermic morphologically uniform teeth: awl-shaped, with a long dorsal barb, an elongate adapical opening and a swollen base with coarse external texture (Fig. 6G-I). All PSHs possess small eyes at the outer lower bases of cylindrical cephalic tentacles.

Geographical and bathymetrical distributions

The genus-level clade *Gladiobela* is recorded from three marine realms (sensu Costello *et al.* 2017) (Fig. 1A, C) and *Pagodibela* clade from at least seven marine realms (Fig. 1B, D).

Gladiobela exhibits a wide bathymetric range, from 470 to 4750 metres, and *Pagodibela* from 318 to 1013 metres (Fig. 8). The sister clades G1 and G2, G4 and G6 are known only from off Australia, where they are restricted to bathyal and abyssal depths of the temperate south (Fig. 1A). The three former PSHs are not recorded micro-sympatrically (e.g. in the same trawl haul): G1 exhibits a disjunct distribution with the majority of records in the GAB and a single record in the Hunter CMR (depth range 2474-3389 m); G2 occurs between (off) the far southern coast of NSW and into the Bass Strait (depth range 4133-4750 m), whereas

G4 is known from a single locality in the Hunter CMR (3980 m). G6, known only from a sole individual, was collected at the same site as G1 in the Hunter CMR. G3 is known from two widely separated localities, both geographically and bathymetrically, namely in the East Gippsland CMR, at 3850 metres and NW Choiseul, Solomon Islands, between 1083 and 1100 metres. G5 is recorded from the Hunter CMR and Canal de l'Havannah, New Caledonia, with depth records occurring between 951 and 1006 metres.

For *Pagodibela*, P2 and P3 are only known as single specimens from the Coral Sea and GAB respectively, of which the former is known from approximately 1000 metres and the latter approximately 370 metres. Conversely, P1 is widely distributed between (off) North Queensland, via the Coral Sea, New Caledonia and eastward to the Society Islands at a depth range of 450-1013 metres. PA has the most widespread known distribution of all *Pagodibela* PSHs, occurring in at least four marine realms between the South Pacific and off the east African coast (Fig. 1D).

PSH to SSH conversion

Comparative examination of the morphological, geographic and bathymetric data available was employed to attempt the conversion of PSHs to SSHs. As generating morphological data for most species with distribution outside Australian waters was beyond the scope of this study, testing of five PSHs (i.e. GA-GE), out of the total of fourteen retrieved by ABGD, was not attempted and these are pending further sampling and taxonomic investigation. As detailed below, all remaining nine PSHs retrieved by ABGD, namely G1-G5, PA and P1-P3 satisfied the three conditions described in the methodological section. G1 and G2 corresponded to highly supported clades (BPP and BS=100%; Fig. 2) in a sister relationship. Both exhibited low intra-PSH genetic distance (average 0.06% and 0.05% respectively; Table 1) and comparatively high reciprocal genetic distance (average 5.4%; Table 1). Both G1 and G2 could be distinguished from all other PSHs by their distinctly carinated shells (Fig. 3A-B). G1 could be differentiated from G2 by their smaller, broader shells (Fig. 4) with a carina that is comparatively less pronounced. In addition, their bathymetrical range did not overlap (Fig. 8). The genetic, morphological and bathymetrical distinction between G1 and G2 was maintained in spite of their apparent high dispersal potential (as inferred by the multispiral protoconch) and their sympatry in the South Australia realm (Fig. 1A).

Clade G3 was highly supported (BPP and BS=100%), exhibiting values of intra-PSH genetic distances (average ~1%; Table 1) well below values of reciprocal between-PSH genetic distance with its most closely related PSHs (4% with both GE and GD; Table 1). Its shell was the smallest and most elongate of all other PSHs (Fig. 4) and could readily be distinguished by its raised peripheral cord (Fig. 3C).

G4 corresponded to a highly supported clade (BPP and BS=100%), exhibiting values of intra-PSH genetic distances (average 0.5%; Table 1) and comparatively high genetic distance with its most closely related PSH, GA (5.8%; Table 1). It could be clearly differentiated from all other PSHs by its shell exhibiting a long, clearly demarcated siphonal canal (Fig. 3D) and by its uniquely long hypodermic teeth (Fig. 6F).

Clade G5 was highly supported (BPP and BS=100%) and included a single haplotype that exhibited a large genetic distance from its most closely related PSH, GC (average 7.9%; Table 1). All shells of this PSH shared distinctively rounded lower teleoconch whorls (Fig. 3E) that allowed their differentiation from shells of all other PSH in the *Gladiobela* clade.

Along with the aforementioned comparatively high values of inter-PSHs genetic p-distance in 12S (Table S2), the shell of G6 could be differentiated from that of all other PSHs by its broad whorls with opisthocline axial ribs, and by its comparatively rounded shoulder (Fig. 3F). Such genetic and morphological differentiation was maintained in spite of its sympatry with G1 at the boundary between the two marine realms encompassing the Australian seas (Fig. 1A).

PA and P1 both corresponded to highly supported clades (BPP=98% and BS=93%, BPP and BS=99% respectively; Table 2) showing comparatively high values of reciprocal genetic differentiation (average 4.7%; Table 2). These two PSHs exhibited similar shells that could be differentiated from other *Pagodibela* PSHs by their comparatively thicker and more elongate shells. However, PA and P1 could be differentiated from each other based on shell sculpture - while shells of P1 possess juvenile whorls with weakly opisthocline axial riblets extending across the periphery (although weakening towards suture), in shells of PA the axial elements were significantly weaker, and there was a prominent, slightly gemmate subsutural cord in the early- to median teleoconch whorls (Fig. 3H and 3G respectively). In both PA and P1, the overall shell shape was rather conserved across its constituent samples. The minor differences observed among PA shells in their peripheral sculpture (smooth,

carinate or tuberculate), were consistent with distributional patterns and thus interpreted as intraspecific geographical variation.

The only sample included in P2 was separated from the sister pair PA and P1 by high values of genetic distance (4.4 and 4.8% respectively; Table 1). The pagodiform shell of P2 exhibited a gemmate carina that was unique among PSHs of *Pagodibela*. This distinctiveness was maintained in spite of geographic and bathymetric overlap with P1 in the Coral Sea. Clade P3 was the sister group of all other *Pagodibela* PSHs, revealing comparatively high values of reciprocal genetic distance with all congeneric PSHs (>6.3%; Table 2). It included only one sample with a uniquely thin, fragile shell with comparatively rounded whorls (Fig. 3J), which differentiated it from any other PSH within the *Pagodibela* clade.

Assigning names to SSHs

A search was conducted for all names available and potentially applicable to the nine SSHs resulting from the conversion process described above. By consulting the relevant literature on Raphitomidae (e.g. Bouchet and Sysoev 2001; Bouchet and Warren 1980; Sysoev and Bouchet 2001) and by comparison of molecular and morphological data available on type specimens with the data generated on sequenced specimens, we found three names applicable to three SSHs. Two SSHs, G1 and P2, included the type material of two species, *G. angulata* and *P. maia* respectively, and could therefore be readily respectively associated with these species. As its constituent specimens shared shells that closely resembled the holotype of *Gymnobela baruna* Sysoev, 1997 (Fig. 3G), clade PA was attributed to this taxon, thus requiring a formal transfer of this species to *Pagodibela* as hereby proposed (*Pagodibela baruna* n. comb.). As no available names could be found for the remaining six SSHs, new taxon names were assigned, namely *G. abyssicola* n. sp. (G2), *G. acris* n. sp. (G3), *G. stupa* n. sp. (G4), *G. vitrea* n. sp. (G5), *G. sinuosa* n. sp. (G6), *P. pacifica* n. sp. (P1) and *P. meridionalis* n. sp. (P3). Formal taxonomic descriptions of these newly recognised species are provided below.

Discussion

Phylogenetic relationships and generic taxonomy

Building on the five-gene phylogeny of Criscione *et al.* (2020), that established the phylogenetic framework upon which *Gladiobela* and *Pagodibela* were recognised and described, it is shown herein that there is strong support in both BI and ML analyses for their monophyly (Fig. 2).

The integrity of these genera is corroborated by radular features diagnostic for each genus.

The radula of *Gladiobela* is characterised by hypodermic awl-shaped teeth with an elongate adapical opening, a very long dorsal blade about half the length of the shaft, a (mostly) broad, angular base and a broad, medium long ligament (Fig. 6A-F). Members of *Pagodibela* exhibit evenly tapering awl-shaped hypodermic teeth with a comparatively narrow, sloping base with coarse external texture, and a comparatively small, short ligament (Fig. 6G-I). The wide, strongly perpendicular base and the long posterior extension, particularly noticeable in *G. angulata*, *G. abyssicola* and, *G. acris* (Fig. 6A, C, E; Fig. 7) are particularly prominent features, notably the crescent-shaped indentation around the base of the shaft (Fig. 7A).

While nothing is known of any potential corresponding features in the proboscis interior of these taxa, such as the presence and nature of an epithelial pad seen in several ‘turrid’ lineages (Kantor and Taylor 2002; Medinskaya 1999), the following speculations can nevertheless be made: the long posterior extension (Fig. 7A) facilitates physical contact with the internal proboscis (thus the area which can be attached), while the crescentic indentation possibly facilitates the proboscis sphincter in holding the tooth securely. A firm, secure grip can hypothetically perform a number of functions, such as aiding in speed and precision during attacks and in securing tooth recovery after- or between attacks (thus assisting in both performing successive stabs and conserving teeth).

While the general configuration of the radula of *G. stupa* conforms with that of its congeners, this species is a notable outlier, due to its very long hypodermic tooth (Fig. 6F). Bouchet and Warren (1980; p. 5) stated that ‘it must be remembered that the radula is an organ for capture of food’; the fact that *G. stupa* possesses extremely long teeth compared to its congeners (Fig. 6F) does suggest that the radular morphology of the group may not purely be ascribed to phylogenetic signal, but that feeding mechanism exerts some selective pressure on their morphology. A similar anomalous enlargement of the radula while retaining the overall tooth configuration (i.e., size and configuration of barbs, length of

adapical opening, base morphology, etc.) of its congeners is also seen in a hitherto unnamed species of *Austrobel* Criscione, Hallan, Fedosov & Puillandre 2020 (unpublished data). The morphology of the radula reflects feeding mechanism to a larger extent than the phylogenetic signal in cone snails (Olivera *et al.* 2015; Puillandre *et al.* 2014). However, dietary habits are not sufficiently known for the Raphitomidae and little inference can be made with regards to the respective influences by phylogenetic signal and feeding in shaping their radular morphology. The radulae of *Pagodibela* species examined here are highly similar (Fig. 6G-J), and therefore present a solid diagnostic generic-level character. In both genera, shells are heterogeneous, but in gross morphology the overall pagodiform shell of *Pagodibela* is a recognisable character in its composite taxa (Fig. 3G-J). While some species are similar in shell morphology (notably *G. angulata* and *G. abyssicola*), *Gladiobela* cannot readily be circumscribed based on its shell at the genus-level (Fig. 3A-F). At the species-level, genetic distinctiveness as shown by ABGD and sequence divergence (Tables 1, 2), demonstrable differences in shell morphology and dimensions (Figs 3, 4) and to a lesser extent radular morphology (particularly for *Pagodibela*, see Fig. 6G-J), translate into robust hypotheses for all the new species described herein. The genetic distinctiveness reported at the intra- and interspecific levels for the two genera (Tables 1, 2) is comparable, but overall lower than those reported for the raphitomid genera *Kermia* W. R. B. Oliver, 1915 and *Pseudodaphnella* Boettger, 1895 (Fedosov and Puillandre 2012), and significantly lower than those reported for *Hemilienardia* Boettger, 1895 (Fedosov *et al.* 2017). This could be explained by differences in population effective size, with mutations being fixed more rapidly in smaller populations due to genetic drift.

Biogeographical and bathymetrical patterns

Most species of *Gladiobela* named herein occur within an area corresponding approximately to the South Australia marine realm of Costello *et al.* (2017). Unsurprisingly, the records are concentrated in the areas of sampling: a relatively restricted portion of the GAB and on a section of the temperate E Australian coast between NE Tasmania and the Hunter CMR (Fig. 1A). As neighbouring regions with comparable environmental conditions remain virtually unexplored, it is plausible that disjunct distributions, like that observed for *G. angulata* (Fig. 1A), are the result of sampling bias, rather than a reflection of any underlying biological process. In *G. angulata*, the mean genetic p-distance between the Hunter CMR COI

haplotype and the GAB haplotypes is low (0.4%), when compared with the range of p-distances calculated within the GAB sequences (0.2-2.0%), indicating very recent or ongoing gene flow between the two areas. It remains unclear whether genetic connectivity in *G. angulata* is realised through a stepping-stone process, involving additional geographically intervening populations, or through long range dispersal of the planktotrophic larva (or both).

In a scenario of a continuous distribution of *G. angulata*, there would be potential range overlap with its sister taxon, *G. abyssicola*, off the southeast Australian coast. However, the two taxa are not recorded in micro-sympatry. Additionally, there is no recorded overlap in their bathymetric ranges, with an approximately 650-metre gap between their lower and upper bathymetric extremes (Fig. 8), despite some sampling coverage within this gap at corresponding areas. It is conceivable that the two taxa have partitioned into separate bathymetric niches, although the present knowledge of their ecological requirements is insufficient to explain the mechanism involved. Separate bathymetric distributions of sister species have been previously reported for at least three conoidean genera, namely *Bathytoma* Harris & Burrows, 1891, *Lophiotoma* T. L. Casey, 1904 and *Cryptogemma* Dall, 1918 (Turridae) (Puillandre *et al.* 2017; Puillandre *et al.* 2010b; Zaharias *et al.* 2020) and presented as examples of speciation where bathymetric niche partitioning is the driver of genetic isolation in absence of topographic barriers.

The two records of *G. acris* are separated by an entire marine realm (Fig. 1A, C) in which there are no records despite moderately comprehensive sampling in recent times and in the relevant depth range (O'Hara 2019), and within which other congeners (Fig. 1A) as well as several other raphitomids have been recorded (Criscione *et al.* 2020). Similarly, *G. vitrea* is recorded from widely separated localities (Hunter CMR and New Caledonia), although both in the same marine realm (Fig. 1A) and both within a relatively narrow depth range when compared to *G. acris* (Fig. 8). Assuming that all species of *Gladiobela* have similar dispersal capabilities, it is plausible that the difference in intraspecific p-distance between *G. acris* (average 1.1%; Table 1) and *G. vitrea* (one haplotype only) is the result of their difference in geographical and bathymetrical distribution.

The comparatively wide geographic distributions of *P. pacifica*, *P. baruna*, *G. acris* and *G. vitrea* are not entirely unexpected given the mounting evidence of wide distributions in deep-sea 'turrids' (Bouchet and Warren 1980; Zaharias *et al.* 2020; Criscione *et al.*, *subm.*).

Our results suggest that *Gladiobela* may comprise species that are comparatively common (e.g., *G. angulata*/*G. abyssicola*) and some of which may be either rare in terms of their abundance or exhibit fragmented distributions (or both).

The bathymetric range of *G. acris* (about 2770 m) (Fig. 8) possibly constitutes the widest ever reported for a conoidean species. While similarly wide depth ranges have been documented for a number of deep-sea ‘turrids’ [including some raphitomids (Bouchet and Waren 1980)], the wide range of the trans-oceanic turrid *C. phymatias* (about 2000 m) is so far the only one reported with support from genetic evidence (Zaharias *et al.* 2020). Due to the scarcity of material for most other species studied here, little inference can be made with regards to their bathymetric zonation.

Challenges to deep-sea ‘turrid’ taxonomy

While extremely diverse, most ‘turrids’ are commonly found in low to very low abundance, frequently even as single individuals (Bouchet *et al.* 2009; Todd and Rawlings 2014). The findings of this study largely conform to that observation, with *P. maia*, *P. meridionalis* and *G. sinuosa* known from only single specimens and *G. acris* n. sp. and *G. vitrea* n. sp. known from two individuals each. Such scarcity of material makes meaningful comparison between taxa with regards to a range of characters difficult. Limited inference can be made about relative size and maturity, as the lack of terminal shell growth makes it difficult to ascertain if a specimen has attained maturity, particularly in the absence of comparative material. While the number of teleoconch whorls may be an indicator of maturity, Bouchet and Waren (1980) suggested that this may not be a reliable character for some taxa, as terminal shell growth has been observed in taxa with very few teleoconch whorls. While the challenge of assessing maturity persists also where sample populations are larger, a growth series can at least provide some insights into any developmental changes that may occur with increasing size. Studies on the genus *Cryptogemma* of the Turridae *sensu stricto* (Kantor and Sysoev 1991; Zaharias *et al.* 2020), suggest that the characteristic apertural notch and a large penial appendage in *Cryptogemma praesignis* (Smith, 1895) are both features attained in maturity and which are absent in immature individuals. Criscione *et al.* (2020) reported developmental changes in the eye morphology of *Nodothauma magnifica* Criscione, Hallan, Fedosov & Puillandre, 2020, in which juvenile and young adults may possess large eyes which with maturity become obscured by epidermis. With species known

only from single or very few specimens, such characters may be readily missed. So, what should then be considered an appropriate threshold in terms of available material for describing a new deep-sea 'turrid'? The absolute minimum ought to be a molecular voucher linked to a type (Puillandre *et al.* 2017) and providing details of radular- and other non-shell characters where available. Satisfying these criteria, meaningful species descriptions can be conducted even where limited material is known. Any effort towards inventorying the diversity of 'turrids' is vital to the understanding of their evolution and to the characterization of turritoxins (e.g. Gonzales and Saloma 2014; Lopez-Vera *et al.* 2004; Puillandre *et al.* 2012a), far lesser known than the pharmacologically relevant conotoxins (Conidae; e.g. Prashanth *et al.* 2014) and teretoxins (Terebridae; e.g. Gorson *et al.* 2015). A molecular type voucher also allows for a cumulative taxonomic process, where any future conspecific material suitable for DNA analysis can then be readily identified, and systematic descriptions revised accordingly where new anatomical and/or morphological data are obtained. However, where scarce material (even single individuals) cannot be analysed molecularly, particularly where only the shell is available for study, new species descriptions of deep-sea 'turrids' are virtually meaningless; in fact, such descriptions may complicate integrative taxonomic efforts on this group by the proliferation of taxon names that can never reliably serve as references to any future anatomical and molecular study. With tendencies in several taxa toward shell plasticity, geographically and bathymetrically widespread distributions, and low abundance (Bouchet *et al.* 2009; Bouchet and Waren 1980; Criscione *et al.* 2020; Kantor *et al.* 2008; Zaharias *et al.* 2020), taxonomic endeavours on 'turrids' pose logistical as well as theoretical challenges best met by integrative, and preferably collaborative efforts to enable optimal sharing of data, material, and expertise. The numerous synonyms in *Cryptogemma* (Zaharias *et al.* 2020) are a salient recent example of how integrative taxonomy is critical to constraining and understanding morphological heterogeneity and elucidating biogeographical patterns at the species level. Todd and Rawlings (2014) give examples of how taxonomic efforts on *Polystira* (Turridae) have resulted in greatly underestimated distribution ranges due to a lack of examination of museum holdings, and where taxonomic decisions have been made with 'relatively few comparisons with other taxa' (p. 470). The results herein further illustrate the need for the integrative approach, associated with a high sampling effort, without which inadequate or

589 redundant taxonomic decisions can too readily be made due to lacking consultation with the
590 broader taxonomic, biogeographical and molecular contexts.

For Review Only

Systematics

General remarks

If not stated otherwise, holotypes are dissected ethanol-preserved specimens and all systematic descriptions are based on the holotype. Shell whorls counts (approximated to one decimal unit) are reported with reference to intact whorls only. When applicable, the expression 'at least' is used in combination with the whorl count to indicate potential additional missing whorls that could not be counted. Shell and head-foot colouration reported in the descriptions are based on observations performed prior to fixation, and thus may not be fully reflected in the illustrations provided (Figs 3, 5).

Measurements of radular features, mainly the length of the adapical opening and the dorsal blade, are given as ratios of the length of the shaft. The 'shaft' is here defined as the entire length of the tooth minus the base, where there is a notable swelling and angulation that clearly differentiates it from the comparatively thin-walled hypodermic, rolled structure. This is done to ensure consistency with the terminology used in Criscione *et al.* (2020).

Superfamily Conoidea Fleming, 1822

Family Raphitomidae Bellardi, 1875

Genus *Gladiobela* Criscione, Hallan, Puillandre and Fedosov, 2020

Diagnosis

Shell (SH=13.5-27.3, SW=7.5-14.0) fusiform-biconical, broadly- to elongate- biconical, thin-walled, semi-translucent to opaque. Protoconch multispiral, orange, cyrthoconoid, with up to four whorls with diagonally cancellate sculpture. Teleoconch of four to eight whitish, cream to orange whorls, suture impressed. Whorl profile medium- to very broad, with wide, rather lightly concave to straight subsutural ramp, indistinctly to clearly demarcated from whorl periphery; distinctly angulated shoulder sometimes bearing clearly defined carina situated at mid-height to abapical third. Lower portion of whorl sub-cylindrical or slightly narrowed toward suture. Teleoconch sculpture of spirals only (striae) or spiral cords and axial riblets/ribs. Subsutural ramp sculpture of axial growth lines to slightly raised riblets, spirals absent to very faint. Last adult whorl evenly convex or with slight concavity below carina, evenly convex below carina (in latter) or below subsutural ramp, clearly demarcated from rather straight, subcylindrical to tapering siphonal canal. Aperture elongate, about 40% to half total shell length; outer lip thin, unsculptured. Inner lip whitish, gently recurved, with

623 or without spiral cords extending onto columella. No distinct callus. Anal sinus wide to very
624 wide, (moderately) deep, u-shaped.

625 Animal uniform whitish to cream. Cephalic tentacles short to rather long. Eyes very small.
626 Radula of straight to slightly curved, medium to very long hypodermic teeth (150-460 µm in
627 length); no ventral barb; dorsal blade extremely long, from about 1/3 to half of length of
628 shaft; adapical opening very elongate to subtriangular, rather narrow, ranging from about
629 1/10 to 1/3 of length of shaft. Base broad to very broad, with or without distinctly indented
630 'shelf' perpendicular to shaft; large dorsal wall extending posteriorly, with numerous
631 internal pits or folds; exterior of base with fine texture; basal opening large, subcircular.
632 Ligament broad.

633

634 Remarks

635 *Gladiobela* can be differentiated from other raphitomid genera by the following combined
636 characters: a (generally) broadly to elongate fusiform shell with a large aperture extending
637 about half of total shell length; a weakly to distinctly carinate shoulder (notably in juvenile
638 teleoconch whorls); rather dense, evenly set spiral cords throughout periphery of
639 teleoconch whorls (include base of last adult whorl); straight to slightly curved hypodermic
640 teeth with a very long dorsal blade, elongate adapical opening, a (generally) very broad,
641 distinctly angular base and a broad, medium long ligament. In terms of shell morphology,
642 *Gladiobela* bears some superficial resemblance to a number of other Australian deep-sea
643 raphitomid genera including *Biconitoma*, *Aplotoma*, *Pueridaphne* and *Fusobela* (all Criscione
644 et al., 2020), all of which exhibit comparatively broadly fusiform shells where the length of
645 the aperture is approximately half of total shell length. However, *Biconitoma* and *Aplotoma*
646 differ from *Gladiobela* in their opaque, chalky shells, which also exhibit prominent spiral
647 cords. *Pueridaphne* is characterised by a finely cancellate sculpture and a deep, wide anal
648 sinus (Criscione et al. 2020), whereas *Fusobela* bears distinctly rounded whorls with a very
649 weakly defined subsutural ramp. Additionally, these genera differ from *Gladiobela* with
650 respect to a number of anatomical characters (see Criscione et al. 2020)

651 The ranges for this genus are here expanded from those provided in Criscione et al. (2020),
652 with a reported bathymetric range of 470-4750 metres (Fig. 8) and occurring in the GAB,
653 Tasman Sea, Coral Sea, New Caledonia and the Solomon Islands (Fig. 1A, C).

654

Gladiobela abyssicola n. sp.

(Figs 3B, 6E)

Material examined

Holotype: Australia, NSW, off Bermagui, (-36.351, 150.914), IN2017_V03_043, 4750-4763 m, (AMS C.571656). COI: MT081415.

Paratype material: As for holotype, 1 wet (AMS C.571717), 1 wet (AMS C.519389), Australia, Bass Strait, (-39.552, 149.553), IN2017_V03_030, 4133-4197 m, 1 wet (AMS C.519329).

Etymology

In reference to its presence in the abyssal zone, derived from 'abyssus' (Latin=abyss) and -colus (New Latin=inhabitant). Adjective of feminine gender.

Distribution

Known from abyssal waters off the southern coast of NSW and Bass Strait, Australia.

Shell (SH=25.6 mm, SW=12.8 mm) broadly fusiform-biconical, rather thin-walled, semi-translucent. Protoconch eroded. Teleoconch of at least 5.2 rather uniformly cream whorls, suture impressed. Whorls broad, with very wide, lightly concave to straight subsutural ramp; well-defined carina situated at approximately mid-height of whorl, periphery subcylindrical. Axial sculpture of growth lines only, on early whorls forming slightly raised, densely set riblets. Spiral sculpture of evenly paced, densely set subperipheral cords (about 6 on median whorl, 8 on penultimate whorl, 40+ on last whorl), few weaker supra-peripheral cords present immediately above carina. Last adult whorl with slight concavity immediately below carina, later - evenly convex, rather clearly demarcated from slightly tapering, moderately long siphonal canal. Aperture elongate, approximately equal to spire length; outer lip thin, unsculptured. Inner lip whitish, gently recurved, spiral cords extending uninterrupted onto columella. No distinct callus.

Anatomy (based on AMS C.571656 [female] and AMS C.519329 [male]). Animal uniform whitish. Cephalic tentacles broad, muscular, short to medium length, somewhat tapering toward blunt tip; miniscule eyespots situated at their outer lower bases. Short, muscular

687 introvert. Proboscis long; venom gland very long, white, convoluted; muscle bulb large,
 688 elongate, lustrous; large radular sac. Oviduct large. Penis narrow, simple, no obvious glands
 689 or swellings.

690 Radula (based on AMS C.519389 and AMS C.571717) of straight to slightly curved
 691 hypodermic teeth attaining 215 μm in length; no ventral barb; dorsal blade sharp, extremely
 692 long, approximately half of length of shaft; adapical opening very elongate, rather narrow,
 693 about 1/3-1/4 of length of shaft. Base broad, with distinct crescentic, slightly excavated
 694 shelf more or less perpendicular to orientation of tooth; large dorsal platform extending
 695 posteriorly, with numerous, densely arranged folds on inner surface; exterior of base with
 696 comparatively fine texture; basal opening large, subcircular. Ligament broad.

697

698 Remarks

699 *G. abyssicola* n. sp. is the sister taxon to *G. angulata*, with which it shares notable
 700 similarities in shell- and radular morphology. In terms of shell morphology, *G. abyssicola*
 701 possesses a more acute carina, which forms an elevated spiral cord at the whorl periphery
 702 and a slightly shorter, less attenuated siphonal canal (Fig. 3B). Compared to its sister taxon,
 703 *G. abyssicola* has larger and more slender shells (Fig. 4). It can readily be differentiated from
 704 the remaining *Gladiobela* spp. by its distinctly carinate shell. Of all *Gladiobela* and
 705 *Pagodibela* species, *G. abyssicola* n. sp. and *G. angulata* are the only to appear in
 706 comparative abundance. The two latter species occupy different bathymetric ranges, in
 707 which *G. abyssicola* is recorded only from abyssal depths (~4100-4800 m) (Fig. 8). *Gladiobela*
 708 *abyssicola* constitutes the deepest-living conoidean gastropod to be described from
 709 Australian waters.

710

711 *Gladiobela acris* n. sp.

712 (Figs 3C, 5A, 6C)

713

714 Material examined:

715 Holotype: Australia, VIC, East Gippsland CMR, (-38.479, 150.185), IN2017_V03_032, 3850-
 716 3853 m, 1 wet (AMS C.571697). COI: MN983181.

717 Paratype: Solomon Islands, (-6.417, 156.35), SOLOMON_2, CP2231, 1083-1100 m, 1 wet
 718 (MNHN-IM-2009-19029).

719

720 Etymology

721 In reference to the pointed shape of its shell, derived from 'acer' (Latin=pointed). Adjective
722 of feminine gender.

723

724 Distribution

725 Distribution: Known only from the Hunter Commonwealth Reserve, NSW, Australia and NW
726 Choiseul, Solomon Islands. Potentially widespread.

727

728 Shell (SH=19.0 mm, SW=7.5 mm) fusiform-biconical, thin, semi-translucent, with tall,
729 orthoconoid spire. Protoconch multispiral, orange, with at least four whorls. PI largely
730 eroded; PII with indistinctly shouldered median whorl, sculpture of axial riblets on shoulder
731 slope changing to diagonally cancellate on whorl periphery. Protoconch-teleoconch
732 transition well-defined, broadly sinuate. Teleoconch of eight uniformly white whorls, suture
733 deeply impressed. Whorls medium-broad, with wide, steep, flat subsutural ramp followed
734 by cylindrical low periphery limited to abapical third in early whorls and subsequently
735 occupying about half of whorl height. Periphery notably raised on early whorls, having
736 appearance of strongly widened cord, in later whorls transition from subsutural ramp to
737 whorl periphery with clear angulation forming distinct shoulder at abapical third of whorl.
738 Axial sculpture of regularly arranged, rounded opisthocline ribs on whorl periphery (20+ on
739 penultimate and last whorls), rapidly weakening and becoming obsolete toward base of last
740 whorl. Spiral sculpture of evenly spaced, gently undulating spiral cords, also confined to
741 whorl periphery (3-4 on mature whorls, 15+ on last whorl). Microsculpture of growth lines,
742 forming arcuate riblets on subsutural ramp, reflecting outline of anal sinus. Last adult whorl
743 evenly convex below subsutural ramp, clearly demarcated from long, tapering siphonal
744 canal. Aperture very elongate, narrow, approximately half of shell length; outer lip thin,
745 unsculptured. Inner lip whitish, distinctly recurved, no distinct callus. Anal sinus wide,
746 moderately deep, u-shaped.

747 Cephalic tentacles long, cylindrical; eyes very small. Muscular bulb elongate.

748 Radula (Fig. 6C) of straight to slightly curved hypodermic teeth attaining 175 μ m in length;
749 no ventral barb; dorsal blade sharp, extremely long, approximately half of length of shaft;
750 adapical opening very elongate, rather narrow, about 1/3 of length of shaft. Base broad,

with distinct crescentic, slightly excavated shelf more or less perpendicular to orientation of tooth; 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 species exhibits the smallest and most slender shell of all congeners (Fig. 4) and it is characterised by its distinctly raised whorl periphery. While differing significantly from the sister taxa *G. angulata/abyssicola* in its shell morphology, it possesses a similar radula with a broad, angular base with a crescentic indentation around the lower shaft (Fig. 6C). Its only two records (Fig. 1A) suggest a wide bathymetric range of at least 2760 metres (Fig. 8).

Gladiobela sinuosa n. sp.

(Figs 3F, 6D)

Material examined:

Holotype: Australia, NSW, Hunter CMR, (-32.575, 153.162), IN2017_V03_070, 2474-2595 m, (AMS C.571625).

In reference to the undulating pattern of its shells axial sculpture, derived from 'sinuosus' (Latin=sinuuous, flexuous). Adjective of feminine gender.

Distribution

Known from a single locality in the Hunter CMR, NSW.

Shell (SL=25.6 mm, SW=14.1 mm) broadly fusiform, rather thin, opaque. Protoconch at least two heavily eroded, orange whorls with diagonally cancellate sculpture. Teleoconch of at least five uniformly whitish whorls, suture deeply impressed. Whorls very broad, tumid, with very wide subsutural ramp, straight in early whorls then weakly concave in later whorls; distinctly angulated shoulder at mid-height of whorl, relatively consistent throughout. Axial

sculpture of raised, sharp, evenly interspaced opisthocline ribs below subsutural ramp (25+ on penultimate whorl, 30+ on last whorl), becoming subobsolete toward base of last whorl. Spiral sculpture of densely set, evenly spaced, straight to somewhat undulating cords below subsutural ramp (12+ on penultimate whorl, 50+ on last whorl), weakening towards base of last whorl. Microsculpture of growth lines only, forming semi-regularly spaced arcuate riblets on subsutural ramp. Anal sinus broad, moderately deep, u-shaped. Aperture elongate-pyriform.

Cephalic tentacles muscular, long, cylindrical. Extremely reduced eye spots on outer lower base of tentacles. Mantle roof with large oviduct; ctenidium large, covering much of length of mantle roof; osphradium large. Proboscis long, conical; radular sac of medium size; venom gland long; muscular bulb large.

Radula of straight to slightly curved hypodermic teeth attaining 180 μm in length; no ventral barb; dorsal blade sharp, very long, ranging between 1/3 and half of length of shaft; adapical opening elongate-triangular, about 1/4 of length of shaft. Base rather broad, with distinct crescentic, steep shelf more or less perpendicular to orientation of tooth; large dorsal platform, extending posteriorly, with numerous, densely arranged folds and pits on inner surface; exterior of base with comparatively fine texture; basal opening large, subcircular. Ligament broad.

Remarks:

This new taxon exhibits the largest and least slender shell of all congeners (Fig. 4), which can readily be differentiated by its broad whorls with opisthocline axial ribs and comparatively rounded shoulder, the latter usually more prominent in most other taxa (see below for comparison with *G. vitrea*). The siphonal canal is broken in the only specimen available, thus the length of both the aperture and the siphonal canal could not be ascertained. The intestine contained ample polychaete fragments.

Gladiobela stupa n. sp.

(Figs 3D, 5F, 6F)

Material examined:

815 Holotype: Australia, NSW, Hunter CMR, (-32.138, 153.527), IN2017_V03_078, 3980-4029 m,
816 1 wet (AMS C.571683). COI: MN983183.

817 Paratype: As for holotype (AMS C.519345).

818

819 Etymology

820 In reference to the shape of its shell, somewhat recalling some sacred Buddhist buildings,
821 derived from the Latinised term 'stupa'. Noun of feminine gender in apposition.

822

823 Shell (SH=20.9 mm, SW=10.6 mm) broadly fusiform, rather thin, semi-translucent.

824 Protoconch eroded. Teleoconch of at least 5 uniformly orange whorls, suture impressed.

825 Whorls broad, with wide, straight, poorly defined subsutural ramp. Lower portion of whorl

826 convex, with shell periphery situated at lower third of whorl, producing slightly pagodiform

827 spire outline. Axial sculpture of growth lines only, most noticeable as slightly raised, rather

828 evenly spaced arcuate riblets on subsutural ramp. Spiral sculpture of densely set, low, spiral

829 cords (8+ on penultimate whorl, 30+ on last whorl), somewhat undulating, at irregular

830 intervals distorted by growth lines. Last adult whorl evenly convex below subsutural ramp,

831 very clearly demarcated from straight, long siphonal canal. Aperture elongate,

832 approximately equal to spire length; outer lip thin, unsculptured, convex at its mid-height,

833 its anterior part extended towards end of siphonal canal. Inner lip orange, rather straight,

834 no distinct callus. Anal sinus wide, deep, u-shaped.

835 Penis large, thick, muscular, club-shaped, with near-distal swelling and distal seminal papilla;

836 dense latitudinal folds. Cephalic tentacles long, muscular, cylindrical, with distinct

837 longitudinal groove. Minuscule eyespots on outer lower base of tentacles.

838 Radula (based on AMS C.571683 and AMS C.519345) of very long, narrow, straight

839 hypodermic teeth attaining 460 μ m in length; no ventral barb; dorsal blade sharp, extremely

840 long, approximately 40% of shaft length; adapical opening elongate, rather narrow, about

841 1/10 of length of shaft. Base rather broad, with large dorsal platform extending posteriorly,

842 with numerous, densely arranged pits on inner surface; exterior of base with comparatively

843 fine texture; basal opening rather large. Ligament broad.

844

845 Remarks

In terms of shell morphology, *G. stupa* is most similar to *G. angulata* and *G. abyssicola*, from which it can readily be differentiated by its distinctly less shouldered whorl profile (Fig. 3D), and the comparatively sharper concavity, where the outer lip meets the siphonal canal, the latter of which is also markedly longer in the observed material. Its radula is considerably longer than that of any of its congeners (Fig. 6F).

A longitudinal groove in the cephalic tentacles is also observed for *Pueridaphne cirrisulcata* Criscione, Hallan, Fedosov & Puillandre, 2020 (Criscione *et al.* 2020; Fig. S4). *Gladiobela stupa* n. sp. is differentiated from the former in its orange shell with a rather long, clearly delineated siphonal canal, its very long radular teeth, and in the former having a reddish-brown animal and cancellate sculpture of the teleoconch.

Gladiobela vitrea n. sp.

(Figs 3E, 5C, 6B)

Material examined:

Holotype: Australia, NSW, Hunter CMR, (-32.479, 152.994), IN2017_V03_069, 1006-1036 m, (AMS C.482311). COI: MN983184.

Paratype: New Caledonia, Canal de l'Havannah, (-22.267, 167.383), EXBODI, CP3793, 951-1180 m, 1 wet (MNHN-IM-2013-52094).

Etymology

In reference to its transparent, somewhat glass-like shell, derived from 'vitreus' (Latin=made of glass). Adjective of feminine gender.

Distribution: Known only from the Hunter CMR, NSW, Australia and Canal de l'Havannah, New Caledonia. Potentially widespread.

Shell (SH=21.4, SW=9.5) elongate-fusiform, rather thin-walled, semi-translucent. Protoconch orange, cyrtoconoid, multispiral, of at least 4 evenly convex whorls. Sculpture diagonally cancellate. Protoconch teleoconch transition, wide, narrowly sinuated. Teleoconch of 6.5 uniformly whitish whorls, suture impressed. Whorls medium broad, with wide subsutural ramp, moderately straight, rather poorly demarcated; early to median whorls with distinct

878 carina at lower third mark, with rounded shoulder on median whorl, penultimate and last
879 whorl rather evenly convex. Axial sculpture of growth lines only, on early whorls forming
880 slightly raised, semi-regular riblets. Spiral sculpture of regularly set, distinct, straight to
881 somewhat undulating spiral cords (about 13 on penultimate whorl, 40+ on last whorl),
882 commencing below subsutural ramp, evenly pronounced except for last whorl where they
883 weaken towards base. Last adult whorl evenly convex below subsutural ramp, clearly
884 demarcated from medium long, subcylindrical siphonal canal. Aperture elongate, about 40%
885 of total shell length; outer lip thin, unsculptured. Inner lip whitish, very gently curved. No
886 distinct callus. Anal sinus wide, moderately deep, u-shaped.
887 Eyes very small. Anal gland rather long. Radular sac small, bearing few teeth; muscular bulb
888 large.
889 Radula of straight to gently curved, tapering hypodermic teeth attaining 140 µm in length;
890 no ventral barb; dorsal blade long, approximately 1/3 of length of shaft; adapical opening
891 elongate, rather narrow, about 1/4 of length of shaft. Base rather broad; large dorsal
892 platform, extending posteriorly, bearing numerous internal pits; exterior of base with
893 comparatively fine texture; basal opening large. Ligament broad.

894

895 Remarks

896 This new species is readily differentiated from its congeners in its comparatively elongate
897 shell with a comparatively taller spire (with the height of the aperture is about 40% of total
898 shell length) and its relatively short siphonal canal. With the exception of *G. sinuosa*, all
899 other *Gladiobela* species treated herein (*G. angulata*, *G. abyssicola*, *G. acris* and *G. stupa*)
900 possess an angulate whorl profile, which is more or less evenly convex in *G. vitrea*. It can be
901 differentiated from *G. sinuosa* by its far narrower shell and its absence of axial ribs.

902

903

904 *Pagodibela* Criscione, Hallan, Puillandre and Fedosov, 2020

905

906 Type species *Pagodibela maia* Criscione, 2020 by monotypy and original designation.

907

908 Diagnosis

909 Shell (SL=16-36 mm, SW=6-12 mm), fusiform-biconical, thin-walled, semi-translucent.
910 Protoconch multispiral (2.5-3.5 whorls), orange, broadly conical, cyrtconoid, sculpture
911 diagonally cancellate. Teleoconch of 5.7-8.5 whorls, whitish to pale cream, suture
912 impressed, whorl profile indistinctly angulated to pagodiform. Subsutural ramp wide,
913 straight, indistinctly to clearly demarcated from whorl periphery. Lower portion of whorl
914 sub-cylindrical or narrowing toward suture. Teleoconch sculpture of spirals only (striae) or
915 spiral cords and axial riblets. Subsutural ramp sculpture of axials only (growth lines or
916 riblets) or of spiral cords and axial riblets. Last adult whorl evenly convex below subsutural
917 ramp, clearly demarcated from stout, tapering siphonal canal. Aperture elongate,
918 approximately 40% to half of shell length; outer lip thin; inner lip whitish, with thin callus,
919 straight. Anal sinus narrow to broad, shallow to moderately deep, u-shaped.

920

921 Head wide, cephalic tentacles of median size, cylindrical; small black eyes situated at their
922 bases. Penis small, simple. Proboscis elongate, conical; venom gland short with large
923 muscular bulb. Osphradium large, approximately 2/3 of ctenidium length, and of equal
924 width. Rhyncocoel not capacious; proboscis small, shifted leftward; venom gland long, on
925 right; muscular bulb very large.

926

927 Radular teeth of hypodermic type, slender, straight to slightly curved, ~140-200 µm in
928 length; barbs absent; dorsal blade nearly half of length of shaft; adapical opening very
929 narrow to narrow and elongate, 1/4 to 1/3 of length of shaft; base comparatively narrow,
930 steep, with coarse external texture; lateral process very weak; basal opening subcircular;
931 ligament small, short.

932

933 Remarks

934 *Pagodibela* can be differentiated from other raphitomid genera by the following combined
935 characters: a (generally) distinctly pagodiform shell (notably in juvenile and subadult
936 juvenile whorls), a medium- to tall spire, and awl-shaped, evenly tapering hypodermic teeth
937 with a comparatively narrow, steep base with coarse external texture. It can be
938 differentiated from the similarly named raphitomid genus *Pagodidaphne* Shuto, 1983
939 (comparison made with type species *P. colmani* Shuto, 1983) by the very prominent spiral
940 sculpture, tall cylindrical periphery and tall aperture of the latter. *Pagodibela*, particularly

the tall-spined *P. baruna* and *P. pacifica*, bears superficial resemblance to tall-spined members of *Typhlosyrinx* Thiele, 1925 and *Leiosyrinx* Bouchet & Sysoev, 2001, but can be differentiated from both of the latter in the (generally) distinctly pagodiform early teleoconch whorls in *Pagodibela*, and also in details of the radula, with the type species *T. vepallida* (Martens, 1902) and *T. supracostata* (Schepman, 1913) shown to have two distinct barbs, and the *L. immedicata* Bouchet & Sysoev, 2001 (genus type species) and *L. matsukumai* Bouchet & Sysoev, 2001 both exhibiting comparatively short (both <100 µm) teeth with short blades and very large, broad bases (Bouchet and Sysoev 2001). Furthermore, the molecular phylogeny by Criscione *et al.* (2020) recovered *Typhlosyrinx* and *Pagodibela* in separate, non-sister clades. The ranges for this genus are here expanded from those provided in Criscione *et al.* (2020), with a bathymetric range of 318-1013 metres (Fig. 8) and occurring in the GAB, temperate to tropical eastern Australia, and large swathe of the Indo-Pacific, from the central South Pacific, PNG, Indonesia and north toward Taiwan, and to the far western Indian Ocean off the East African coast (Fig. 1B, D).

Pagodibela baruna (Sysoev, 1997)
(Fig. 3G)

Gymnobela baruna Sysoev, 1997: 339, figs 6, 49-50.

Material examined

Holotype: Indonesia, Kai Islands, N of channel between small and Big Kai Island (-5.230, 133.000), KARUBAR, CC21, 688-694 m.

Paratype: As for holotype.

Other material: Glorioso Islands, (-12.5, 44.933), BIOMAGLO, DW4863, 606-610 m, 1 wet (MNHN-IM-2013-62987); New Caledonia, Chesterfield Islands, (-21.483, 162.600), EBISCO, CP2651, 883-957 m, 1 wet (MNHN-IM-2007-42312); (-21.683, 166.617), EXBODI, CP3809, 685-880 m, 1 wet (MNHN-IM-2009-29111); PNG, (-4.967, 145.833), BIOPAPUA, CP3708, 502-529 m, 1 wet (MNHN-IM-2009-17156), 1 wet (MNHN-IM-2009-17197); (-9.150, 152.250), BIOPAPUA, CP3739, 503-546 m, 1 wet (MNHN-IM-2009-17116); (-4.733, 146.183), PAPUA_NIUGINI, CP3979, 540-580 m, 1 wet (MNHN-IM-2013-19691); (-5.183, 147.050), PAPUA_NIUGINI, CP3981, 688 m, 1 wet (MNHN-IM-2013-19729); (-5.367, 145.85),

PAPUA_NIUGINI, CP4026, 620-677 m, 1 wet (MNHN-IM-2013-9836). Solomon Islands, (-7.717, 156.417), SALOMON_2, CP2246, 664-682 m, 1 wet (MNHN-IM-2007-42518); (-7.750, 156.933), SALOMON_2, CP2269, 768-890 m, 1 wet (MNHN-IM-2007-42519); (-9.150, 158.983), SALOMON_2, CP2176, 600-875 m, 1 wet (MNHN-IM-2007-42528). South Madagascar, (-25.617, 46.367), ATIMO_VATAE, CP3566/DW3565, 618-624 m, 1 wet (MNHN-IM-2009-14887); Taiwan, (16.233, 114.500), ZhongSha_2015, CP4153, 318 m, 1 wet (MNHN-IM-2013-59316); (16.250, 114.567), ZhongSha_2015, CP4154, 321-326 m, 1 wet (MNHN-IM-2013-59352). Vanuatu, (-16.717, 167.983), BOA1, CP2465, 770-799 m, 1 wet (MNHN-IM-2007-17695).

Distribution: W Pacific: Indonesia, PNG, New Caledonia and Vanuatu in the south; Taiwan in the north. SW Indian Ocean: Madagascar and Glorioso Islands.

Remarks

G. baruna was previously known exclusively for its live-collected holotype (Fig. 3D) and the shell of its paratype (Sysoev 1997, fig. 50), both collected off the Kai Islands (Indonesia). As already noted by Sysoev (1997, p. 339), the two specimens differ mainly in the prominence of their shell sculpture, specifically with the paratype exhibiting a distinctively more pronounced shoulder. The examination of shells of *P. baruna* conducted in this study, reveals that, while the first 4-5 teleoconch whorls are distinctively more shouldered in all studied shells, only some specimens have shells exhibiting this feature on subsequent (5+) whorls.

The degree of prominence of the whorl angulation, as well as of other sculptural elements, varies across the sample along a morphological continuum, suggesting that such differences are likely to be the expression of intraspecific variability.

In our molecular analysis (Fig. 2), sequences of this species form a strongly supported clade, exhibiting significant genetic structure, which is largely consistent with geographical patterns. The comparatively low average intraspecific pairwise distance in COI (less than 2%), along with the relative homogeneity in shell morphology, suggest that no further taxonomic splitting is required.

The inclusion of additional material into *P. baruna*, results in an expansion of the geographical and bathymetrical ranges of this taxon, now spanning over 13,000 kilometres, from the SW to the NW Pacific, to the W Indian Ocean, at depths between 318 and 883 m. Given the widespread occurrence of shell character homoplasy in the Conoidea (Bouchet *et al.* 2011; Hallan *et al.* 2020; Kantor *et al.* 2018), the shell-based attribution of the material studied herein to this taxon is considered tentative. Further investigation, based on sequence data of freshly collected topotypical material of *G. baruna*, supplemented by anatomical data, will elucidate whether the taxon studied herein is indeed *G. baruna* or an additional, yet unnamed and conchologically similar species.

Pagodibela meridionalis n. sp.

(Figs 3J, 5E, 6H)

Material examined

Holotype: Australia, SA, GAB, (-35.043, 134.079), IN2015_C02_126, 367-409 m, (SAMA D44173). COI: MN983189.

Etymology

For its presence in the southernmost part of the genus range, derived from 'meridionalis' (Latin=from the south). Adjective of feminine gender.

Shell

Shell (SL=19 mm, SW=8 mm), fusiform-biconical, thin-walled, semi-translucent. Protoconch orange, broadly conical, of at least three gently convex, diagonally cancellate whorls. Teleoconch of 6.5 pale cream whorls, suture impressed, whorl profile convex, with moderate, non-carinate angulation at periphery. Subsutural ramp wide, straight, indistinctly demarcated from rounded whorl periphery located at whorl mid-height. Lower portion of whorl sub-cylindrical, narrowing towards lower suture. Subsutural ramp sculpture of dense arcuate growth lines, reflecting shape of anal sinus. Sculpture of regularly spaced, fine, shallow striae, uniformly pronounced over entire shell surface, and dense collabral growth lines. Last adult whorl evenly convex below subsutural ramp, clearly demarcated from stout, tapering whitish siphonal canal with wide opening. Aperture elongate, approximately half of

shell length; outer lip thin; inner lip whitish, with thin callus, straight. Anal sinus moderately deep, u-shaped.

Head wide, cephalic tentacles of median size, cylindrical; small black eyes situated at their bases. Osphradium large, approximately 2/3 of ctenidium length, and of equal width.

Rhyncocoel not capacious; proboscis small, shifted leftward; venom gland long, on right; muscular bulb very large.

Radular teeth of hypodermic type, attaining about 200 µm in length, straight to slightly curved, somewhat loosely rolled; barbs absent; dorsal blade nearly half of length of shaft; adapical opening wide and elongate, approximately 1/4 of length of shaft; base comparatively narrow, steep with coarse external texture; lateral process very weak; basal opening large, subcircular. Ligament short, small.

Remarks

This new taxon can be differentiated from the *Pagodibela* spp. studied herein based on its thin, semi-translucent, smooth shell with no distinct carina. *Pagodibela baruna* (Sysoev, 1997) is superficially similar in also having a comparatively smooth (in adults), tall-spined shell, but the latter is opaque and chalky in texture, possesses a significantly taller spire, and more marked angulations at the shoulder in early teleoconch whorls and a comparatively prominent, gemmate supra-sutural cord in early teleoconch whorls (Fig. 3G). None of the *Pagodibela* spp. can readily be differentiated on the basis of radular morphology only (Fig. 6G-I).

This is the only *Pagodibela* taxon from temperate Australia, where it is known only from upper bathyal depths in the GAB.

Pagodibela pacifica n. sp.

(Figs 3H, 6J)

Material examined

Holotype: New Caledonia, Chesterfield Islands, (-20.967, 160.967), EBISCO, CP2645, 641-652 m, (MNHN-IM-2007-17844). COI: EU015652.

1066 Paratypes: Tuamotu Archipelago, (-17.783, -149.383), TARASOC, DW3489, 450-720 m, 1 wet
1067 (MNHN-IM-2007-38860); New Caledonia, (-22.283, 171.3), EXBODI, DW3876, 518-833 m,
1068 (MNHN-IM-2009-29189); New Caledonia, (-23.283, 167.933), KANACONO, CP4750, 750-850
1069 m, 1 wet (MNHN-IM-2013-69658); Australia, QLD, Coral Sea CMR, (-23.587, 154.194),
1070 IN2017_V03_121, 1013-1093 m, 1 wet (AMS C.519402).

1071

1072 Etymology

1073 For its wide distribution across the Pacific Ocean, derived from 'pacificus' (New Latin=from
1074 the Pacific Ocean). Adjective of feminine gender.

1075

1076 Distribution

1077 Widespread; recorded from off north Queensland, Coral Sea, New Caledonia and to the
1078 Society Islands.

1079

1080 Shell (SL=30 mm, SW=11 mm) elongate, fusiform-biconical, moderately thin-walled, rather
1081 opaque. Protoconch of 3.5 whorls, broadly cyrthoconoid, light orange. Protoconch 2 with
1082 distinct diagonally cancellate sculpture throughout whorl height. Protoconch-teleoconch
1083 transition somewhat weakly defined, only detectable by change in sculpture pattern.
1084 Teleoconch of 8.5 whorls, pale cream; suture deeply impressed. Whorl profile distinctly
1085 angulated, with peripheral carina in early to median teleoconch whorls and rounded
1086 angulation in mature whorls. Subsutural ramp wide, straight, concluded by peripheral carina
1087 at about mid-height of whorl in early to median teleoconch whorls. Lower portion of whorl
1088 subcylindrical or slightly narrowed towards lower suture. Subsutural ramp sculpture of
1089 arcuate riblets, reflecting shape of anal sinus, intersected by narrow raised spiral cords,
1090 forming somewhat reticulate pattern in juvenile whorls; arcuate riblets continuous across
1091 periphery of early to median teleoconch whorls, strongly opisthocline, sub-obsolete to
1092 absent in subsequent whorls. Spiral sculpture of supra-peripheral cords in early to median
1093 teleoconch whorls, forming weak nodules at intersections with arcuate riblets, with cords
1094 less prominent and more densely set in subsequent whorls. Last adult whorl evenly convex
1095 below subsutural ramp, clearly demarcated from broad, stout siphonal canal with distinct
1096 concavity on left side (when seen in apertural view, Fig. 3H). Aperture elongate,

approximately 40% of total shell length; outer lip thin, unsculptured; inner lip whitish, with thin callus, slightly recurved. Anal sinus moderately wide and deep, u-shaped. Radula (based on paratype AMS C.519402) of hypodermic type, approximately 140 μm long, straight to slightly curved; barbs absent; dorsal blade sharp, nearly half of length of shaft; adapical opening narrow and elongate, 1/3 of length of shaft; base comparatively narrow, steep, with coarse external texture; lateral process very weak; basal opening large, subcircular. Ligament short, small.

Remarks

This species can be recognised by its elongate, slender shell with strongly carinated early teleoconch whorls. It is rather similar to the sister taxon *P. baruna* in its shell morphology, with both species exhibiting comparatively large, elongate shells with distinctly pagodiform early to median teleoconch whorls (Fig. 3G, H). However, when compared to the holotype of the latter (Fig. 3G), *P. pacifica* is comparatively smaller, less opaque, and possessing more prominent axial ribs and carina on early teleoconch whorls, and does not possess a distinct, gemmate supra-sutural cord in early teleoconch whorls (Fig. 3G, H).

This new species, along with the sister species *G. baruna*, appear to be the most geographically and bathymetrically widespread members of the genus. However, unlike the sister species *G. angulata/abyssicola* (Fig. 3A, B) they are not allopatric, with largely overlapping bathymetric ranges and with both taxa occurring in the New Caledonian region (Figs 1, 8).

1118 Conflict of interest

1119 The authors declare no conflicts of interest.

1120

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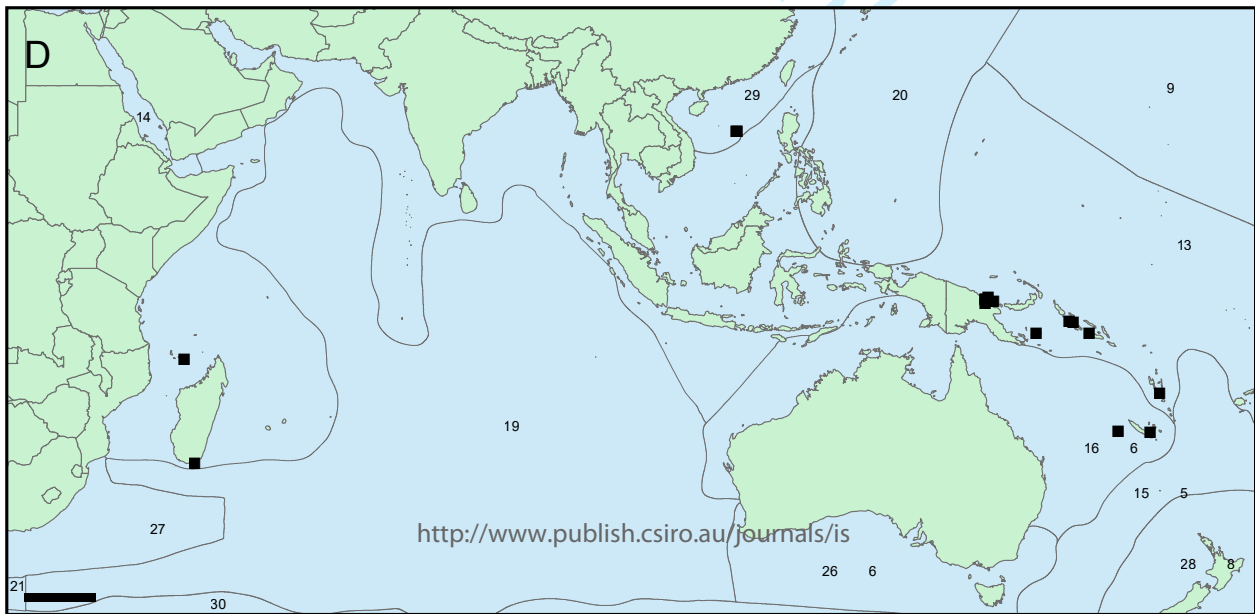
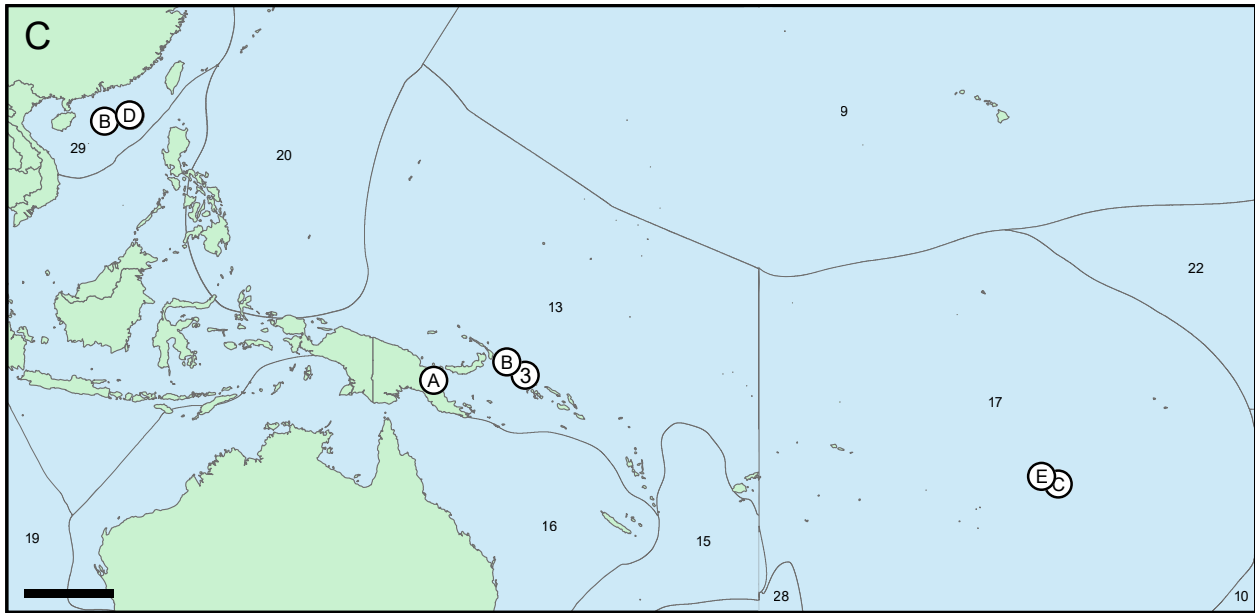
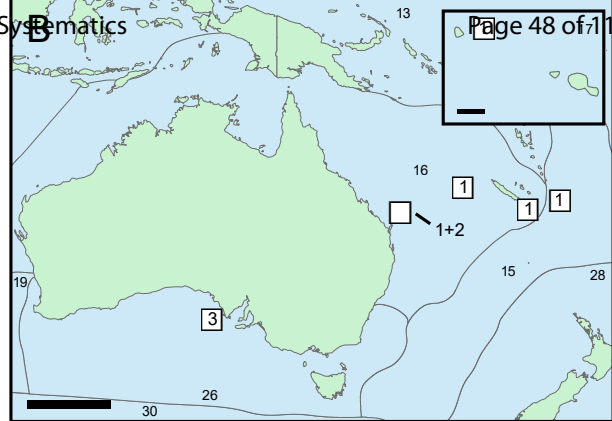
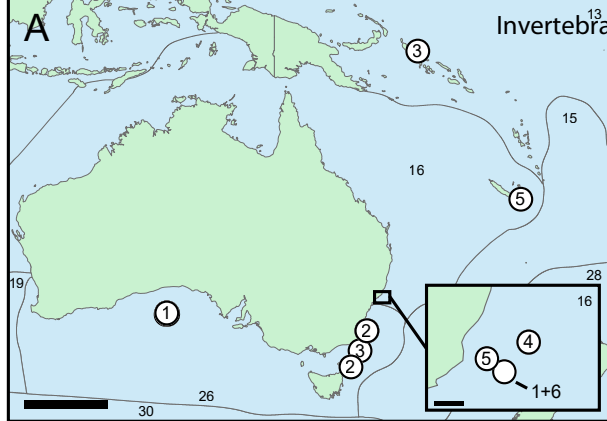
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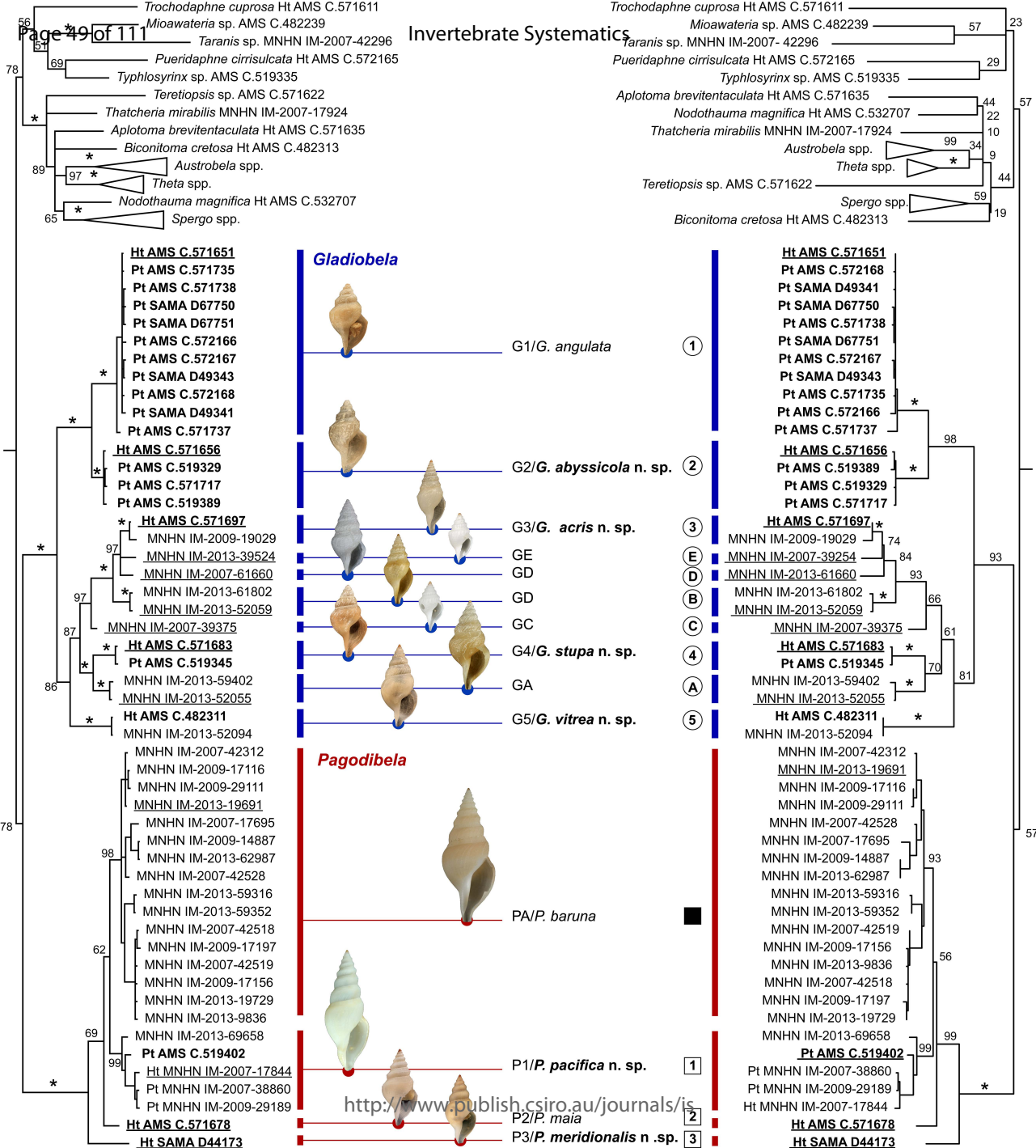
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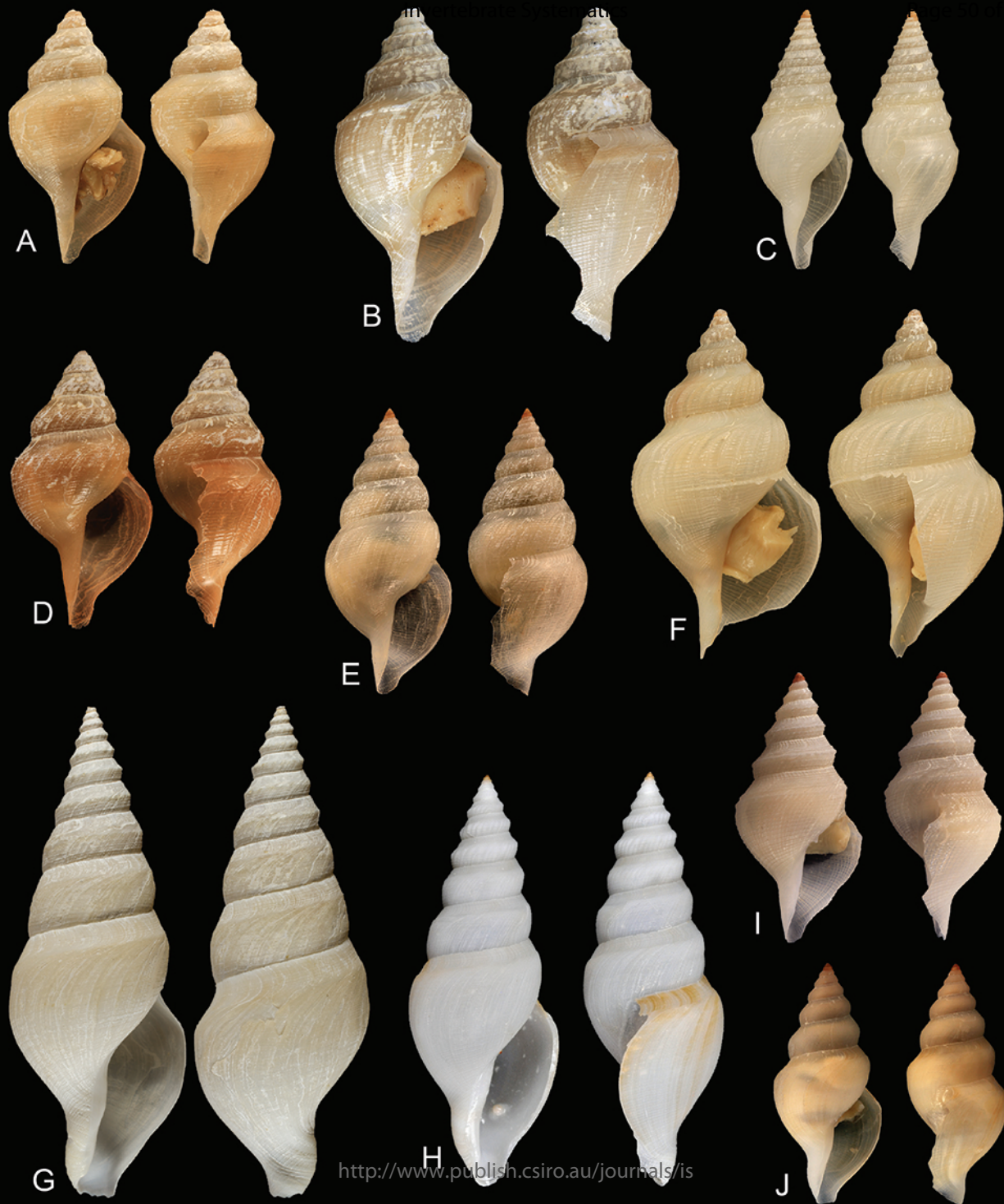
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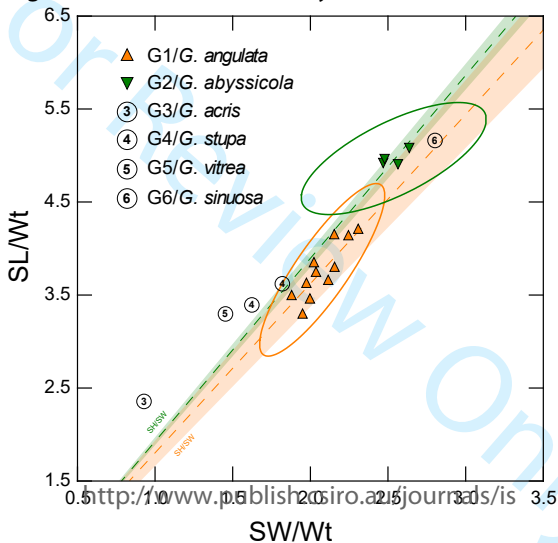
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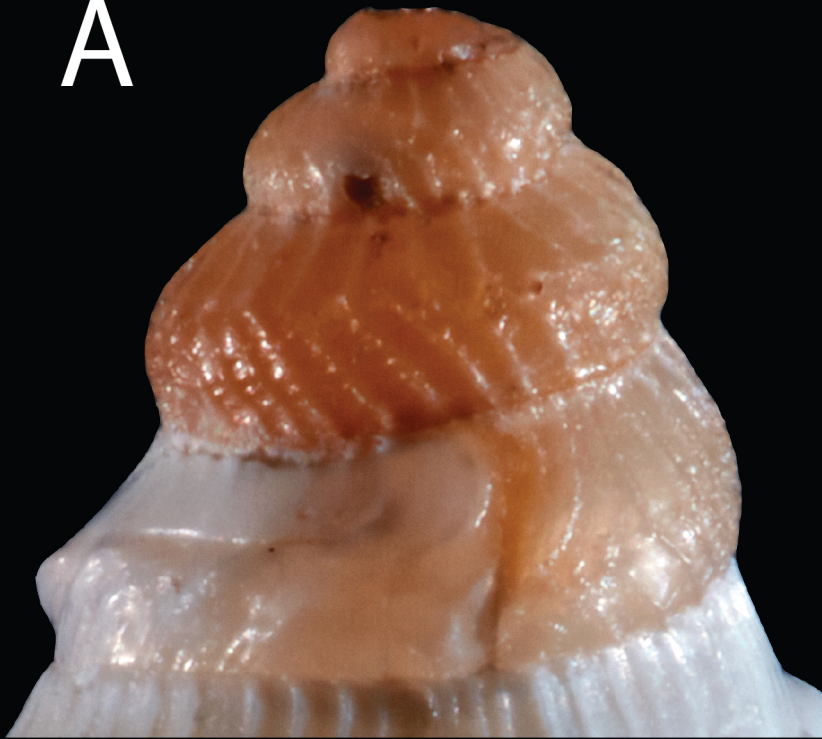




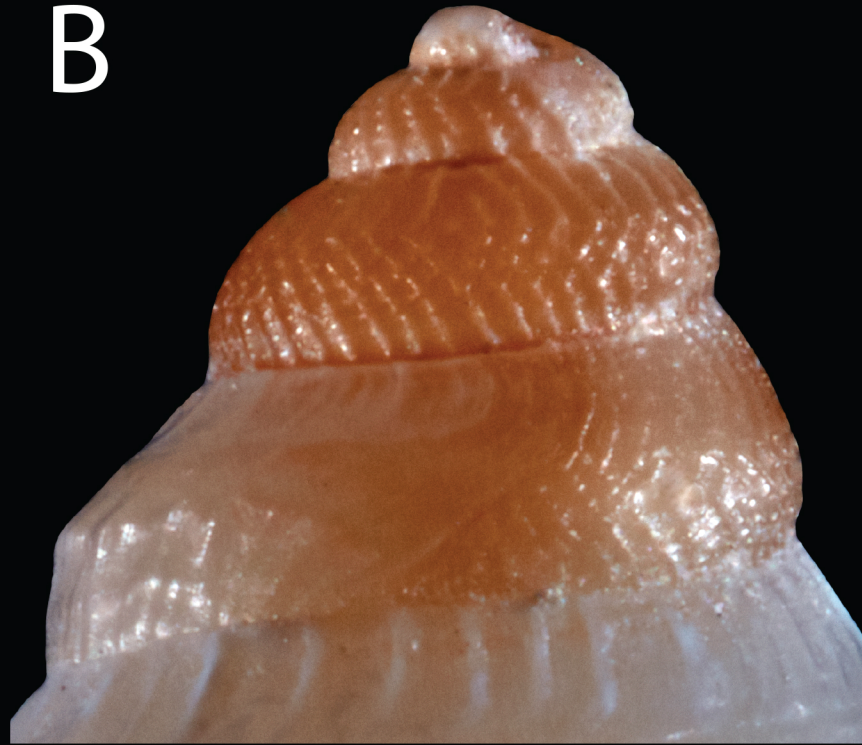




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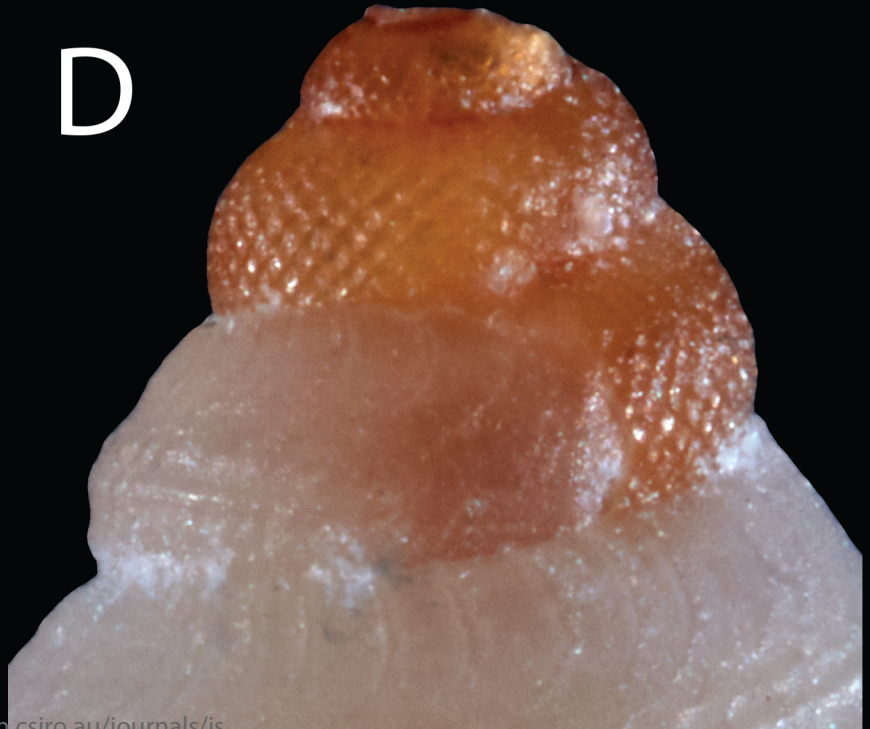
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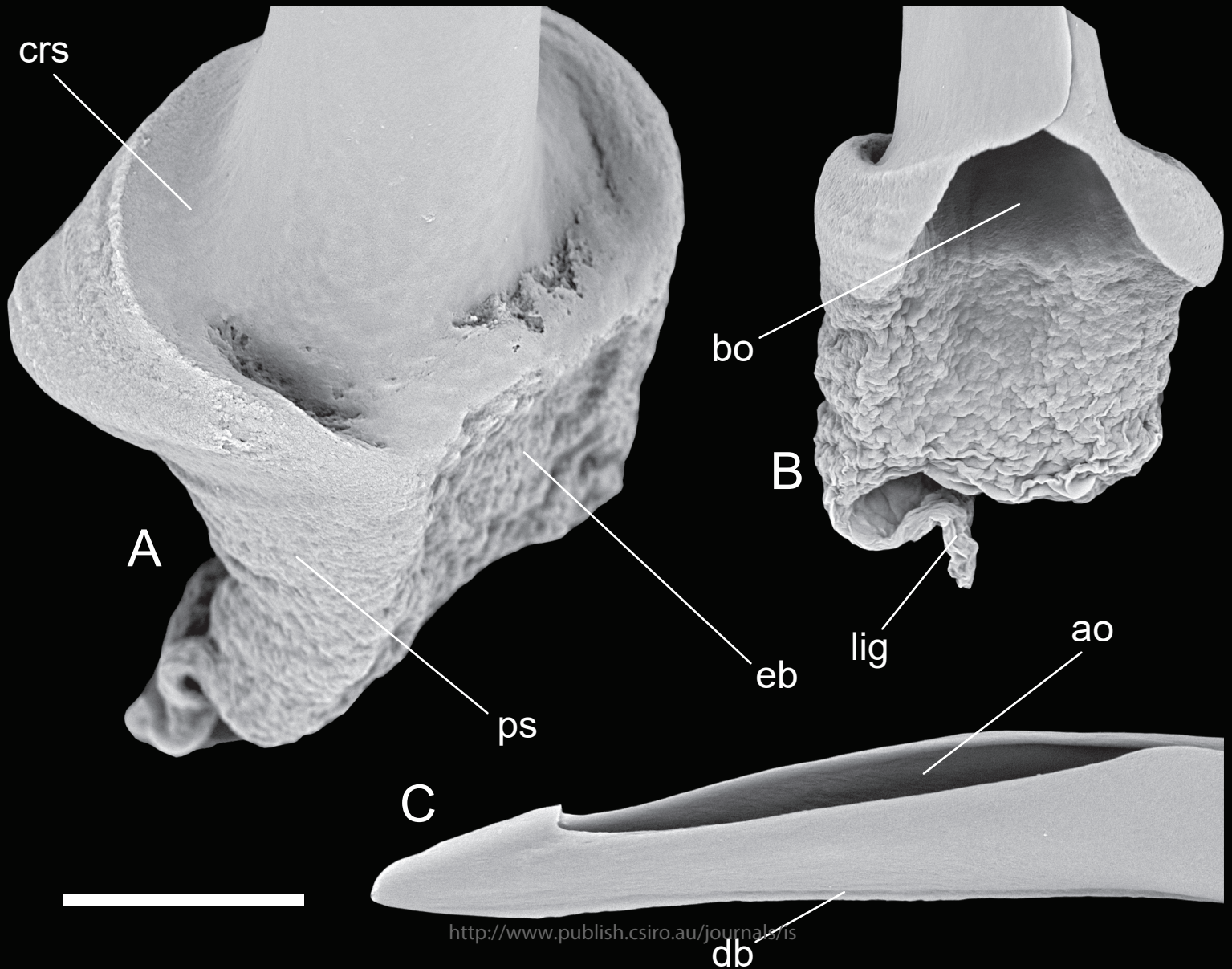
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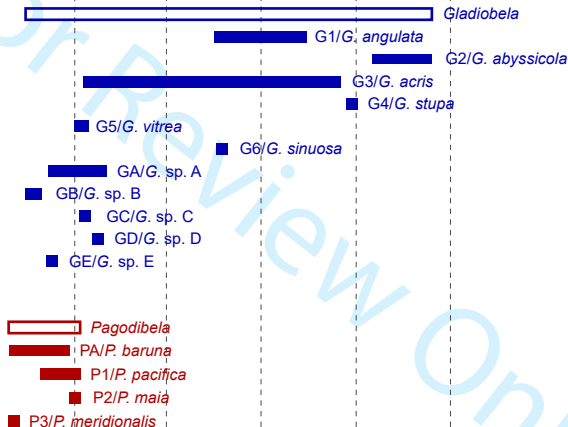


D









	G1/ang	G3/acr	G2/aby	G4/stu	G5/vit	GA	GB	GC	GD	GE
G1/ang	0.006							min	max	mean
G3/acr	0.105	0.011					within	0.000	0.011	0.005
G2/aby	0.054	0.101	0.005				between	0.040	0.117	0.082
G4/stu	0.098	0.088	0.090	0.005						
G5/vit	0.101	0.106	0.106	0.087	0.000					
GA	0.098	0.076	0.090	0.058	0.099	0.006				
GB	0.101	0.049	0.099	0.080	0.104	0.069	0.005			
GC	0.097	0.057	0.093	0.071	0.079	0.062	0.060	-		
GD	0.110	0.040	0.108	0.084	0.103	0.071	0.043	0.067	-	
GE	0.114	0.040	0.117	0.094	0.109	0.076	0.052	0.061	0.040	-

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	PA/bar	P1/pac	P2/mai	P3/mer				
PA/bar	0.019					min	max	mean
P1/pac	0.047	0.018			within	0.018	0.019	0.018
P2/mai	0.044	0.048	-		between	0.044	0.071	0.056
P3/mer	0.063	0.071	0.065	-				

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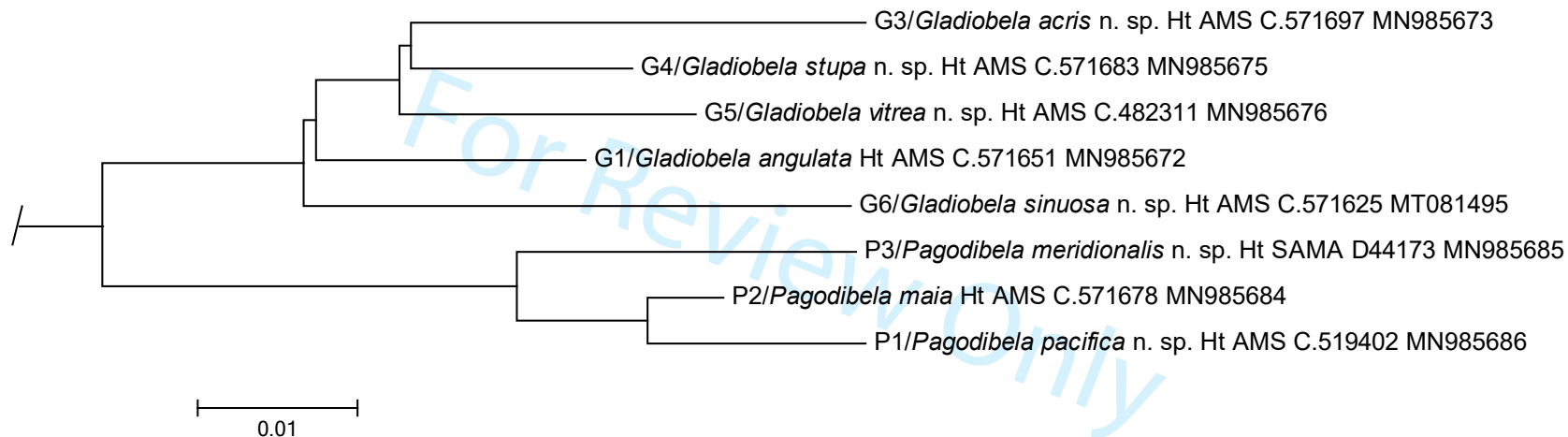


Figure S1 - Detail of the optimal Neighbor-Joining tree based on 179 12S sequences of species of Raphitomidae. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary p-distances used to infer the phylogenetic tree.

GenBank accession numbers (MN-) are indicated on branch labels. publish.csiro.au/journals/is

Table S1 – Museum registration numbers, voucher status, locality, BOLD ids and GenBank accession numbers of samples used for the molecular analyses. Names of species described herein are in bold.

Taxon	Museum	Registration no.	voucher	Locality/Expedition	BOLD id	COI	12S
Ingroup							
Gladiobela abyssicola n. sp.	AMS	C.571656	Ht	Australia, NSW, off Bermagui, (-36.351, 150.914), IN2017_V03_043, 4750-4763 m.		MT081415	
	AMS	C.571717	Pt	Australia, NSW, off Bermagui, (-36.351, 150.914), IN2017_V03_043, 4750-4763 m.		MN983182	
	AMS	C.519329	Pt	Australia, TAS, Bass Strait, (-39.552, 149.553), IN2017_V03_030, 4133-4197 m.		MT081413	
	AMS	C.519389	Pt	Australia, NSW, off Bermagui, (-36.351, 150.914), IN2017_V03_043, 4750-4763 m.		MT081414	
Gladiobela acris n. sp.	AMS	C.571697	Ht	Australia, VIC, East Gippsland CMR, (-38.479, 150.185), IN2017_V03_032, 3850-3853 m.		MN983181	MN985673
	MNHN	IM-2009-19029	Pt	Solomon Islands, (-6.417, 156.35), SOLOMON_2, CP2231, 1083-1100 m.	CONO3079-20	MT256948	
<i>Gladiobela angulata</i> Criscione et al., 2020	AMS	C.571651	Ht	Australia, NSW, Hunter CMR, (-32.575, 153.162), IN2017_V03_070, 2474-2595 m.		MN983180	MN985672
	AMS	C.571735	Pt	Australia, GAB, (-34.452, 129.492), IN2017_C01_197, 3235-3350 m.		MT081403	
	AMS	C.572166	Pt	Australia, GAB, (-34.452, 129.492), IN2017_C01_197, 3235-3350 m.		MT081404	
	AMS	C.572167	Pt	Australia, GAB, (-34.452, 129.492), IN2017_C01_197, 3235-3350 m.		MT081405	
	AMS	C.571737	Pt	Australia, GAB, (-34.452, 129.492), IN2017_C01_197, 3235-3350 m.		MT081406	
	AMS	C.571738	Pt	Australia, GAB, (-34.452, 129.492), IN2017_C01_197, 3235-3350 m.		MT081407	
	AMS	C.572168	Pt	Australia, GAB, (-34.452, 129.492), IN2017_C01_197, 3235-3350 m.		MT081408	
	SAMA	D49341	Pt	Australia, GAB, (-34.574, 129.572), IN2017_C01_198, 3389-3540 m.		MT081409	
	SAMA	D67750	Pt	Australia, GAB, (-34.574, 129.572), IN2017_C01_198, 3389-3540 m.		MT081410	
	SAMA	D67751	Pt	Australia, GAB, (-34.574, 129.572), IN2017_C01_198, 2474-2595 m.		MT081411	
	SAMA	D49343	Pt	Australia, GAB, (-34.452, 129.492), IN2017_C01_197, 3235-3350 m.		MT081412	
Gladiobela sinuosa n. sp.	AMS	C.571625	Ht	Australia, NSW, Hunter CMR, (-32.575, 153.162), IN2017_V03_070, 2474-2595 m.		-	MT081495
Gladiobela stupa n. sp.	AMS	C.571683	Ht	Australia, NSW, Hunter CMR, (-32.138, 153.527), IN2017_V03_078, 3980-4029 m.		MN983183	MN985675
Gladiobela stupa n. sp.	AMS	C.519345	Pt	Australia, NSW, Hunter CMR, (-32.138, 153.527), IN2017_V03_078, 3980-4029 m.		MT081416	
Gladiobela vitrea n. sp.	AMS	C.482311	Ht	Australia, NSW, Hunter CMR, (-32.479, 152.994), IN2017_V03_069, 1006-1036 m.		MN983184	MN985676
	MNHN	IM-2013-52094	Pt	New Caledonia, (-22.267, 167.383), EXBODI, CP3793, 951-1180 m.	CONO3087-20	MT256973	
<i>Gladiobela</i> sp. A	MNHN	IM-2013-52055		Papua New Guinea, (-6.933, 147.133), BIOPAPUA, CP3632, 700-740 m.	CONO3085-20	MT256949	
<i>Gladiobela</i> sp. A	MNHN	IM-2013-59402		Taiwan, (19.8, 116.483), ZhongSha_2015, CP4157, 1205-1389 m.	CONO3091-20	MT256959	
<i>Gladiobela</i> sp. B	MNHN	IM-2013-52059		Papua New Guinea, (-5.067, 154.483), BIOPAPUA, CP3755, 662 m.	CONO3086-20	MT256969	
<i>Gladiobela</i> sp. B	MNHN	IM-2013-61802		Taiwan, (19.217, 113.933), ZhongSha_2015, DW4138, 470-494 m.	CONO3090-20	MT256961	
<i>Gladiobela</i> sp. C	MNHN	IM-2007-39375		Tuamotu Archipelago, (-17.45, -149.833), TARASOC, DW3462, 1000-1145 m.	CONO3074-20	MT256957	
<i>Gladiobela</i> sp. D	MNHN	IM-2013-61660		Taiwan, (19.833, 116.45), ZhongSha_2015, CP4134, 1128-1278 m.	CONO3092-20	MT256951	
<i>Gladiobela</i> sp. E	MNHN	IM-2007-39254		Tuamotu Archipelago, (-16.7, -151.517), TARASOC, CP3449, 780 m.	CONO3073-20	MT256972	
<i>Pagodibela baruna</i> (Sysoev, 1997)	MNHN	IM-2009-29111		New Caledonia, (-21.683, 166.617), EXBODI, CP3809, 685-880 m.	CONO3080-20	MT256963	
	MNHN	IM-2007-42312		New Caledonia, Chesterfield Islands, (-21.483, 162.6), EBISCO, CP2651, 883-957 m.	CONO578-08	MT256968	
	MNHN	IM-2013-19691		Papua New Guinea, (-4.733, 146.183), PAPUA_NIUGINI, CP3979, 540-580 m.	CONO3084-20	MT256955	
	MNHN	IM-2009-17156		Papua New Guinea, (-4.967, 145.833), BIOPAPUA, CP3708, 502-529 m.	CONO3076-20	MT256954	

	MNHN	IM-2009-17197		Papua New Guinea, (-4.967, 145.833), BIOPAPUA, CP3708, 502-529 m.	CONO3077-20	MT256950	
	MNHN	IM-2013-19729		Papua New Guinea, (-5.183, 147.05), PAPUA_NIUGINI, CP3981, 688 m.	CONO3082-20	MT256962	
	MNHN	IM-2013-9836		Papua New Guinea, (-5.367, 145.85), PAPUA_NIUGINI, CP4026, 620-677 m.	CONO3083-20	MT256974	
	MNHN	IM-2009-17116		Papua New Guinea, (-9.15, 152.25), BIOPAPUA, CP3739, 503-546 m.	CONO3075-20	MT256960	
	MNHN	IM-2007-42518		Solomon Islands, (-7.717, 156.417), SOLOMON_2, CP2246, 664-682 m.	CONO793-08	MT256966	
	MNHN	IM-2007-42519		Solomon Islands, (-7.75, 156.933), SOLOMON_2, CP2269, 768-890 m.	CONO794-08	MT256953	
	MNHN	IM-2007-42528		Solomon Islands, (-9.15, 158.983), SOLOMON_2, CP2176, 600-875 m.	CONO804-08	MT256967	
	MNHN	IM-2013-62987		Glorioso Islands, (-12.5, 44.933), BIOMAGLO, DW4863, 606-610 m.	CONO3093-20	MT256965	
	MNHN	IM-2009-14887		South Madagascar, (-25.617, 46.367), ATIMO_VATAE, CP3566/DW3565, 618-624 m.	CONO3078-20	MT256958	
	MNHN	IM-2013-59316		Taiwan, (16.233, 114.5), ZhongSha_2015, CP4153, 318 m.	CONO3088-20	MT256964	
	MNHN	IM-2013-59352		Taiwan, (16.25, 114.567), ZhongSha_2015, CP4154, 321-326 m.	CONO3089-20	MT256970	
	MNHN	IM-2007-17695		Vanuatu, (-16.717, 167.983), BOA1, CP2465, 770 m.	CONO143-08	MT256956	
<i>Pagodibela maia</i> Criscione et al., 2020	AMS	C.571678	Ht	Australia, QLD, Coral Sea CMR, (-23.587, 154.194), IN2017_V03_121, 1013-1093 m.		MN983188	MN985684
<i>Pagodibela pacifica</i> n. sp.	MNHN	IM-2007-17844	Ht	New Caledonia, Chesterfield Islands, (-20.967, 160.967), EBISCO, CP2645, 641-652 m.	CONO186-08	EU015652	
	AMS	C.519402	Pt	Australia, QLD, Coral Sea CMR, (-23.587, 154.194), IN2017_V03_121, 1013-1093 m.		MN983190	MN985686
	MNHN	IM-2009-29189	Pt	New Caledonia, (-22.283, 171.3), EXBODI, DW3876, 518-833 m.	CONO3081-20	MT256971	
	MNHN	IM-2013-69658	Pt	New Caledonia, (-23.283, 167.933), KANACONO, CP4750, 750-850 m.	CONO3094-20	MT256947	
	MNHN	IM-2007-38860	Pt	Tuamotu Archipelago, (-17.783, -149.383), TARASOC, DW3489, 450-720 m.	CONO3072-20	MT256952	
<i>Pagodibela meridionalis</i> n. sp.	SAMA	D44173	Ht	Australia, SA, GAB, (-35.043, 134.079), IN2015_C02_126, 367-409 m.		MN983189	MN985685
Outgroups							
<i>Aplotoma brevitentaculata</i> Criscione et al., 2020	AMS	C.571635	Ht	Australia, VIC, East Gippsland CMR, (-37.792, 150.382), IN2017_V03_035, 2338-2581 m.		MN983163	
<i>Austrobela micraulax</i> (Sysoev, 1997)	AMS	C.519275		Australia, QLD, Coral Sea CMR, (-23.587, 154.194), IN2017_V03_121, 1013-1093 m.		MN983164	
<i>Austrobela</i> n. sp. 2	AMS	C.571693		Australia, SA, GAB, (-34.074, 129.182), IN2015_C01_064, 2649-2803 m.		MN983165	
<i>Austrobela</i> n. sp. 3	AMS	C.571670		Australia, SA, GAB, (-34.823, 132.692), IN2015_C02_167, 998-1015 m.		MN983166	
<i>Austrobela</i> n. sp. 4	AMS	C.571644		Australia, NSW, Hunter CMR, (-32.575, 153.162), IN2017_V03_070, 2474-2595 m.		MN983167	
<i>Austrobela rufa</i> Criscione et al., 2020	AMS	C.571699	Pt	Australia, SA, GAB, (-35.345, 134.045), IN2015_C02_134, 1509-1544 m.		MN983168	
<i>Biconitoma cretosa</i> n. sp.	AMS	C.482313	Ht	Australia, NSW, off Byron Bay, (-28.677, 154.203), IN2017_V03_090, 2562-2587 m.		MN983169	
<i>Mioawateria</i> n. sp. 1	AMS	C.482239		Australia, VIC, East Gippsland CMR, (-37.815, 150.373), IN2017_V03_040, 2600-2746 m.		MN983186	
<i>Nodothauma magnifica</i> Criscione et al., 2020	AMS	C.532707	Ht	Australia, SA, GAB, (-35.558, 134.083), IN2015_C02_137, 1927-1995 m.		MN983187	
<i>Pueridaphne cirrisulcata</i> Criscione et al., 2020	AMS	C.572165	Ht	Australia, SA, GAB, (-34.452, 129.492), IN2017_C01_197, 3235-3350 m.		MN983198	
<i>Spergo fusiformis</i> (Habe, 1962)	AMS	C.482154		Australia, QLD, Coral Sea CMR, (-23.587, 154.194), IN2017_V03_121, 1013-1093 m.		MN983201	
<i>Spergo</i> n. sp. 1	AMS	C.519290		Australia, TAS, Freycinet CMR, (-41.731, 149.12), IN2017_V03_004, 2751-2820 m.		MN983202	
<i>Spergo</i> n. sp. 2	AMS	C.519331		Australia, Bass Strait, (-39.552, 149.553), IN2017_V03_030, 4133-4197 m.		MN983203	
<i>Spergo</i> n. sp. 3	AMS	C.519392		Australia, TAS, Flinders CMR, (-40.473, 149.397), IN2017_V03_015, 4114-4139 m.		MN983204	
<i>Spergo</i> n. sp. 4	AMS	C.571638		Australia, NSW, Hunter CMR, (-32.575, 153.162), IN2017_V03_070, 2474-2595 m.		MN983205	
<i>Spergo</i> sp.	MNHN	IM-2007-17841		New Caledonia, (-21.533, 162.5), EBISCO, CP2648, 458-750 m.	CONO184-08	EU015650	
<i>Taranis</i> sp.	MNHN	IM-2007-42296		Philippines, Aurora, off Dipaculao, (15.95, 121.833), AURORA 2007, CP2749, 473 m.	CONO561-08	HQ401584	

<i>Teretiopsis</i> sp.	AMS	C.571622		Australia, QLD, Coral Sea CMR, (-23.587, 154.194), IN2017_V03_121, 1013-1093 m.		MN983206
<i>Thatcheria mirabilis</i> Angas, 1877	MNHN	IM-2007-17924		Solomon Islands, (-8.283, 160), SOLOMON 2, CP2184, 464-523 m.	CONO349-08	EU015736
<i>Theta lyronuclea</i> (A. H. Clarke, 1959)	AMS	C.482290		Australia, NSW, Jervis CMR, (-35.114, 151.469), IN2017_V03_053, 3952-4011 m.		MN983207
<i>Theta</i> n. sp. 2	AMS	C.532711		Australia, SA, GAB, (-35.818, 134.109), IN2015_C02_141, 2800-2852 m.		MN983209
<i>Theta</i> n. sp. 3	AMS	C.571657		Australia, NSW, Hunter CMR, (-32.575, 153.162), IN2017_V03_070, 2474-2595 m.		MN983210
<i>Trochodaphne cuprosa</i> Criscione et al., 2020	AMS	C.571611	Ht	Australia, NSW, Jervis CMR, (-35.333, 151.258), IN2017_V03_056, 2650-2636 m.		MN983211
<i>Typhlosyrinx</i> sp.	AMS	C.519335		Australia, NSW, off Byron Bay, (-28.054, 154.083), IN2017_V03_100, 999-1013 m.		MN983212

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Table S2. Inter-PSHs/specific genetic differentiation of 12S sequences in *Gladiobela* by means of p-distances. Reciprocal distances of G6/*G. sinuosa* shaded. Species codes: acr, *G. acris* n. sp.; ang, *G. angulata*.; sin, *G. sinuosa* n. sp.; stu, *G. stupa* n. sp.; vit, *G. vitrea* n. sp. Codes of species described herein in bold.

	G3/acr	G1/ang	G6/sin	G4/stu
G1/ang	0.051			
G6/sin	0.066	0.051		
G4/stu	0.042	0.035	0.053	
G5/vit	0.046	0.040	0.061	0.033

Figure captions

Figure 1. Distribution of taxa studied herein. (A) Records of sequenced specimens of *Gladiobela* in Australian waters (numbered circles). Inset: section of the Hunter region coast where four different records occur in close vicinity. (B) Records of sequenced specimens of *Pagodibela* with distribution in Australian waters (numbered squares). Inset: record of *P. pacifica* in the Tuamotu Archipelago. (C) Records of sequenced specimens of *Gladiobela* outside Australian waters (lettered and numbered circles). (D) Records of sequenced specimens of PA/*Pagodibela baruna* (Sysoev, 1997) (black squares). Numbers in circles indicate PSHs/species of *Gladiobela* (1 – G1/*G. angulata*, 2 – G2/*G. abyssicola*, 3 – G3/*G. acris*, 4 – G4/*G. stupa*, 5 – G5/*G. vitrea*, 6 – *G. sinuosa*). Letters in circles indicate PSHs of *Gladiobela* with distribution outside Australia (A – GA, B – GB, C – GC, D – GD, E – GE). Numbers in squares indicate PSHs/species of *Pagodibela* (1 – P1/*P. pacifica*, 2 – P2/*P. maia*, 3 – P3/*P. meridionalis*). Records of micro-sympatry (see text) are indicated by numbers connected by '+'. Thin lines mark limits among marine realms (numbered as in Costello et al., 2017). Main scalebars = 1000 km, insets scalebars = 50 Km.

Figure 2. Bayesian consensus phylogram (BI, left) and Maximum-Likelihood tree (ML, right) based on analyses of the COI sequences dataset. Clades containing congeneric species in the outgroup are collapsed. Numbers above branches indicate nodal support (%) by Bayesian posterior probabilities (BPP) and ML bootstrap (BS). For both BPP and BS values of 100% are represented by asterisks. Support values for clades below the species level are omitted. Names of species described herein, and sequences of Australian samples are in bold. Vertical bars mark distinct primary species hypotheses (PSHs) as delimited by the ABGD method. Samples whose shells are figured (scale bar = 10 mm) are underlined.

Figure 3. Shells of PSHs/species studied herein. (A) G1/*Gladiobela angulata* Criscione et al., 2020 holotype AMS C.571561; (B) G2/*Gladiobela abyssicola* n. sp., holotype AMS C.571656; (C) G3/*Gladiobela acris* n. sp., holotype AMS C.571697; (D) G4/*Gladiobela stupa* n. sp., holotype AMS C.571683; (E) G5/*Gladiobela vitrea* n. sp., holotype AMS C.482311; (F) *Gladiobela sinuosa* n. sp., holotype AMS C. 571625; (G) PA/*Pagodibela baruna* (Sysoev, 1997) n. comb., holotype MNHN IM-2000-2772; (H) P1/*Pagodibela pacifica* n. sp., holotype

MNHN IM-2007-17844; (I) P2/*Pagodibela maia* Criscione, 2020, holotype AMS C.571678; (J) P3/*Pagodibela meridionalis* n. sp., holotype SAMA D44173. Scale bar = 10 mm.

Figure 4. Scatter plot of SW and SH ratios with Wt for all measured shells of *Gladiobela*. 95% confidence ellipses are drawn for species represented by more than 4 shells. Shaded areas correspond to portion of morpho-space delimited by minimum and maximum values of SH/SW for species represented by more than 4 shells. Dashed lines represent mean SH/SW values.

Figure 5. Larval shells of PSHs/species studied herein. (A) G3/*Gladiobela acris* n. sp., holotype AMS C.571697; (B) G4/*Gladiobela stupa* n. sp., holotype AMS C.571683; (C) G5/*Gladiobela vitrea* n. sp., holotype AMS C.482311; (D) P2/*Pagodibela maia* Criscione, 2020, holotype AMS C.571678; (E) P3/*Pagodibela meridionalis* n. sp., holotype SAMA D44173. Scale bar = 500 μ m.

Figure 6. Hypodermic teeth of PSHs/species studied herein. (A) G1/*Gladiobela angulata* Criscione et al., 2020, holotype AMS C.571561; (B) G5/*Gladiobela vitrea* n. sp., holotype AMS C.482311; (C) G3/*Gladiobela acris* n. sp., holotype AMS C.571697; (D) *Gladiobela sinuosa* n. sp., holotype AMS C. 571625; (E) G2/*Gladiobela abyssicola* n. sp., paratype AMS C.519389; (F) G4/*Gladiobela stupa* n. sp., paratype AMS C.519345; (G) P2/*Pagodibela maia* Criscione, 2020, holotype AMS C.571678; (H) P3/*Pagodibela meridionalis* n. sp., holotype SAMA D44173; (J) P2/*Pagodibela pacifica* n. sp., holotype MNHN IM-2007-17844. Scale bar = 100 μ m. Db = dorsal blade.

Figure 7. Radular details of *Gladiobela* PSHs/species (A) G1/*Gladiobela angulata* Criscione et al., 2020, holotype AMS C.571561, showing dorso-lateral view of tooth base, with crescent-shaped indentation (crs), posterior shelf (ps) and sculpture of external base (eb); (B) G1/*G. angulata* paratype AMS C.571737, showing basal opening (bo) and short ligament (lig); (C) G2/*G. abyssicola* n. sp., paratype AMS C.519389, showing adapical opening (ao) and dorsal blade (db). Scale bar = 20 μ m.

Figure 8. Bathymetric ranges of taxa studied herein as inferred from records of sequenced specimens. Species represented by a single record are indicated by a square.

Table 1. Intra- and inter-PSHs/specific genetic differentiation of COI sequences in *Gladiobela* by means of p-distances. Intra-PSH/specific distances shaded. Inset: minimum, maximum and average intra- and inter-PSHs/specific p-distances within *Gladiobela*. Species codes: aby, *G. abyssicola* n. sp.; acr, *G. acris* n. sp.; ang, *G. angulata*.; stu, *G. stupa* n. sp.; vit, *G. vitrea* n. sp. Codes of species described herein in bold.

Table 2. Intra- and inter-PSHs/specific genetic differentiation of COI sequences in *Pagodibela* by means of p-distances. Intra-PSH/specific distances shaded. Inset: minimum, maximum and average intra- and inter-PSHs/specific p-distances within *Pagodibela*. Species codes: bar, *P. baruna*; P.; mai, *P. maia*; pac, *P. pacifica* n. sp.; P.; pho, *P. meridionalis* n. sp. Codes of species described herein in bold.

Tables captions

Table 1. Intra- and inter-PSHs/specific genetic differentiation of COI sequences among *Gladiobela* PSHs/species by means of p-distances. Intra-PSHs/specific distances shaded. Inset: minimum, maximum and average intra- and inter-PSHS/specific p-distances within *Gladiobela*. Species codes: acr, *G. acris* n. sp.; ang, *G. angulata*; car, *G. abyssicola* n. sp.; stu, *G. stupa* n. sp.; vit, *G. vitrea* n. sp. Codes of species described herein in bold.

Table 2. Table 1. Intra- and inter-PSHs/specific genetic differentiation of COI sequences among *Pagodibela* PSHs/species by means of p-distances. Intra-PSHs/specific distances shaded. Inset: minimum, maximum and average intra- and inter-PSHS/specific p-distances within *Pagodibela*. Species codes: bar, *P. baruna*; *P.*; mai, *P. maia*; pac, *P. pacifica* n. sp.; *P.*; pho, *P. meridionalis* n. sp. Codes of species described herein in bold.

Few and far apart: integrative taxonomy of Australian species of *Gladiobela* and *Pagodibela* (Conoidea: Raphitomidae) reveals patterns of wide distributions and low abundance

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Running title: Molecular systematics of *Gladiobela* and *Pagodibela*

24 Abstract

25 The deep-sea malacofauna of temperate Australia remains comparatively poorly known.
26 However, a recent influx of DNA-suitable material obtained from a series of deep-sea cruises
27 facilitated integrative taxonomic study on the Conoidea (Caenogastropoda:
28 Neogastropoda). Building on a recent molecular phylogeny of the conoidean family
29 Raphitomidae, this study focussed on the genera *Gladiobela* and *Pagodibela* (both Criscione
30 et al., 2020). We subjected a comprehensive mtDNA COI dataset of deep-sea raphitomids to
31 ABGD barcode gap detection, which recognised 14 primary species hypotheses (PSHs), nine
32 of which were converted to secondary species hypotheses (SSHs). Following the additional
33 examination of the shell and hypodermic radula features, as well as consideration of
34 bathymetric and geographic data, seven of these PSHs were recognised as new to science
35 and given full species rank. Subsequently, full systematic descriptions were provided herein.
36 Of these, five were attributed to *Gladiobela* (three of which are endemic to Australia and
37 with two more widely distributed) and two were placed in *Pagodibela* (one endemic to
38 southern Australia and one widespread in the Pacific). The rarity of many ‘turrids’ reported
39 in previous studies was confirmed herein, as particularly indicated by highly disjunct
40 geographic records for two taxa. Additionally, several of the studied taxa exhibited wide
41 Indo-Pacific distributions, suggesting that wide geographic ranges in deep-sea ‘turrids’ may
42 be more common than previously assumed. Finally, impediments to deep-sea ‘turrid’
43 taxonomy in the light of such comparative rarity and unexpectedly wide distributions were
44 discussed.

45 Introduction

46 It is a well-known notion among malacologists that ‘turrids’ – members of the hyper-diverse
47 superfamily Conoidea (Caenogastropoda: Neogastropoda) not including Conidae and
48 Terebridae and historically treated as Turridae (herein referred to as ‘turrids’ to clearly
49 distinguish from Turridae *sensu stricto*) – are a particularly challenging group taxonomically.
50 Hedley (1922: p. 213) stated that ‘the marine gasteropods [sic] embraced in the family
51 Turridae (formerly Pleurotomidae) are considered by those who meddle with them to be
52 more perplexing than any other molluscan family’. The literature provides numerous
53 examples in support of that statement, such as ‘turrid pairs’, where separate species (not
54 necessarily sister taxa) have virtually indistinguishable teleoconch morphologies but
55 differing protoconchs (Powell 1942) or where even species from different families cannot be
56 readily differentiated based on shell characters (Hallan *et al.* 2020; Kantor *et al.* 2018;
57 Sysoev and Kantor 1990). Other impediments to ‘turrid’ taxonomic study include low
58 abundances in many taxa and relative difficulty in collecting due to their largely subtidal
59 habitats (Bouchet and Waren 1980; Todd and Rawlings 2014). Challenges with ‘turrid’
60 taxonomy are further exacerbated in the deep sea, where protoconchs are commonly
61 eroded or missing entirely (Criscione *et al.* 2020), and sculptural elements of the teleoconch
62 may be significantly worn owing to the dissolution of CaCO₃ (Burton 1998). Furthermore,
63 some deep-sea taxa exhibit an overall lack of indicators of terminal shell growth [such as
64 apertural thickening, formation of a varix, or similar (Bouchet and Waren 1980)]. In these
65 cases, inferences about the stage of maturity (and therefore about representative adult
66 size) are difficult, particularly where material is scarce. Paraphrasing the sentiment by
67 Marshall (1983) that material of Triphoridae ought not to be described in the absence of an
68 intact protoconch, Puillandre *et al.* (2017) emphasised that no new ‘turrids’ should be
69 described without molecular data, preferably designating a molecular voucher as a type.
70 This is particularly true for deep-sea material, given the issues raised above.
71 When conducting ‘turrid’ systematics research, notably on deep-sea taxa, there is also the
72 need to consult with taxonomic work on species that may occur far beyond conventionally
73 expected geographic limits of conspecific taxa. A study by Zaharias *et al.* (2020)
74 demonstrated that several deep-sea species of the genus *Cryptogemma* Dall, 1918
75 (Turridae) exhibit notably wide distributions. Corroborated by mitochondrial DNA evidence,
76 one species, *C. phymatias* (R. B. Watson, 1886) was shown to have a trans-oceanic

distribution, arguably providing the first molecularly confirmed such case in a benthic gastropod. Such unexpectedly wide geographic ranges may routinely escape the attention of taxonomists, notably where morphologically heterogeneous taxa are concerned; Zaharias *et al.* (2020) synonymised several species names attributable to *Cryptogemma*, suggesting that while analyses of molecular data commonly reveal unnamed taxa in the Conoidea (e.g., Fedosov and Puillandre 2012; Puillandre *et al.* 2010a), taxonomic over-splitting may also occur, arguably in part as a consequence of underestimated distribution ranges. While trans-oceanic ranges, such as that documented for *C. phymatias*, appear to be exceptionally rare based on existing evidence, wide distributions in the deep sea, particularly in the Conoidea, may not be so uncommon. Bouchet and Waren (1980) noted that among their deep-sea study material from the Western and Eastern Atlantic, there was a 34% species overlap between the two regions, suggesting that a significant portion of deep-sea ‘turrids’ may have ocean-wide distributions. Furthermore, they predicted that percentage would increase with additional study.

The deep-sea Australian malacofauna has, until recently, remained among the most poorly known in the Indo-Pacific region owing to a lack of study material, particularly that suitable for molecular analysis (Criscione *et al.* 2020). However, recent deep-sea expeditions in southern and eastern Australia, notably aboard the research vessel *Investigator*, have delivered a wealth of material from several major groups of the Mollusca (see MacIntosh *et al.* 2018; O'Hara 2019). The extremely diverse superfamily Conoidea is prevalent in these samples, and now subject to ongoing collaborative study between the Australian Museum, Sydney (AM) and the Muséum National d'Histoire Naturelle, Paris (MNHN) (Criscione *et al.* 2020; Hallan *et al.* 2020; Zaharias *et al.* 2020). The ‘turrid’ family Raphitomidae is particularly well-represented among this conoidean material (O'Hara 2019). A recent molecular phylogeny by Criscione *et al.* (2020) revealed a considerable diversity of previously unknown deep-sea raphitomid lineages and included the description of twelve new genera. Building on the classification framework set out by this latter study, two of the genera described therein are further treated here: *Gladiobela* Criscione *et al.*, 2020 and *Pagodibela* Criscione *et al.*, 2020. *Gladiobela angulata* Criscione *et al.*, 2020, type species of its genus, is known from bathyal depths (3350–3807 m) of the Great Australian Bight (henceforth GAB), and from a single locality off the NSW Central Coast (~2600 m). This study describes five additional species of *Gladiobela*, three of which are possibly endemic to

109 temperate Australia, and two potentially widespread in the eastern Indo-Pacific, with all
110 members of the genus occurring from bathyal to abyssal depths (~500-4850 m). *Pagodibela*
111 *maia* Criscione, 2020, type species of its genus, is known only from a single record from the
112 Coral Sea (~1000 m). Two additional species of *Pagodibela*, one from the GAB and the other
113 from north Queensland to the Society Islands, are also described herein. Generic diagnoses
114 are provided for both genera, as well as details of the shell and venom apparatus.
115 Furthermore, morphological characters, as well as patterns of bathymetry and biogeography
116 are presented. Finally, impediments to future 'turrid' systematics given their comparative
117 scarcity (in terms of number of individuals) and unusually wide distributions at the species-
118 level are discussed.

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Materials and methods

Taxon sampling

The samples studied herein were selected from among all deep-sea Raphitomidae ethanol-preserved material from the malacological collections of the Australian Museum, Sydney (AMS), the South Australian Museum, Adelaide (SAMA) and the Muséum national d'Histoire naturelle, Paris (MNHN). As a result of ongoing systematic research on the Conoidea at the AMS and MNHN, several hundreds sequences of the mitochondrial gene cytochrome c oxidase subunit 1 (COI) were obtained from a few hundreds largely undescribed representative raphitomid taxa. In order to assist with the selection of the study material, a pilot analysis was performed on a dataset including all raphitomid COI sequences, using the neighbour-joining method (NJ) (Saitou and Nei 1987) implemented in MEGA 7 (Kumar *et al.* 2016). The dataset encompassed sequences of the type species of many deep-sea raphitomid genera, including the holotypes of *G. angulata* (MN983180) and *P. maia* (MN983188). A subset of sequences was generated which included all COI sequences that in the resulting tree (not shown) were more closely related to the sequences of either of the two holotypes than to any type species of any other raphitomid genus in the dataset. The dataset thus obtained (henceforth referred to as 'ingroup') forms the basis for the molecular analysis described below. Additional material relevant to this study, but for which attempts of amplifying COI failed, was selected based on the results of a NJ analysis (see below) of a dataset comprising all 12S sequences available for raphitomids. This dataset, albeit much smaller than the COI one (about 200 sequences), included sequences of the holotypes of type species of *Gladiobela* (MN985672) and *Pagodibela* (MN985684). A subset of 12S sequences was formed with these and other sequences that in the resulting tree (not shown) were ~~to them~~ more closely related to them than to any type species of any other raphitomid genus in the dataset.

Among the ingroup specimens, morphological examination was only conducted on those collected in Australian waters and some of those collected outside Australia (see Results). Geographic and bathymetric data were available for all ingroup specimens. Geographic distributions were assessed with reference to marine biogeographic realms as delimited in Costello *et al.* (2017). According to Bouchet *et al.* (2008), when inferring species distributions from sampling depth intervals, only shallower depth values were considered, as there is no evidence that the species collected occurs beyond that value.

151

152 Molecular methods

153 Molecular work was performed in laboratories at two different Institutions (AMS and
154 MNHN). Unless otherwise stated, the same methodology was followed by both laboratories.

155 DNA extraction was performed on at least one specimen per morphospecies per collecting
156 site. DNA was extracted from small pieces of foot muscle by use of a Bioline Isolate II
157 Genomic DNA extraction kit for animal tissue, following the standard procedure of the
158 manual (AM) or using the Epmotion 5075 robot (Eppendorf), following the
159 recommendations by the manufacturer (MNHN). Fragments of the two mitochondrial genes
160 COI and 12S were amplified using the primer pairs LCO1490/HCO2198 (Folmer *et al.* 1994)
161 and 12S-I/12S-III for 12S (Simon *et al.* 1991). PCR reactions were performed in volumes of 25
162 μ l, containing 3 ng DNA, 1X Qiagen CoralLoad PCR Buffer, 2.5mM $MgCl_2$, 0.25mM dNTP,
163 0.5mM of each primer, 0.5 μ g/ μ l of BSA and 0.2 μ l of Bioline MyTaq DNA polymerase.
164 Amplification consisted of an initial denaturation step at 94°C for 4 min, followed by 37
165 cycles of denaturation at 94°C for 30 s, annealing at 50°C (COI) or 57°C (12S) for 30 s,
166 followed by extension at 72°C for 1 min. The final extension was conducted at 72°C for 5
167 min.

168 PCR products were purified and sequenced by the Macrogen (AMS) and Eurofins (MNHN)
169 sequencing facilities. When necessary, chromatograms were manually corrected for
170 misreads and forward and reverse strands were merged into one sequence file using
171 CodonCode Aligner v. 9.0.1 (CodonCode Corporation, Dedham, MA). COI sequences did not
172 require alignment as these had identical lengths of 658 bp after trimming of the primer
173 sites. Alignments of 12S sequences were generated using MUSCLE as implemented in
174 MEGA7 (Kumar *et al.* 2016).

175 Phylogenetic analyses were conducted on the COI dataset, using Maximum Likelihood (ML)
176 and Bayesian inference (BI) methods. All sequences used deposited in GenBank (Table S1).
177 Sequences of thirteen deep-sea raphitomid genera were added to serve as outgroups (Table
178 S1). Their selection was based on a multi-gene (mitochondrial and nuclear) phylogeny
179 containing many southern and south-eastern Australian Raphitomidae (Criscione *et al.*
180 2020). ML was performed using the program MEGA7 with Nearest-Neighbour-Interchange
181 (NNI) as heuristic method and automatic generation of the initial tree. One thousand
182 bootstrap replicates (BS) were performed to assess the topology support. The BI analysis

was performed in MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) and included 2 runs of 10^7 generations, with 4 chains each and a sampling frequency of one tree per 1,000 generations. Other parameters were set to default. A consensus tree was then calculated after checking for chain convergence and discarding the first 25% trees as burn-in. Prior to the model-based ML phylogenetic analyses, TN93+G+I was identified as best-fit model of nucleotide substitution by means of the Bayesian Information Criterion as implemented in MEGA 7 (Kumar *et al.* 2016). According to MrBayes manual (p. 94), a priori model testing was not performed, and the GTR+G+I model was applied to the BI analysis. Nodal support was assessed by values of Bayesian posterior clade probabilities (BPP).

Due to the smaller number of sequences selected to form the 12S dataset, a NJ analysis only was deemed sufficient to represent the phylogenetic relationships based on this gene. This analysis was performed in MEGA 7 (Kumar *et al.* 2016). Uncorrected pairwise genetic distances were calculated using MEGA7 with the option 'pair-wise deletion of gaps'.

Morphological examinations

All studied samples consisted of soft parts and shells, which had been separated following the methodology (drilling or microwaving) mentioned in Criscione *et al.* (2020). We studied shell morphology and (when possible) internal anatomy, including radular morphology. Shells were affixed to plasticine and positioned with their vertical axis parallel to the observation plane. Each shell was then photographed from above using a Canon EOS 6D digital SLR camera. Maximum shell length (SL) and width (SW) were measured on digitised images using the calibrated ruler tool in Adobe Photoshop CC v.20.0.6 and measurements rounded to the nearest 0.1 mm. The number of shell whorls was counted under a Leica MZ8 stereomicroscope, according to Bouchet and Kantor (2004). While it was possible to obtain the number of teleoconch whorls (Wt) for all studied specimens, protoconch whorls could only be counted occasionally due to widespread erosion of the apex. In order to capture the shell proportions regardless of their size, the ratios SL/SW, SL/Wt and SW/Wt were generated. Ideally, to prevent the effects of allometry, only shells at terminal growth could be used in the morphometric analysis of this study. However, terminal growth could not be assessed for the samples of this study (see above). As an approximation, shells of a given PSHs were assumed to have reached terminal growth when their Wt ~~was~~were within one

unit of the maximum Wt value observed for that given PSHs. Based on the data obtained, descriptive statistics and plots were produced in SYSTAT v.13.1 (Systat Software, Inc., 2009). Anatomical studies were conducted on animals removed from ethanol and briefly rehydrated in distilled water. Using standard dissection tools, the venom apparatus was excised and the radular sac isolated and placed on a glass slide; during this 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 were rinsed repeatedly in distilled water, then separated into individuals and ligament-connected pairs/smaller clusters. 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.

Species delimitation

The Automatic Barcode Gap Discovery (ABGD) (Puillandre *et al.* 2012b) was applied for primary species delimitation to the dataset containing all COI ingroup sequences. The web-based version of ABGD (<https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html>) was used with a p-distance model. The relative gap width (X) was set to 1 and other parameters left to default. Resulting ABGD groups were considered primary species hypotheses, henceforth referred to as PSHs. Following Puillandre *et al.* (2012c), conversion of PSHs to secondary species hypotheses (SSHs) was conducted through comparative examination of morphological characters as well as through evaluation of geographic and bathymetric data. In particular, for each PSH examined, the co-occurrence of the following conditions was considered evidence supporting such conversion: (i) the PSH is a highly supported clade (BPP>98% and BS > 90%), (ii) the PSH shows lower values of intra-PSH genetic p-distance in COI when compared with values of inter-PSH distances measured with the most closely related PSH, (iii) all its constituent specimens share at least one distinctive morphological feature deemed not to be polymorphic or ecophenotypic, and without exhibiting intermediate forms. When the above criteria were met, the presence of genetic or morphological divergence and/or bathymetrical partitioning in sympatry was considered additional evidence supporting species delimitation. Clearly, when PSHs are represented by one sequence only, criteria (i) and (ii) cannot be assessed. In those cases, the decision was guided by presence of additional bathymetrical and morphological evidence ~~(such as that~~

~~described above~~) as well as comparisons with intra-generic patterns of genetic distance.

When available, species names were assigned to SSHs based on the current taxonomy. New species names were introduced when no names were available, and formal descriptions for these taxa are given in the systematic section below.

Abbreviations

CMR=Commonwealth Marine Reserve; Ht=holotype; NSW=New South Wales; PNG= Papua New Guinea; Pt=paratype; QLD=Queensland, SA=South Australia, TAS=Tasmania; VIC=Victoria; wet=number of ethanol-preserved (wet) specimens.

Results

Molecular studies

Molecular analyses were based on a total of 75 COI sequences (42 newly produced and 33 GenBank-sourced) generated from specimens collected off Australia during the expeditions IN2015_C01, IN2015_C02 (GAB) and IN2017_V03 (Tasman and Coral Seas) and other localities of the tropical and temperate Indian and Pacific Oceans, during a number of voyages that formed part of the Tropical Deep-sea Benthos programme of MNHN (Fig. 1, Table S1). The dataset analysed included 51 ingroup sequences and 24 sequences representing 24 deep-water raphitomid species of 13 different genera that were used as outgroups

Except for extremely low and high prior values, the ABGD analysis of the COI ingroup dataset consistently returned a partition with 14 groups of sequences (PSHs). Among all PSHs (Fig. 2), five (G1, G2, G4, P2 and P3) contain exclusively Australian samples, three (G3, G5 and P1) include samples from Australian seas and beyond, while the remaining six (GA-GE and PA) encompass sequences from outside Australian waters.

The BI and ML analyses generated trees with nearly identical topologies, showing only minor differences in the relative position of individual sequences within some of the PSH clades (Fig. 2). Clades representing PSH-level relationships and above were generally well-supported, with very few exceptions. In both analyses, two major genus-level clades were retrieved, namely *Gladiobela* (BPP=100%, BS=93%) and *Pagodibela* (BPP and BS=100%).

These two clades included ten and four PSHs respectively, all forming well-supported (in

terms of nodal support: BPP>98%; BS>90%) and well-differentiated (in terms of branch lengths) PSH clades.

Within the two genus-level clades, there was no overlap between intra- and inter-PSH distances. In the *Gladiobela* clade, the intra-PSH pairwise distances in COI ranged from 0 to 1.1 % (average=0.5 %) with inter-PSH distances ranging from 4.0 to 11.7 % (average=8.2 %) (Table 1). The lowest inter-PSH distances were observed between GD and GE and the highest intra-PSH distances were found within G3. In the *Pagodibela* clade, the intra-PSH pairwise distances were between 1.8 and 1.9%, whereas inter-PSH distances ranged from 4.4 to 7.1 % (average=5.6 %) (Table 2). The lowest inter-PSH distances were observed between P2 and PA and the highest intra-PSH distances were found within P1.

The NJ tree obtained analysing the 12S dataset contained four sequences in a cluster, each obtained from samples of four distinct *Gladiobela* PSHs (G1, G3, G4, G5 - as delimited above). One additional sequence (MT081495), from sample AMS C.571625, was the sister group of this former cluster and exhibited values of p-distances (5.1-6.6%; Table S2) with its members that were within the range of those measured for COI between *Gladiobela* PSHs. Additionally, its genetic similarity (in terms of p-distance values) with G1, G3, G4, G5 was greater than that measured with sequences of samples of *Pagodibela* or of any other genus in the analysis (data not shown), suggesting its attribution to *Gladiobela*. Given that 12S largely shares patterns of inheritance with COI, this sample ~~is~~was considered an additional *Gladiobela* PSH (G6) to undergo further testing for conversion to SSH.

297

298 Morphological studies

Shell morphology was examined for all sequenced material and internal anatomy, including radular morphology ~~was studied~~ (when possible) for at least two sequenced specimens per PSH. The *Gladiobela* clade contains three PSHs (G1, G2 and G4) exhibiting a gross shell morphology, whorl profile and sculptural elements that are comparatively similar (Fig. 3A, B, D), whereas the remaining taxa possess heterogeneous shell morphologies, including high-spired and broad fusiform shells with varying sculpture (Fig. 3).

Due to the limited amount of material available (and specifically of shells at a stage equivalent terminal growth), the sample size was too small to permit inclusion of all PSHs in a statistically rigorous morphometric analysis at this time. A scatterplot of SW/Wt and SH/Wt for *Gladiobela* (Fig. 4) revealed that G1 and G2 can be differentiated by shell size

(with the latter exhibiting larger values of both length and width) and proportions (with the latter showing a larger SH/SW ratio). The plot shows that G3 has the smallest and most slender shell of all congeners, while G6 has the largest and broadest shell.

As protoconchs were largely eroded (an intact protoconch could not be observed for all species), this character will not be given much emphasis herein. However, all larval shells that could be examined were multispiral and exhibited the typical raphitomid diagonally cancellate sculpture (Fig. 5).

All members of *Gladiobela* shared hypodermic, somewhat tightly rolled teeth with a very long dorsal blade (Fig. 6A), elongate adapical opening and moderately broad to very broad base (Fig. 6). The sister taxa G1, G2 and G3 can be characterised by teeth with extremely long dorsal blades and a very broad, angular base with a crescent-shaped indentation around the perimeter of the lower shaft and an elongate posterior extension (Fig. 7); G4 is a notable outlier with an extremely long tooth compared to its congeners (Fig. 6F), whereas G5 and G6 possess teeth with a narrower, less angular base (Fig. 6B, D). All members exhibit moderate to long, tapering to cylindrical cephalic tentacles with very small eyespots at their lower outer bases.

Pagodibela PSHs vary notably in shell morphology, from strongly pagodiform with prominent sculpture, to subconical and comparatively smooth (Fig. 3G-J). Their radulae consist of hypodermic morphologically uniform teeth: awl-shaped, with a long dorsal barb, an elongate adapical opening and a swollen base with coarse external texture (Fig. 6G-I). All PSHs possess small eyes at the outer lower bases of cylindrical cephalic tentacles.

Geographical and bathymetrical distributions

The genus-level clade *Gladiobela* is recorded from three marine realms (sensu Costello *et al.* 2017) (Fig. 1A, C) and *Pagodibela* clade from at least seven marine realms (Fig. 1B, D).

Gladiobela exhibits a wide bathymetric range, from 470 to 4750 metres, and *Pagodibela* from 318 to 1013 metres (Fig. 8). The sister clades G1 and G2, G4 and G6 are known only from off Australia, where they are restricted to bathyal and abyssal depths of the temperate south (Fig. 1A). The three former PSHs are not recorded micro-sympatrically (e.g. in the same trawl haul): G1 exhibits a disjunct distribution with the majority of records in the GAB and a single record in the Hunter CMR (depth range 2474-3389 m); G2 occurs between (off) the far southern coast of NSW and into the Bass Strait (depth range 4133-4750 m), whereas

G4 is known from a single locality in the Hunter CMR (3980 m). G6, known only from a sole individual, was collected at the same site as G1 in the Hunter CMR. G3 is known from two widely separated localities, both geographically and bathymetrically, namely in the East Gippsland CMR, at 3850 metres and NW Choiseul, Solomon Islands, between 1083 and 1100 metres. G5 is recorded from the Hunter CMR and Canal de l'Havannah, New Caledonia, with depth records occurring between 951 and 1006 metres.

For *Pagodibela*, P2 and P3 are only known as single specimens from the Coral Sea and GAB respectively, of which the former is known from approximately 1000 metres and the latter approximately 370 metres. Conversely, P1 is widely distributed between (off) North Queensland, via the Coral Sea, New Caledonia and eastward to the Society Islands at a depth range of 450-1013 metres. PA has the most widespread known distribution of all *Pagodibela* PSHs, occurring in at least four marine realms between the South Pacific and off the east African coast (Fig. 1D).

PSH to SSH conversion

Comparative examination of the morphological, geographic and bathymetric data available was employed to attempt the conversion of PSHs to SSHs. As generating morphological data for most species with distribution outside Australian waters was beyond the scope of this study, testing of five PSHs (i.e. GA-GE), out of the total of fourteen retrieved by ABGD, was not attempted and these are pending further sampling and taxonomic investigation. As detailed below, all remaining nine PSHs retrieved by ABGD, namely G1-G5, PA and P1-P3 satisfied the three conditions described in the methodological section. G1 and G2 corresponded to highly supported clades (BPP and BS=100%; Fig. 2) in a sister relationship. Both exhibited low intra-PSH genetic distance (average 0.06% and 0.05% respectively; Table 1) and comparatively high reciprocal genetic distance (average 5.4%; Table 1). Both G1 and G2 could be distinguished from all other PSHs by their distinctly carinated shells (Fig. 3A-B). G1 could be differentiated from G2 by their smaller, broader shells (Fig. 4) with a carina that is comparatively less pronounced. In addition, their bathymetrical range did not overlap (Fig. 8). The genetic, morphological and bathymetrical distinction between G1 and G2 was maintained in spite of their apparent high dispersal potential (as inferred by the multispiral protoconch) and their sympatry in the South Australia realm (Fig. 1A).

Clade G3 was highly supported (BPP and BS=100%), exhibiting values of intra-PSH genetic distances (average ~1%; Table 1) well below values of reciprocal between-PSH genetic distance with its most closely related PSHs (4% with both GE and GD; Table 1). Its shell was the smallest and most elongate of all other PSHs (Fig. 4) and could readily be distinguished by its raised peripheral cord (Fig. 3C).

G4 corresponded to a highly supported clade (BPP and BS=100%), exhibiting values of intra-PSH genetic distances (average 0.5%; Table 1) and comparatively high genetic distance with its most closely related PSH, GA (5.8%; Table 1). It could be clearly differentiated from all other PSHs by its shell exhibiting a long, clearly demarcated siphonal canal (Fig. 3D) and by its uniquely long hypodermic teeth (Fig. 6F).

Clade G5 was highly supported (BPP and BS=100%) and included a single haplotype that exhibited a large genetic distance from its most closely related PSH, GC (average 7.9%; Table 1). All shells of this PSH shared distinctively rounded lower teleoconch whorls (Fig. 3E) that allowed their differentiation from shells of all other PSH in the *Gladiobela* clade.

Along with the aforementioned comparatively high values of inter-PSHs genetic p-distance in 12S (Table S2), the shell of G6 could be differentiated from that of all other PSHs by its broad whorls with opisthocline axial ribs, and by its comparatively rounded shoulder (Fig. 3F). Such genetic and morphological differentiation was maintained in spite of its sympatry with G1 at the boundary between the two marine realms encompassing the Australian seas (Fig. 1A).

PA and P1 both corresponded to highly supported clades (BPP=98% and BS=93%, BPP and BS=99% respectively; Table 2) showing comparatively high values of reciprocal genetic differentiation (average 4.7%; Table 2). These two PSHs exhibited similar shells that could be differentiated from other *Pagodibela* PSHs by their comparatively thicker and more elongate shells. However, PA and P1 could be differentiated from each other based on shell sculpture - while shells of P1 possess juvenile whorls with weakly opisthocline axial riblets extending across the periphery (although weakening towards suture), in shells of PA the axial elements were significantly weaker, and there was a prominent, slightly gemmate subsutural cord in the early- to median teleoconch whorls (Fig. 3H and 3G respectively). In both PA and P1, the overall shell shape was rather conserved across its constituent samples. The minor differences observed among PA shells in their peripheral sculpture (smooth,

carinate or tuberculate), were consistent with distributional patterns and thus interpreted as intraspecific geographical variation.

The only sample included in P2 was separated from the sister pair PA and P1 by high values of genetic distance (4.4 and 4.8% respectively; Table 1). The pagodiform shell of P2 exhibited a gemmate carina that was unique among PSHs of *Pagodibela*. This distinctiveness was maintained in spite of geographic and bathymetric overlap with P1 in the Coral Sea. Clade P3 was the sister group of all other *Pagodibela* PSHs, revealing comparatively high values of reciprocal genetic distance with all congeneric PSHs (>6.3%; Table 2). It included only one sample with a uniquely thin, fragile shell with comparatively rounded whorls (Fig. 3J), which differentiated it from any other PSH within the *Pagodibela* clade.

Assigning names to SSHs

A search was conducted for all names available and potentially applicable to the nine SSHs resulting from the conversion process described above. By consulting the relevant literature on Raphitomidae (e.g. Bouchet and Sysoev 2001; Bouchet and Warren 1980; Sysoev and Bouchet 2001) and by comparison of molecular and morphological data available on type specimens with the data generated on sequenced specimens, we found three names applicable to three SSHs. Two SSHs, G1 and P2, included the type material of two species, *G. angulata* and *P. maia* respectively, and could therefore be readily respectively associated with these species. As its constituent specimens shared shells that closely resembled the holotype of *Gymnobela baruna* Sysoev, 1997 (Fig. 3G), clade PA was attributed to this taxon, thus requiring a formal transfer of this species to *Pagodibela* as hereby proposed (*Pagodibela baruna* n. comb.). As no available names could be found for the remaining six SSHs, new taxon names were assigned, namely *G. abyssicola* n. sp. (G2), *G. acris* n. sp. (G3), *G. stupa* n. sp. (G4), *G. vitrea* n. sp. (G5), *G. sinuosa* n. sp. (G6), *P. pacifica* n. sp. (P1) and *P. meridionalis* n. sp. (P3). Formal taxonomic descriptions of these newly recognised species are provided below.

Discussion

Phylogenetic relationships and generic taxonomy

Building on the five-gene phylogeny of Criscione *et al.* (2020), that established the phylogenetic framework upon which *Gladiobela* and *Pagodibela* were recognised and described, it is shown herein that there is strong support in both BI and ML analyses for their monophyly (Fig. 2).

The integrity of these genera is corroborated by radular features diagnostic for each genus.

The radula of *Gladiobela* is characterised by hypodermic awl-shaped teeth with an elongate apical opening, a very long dorsal blade about half the length of the shaft, a (mostly) broad, angular base and a broad, medium long ligament (Fig. 6A-F). Members of *Pagodibela* exhibit evenly tapering awl-shaped hypodermic teeth with a comparatively narrow, sloping base with coarse external texture, and a comparatively small, short ligament (Fig. 6G-I). The wide, strongly perpendicular base and the long posterior extension, particularly noticeable in *G. angulata*, *G. abyssicola* and, *G. acris* (Fig. 6A, C, E; Fig. 7) are particularly prominent features, notably the crescent-shaped indentation around the base of the shaft (Fig. 7A).

While nothing is known of any potential corresponding features in the proboscis interior of these taxa, such as the presence and nature of an epithelial pad seen in several ‘turrid’ lineages (Kantor and Taylor 2002; Medinskaya 1999), the following speculations can nevertheless be made: the long posterior extension (Fig. 7A) facilitates physical contact with the internal proboscis (thus the area which can be attached), while the crescentic indentation possibly facilitates the proboscis sphincter in holding the tooth securely. A firm, secure grip can hypothetically perform a number of functions, such as aiding in speed and precision during attacks and in securing tooth recovery after- or between attacks (thus assisting in both performing successive stabs and conserving teeth).

While the general configuration of the radula of *G. stupa* conforms with that of its congeners, this species is a notable outlier, due to its very long hypodermic tooth (Fig. 6F). Bouchet and Warren (1980; p. 5) stated that ‘it must be remembered that the radula is an organ for capture of food’; the fact that *G. stupa* possesses extremely long teeth compared to its congeners (Fig. 6F) does suggest that the radular morphology of the group may not purely be ascribed to phylogenetic signal, but that feeding mechanism exerts some selective pressure on their morphology. A similar anomalous enlargement of the radula while retaining the overall tooth configuration (i.e., size and configuration of barbs, length of

adapical opening, base morphology, etc.) of its congeners is also seen in a hitherto unnamed species of *Austrobel* Criscione, Hallan, Fedosov & Puillandre 2020 (unpublished data). The morphology of ~~the~~ radula reflects feeding mechanism to a larger extent than the phylogenetic signal in cone snails (Olivera *et al.* 2015; Puillandre *et al.* 2014). However, dietary habits are not sufficiently known for the Raphitomidae and little inference can be made with regards to the respective influences by phylogenetic signal and feeding in shaping their radular morphology. The radulae of *Pagodibela* species examined here are highly similar (Fig. 6G-J), and therefore present a solid diagnostic generic-level character. In both genera, shells are heterogeneous, but in gross morphology the overall pagodiform shell of *Pagodibela* is a recognisable character in its composite taxa (Fig. 3G-J). While some species are similar in shell morphology (notably *G. angulata* and *G. abyssicola*), *Gladiobela* cannot readily be circumscribed based on its shell at the genus-level (Fig. 3A-F). At the species-level, genetic distinctiveness as shown by ABGD and sequence divergence (Tables 1, 2), demonstrable differences in shell morphology and dimensions (Figs 3, 4) and to a lesser extent radular morphology (particularly for *Pagodibela*, see Fig. 6G-J), translate into robust hypotheses for all the new species described herein. The genetic distinctiveness reported at the intra- and interspecific levels for the two genera (Tables 1, 2) is comparable, but overall lower than those reported for the raphitomid genera *Kermia* W. R. B. Oliver, 1915 and *Pseudodaphnella* Boettger, 1895 (Fedosov and Puillandre 2012), and significantly lower than those reported for *Hemilienardia* Boettger, 1895 (Fedosov *et al.* 2017). This could be explained by differences ~~e.g.~~ in population effective size, ~~with the~~ mutations being fixed more rapidly in smaller populations due to genetic drift, ~~or in evolutionary rates, the compared taxa living in different environments that could have different impact on rates of molecular evolution.~~

Biogeographical and bathymetrical patterns

Most species of *Gladiobela* named herein occur within an area corresponding approximately to the South Australia marine realm of Costello *et al.* (2017). Unsurprisingly, the records are concentrated in the areas of sampling: a relatively restricted portion of the GAB and on a section of the temperate E Australian coast between NE Tasmania and the Hunter CMR (Fig. 1A). As neighbouring regions with comparable environmental conditions remain virtually unexplored, it is plausible that disjunct distributions, like that observed for *G. angulata* (Fig.

1A), are the result of sampling bias, rather than a reflection of any underlying biological process. In *G. angulata*, the mean genetic p-distance between the Hunter CMR COI haplotype and the GAB haplotypes is low (0.4%), when compared with the range of p-distances calculated within the GAB sequences (0.2-2.0%), indicating very recent or ongoing gene flow between the two areas. It remains unclear whether genetic connectivity in *G. angulata* is realised through a stepping-stone process, involving additional geographically intervening populations, or through long range dispersal of the planktotrophic larva (or both).

In a scenario of a continuous distribution of *G. angulata*, there would be potential range overlap with its sister taxon, *G. abyssicola*, off the southeast Australian coast. However, the two taxa are not recorded in micro-sympatry. Additionally, there is no recorded overlap in their bathymetric ranges, with an approximately 650-metre gap between their lower and upper bathymetric extremes (Fig. 8), despite some sampling coverage within this gap at corresponding areas. It is conceivable that the two taxa have partitioned into separate bathymetric niches, although the present knowledge of their ecological requirements is insufficient to explain the mechanism involved. Separate bathymetric distributions of sister species have been previously reported for at least three conoidean genera, namely *Bathytoma* Harris & Burrows, 1891, *Lophiotoma* T. L. Casey, 1904 and *Cryptogemma* Dall, 1918 (Turridae) (Puillandre *et al.* 2017; Puillandre *et al.* 2010b; Zaharias *et al.* 2020) and presented as examples of speciation where bathymetric niche partitioning is the driver of genetic isolation in absence of topographic barriers.

The two records of *G. acris* are separated by an entire marine realm (Fig. 1A, C) in which there are no records despite moderately comprehensive sampling in recent times and in the relevant depth range (O'Hara 2019), and within which other congeners (Fig. 1A) as well as several other raphitomids have been recorded (Criscione *et al.* 2020). Similarly, *G. vitrea* is recorded from widely separated localities (Hunter CMR and New Caledonia), although both in the same marine realm (Fig. 1A) and both within a relatively narrow depth range when compared to *G. acris* (Fig. 8). Assuming that all species of *Gladiobela* have similar dispersal capabilities, it is plausible that the difference in intraspecific p-distance between *G. acris* (average 1.1%; Table 1) and *G. vitrea* (one haplotype only) is the result of their difference in geographical and bathymetrical distribution.

The comparatively wide geographic distributions of *P. pacifica*, *P. baruna*, *G. acris* and *G. vitrea* are not entirely unexpected given the mounting evidence of wide distributions in deep-sea 'turrids' (Bouchet and Waren 1980; Zaharias *et al.* 2020; Criscione *et al.*, *subm.*). Our results suggest that *Gladiobela* may comprise species that are comparatively common (e.g., *G. angulata*/*G. abyssicola*) and some of which may be either rare in terms of their abundance or exhibit fragmented distributions (or both).

The bathymetric range of *G. acris* (about 2770 m) (Fig. 8) possibly constitutes the widest ever reported for a conoidean species. While similarly wide depth ranges have been documented for a number of deep-sea 'turrids' [including some raphitomids (Bouchet and Waren 1980)], the wide range of the trans-oceanic turrid *C. phymatias* (about 2000 m) is so far the only one reported with support from genetic evidence (Zaharias *et al.* 2020). Due to the scarcity of material for most other species studied here, little inference can be made with regards to their bathymetric zonation.

Challenges to deep-sea 'turrid' taxonomy

While extremely diverse, most 'turrids' are commonly found in low to very low abundance, frequently even as single individuals (Bouchet *et al.* 2009; Todd and Rawlings 2014). The findings of this study largely conform to that observation, with *P. maia*, *P. meridionalis* and *G. sinuosa* known from only single specimens and *G. acris* n. sp. and *G. vitrea* n. sp. known from two individuals each. Such scarcity of material makes meaningful comparison between taxa with regards to a range of characters difficult. Limited inference can be made about relative size and maturity, as the lack of terminal shell growth makes it difficult to ascertain if a specimen has attained maturity, particularly in the absence of comparative material. While the number of teleoconch whorls may be an indicator of maturity, Bouchet and Waren (1980) suggested that this may not be a reliable character for some taxa, as terminal shell growth has been observed in taxa with very few teleoconch whorls. While the challenge of assessing maturity persists also where sample populations are larger, a growth series can at least provide some insights into any developmental changes that may occur with increasing size. Studies on the genus *Cryptogemma* of the Turridae *sensu stricto* (Kantor and Sysoev 1991; Zaharias *et al.* 2020), suggest that the characteristic apertural notch and a large penial appendage in *Cryptogemma praesignis* (Smith, 1895) are both features attained in maturity and which are absent in immature individuals. Criscione *et al.*

(2020) reported developmental changes in the eye morphology of *Nodothauma magnifica* Criscione, Hallan, Fedosov & Puillandre, 2020, in which juvenile and young adults may possess large eyes which with maturity become obscured by epidermis. With species known only from single or very few specimens, such characters may be readily missed. So, what should then be considered an appropriate threshold in terms of available material for describing a new deep-sea 'turrid'? The absolute minimum ought to be a molecular voucher linked to a type (Puillandre *et al.* 2017) and providing details of radular- and other non-shell characters where available. Satisfying these criteria, meaningful species descriptions can be conducted even where limited material is known. Any effort towards inventorying the diversity of 'turrids' is vital to the understanding of their evolution and to the characterization of turritoxins (e.g. Gonzales and Saloma 2014; Lopez-Vera *et al.* 2004; Puillandre *et al.* 2012a), far lesser known than the pharmacologically relevant conotoxins (Conidae; e.g. Prashanth *et al.* 2014) and teretoxins (Terebridae; e.g. Gorson *et al.* 2015). A molecular type voucher also allows for a cumulative taxonomic process, where any future conspecific material suitable for DNA analysis can then be readily identified, and systematic descriptions revised accordingly where new anatomical and/or morphological data are obtained. However, where scarce material (even single individuals) cannot be analysed molecularly, particularly where only the shell is available for study, new species descriptions of deep-sea 'turrids' are virtually meaningless; in fact, such descriptions may complicate integrative taxonomic efforts on this group by the proliferation of taxon names that can never reliably serve as references to any future anatomical and molecular study. With tendencies in several taxa toward shell plasticity, geographically and bathymetrically widespread distributions, and low abundance (Bouchet *et al.* 2009; Bouchet and Waren 1980; Criscione *et al.* 2020; Kantor *et al.* 2008; Zaharias *et al.* 2020), taxonomic endeavours on 'turrids' pose logistical as well as theoretical challenges best met by integrative, and preferably collaborative efforts to enable optimal sharing of data, material, and expertise. The numerous synonyms in *Cryptogemma* (Zaharias *et al.* 2020) are a salient recent example of how integrative taxonomy is critical to constraining and understanding morphological heterogeneity and elucidating biogeographical patterns at the species level. Todd and Rawlings (2014) give examples of how taxonomic efforts on *Polystira* (Turridae) have resulted in greatly underestimated distribution ranges due to a lack of examination of museum holdings, and where taxonomic decisions have been made with 'relatively few

589 comparisons with other taxa' (p. 470). The results herein further illustrate the need for the
590 integrative approach, associated with a high sampling effort, without which inadequate or
591 redundant taxonomic decisions can too readily be made due to lacking consultation with the
592 broader taxonomic, biogeographical and molecular contexts.

For Review Only

Systematics

General remarks

If not stated otherwise, holotypes are dissected ethanol-preserved specimens and all systematic descriptions are based on the holotype. Shell whorls counts (approximated to one decimal unit) are reported with reference to intact whorls only. When applicable, the expression 'at least' is used in combination with the whorl count to indicate potential additional missing whorls that could not be counted. Shell and head-foot colouration reported in the descriptions are based on observations performed prior to fixation, and thus may not be fully reflected in the illustrations provided (Figs 3, 5). Measurements of radular features, mainly the length of the adapical opening and the dorsal blade, are given as ratios of the length of the shaft. The 'shaft' is here defined as the entire length of the tooth minus the base, where there is a notable swelling and angulation that clearly differentiates it from the comparatively thin-walled hypodermic, rolled structure. This is done to ensure consistency with the terminology used in Criscione *et al.* (2020).

Superfamily Conoidea Fleming, 1822

Family Raphitomidae Bellardi, 1875

Genus *Gladiobela* Criscione, Hallan, Puillandre and Fedosov, 2020

Diagnosis

Shell (SH=13.5-27.3, SW=7.5-14.0) fusiform-biconical, broadly- to elongate- biconical, thin-walled, semi-translucent to opaque. Protoconch multispiral, orange, cyrthoconoid, with up to four whorls with diagonally cancellate sculpture. Teleoconch of four to eight whitish, cream to orange whorls, suture impressed. Whorl profile medium- to very broad, with wide, rather lightly concave to straight subsutural ramp, indistinctly to clearly demarcated from whorl periphery; distinctly angulated shoulder sometimes bearing clearly defined carina situated at mid-height to abapical third. Lower portion of whorl sub-cylindrical or slightly narrowed toward suture. Teleoconch sculpture of spirals only (striae) or spiral cords and axial riblets/ribs. Subsutural ramp sculpture of axial growth lines to slightly raised riblets, spirals absent to very faint. Last adult whorl evenly convex or with slight concavity below carina, evenly convex below carina (in latter) or below subsutural ramp, clearly demarcated from rather straight, subcylindrical to tapering siphonal canal. Aperture elongate, about 40% to half total shell length; outer lip thin, unsculptured. Inner lip whitish, gently recurved, with

625 or without spiral cords extending onto columella. No distinct callus. Anal sinus wide to very
626 wide, (moderately) deep, u-shaped.

627 Animal uniform whitish to cream. Cephalic tentacles short to rather long. Eyes very small.
628 Radula of straight to slightly curved, medium to very long hypodermic teeth (150-460 μm in
629 length); no ventral barb; dorsal blade extremely long, from about 1/3 to half of length of
630 shaft; adapical opening very elongate to subtriangular, rather narrow, ranging from about
631 1/10 to 1/3 of length of shaft. Base broad to very broad, with or without distinctly indented
632 'shelf' perpendicular to shaft; large dorsal wall extending posteriorly, with numerous
633 internal pits or folds; exterior of base with fine texture; basal opening large, subcircular.
634 Ligament broad.

635

636 Remarks

637 *Gladiobela* can be differentiated from other raphitomid genera by the following combined
638 characters: a (generally) broadly to elongate fusiform shell with a large aperture extending
639 about half of total shell length; a weakly to distinctly carinate shoulder (notably in juvenile
640 teleoconch whorls); rather dense, evenly set spiral cords throughout periphery of
641 teleoconch whorls (include base of last adult whorl); straight to slightly curved hypodermic
642 teeth with a very long dorsal blade, elongate adapical opening, a (generally) very broad,
643 distinctly angular base and a broad, medium long ligament. In terms of shell morphology,
644 *Gladiobela* bears some superficial resemblance to a number of other Australian deep-sea
645 raphitomid genera including *Biconitoma*, *Aplotoma*, *Pueridaphne* and *Fusobela* (all Criscione
646 et al., 2020), all of which exhibit comparatively broadly fusiform shells where the length of
647 the aperture is approximately half of total shell length. However, *Biconitoma* and *Aplotoma*
648 differ from *Gladiobela* in their opaque, chalky shells, which also exhibit prominent spiral
649 cords. *Pueridaphne* is characterised by a finely cancellate sculpture and a deep, wide anal
650 sinus (Criscione et al. 2020), whereas *Fusobela* bears distinctly rounded whorls with a very
651 weakly defined subsutural ramp. Additionally, these genera differ from *Gladiobela* with
652 respect to a number of anatomical characters (see Criscione et al. 2020)

653 The ranges for this genus are here expanded from those provided in Criscione et al. (2020),
654 with a reported bathymetric range of 470-4750 metres (Fig. 8) and occurring in the GAB,
655 Tasman Sea, Coral Sea, New Caledonia and the Solomon Islands (Fig. 1A, C).

656

Gladiobela abyssicola n. sp.

(Figs 3B, 6E)

Material examined

Holotype: Australia, NSW, off Bermagui, (-36.351, 150.914), IN2017_V03_043, 4750-4763 m, (AMS C.571656). COI: MT081415.

Paratype material: As for holotype, 1 wet (AMS C.571717), 1 wet (AMS C.519389), Australia, Bass Strait, (-39.552, 149.553), IN2017_V03_030, 4133-4197 m, 1 wet (AMS C.519329).

Etymology

In reference to its presence in the abyssal zone, derived from 'abyssus' (Latin=abyss) and -colus (New Latin=inhabitant). Adjective of feminine gender.

Distribution

Known from abyssal waters off the southern coast of NSW and Bass Strait, Australia.

Shell (SH=25.6 mm, SW=12.8 mm) broadly fusiform-biconical, rather thin-walled, semi-translucent. Protoconch eroded. Teleoconch of at least 5.2 rather uniformly cream whorls, suture impressed. Whorls broad, with very wide, lightly concave to straight subsutural ramp; well-defined carina situated at approximately mid-height of whorl, periphery subcylindrical. Axial sculpture of growth lines only, on early whorls forming slightly raised, densely set riblets. Spiral sculpture of evenly paced, densely set subperipheral cords (about 6 on median whorl, 8 on penultimate whorl, 40+ on last whorl), few weaker supra-peripheral cords present immediately above carina. Last adult whorl with slight concavity immediately below carina, later - evenly convex, rather clearly demarcated from slightly tapering, moderately long siphonal canal. Aperture elongate, approximately equal to spire length; outer lip thin, unsculptured. Inner lip whitish, gently recurved, spiral cords extending uninterrupted onto columella. No distinct callus.

Anatomy (based on AMS C.571656 [female] and AMS C.519329 [male]). Animal uniform whitish. Cephalic tentacles broad, muscular, short to medium length, somewhat tapering toward blunt tip; miniscule eyespots situated at their outer lower bases. Short, muscular

689 introvert. Proboscis long; venom gland very long, white, convoluted; muscle bulb large,
 690 elongate, lustrous; large radular sac. Oviduct large. Penis narrow, simple, no obvious glands
 691 or swellings.

692 Radula (based on AMS C.519389 and AMS C.571717) of straight to slightly curved
 693 hypodermic teeth attaining 215 μm in length; no ventral barb; dorsal blade sharp, extremely
 694 long, approximately half of length of shaft; adapical opening very elongate, rather narrow,
 695 about 1/3-1/4 of length of shaft. Base broad, with distinct crescentic, slightly excavated
 696 shelf more or less perpendicular to orientation of tooth; large dorsal platform extending
 697 posteriorly, with numerous, densely arranged folds on inner surface; exterior of base with
 698 comparatively fine texture; basal opening large, subcircular. Ligament broad.

699

700 Remarks

701 *G. abyssicola* n. sp. is the sister taxon to *G. angulata*, with which it shares notable
 702 similarities in shell- and radular morphology. In terms of shell morphology, *G. abyssicola*
 703 possesses a more acute carina, which forms an elevated spiral cord at the whorl periphery
 704 and a slightly shorter, less attenuated siphonal canal (Fig. 3B). Compared to its sister taxon,
 705 *G. abyssicola* has larger and more slender shells (Fig. 4). It can readily be differentiated from
 706 the remaining *Gladiobela* spp. by its distinctly carinate shell. Of all *Gladiobela* and
 707 *Pagodibela* species, *G. abyssicola* n. sp. and *G. angulata* are the only to appear in
 708 comparative abundance. The two latter species occupy different bathymetric ranges, in
 709 which *G. abyssicola* is recorded only from abyssal depths (~4100-4800 m) (Fig. 8). *Gladiobela*
 710 *abyssicola* constitutes the deepest-living conoidean gastropod to be described from
 711 Australian waters.

712

713 *Gladiobela acris* n. sp.

714 (Figs 3C, 5A, 6C)

715

716 Material examined:

717 Holotype: Australia, VIC, East Gippsland CMR, (-38.479, 150.185), IN2017_V03_032, 3850-
 718 3853 m, 1 wet (AMS C.571697). COI: MN983181.

719 Paratype: Solomon Islands, (-6.417, 156.35), SOLOMON_2, CP2231, 1083-1100 m, 1 wet
 720 (MNHN-IM-2009-19029).

721

722 Etymology

723 In reference to the pointed shape of its shell, derived from 'acer' (Latin=pointed). Adjective
724 of feminine gender.

725

726 Distribution

727 Distribution: Known only from the Hunter Commonwealth Reserve, NSW, Australia and NW
728 Choiseul, Solomon Islands. Potentially widespread.

729

730 Shell (SH=19.0 mm, SW=7.5 mm) fusiform-biconical, thin, semi-translucent, with tall,
731 orthoconoid spire. Protoconch multispiral, orange, with at least four whorls. PI largely
732 eroded; PII with indistinctly shouldered median whorl, sculpture of axial riblets on shoulder
733 slope changing to diagonally cancellate on whorl periphery. Protoconch-teleoconch
734 transition well-defined, broadly sinuate. Teleoconch of eight uniformly white whorls, suture
735 deeply impressed. Whorls medium-broad, with wide, steep, flat subsutural ramp followed
736 by cylindrical low periphery limited to abapical third in early whorls and subsequently
737 occupying about half of whorl height. Periphery notably raised on early whorls, having
738 appearance of strongly widened cord, in later whorls transition from subsutural ramp to
739 whorl periphery with clear angulation forming distinct shoulder at abapical third of whorl.
740 Axial sculpture of regularly arranged, rounded opisthocline ribs on whorl periphery (20+ on
741 penultimate and last whorls), rapidly weakening and becoming obsolete toward base of last
742 whorl. Spiral sculpture of evenly spaced, gently undulating spiral cords, also confined to
743 whorl periphery (3-4 on mature whorls, 15+ on last whorl). Microsculpture of growth lines,
744 forming arcuate riblets on subsutural ramp, reflecting outline of anal sinus. Last adult whorl
745 evenly convex below subsutural ramp, clearly demarcated from long, tapering siphonal
746 canal. Aperture very elongate, narrow, approximately half of shell length; outer lip thin,
747 unsculptured. Inner lip whitish, distinctly recurved, no distinct callus. Anal sinus wide,
748 moderately deep, u-shaped.

749 Cephalic tentacles long, cylindrical; eyes very small. Muscular bulb elongate.

750 Radula (Fig. 6C) of straight to slightly curved hypodermic teeth attaining 175 μ m in length;
751 no ventral barb; dorsal blade sharp, extremely long, approximately half of length of shaft;
752 apical opening very elongate, rather narrow, about 1/3 of length of shaft. Base broad,

with distinct crescentic, slightly excavated shelf more or less perpendicular to orientation of tooth; 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 species exhibits the smallest and most slender shell of all congeners (Fig. 4) and it is characterised by its distinctly raised whorl periphery. While differing significantly from the sister taxa *G. angulata/abyssicola* in its shell morphology, it possesses a similar radula with a broad, angular base with a crescentic indentation around the lower shaft (Fig. 6C). Its only two records (Fig. 1A) suggest a wide bathymetric range of at least 2760 metres (Fig. 8).

Gladiobela sinuosa n. sp.

(Figs 3F, 6D)

Material examined:

Holotype: Australia, NSW, Hunter CMR, (-32.575, 153.162), IN2017_V03_070, 2474-2595 m, (AMS C.571625).

In reference to the undulating pattern of its shells axial sculpture, derived from 'sinuosus' (Latin=sinuuous, flexuous). Adjective of feminine gender.

Distribution

Known from a single locality in the Hunter CMR, NSW.

Shell (SL=25.6 mm, SW=14.1 mm) broadly fusiform, rather thin, opaque. Protoconch at least two heavily eroded, orange whorls with diagonally cancellate sculpture. Teleoconch of at least five uniformly whitish whorls, suture deeply impressed. Whorls very broad, tumid, with very wide subsutural ramp, straight in early whorls then weakly concave in later whorls; distinctly angulated shoulder at mid-height of whorl, relatively consistent throughout. Axial

sculpture of raised, sharp, evenly interspaced opisthocline ribs below subsutural ramp (25+ on penultimate whorl, 30+ on last whorl), becoming subobsolete toward base of last whorl. Spiral sculpture of densely set, evenly spaced, straight to somewhat undulating cords below subsutural ramp (12+ on penultimate whorl, 50+ on last whorl), weakening towards base of last whorl. Microsculpture of growth lines only, forming semi-regularly spaced arcuate riblets on subsutural ramp. Anal sinus broad, moderately deep, u-shaped. Aperture elongate-pyriform.

Cephalic tentacles muscular, long, cylindrical. Extremely reduced eye spots on outer lower base of tentacles. Mantle roof with large oviduct; ctenidium large, covering much of length of mantle roof; osphradium large. Proboscis long, conical; radular sac of medium size; venom gland long; muscular bulb large.

Radula of straight to slightly curved hypodermic teeth attaining 180 μm in length; no ventral barb; dorsal blade sharp, very long, ranging between 1/3 and half of length of shaft; adapical opening elongate-triangular, about 1/4 of length of shaft. Base rather broad, with distinct crescentic, steep shelf more or less perpendicular to orientation of tooth; large dorsal platform, extending posteriorly, with numerous, densely arranged folds and pits on inner surface; exterior of base with comparatively fine texture; basal opening large, subcircular. Ligament broad.

Remarks:

This new taxon exhibits the largest and least slender shell of all congeners (Fig. 4), which can readily be differentiated by its broad whorls with opisthocline axial ribs and comparatively rounded shoulder, the latter usually more prominent in most other taxa (see below for comparison with *G. vitrea*). The siphonal canal is broken in the only specimen available, thus the length of both the aperture and the siphonal canal could not be ascertained. The intestine contained ample polychaete fragments.

Gladiobela stupa n. sp.

(Figs 3D, 5F, 6F)

Material examined:

817 Holotype: Australia, NSW, Hunter CMR, (-32.138, 153.527), IN2017_V03_078, 3980-4029 m,
818 1 wet (AMS C.571683). COI: MN983183.

819 Paratype: As for holotype (AMS C.519345).

820

821 Etymology

822 In reference to the shape of its shell, somewhat recalling some sacred Buddhist buildings,
823 derived from the Latinised term 'stupa'. Noun of feminine gender in apposition.

824

825 Shell (SH=20.9 mm, SW=10.6 mm) broadly fusiform, rather thin, semi-translucent.

826 Protoconch eroded. Teleoconch of at least 5 uniformly orange whorls, suture impressed.

827 Whorls broad, with wide, straight, poorly defined subsutural ramp. Lower portion of whorl

828 convex, with shell periphery situated at lower third of whorl, producing slightly pagodiform

829 spire outline. Axial sculpture of growth lines only, most noticeable as slightly raised, rather

830 evenly spaced arcuate riblets on subsutural ramp. Spiral sculpture of densely set, low, spiral

831 cords (8+ on penultimate whorl, 30+ on last whorl), somewhat undulating, at irregular

832 intervals distorted by growth lines. Last adult whorl evenly convex below subsutural ramp,

833 very clearly demarcated from straight, long siphonal canal. Aperture elongate,

834 approximately equal to spire length; outer lip thin, unsculptured, convex at its mid-height,

835 its anterior part extended towards end of siphonal canal. Inner lip orange, rather straight,

836 no distinct callus. Anal sinus wide, deep, u-shaped.

837 Penis large, thick, muscular, club-shaped, with near-distal swelling and distal seminal papilla;

838 dense latitudinal folds. Cephalic tentacles long, muscular, cylindrical, with distinct

839 longitudinal groove. Minuscule eyespots on outer lower base of tentacles.

840 Radula (based on AMS C.571683 and AMS C.519345) of very long, narrow, straight

841 hypodermic teeth attaining 460 μ m in length; no ventral barb; dorsal blade sharp, extremely

842 long, approximately 40% of shaft length; adapical opening elongate, rather narrow, about

843 1/10 of length of shaft. Base rather broad, with large dorsal platform extending posteriorly,

844 with numerous, densely arranged pits on inner surface; exterior of base with comparatively

845 fine texture; basal opening rather large. Ligament broad.

846

847 Remarks

In terms of shell morphology, *G. stupa* is most similar to *G. angulata* and *G. abyssicola*, from which it can readily be differentiated by its distinctly less shouldered whorl profile (Fig. 3D), and the comparatively sharper concavity, where the outer lip meets the siphonal canal, the latter of which is also markedly longer in the observed material. Its radula is considerably longer than that of any of its congeners (Fig. 6F).

A longitudinal groove in the cephalic tentacles is also observed for *Pueridaphne cirrisulcata* Criscione, Hallan, Fedosov & Puillandre, 2020 (Criscione *et al.* 2020; Fig. S4). *Gladiobela stupa* n. sp. is differentiated from the former in its orange shell with a rather long, clearly delineated siphonal canal, its very long radular teeth, and in the former having a reddish-brown animal and cancellate sculpture of the teleoconch.

Gladiobela vitrea n. sp.

(Figs 3E, 5C, 6B)

Material examined:

Holotype: Australia, NSW, Hunter CMR, (-32.479, 152.994), IN2017_V03_069, 1006-1036 m, (AMS C.482311). COI: MN983184.

Paratype: New Caledonia, Canal de l'Havannah, (-22.267, 167.383), EXBODI, CP3793, 951-1180 m, 1 wet (MNHN-IM-2013-52094).

Etymology

In reference to its transparent, somewhat glass-like shell, derived from 'vitreous' (Latin=made of glass). Adjective of feminine gender.

Distribution: Known only from the Hunter CMR, NSW, Australia and Canal de l'Havannah, New Caledonia. Potentially widespread.

Shell (SH=21.4, SW=9.5) elongate-fusiform, rather thin-walled, semi-translucent. Protoconch orange, cyrtoconoid, multispiral, of at least 4 evenly convex whorls. Sculpture diagonally cancellate. Protoconch teleoconch transition, wide, narrowly sinuated. Teleoconch of 6.5 uniformly whitish whorls, suture impressed. Whorls medium broad, with wide subsutural ramp, moderately straight, rather poorly demarcated; early to median whorls with distinct

880 carina at lower third mark, with rounded shoulder on median whorl, penultimate and last
881 whorl rather evenly convex. Axial sculpture of growth lines only, on early whorls forming
882 slightly raised, semi-regular riblets. Spiral sculpture of regularly set, distinct, straight to
883 somewhat undulating spiral cords (about 13 on penultimate whorl, 40+ on last whorl),
884 commencing below subsutural ramp, evenly pronounced except for last whorl where they
885 weaken towards base. Last adult whorl evenly convex below subsutural ramp, clearly
886 demarcated from medium long, subcylindrical siphonal canal. Aperture elongate, about 40%
887 of total shell length; outer lip thin, unsculptured. Inner lip whitish, very gently curved. No
888 distinct callus. Anal sinus wide, moderately deep, u-shaped.
889 Eyes very small. Anal gland rather long. Radular sac small, bearing few teeth; muscular bulb
890 large.
891 Radula of straight to gently curved, tapering hypodermic teeth attaining 140 μm in length;
892 no ventral barb; dorsal blade long, approximately 1/3 of length of shaft; adapical opening
893 elongate, rather narrow, about 1/4 of length of shaft. Base rather broad; large dorsal
894 platform, extending posteriorly, bearing numerous internal pits; exterior of base with
895 comparatively fine texture; basal opening large. Ligament broad.

896

897 Remarks

898 This new species is readily differentiated from its congeners in its comparatively elongate
899 shell with a comparatively taller spire (with the height of the aperture is about 40% of total
900 shell length) and its relatively short siphonal canal. With the exception of *G. sinuosa*, all
901 other *Gladiobela* species treated herein (*G. angulata*, *G. abyssicola*, *G. acris* and *G. stupa*)
902 possess an angulate whorl profile, which is more or less evenly convex in *G. vitrea*. It can be
903 differentiated from *G. sinuosa* by its far narrower shell and its absence of axial ribs.

904

905

906 *Pagodibela* Criscione, Hallan, Puillandre and Fedosov, 2020

907

908 Type species *Pagodibela maia* Criscione, 2020 by monotypy and original designation.

909

910 Diagnosis

911 Shell (SL=16-36 mm, SW=6-12 mm), fusiform-biconical, thin-walled, semi-translucent.
912 Protoconch multispiral (2.5-3.5 whorls), orange, broadly conical, cyrtconoid, sculpture
913 diagonally cancellate. Teleoconch of 5.7-8.5 whorls, whitish to pale cream, suture
914 impressed, whorl profile indistinctly angulated to pagodiform. Subsutural ramp wide,
915 straight, indistinctly to clearly demarcated from whorl periphery. Lower portion of whorl
916 sub-cylindrical or narrowing toward suture. Teleoconch sculpture of spirals only (striae) or
917 spiral cords and axial riblets. Subsutural ramp sculpture of axials only (growth lines or
918 riblets) or of spiral cords and axial riblets. Last adult whorl evenly convex below subsutural
919 ramp, clearly demarcated from stout, tapering siphonal canal. Aperture elongate,
920 approximately 40% to half of shell length; outer lip thin; inner lip whitish, with thin callus,
921 straight. Anal sinus narrow to broad, shallow to moderately deep, u-shaped.

922

923 Head wide, cephalic tentacles of median size, cylindrical; small black eyes situated at their
924 bases. Penis small, simple. Proboscis elongate, conical; venom gland short with large
925 muscular bulb. Osphradium large, approximately 2/3 of ctenidium length, and of equal
926 width. Rhyncocoel not capacious; proboscis small, shifted leftward; venom gland long, on
927 right; muscular bulb very large.

928

929 Radular teeth of hypodermic type, slender, straight to slightly curved, ~140-200 μ m in
930 length; barbs absent; dorsal blade nearly half of length of shaft; adapical opening very
931 narrow to narrow and elongate, 1/4 to 1/3 of length of shaft; base comparatively narrow,
932 steep, with coarse external texture; lateral process very weak; basal opening subcircular;
933 ligament small, short.

934

935 Remarks

936 *Pagodibela* can be differentiated from other raphitomid genera by the following combined
937 characters: a (generally) distinctly pagodiform shell (notably in juvenile and subadult
938 juvenile whorls), a medium- to tall spire, and awl-shaped, evenly tapering hypodermic teeth
939 with a comparatively narrow, steep base with coarse external texture. It can be
940 differentiated from the similarly named raphitomid genus *Pagodidaphne* Shuto, 1983
941 (comparison made with type species *P. colmani* Shuto, 1983) by the very prominent spiral
942 sculpture, tall cylindrical periphery and tall aperture of the latter. *Pagodibela*, particularly

the tall-spined *P. baruna* and *P. pacifica*, bears superficial resemblance to tall-spined members of *Typhlosyrinx* Thiele, 1925 and *Leiosyrinx* Bouchet & Sysoev, 2001, but can be differentiated from both of the latter in the (generally) distinctly pagodiform early teleoconch whorls in *Pagodibela*, and also in details of the radula, with the type species *T. vepallida* (Martens, 1902) and *T. supracostata* (Schepman, 1913) shown to have two distinct barbs, and the *L. immedicata* Bouchet & Sysoev, 2001 (genus type species) and *L. matsukumai* Bouchet & Sysoev, 2001 both exhibiting comparatively short (both <100 µm) teeth with short blades and very large, broad bases (Bouchet and Sysoev 2001). Furthermore, the molecular phylogeny by Criscione *et al.* (2020) recovered *Typhlosyrinx* and *Pagodibela* in separate, non-sister clades. The ranges for this genus are here expanded from those provided in Criscione *et al.* (2020), with a bathymetric range of 318-1013 metres (Fig. 8) and occurring in the GAB, temperate to tropical eastern Australia, and large swathe of the Indo-Pacific, from the central South Pacific, PNG, Indonesia and north toward Taiwan, and to the far western Indian Ocean off the East African coast (Fig. 1B, D).

Pagodibela baruna (Sysoev, 1997)
(Fig. 3G)

Gymnobela baruna Sysoev, 1997: 339, figs 6, 49-50.

Material examined

Holotype: Indonesia, Kai Islands, N of channel between small and Big Kai Island (-5.230, 133.000), KARUBAR, CC21, 688-694 m.

Paratype: As for holotype.

Other material: Glorioso Islands, (-12.5, 44.933), BIOMAGLO, DW4863, 606-610 m, 1 wet (MNHN-IM-2013-62987); New Caledonia, Chesterfield Islands, (-21.483, 162.600), EBISCO, CP2651, 883-957 m, 1 wet (MNHN-IM-2007-42312); (-21.683, 166.617), EXBODI, CP3809, 685-880 m, 1 wet (MNHN-IM-2009-29111); PNG, (-4.967, 145.833), BIOPAPUA, CP3708, 502-529 m, 1 wet (MNHN-IM-2009-17156), 1 wet (MNHN-IM-2009-17197); (-9.150, 152.250), BIOPAPUA, CP3739, 503-546 m, 1 wet (MNHN-IM-2009-17116); (-4.733, 146.183), PAPUA_NIUGINI, CP3979, 540-580 m, 1 wet (MNHN-IM-2013-19691); (-5.183, 147.050), PAPUA_NIUGINI, CP3981, 688 m, 1 wet (MNHN-IM-2013-19729); (-5.367, 145.85),

PAPUA_NIUGINI, CP4026, 620-677 m, 1 wet (MNHN-IM-2013-9836). Solomon Islands, (-7.717, 156.417), SALOMON_2, CP2246, 664-682 m, 1 wet (MNHN-IM-2007-42518); (-7.750, 156.933), SALOMON_2, CP2269, 768-890 m, 1 wet (MNHN-IM-2007-42519); (-9.150, 158.983), SALOMON_2, CP2176, 600-875 m, 1 wet (MNHN-IM-2007-42528). South Madagascar, (-25.617, 46.367), ATIMO_VATAE, CP3566/DW3565, 618-624 m, 1 wet (MNHN-IM-2009-14887); Taiwan, (16.233, 114.500), ZhongSha_2015, CP4153, 318 m, 1 wet (MNHN-IM-2013-59316); (16.250, 114.567), ZhongSha_2015, CP4154, 321-326 m, 1 wet (MNHN-IM-2013-59352). Vanuatu, (-16.717, 167.983), BOA1, CP2465, 770-799 m, 1 wet (MNHN-IM-2007-17695).

984

Distribution: W Pacific: Indonesia, PNG, New Caledonia and Vanuatu in the south; Taiwan in the north. SW Indian Ocean: Madagascar and Glorioso Islands.

987

Remarks

G. baruna was previously known exclusively for its live-collected holotype (Fig. 3D) and the shell of its paratype (Sysoev 1997, fig. 50), both collected off the Kai Islands (Indonesia). As already noted by Sysoev (1997, p. 339), the two specimens differ mainly in the prominence of their shell sculpture, specifically with the paratype exhibiting a distinctively more pronounced shoulder. The examination of shells of *P. baruna* conducted in this study, reveals that, while the first 4-5 teleoconch whorls are distinctively more shouldered in all studied shells, only some specimens have shells exhibiting this feature on subsequent (5+) whorls.

The degree of prominence of the whorl angulation, as well as of other sculptural elements, varies across the sample along a morphological continuum, suggesting that such differences are likely to be the expression of intraspecific variability.

In our molecular analysis (Fig. 2), sequences of this species form a strongly supported clade, exhibiting significant genetic structure, which is largely consistent with geographical patterns. The comparatively low average intraspecific pairwise distance in COI (less than 2%), along with the relative homogeneity in shell morphology, suggest that no further taxonomic splitting is required.

The inclusion of additional material into *P. baruna*, results in an expansion of the geographical and bathymetrical ranges of this taxon, now spanning over 13,000 kilometres, from the SW to the NW Pacific, to the W Indian Ocean, at depths between 318 and 883 m. Given the widespread occurrence of shell character homoplasy in the Conoidea (Bouchet *et al.* 2011; Hallan *et al.* 2020; Kantor *et al.* 2018), the shell-based attribution of the material studied herein to this taxon is considered tentative. Further investigation, based on sequence data of freshly collected toptotypical material of *G. baruna*, supplemented by anatomical data, will elucidate whether the taxon studied herein is indeed *G. baruna* or an additional, yet unnamed and conchologically similar species.

Pagodibela meridionalis n. sp.

(Figs 3J, 5E, 6H)

Material examined

Holotype: Australia, SA, GAB, (-35.043, 134.079), IN2015_C02_126, 367-409 m, (SAMA D44173). COI: MN983189.

Etymology

For its presence in the southernmost part of the genus range, derived from ‘meridionalis’ (Latin=from the south). Adjective of feminine gender.

Shell

Shell (SL=19 mm, SW=8 mm), fusiform-biconical, thin-walled, semi-translucent. Protoconch orange, broadly conical, of at least three gently convex, diagonally cancellate whorls. Teleoconch of 6.5 pale cream whorls, suture impressed, whorl profile convex, with moderate, non-carinate angulation at periphery. Subsutural ramp wide, straight, indistinctly demarcated from rounded whorl periphery located at whorl mid-height. Lower portion of whorl sub-cylindrical, narrowing towards lower suture. Subsutural ramp sculpture of dense arcuate growth lines, reflecting shape of anal sinus. Sculpture of regularly spaced, fine, shallow striae, uniformly pronounced over entire shell surface, and dense collabral growth lines. Last adult whorl evenly convex below subsutural ramp, clearly demarcated from stout, tapering whitish siphonal canal with wide opening. Aperture elongate, approximately half of

1037 shell length; outer lip thin; inner lip whitish, with thin callus, straight. Anal sinus moderately
1038 deep, u-shaped.

1039 Head wide, cephalic tentacles of median size, cylindrical; small black eyes situated at their
1040 bases. Osphradium large, approximately 2/3 of ctenidium length, and of equal width.

1041 Rhyncocoel not capacious; proboscis small, shifted leftward; venom gland long, on right;
1042 muscular bulb very large.

1043 Radular teeth of hypodermic type, attaining about 200 µm in length, straight to slightly
1044 curved, somewhat loosely rolled; barbs absent; dorsal blade nearly half of length of shaft;
1045 adapical opening wide and elongate, approximately 1/4 of length of shaft; base
1046 comparatively narrow, steep with coarse external texture; lateral process very weak; basal
1047 opening large, subcircular. Ligament short, small.

1048

1049 Remarks

1050 This new taxon can be differentiated from the *Pagodibela* spp. studied herein based on its
1051 thin, semi-translucent, smooth shell with no distinct carina. *Pagodibela baruna* (Sysoev,
1052 1997) is superficially similar in also having a comparatively smooth (in adults), tall-spined
1053 shell, but the latter is opaque and chalky in texture, possesses a significantly taller spire, and
1054 more marked angulations at the shoulder in early teleoconch whorls and a comparatively
1055 prominent, gemmate supra-sutural cord in early teleoconch whorls (Fig. 3G). None of the
1056 *Pagodibela* spp. can readily be differentiated on the basis of radular morphology only (Fig.
1057 6G-I).

1058 This is the only *Pagodibela* taxon from temperate Australia, where it is known only from
1059 upper bathyal depths in the GAB.

1060

1061

1062 *Pagodibela pacifica* n. sp.

1063 (Figs 3H, 6J)

1064

1065 Material examined

1066 Holotype: New Caledonia, Chesterfield Islands, (-20.967, 160.967), EBISCO, CP2645, 641-652
1067 m, (MNHN-IM-2007-17844). COI: EU015652.

1068 Paratypes: Tuamotu Archipelago, (-17.783, -149.383), TARASOC, DW3489, 450-720 m, 1 wet
1069 (MNHN-IM-2007-38860); New Caledonia, (-22.283, 171.3), EXBODI, DW3876, 518-833 m,
1070 (MNHN-IM-2009-29189); New Caledonia, (-23.283, 167.933), KANACONO, CP4750, 750-850
1071 m, 1 wet (MNHN-IM-2013-69658); Australia, QLD, Coral Sea CMR, (-23.587, 154.194),
1072 IN2017_V03_121, 1013-1093 m, 1 wet (AMS C.519402).

1073

1074 Etymology

1075 For its wide distribution across the Pacific Ocean, derived from 'pacificus' (New Latin=from
1076 the Pacific Ocean). Adjective of feminine gender.

1077

1078 Distribution

1079 Widespread; recorded from off north Queensland, Coral Sea, New Caledonia and to the
1080 Society Islands.

1081

1082 Shell (SL=30 mm, SW=11 mm) elongate, fusiform-biconical, moderately thin-walled, rather
1083 opaque. Protoconch of 3.5 whorls, broadly cyrthoconoid, light orange. Protoconch 2 with
1084 distinct diagonally cancellate sculpture throughout whorl height. Protoconch-teleoconch
1085 transition somewhat weakly defined, only detectable by change in sculpture pattern.
1086 Teleoconch of 8.5 whorls, pale cream; suture deeply impressed. Whorl profile distinctly
1087 angulated, with peripheral carina in early to median teleoconch whorls and rounded
1088 angulation in mature whorls. Subsutural ramp wide, straight, concluded by peripheral carina
1089 at about mid-height of whorl in early to median teleoconch whorls. Lower portion of whorl
1090 subcylindrical or slightly narrowed towards lower suture. Subsutural ramp sculpture of
1091 arcuate riblets, reflecting shape of anal sinus, intersected by narrow raised spiral cords,
1092 forming somewhat reticulate pattern in juvenile whorls; arcuate riblets continuous across
1093 periphery of early to median teleoconch whorls, strongly opisthocline, sub-obsolete to
1094 absent in subsequent whorls. Spiral sculpture of supra-peripheral cords in early to median
1095 teleoconch whorls, forming weak nodules at intersections with arcuate riblets, with cords
1096 less prominent and more densely set in subsequent whorls. Last adult whorl evenly convex
1097 below subsutural ramp, clearly demarcated from broad, stout siphonal canal with distinct
1098 concavity on left side (when seen in apertural view, Fig. 3H). Aperture elongate,

approximately 40% of total shell length; outer lip thin, unsculptured; inner lip whitish, with thin callus, slightly recurved. Anal sinus moderately wide and deep, u-shaped. Radula (based on paratype AMS C.519402) of hypodermic type, approximately 140 μm long, straight to slightly curved; barbs absent; dorsal blade sharp, nearly half of length of shaft; adapical opening narrow and elongate, 1/3 of length of shaft; base comparatively narrow, steep, with coarse external texture; lateral process very weak; basal opening large, subcircular. Ligament short, small.

Remarks

This species can be recognised by its elongate, slender shell with strongly carinated early teleoconch whorls. It is rather similar to the sister taxon *P. baruna* in its shell morphology, with both species exhibiting comparatively large, elongate shells with distinctly pagodiform early to median teleoconch whorls (Fig. 3G, H). However, when compared to the holotype of the latter (Fig. 3G), *P. pacifica* is comparatively smaller, less opaque, and possessing more prominent axial ribs and carina on early teleoconch whorls, and does not possess a distinct, gemmate supra-sutural cord in early teleoconch whorls (Fig. 3G, H).

This new species, along with the sister species *G. baruna*, appear to be the most geographically and bathymetrically widespread members of the genus. However, unlike the sister species *G. angulata/abyssicola* (Fig. 3A, B) they are not allopatric, with largely overlapping bathymetric ranges and with both taxa occurring in the New Caledonian region (Figs 1, 8).

1120 Conflict of interest

1121 The authors declare no conflicts of interest.

1122

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