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ORIGINAL ARTICLE

Molecular phylogenetics of the superfamily Stromboidea (Caenogastropoda): New insights from increased taxon sampling

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Abstract

The superfamily Stromboidea is a clade of morphologically distinctive gastropods which include the iconic Strombidae, or 'true conchs'. In this study, we present the most taxonomically extensive phylogeny of the superfamily to date, using fossil calibrations to produce a chronogram and extant geographical distributions to reconstruct ancestral ranges. From these results, we confirm the monophyly of all stromboidean families; however, six genera are not monophyletic using current generic assignments (Strombidae: *Lentigo*, *Canarium*, *Dolomena*, *Doxander*; Xenophoridae: *Onustus*, *Xenophora*). Within Strombidae, analyses resolve an Indo-West Pacific (IWP) clade sister to an East Pacific/Atlantic clade, together sister to a second, larger IWP clade. Our results also indicate two pulses of strombid diversification within the Miocene, and a Tethyan/IWP origin for Strombidae—both supported by the fossil record. However, conflicts between divergence time estimates and the fossil record warrant further exploration. Species delimitation analyses using the COI barcoding gene support several taxonomic changes. We synonymise *Euprotomus aurora* with *Euprotomus bulla*, *Strombus alatus* with *Strombus pugilis*, *Dolomena abbotti* with *Dolomena labiosa*, and *Dolomena operosa* with *Dolomena vittata*. We identified cryptic species complexes within *Terebellum terebellum*, *Lambis lambis*, *"Canarium" wilsonorum*, *Dolomena turturella* and *Maculastrombus mutabilis*. We reinstate *Rimellopsis laurenti* as a species (previously synonymised with *R. powisii*) and recognise *Harpago chiragra rugosus* and *Lambis truncata sowerbyi* valid at the rank of species. Finally, we establish several new combinations to render *Lentigo*, *Dolomena*, and *Canarium* monophyletic: *Lentigo thersites*, *Dolomena robusta*, *Dolomena epidromis*, *Dolomena turturella*, *Dolomena taeniata*, *Dolomena vanikorensis*, *D. vittata*, *"Canarium" wilsonorum*, *Hawaiistrombus scalariformis*, *Maculastrombus mutabilis*, *Maculastrombus microurceus*.

1 | INTRODUCTION

Members of the gastropod superfamily Stromboidea Rafinesque, 1815 inhabit predominantly shallow tropical and subtropical marine habitats worldwide, with some ranging into deeper and/or temperate waters. Species are characterised by varied and often elaborate shell morphologies (Savazzi, 1991), and some are well known for their large, colourful eyes (Figure 1). Owing to these distinctive features, the Stromboidea, and especially the Strombidae Rafinesque, 1815, have been the subject of numerous comparative morphological studies, with discussion on generic relationships and biogeographic patterns (e.g. Bandel, 2007; Latiolais et al., 2006; Simone, 2005).

Despite this substantial interest in the superfamily, a robust, taxonomically complete phylogeny for Stromboidea is lacking. Recent phylogenetic studies focus primarily on Strombidae, whereas taxon sampling of the other five stromboid families is limited (Irwin et al., 2021; Latiolais et al., 2006; Li, Gu, et al., 2022; Machkour-M'Rabet et al., 2021). This has prevented analysis of generic relationships, or confirmation of reciprocal monophyly among families (except for Strombidae and Xenophoridae Troschel, 1852; Irwin et al., 2021). Analyses within the most recent and taxon-rich phylogenetic study to date did not support the monophyly of several strombid genera (*Canarium*, *Dolomena*, and *Lentigo*), revealing the need for a systematic revision of the family (Irwin et al., 2024).

Studies with more complete taxonomic representation are also useful tools in investigating patterns of biogeography and diversification. When calibrated with the fossil record, phylogenetic analyses allow us to estimate timings of key radiation and divergence events and generate hypotheses on the ecological and geographical factors underpinning these changes. For instance, tectonic movements and concomitant changes to habitats, coastlines, sea level, temperature, and ocean circulation have all had well-documented impacts on marine taxa (e.g., Kohn, 1990; Meyer, 2003; Reid et al., 2010; Vermeij, 1996; Williams, 2007; Wilson et al., 1998). The rich stromboidean fossil record makes this superfamily an excellent subject for time-calibrated phylogenetic studies, with earliest records dating from the Early Jurassic (Gründel et al., 2009, but see Tracey et al., 1993).

In this study, we reconstruct the most taxon rich phylogeny of the Stromboidea to date, with a focus on Strombidae, incorporating time calibrations based on the extensive fossil record. We include sequence data from 53% of currently recognised stromboidean species (59% of strombid species), doubling the taxon sampling in Irwin et al. (2024). This dataset comprises at least one species from all currently accepted strombid genera (except *Mirabilistrombus* and *Amabiliplicatus*); from these, type species are only missing for *Canarium*, *Hawaiistrombus*, *Laevistrombus*, *Titanostrombus* and *Neodilatilabrum* (Supplementary Material S1). We use this framework to inform the systematics of the superfamily and use species delimitation methods to infer primary species hypotheses. We also identify stromboid fossils suitable for calibrating a phylogeny, to estimate the timing of major diversification events and geographic divergences.

2 | METHODS

2.1 | Sample choice

Sampling included at least one representative from 87% of currently recognised stromboidean genera (MolluscaBase, 2023) (Supplementary Material S1), and 93 recognised species, representing 381 newly sequenced specimens; see Supplementary Material S2 for specimen data. Other sequences were sourced from GenBank; those lacking voucher data (Supplementary Material S2) were included if one or more additional specimens of that species (according to initial delimitation analyses) with voucher data were available. Exceptions were made for MN703099 *Stellaria solaris*, MK327366 *Onustus exutus* and DQ525214 *Canarium wilsonorum*, which were included even though we have no vouchers associated with these species, due to interesting initial results and their importance to systematic discussions. Identifications of these two species were consistent with phylogenetic placement in preliminary analyses. Two littorinid species were chosen as outgroups based on a previous study (Irwin et al., 2021) (Supplementary Material S2).

2.2 | DNA extractions, polymerase chain reactions and sanger sequencing

DNA was extracted from ethanol-preserved tissue following Irwin et al. (2021). Fragments of the nuclear 28S rRNA gene (28S) and three mitochondrial genes (cytochrome oxidase subunit I, COI; 16S rRNA, 16S; and 12S rRNA, 12S), were amplified and sequenced following Williams and Ozawa (2006), except most 28S sequences were obtained with a forward primer designed for Stromboidea (Irwin et al., 2021). Sequencing was undertaken at NHMUK or MNHN.

2.3 | Sequence analysis

Sequences were assembled and edited using Sequencher v. 5.4.6 (GeneCodes, Ann Arbor, MI). Several datasets

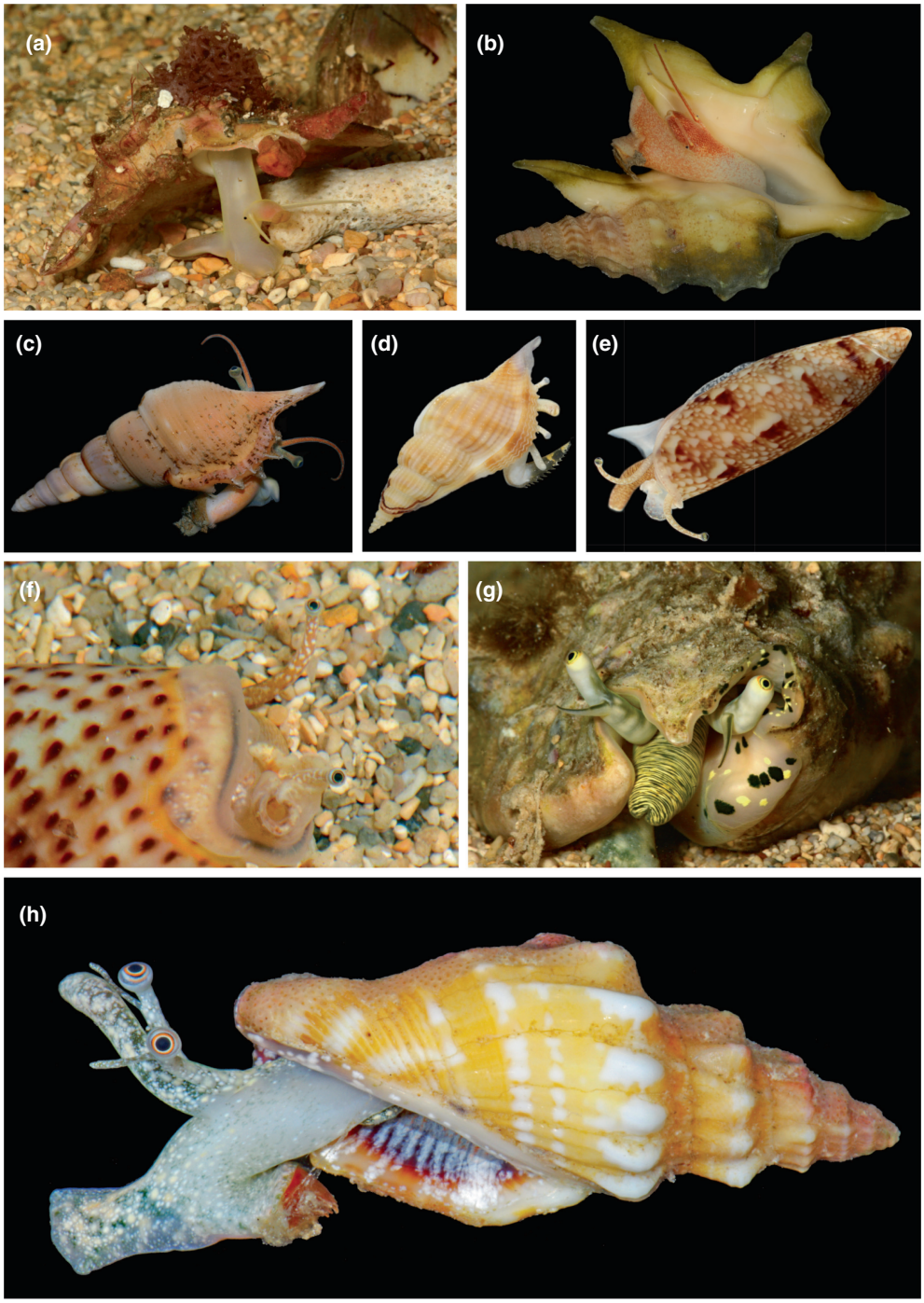


FIGURE 1 Photos of living stromboids: (a) xenophorid *Xenophora solarioides*, Île Sainte-Marie, New Caledonia; (b) aporrhaid *Aporrhais pespelecani*, MNHN-IM-2019-17225, Corsica; (c) rostellariid *Rimellopsis powisii*, MNHN-IM-2007-34492, Philippines; (d) rostellariid *Varicospira cancellata*, MNHN-IM-2013-47468, Papua New Guinea; (e) seraphsid *Terebellum terebellum* D, MNHN-IM-2013-11701, Papua New Guinea; (f) seraphsid *T. terebellum*, Île Néaé, New Caledonia; (g) strombid *Lentigo lentiginosus*, Îlot Tenia, New Caledonia; (h) strombid *Canarium elegans*, MNHN-IM-2013-81518, New Caledonia. Images (a), (f) and (g) taken by David Massemin; remaining images taken by MNHN. Specimens (c)–(e) were sequenced in this study (Supplementary Material S2); see MNHN database for full collection data for specimens (b) and (h).

were produced: (1) datasets for species delimitation analyses comprised 452 and 454 COI sequences (excluding and including outgroups, respectively); (2) datasets for additional single-gene phylogenetic analyses comprised 12S: $n = 199$, 16S: $n = 208$, and 28S: $n = 157$ (including outgroups; Supplementary Material S2); (3) an ingroup-only dataset for the *BEAST analysis including all terminals (472 specimens); (4) an ingroup-only dataset for the

fossil-calibrated BEAST analysis including only 100 terminals (one representative for each putative species delimited in this study). The BEAST dataset included a chimeric sequence for *Varicospira crispata* comprising sequences from different specimens, and three species lacking COI data: *Dolomena japonica*; *Dolomena campbellii*; *Dolomena wienekei* (Supplementary Material S2). Ribosomal RNA genes were aligned in an iterative process via PASTA (Mirarab et al., 2014), using MAFFT L-INS-I (Katoh et al., 2009) to align, OPAL (Wheeler & Kececioglu, 2007) to merge adjacent subset alignments pairs, FASTTREE (Price et al., 2009) to estimate a maximum likelihood tree, GTR + CAT as the nucleotide substitution model, 50% subproblem and centroid decomposition with five iterations and the best alignment determined by likelihood value. Ambiguously aligned regions were excluded via Gblocks 0.91b (Castresana, 2000), with smaller final blocks, gap positions within final blocks and less strict flanking positions allowed; alignment of COI was unambiguous. Putative editing errors were trimmed from GenBank sequence ends (e.g., COI frameshifting indels). The best nucleotide substitution models were chosen via ModelTest-NG (Darriba et al., 2020) using the Akaike Information Criterion: COI, 28S, GTR + I + G; 16S, HKY + I + G; 12S, TrN93 + I + G. Variable and phylogenetically informative sites were identified via IQ-TREE (Minh et al., 2013).

2.4 | Species delimitation

The results of different species delimitation methods for identifying evolutionarily significant units (ESUs) using COI were compared: (1) single threshold general mixed Yule-coalescent model (GMYC; Fujisawa and Barraclough, 2013); (2) single-rate (bPTP; Zhang et al., 2013) and (3) multi-rate Bayesian Poisson Tree Processes (mPTP; Kapli et al., 2017); (4); Automatic Barcode Gap Discovery (ABGD; Puillandre et al., 2012); and (5) Assemble Species by Automatic Partitioning (ASAP; Puillandre et al., 2021). These methods use different criteria to delineate species boundaries (phenetic criteria, ASAP and ABGD; phylogenetic criteria, GMYC, bPTP and mPTP), and vary in performance in other groups, including gastropods (e.g., Aksenova et al., 2018; Goulding et al., 2023; Strong & Whelan, 2019). ESUs were considered putative species (i.e., primary species hypotheses; Puillandre et al., 2012) in *BEAST and BEAST analyses if: (1) ESUs formed a well-supported clade in both BEAST and IQ-TREE COI analyses; (2) ESUs were delimited by at least one method of both phenetic (ABGD and ASAP) and phylogenetic (GMYC, bPTP and mPTP) criteria each. Average interspecific and intraspecific genetic distances for COI were calculated via the Kimura two-parameter model for species with changes proposed to circumscription or rank (K2P; Kimura, 1980) via MEGA v.10.2.6 (Stecher et al., 2020).

ASAP and ABGD analyses were performed with three substitution models (JC, K2P and simple p-distances) via the online servers (ASAP, https://bioinfo.mnhn.fr/abi/public/asap; ABGD, https://bioinfo.mnhn.fr/abi/public/abgd) with default parameters. Only initial partitions were considered in the ABGD analysis (Puillandre et al., 2012). An ultrametric COI tree for the GMYC analysis was produced using Bayesian Inference (BI; Huelsenbeck et al., 2001) via BEAST v.1.10.4 (Drummond & Rambaut, 2007) without fossil calibrations and with an uncorrelated relaxed lognormal clock, a constant population size coalescent prior (more conservative than a Yule prior for species delimitation; Monaghan et al., 2009), and a UPGMA starting tree. The analysis ran for 150,000,000 generations (sampling frequency, 5000). Convergence was checked via Tracer v.1.7.1 (Rambaut et al., 2018); ESS values >200 indicated adequate sampling. The final tree was produced in TreeAnnotator based on 27,000 trees with maximum clade credibility (MCC) and median node heights, and posterior probabilities (PP) calculated by BEAST. We used SPLITS (Ezard et al., 2009) in R v.4.1.3 (R Core Team, 2022) to identify species boundaries. Maximum likelihood (ML; Felsenstein, 1981) trees were produced in IQ-TREE for PTP analyses using the ultrafast bootstrap (UFBoot) feature (Hoang et al., 2018). The mPTP and bPTP models were run via mPTP v.0.2.4 (https://github.com/Pas-Kapli/mptp). Confidence of delimitations was assessed via ten MCMC chains (generations, 100,000,000; sampling frequency, 5000) with 10% burnin; convergence of independent runs was verified with Average Standard Deviation of Delimitation Support Values (ASDDSV; Kapli et al., 2017).

2.5 | Phylogenetic reconstructions

Single-gene BI analyses for 12S, 16S and 28S were produced via MrBayes (v.3.2.2; Huelsenbeck & Ronquist, 2001). Four MCMC chains were run for 100,000,000 generations (sample frequency, 1000). We examined .p files for stationarity and convergence in Tracer; consensus trees were obtained after a 10% burnin. A starting tree for the concatenated BEAST analysis was produced via *BEAST, v.2.6.6 (Bouckaert et al., 2019); the phylogenetic inference of this method is suggested to be superior (Heled & Drummond, 2009). Note that this starting tree was not used to 'fix' the topology, given that initial *BEAST analyses did not recover Xenophoridae + Aporrhaidae + Struthiolariidae, as in previous mitogenome studies (e.g., Irwin et al., 2021), or a monophyletic Rostellariidae. The *BEAST analysis ran for 900,000,000 generations

(sample frequency, 5000) without fossil calibrations (due to computational limitations) and with a Yule tree prior for species-level analyses, a constant coalescent model for population-level analyses, a lognormal clock, and a dataset partitioned by gene fragment. The final species tree was an MCC tree with median node heights and 10% burnin. The time-calibrated phylogeny was produced in BEAST with a dataset partitioned by gene fragment, each gene allowed to evolve at a different rate, a Yule speciation prior, the *BEAST tree as the starting topology, and an uncorrelated relaxed, lognormal clock with four fossil calibrations (Section 2.6). We ran the analysis for 180,000,000 generations (sampling frequency, 3000), and examined log files for convergence. The final species tree was a MCC tree with median node heights, 10% burnin, and PP node support.

2.6 | Fossil calibrations

Based on the earliest undisputed fossil representatives from each family (including extinct subfamilies), preliminary BEAST and *BEAST analyses, and previous mitogenome work (Irwin et al., 2021), four fossil calibrations were used in the BEAST analysis (Table 1; for traits used to identify fossils to family level, see Supplementary Material S3). Initial *BEAST analyses did not recover a monophyletic Rostellariidae Gabb, 1868; therefore, a rostellariid fossil was used to calibrate the crown age of Rostellariidae + Seraphsidae Grey, 1853 (Table 1). Initial BEAST analyses with separate calibrations for Aporrhaidae Grey, 1850 and Struthiolariidae Gabb, 1868 had highly unrealistic node ages; therefore, an aporrhaid fossil was used to calibrate the crown age of Aporrhaidae + Stuthiolariidae (Table 1). A prior study by the authors used the same calibrations without justification (Irwin et al., 2024); a justification of these choices is given below.

2.6.1 | Aporrhaidae + Struthiolariidae

A specimen of *Toarctocera subpunctata* (Münster, 1844) from the Late Toarcian (Baden Württemberg) is the oldest complete aporrhaid specimen recorded in the literature (Gründel et al., 2009, fig. 2). However, numerous older, incomplete specimens (e.g., Terquem, 1855, pl. 17, fig. 5; Moore, 1867, pl. 14, figs 23–25; Piette, 1876, pl. 1, figs 2, 3; Haas, 1953, pl. 16, figs 51, 55; Schubert et al., 2008, fig. 5c) suggest an earlier origin for Aporrhaidae. A specimen of *Alaria hudlestoni* E. Wilson, 1887 from the lower Sinemurian (Lower Lias, Gloucestershire, Wilson, 1887, pl. 5, fig. 13, dated by Gründel et al., 2009) is a damaged

TABLE 1 Fossil calibrations used in BEAST analyses, with age of earliest fossil representative and corresponding geologic age from Gradstein et al. (2020) and calibration parameters.

Name	Age of earliest representative	Geologic age	Mean in real space	Log stdev	Offset	95% interval
Xenophoridae	100.5–93.9	Cenomanian (Upper Cretaceous)	9	8	93.9	95.2–117.5
Aporrhaidae + Struthiolariidae	199.3–190.8	Sinemurian (Lower Jurassic)	12	10	190.8	193.6–221.2
Rostellariidae + Seraphsidae	83.6–66.0	Campanian/Maastrichtian (Upper Cretaceous)	9	7	66.0	67.6–91.0
Strombidae	41.2–47.8	Lutetian (Middle Eocene)	5	5	41.2	42.1–59.3

Note: For complete details and justification of fossil representatives used, see Sections 2.6.2–5.

shell, but has more intact diagnostic characters than earlier representatives (Tracey et al., 1993), and was used to date the crown age of Aporrhaidae + Struthiolariidae (Table 1).

2.6.2 | Xenophoridae

The earliest Xenophoridae is generally dated to the Late Cretaceous (Ponder, 1983). Early specimens are often internal casts, with a trochiform shell shape and scars, or impressions, from the agglutination of foreign objects as the only useful characters for identification to family level (Stephenson, 1952; Wade, 1926) (Figure 1a; Supplementary Material S3). These scars may be confused with taphonomic artefacts. The earliest xenophorid specimen (Kiel & Perrilliat, 2001; Ponder, 1983; Tracey et al., 1993) is a poorly preserved cast of *Xenophora*? sp. with impressions possibly from agglutinated shell fragments (Stephenson, 1952) (USNM PAL 105677, not figured), from the Cenomanian (Woodbine Formation, Texas). A cast and an incomplete shell of *Xenophora leprosa* (Morton, 1834) from the Campanian/Maastrichtian have more convincing scars (Ripley Formation, Tennessee: Wade, 1926, pl. 56, figs 7 and 8; Corsicana Marl, Texas: Stephenson, 1941, figs 17–19). *Acanthoxenophora* Perilliat & Vega 2001 is recorded from the Campanian and possibly the Santonian (Kiel & Krüger, 2006, fig. 11; Pietzonka et al., 2023, fig. 5). However, preliminary analyses with these calibrations led to highly unrealistic node ages; therefore, we use *Xenophora*? sp. (Cenomanian) to date the crown age (Table 1).

2.6.3 | Rostellariidae + Seraphsidae

Hypotheses on the earliest rostellariid range from the Cenomanian–Turonian to the Maastrichtian (Bandel, 2007; Roy, 1996). The oldest specimen according to Tracey et al. (1993) is? *Dientomochilus stueri* from the Coniacian (Condat, France: Cossmann, 1904, pl. 9, figs 5 and 6); however, this is an incomplete internal mould. *Eucalyptraphorus palliatus* (Forbes, 1846) is reported from the Turonian-Coniacian and Maastrichtian-Campanian (Trichinopoly and Ariyalur Groups, India: Stoliczka, 1868, pl. 2, figs 18–20; Acharyya & Lahiri, 1991); the former is a mould, and the latter an incomplete shell. A *Calyptraphorus itamaracensis* specimen (Gramame Formation, Pernambuco, Brazil: Muñiz, 1993, pl. 11, figs 5, 8), reported from the Campanian, was considered the oldest representative by Perrilliat and Vega (1997); however, this formation has since been identified as Maastrichtian (e.g. El Gadi and Brookfield, 1999). Therefore, we use *E. palliatus* (Campanian/Maastrichtian) to date the crown age of Rostellariidae + Seraphsidae (Table 1).

2.6.4 | Strombidae

The earliest strombid record is *Stromboconus suessi* (Bayan, 1870, p. 480) from the Middle Eocene of Roncà, Italy. This specimen is not figured; however, other fossils of *S. suessi* are recorded from the Upper Lutetian of the same locality (Wieneke et al., 2023), which we used to date the crown age of the strombid clade (Table 1).

2.7 | Diversification rate and ancestral range reconstructions

A relative cladogenesis (RC) test, conducted via R package Geiger v.2.0.7 (Pennell et al., 2014), was used to detect significant increases in diversification rate in the time-calibrated tree. The gamma (γ) statistic (Pybus & Harvey, 2000) was used to detect differences in diversification rate using 'lineages through time' (LTT) plots, for (1) stromboidean and (2) strombid lineages. Ancestral ranges were estimated via R package BioGeoBEARS v.1.1.2 (Matzke, 2013), using the time-calibrated tree and a maximum range size of four. Geographic ranges were based on literature records (see Supplementary Material S3). For putative cryptic species, only localities for specimens with molecular data available were included. Eight marine biogeographical regions were from Spalding et al. (2007), modified based on stromboidean ranges: 1, Temperate North-East Atlantic; 2, Western Indo-West Pacific (IWP); 3, Central IWP; 4, Eastern IWP; 5, Temperate New Zealand and Australia; 6, Tropical Eastern Pacific; 7, Tropical West Atlantic; 8, Tropical East Atlantic. The best model according to AIC and AICc was BAYAREA-like + j ($d = 6.3 \times 10^{-5}$; $e = 5.6 \times 10^{-3}$; $j = 0.014$; LnL = −224.0) (Landis et al., 2013; Matzke, 2014).

3 | RESULTS

3.1 | Sequence analysis

COI alignments of 658 bp included 356 variable and 266 phylogenetically informative sites. For the BEAST dataset, 530 bp of 12S sequence (83% of 640 bp), 496 bp of 16S (90% of 554 bp), and 1347 bp of 28S (83% of 1630 bp) remained after removal of ambiguous blocks. Variable and phylogenetically informative sites, respectively, were as follows: 288 and 271 for 12S; 199 and 172 for 16S; 350 and 239 for 28S. For MrBayes and *BEAST datasets, total sequence

length and variable and phylogenetically informative sites, respectively, were as follows: 520 bp, 288 and 272 sites for 12S; 496 bp, 212 and 178 sites for 16S; 1353 bp, 378 and 253 sites for 28S.

3.2 | Species delimitation analyses

COI species delimitation analyses suggested 97 putative stromboid species (not including the three species lacking COI data; Supplementary Material S2, and S4). Most of the species that differed from current species concepts (resulting from the identification of cryptic species complexes, newly synonymised species, previously synonymised species, or changes to taxonomic rank) have sister taxa that are sympatric or co-occur in at least one of the same ecoregions (as defined in Section 2.7) (Table 2). Note that it is unlikely that species termed "cryptic" herein are truly 'cryptic' (i.e., not morphologically diagnosable, even with the benefit of hindsight and genetic data), but species referred to as such in this study are those that are genetically distinguishable species, currently recognised as a single species. Estimated divergence times between taxa with changes to rank or circumscription and their respective sister species/clades were ≥5 Myr, with varying K2P distances (3.7%–12.3%); intraspecific K2P distances ranged from <0.1% to 1.7% (Table 2). All putative species were delimited by ASAP across all distance metrics (JC, ASAP-score 3.5, $p = .018$, $W = 2.6 \times 10^{-4}$, $T_d = 0.029$; K2P, ASAP-score 4.0, $p = .018$, $W = 2.6 \times 10^{-4}$, $T_d = 0.029$; *p*-distance, ASAP-score 3.5, $p = .020$, $W = 1.7 \times 10^{-4}$, $T_d = 0.028$) (Figure 2; Supplementary Material S4 and S5). ABGD recovered 92 ESUs using the JC model ($p = .04$); *p*-values for other models were not significant. Support for the GMYC model was significant (likelihood ratio test (LR): GMYC, 3932; null model (null), 3860; ratio: 145, $p < .001$); the threshold time (−0.012) resulted in 79 clusters (95% CI, 78–82) and 102 ESUs (including species represented by a single specimen; 95% CI, 99–105) (Figure 2; Supplementary Material S4 and S5). Support for the bPTP model was significant (LR: bPTP, 1905; null, 1495; $p < .001$). MCMC chains converged in PTP analyses (both ASDDSV <0.001; mPTP, 86 ESUs; bPTP, 104 ESUs) (Figure 2; Supplementary Material S4 and S5).

Delimitation results conflicted with some current species concepts in Strombidae, Seraphsidae and Rostellariidae and several species are synomised. For Strombidae, the 69 putative species with multiple COI sequences received high to maximal support in all COI trees (PP = 0.99–100; BS = 94–100) (Figure 2; Supplementary Material S4–S6). All methods recognised *Dolomena abbotti* and *D. labiosa* as one species (now *D. labiosa*) with maximal support, as well as *Euprotomus aurora* and *E. bulla* (now *E. bulla*). All methods except GMYC recognised *Strombus pugilis* and *S. alatus* as one species (now *S. pugilis*); low support for GMYC suggested either within-species structure or very close sister species (GMYC = 0.65/0.65) (Figure 2; Supplementary Material S4–S6). ABGD, mPTP and bPTP recognised *Dolomena swainsoni* and *D. dilatata* as one species with maximal support, however, no taxonomic changes are suggested for these species since there is no voucher for *D. swainsoni* and so we cannot rule out the possibility that the specimen we sequenced as '*D. swainsoni*' was misidentified (Figure 2; Supplementary Material S4–S6). ASAP, ABGD, mPTP and bPTP recognised *Dolomena vittata* (formerly *Doxander*) and *D. operosus* as one species (now *D. vittata*) with maximal ASV support for bPTP and mPTP (Figure 2; Supplementary Material S4–S6). However, taxonomic boundaries for *D. vittata* are still somewhat unclear since GMYC delimited two ESUs with maximal support: (1) *D. vittata* (Singapore) + *D. operosus*; (2) *D. vittata* (China) (Figure 2; Supplementary Material S4–S6).

Several cryptic species complexes were identified: specimens identified as *Lambis lambis* based on morphology were split into three putative species (A–C), and *Maculastrombus mutabilis*, *Dolomena turturella* and *"Canarium" wilsonorum* were split into two species each (A, B), all with maximal support except *M. mutabilis* B (GMYC = 0.63) and *D. turturella* A (GMYC = 0.97; bPTP = 0.74, mPTP = 0.9). (Figure 2; Supplementary Material S4–S6). All methods delimited the following sister taxa (formerly subspecies) as separate species with maximal support: *Lambis truncata* and *L. sowerbyi*, and *Harpago chiragra* and *H. rugosus* (Figure 2; Supplementary Material S4–S6). For Rostellariidae, putative species had maximal support in all COI phylogenetic analyses (except *Rostellariella delicatula*; PP = 0.98, BS = 67) and all delimitation methods (Figure 2; Supplementary Material S4–S6). Here, *Rimellopsis laurenti* is distinct from *R. powisii* (Figure 2; Supplementary Material S4–S6) with which it is often synonymised. For Seraphsidae, five putative cryptic species of *Terebellum terebellum* (e.g., Figure 1e) had maximal support in all COI analyses and all delimitation methods except GMYC (GMYC = 0.81/1) (Figure 2; Supplementary Material S4–S6).

3.3 | Phylogenetic analyses

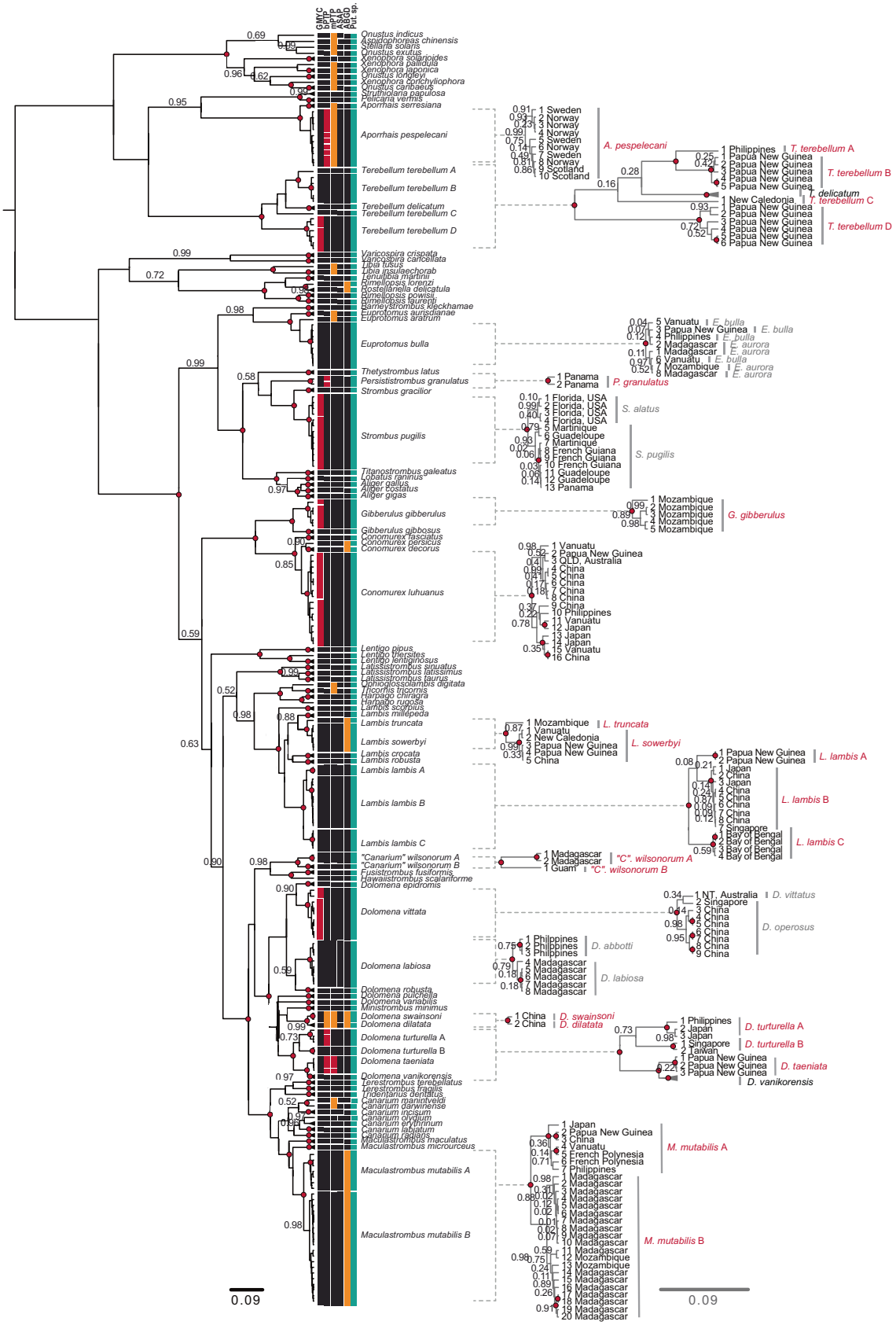
Strombidae was recovered as monophyletic with high to maximal support in all trees (PP = 0.96–1; BS = 100%), as was Seraphsidae (PP = 0.95–1; BS = 100%), Xenophoridae (PP = 0.97–1; BS = 100%), Aporrhaidae and Struthiolariidae (both PP = 1; BS = 100%) (Figures 2 and 3; Supplementary Material S5–S8). The BEAST

TABLE 2 Summary of delimitation analyses for taxa with changes to rank or circumscription (Supplementary Material S2): (1) cryptic species complexes; (2) newly synonymised species; (3) previously synonymised species; (4) changes to taxonomic rank.

N.	Species	Geographical range	Sister species/clade
1. Cryptic species complexes			
15	*Terebellum terebellum* A	Philippines	*T. terebellum* B
16	*Terebellum terebellum* B	Papua New Guinea	*T. terebellum* A
18	*Terebellum terebellum* C	New Caledonia	*T. delicatum*
19	*Terebellum terebellum* D	Papua New Guinea	*T. terebellum* C + *T. delicatum*
64	*Lambis lambis* A	Papua New Guinea	*L. lambis* B + *L. lambis* C
65	*Lambis lambis* B	Japan, China, Singapore	*L. lambis* C
66	*Lambis lambis* C	Bay of Bengal	*L. lambis* B
67	*"Canarium" wilsonorum* A	Madagascar	*"C". wilsonorum* B
68	*"Canarium" wilsonorum* B	Guam	*"C". wilsonorum* A
80	*Dolomena turturella* A	Philippines, Japan	*Dolomena turturella* B
81	*Dolomena turturella* B	Singapore, Taiwan	*Dolomena turturella* A
96	*Maculastrombus mutabilis* A	Papua New Guinea, Vanuatu, Philippines, Japan, China, French Polynesia	*M. mutabilis* B
97	*Maculastrombus mutabilis* B	Madagascar, Mozambique	*M. mutabilis* A
2. Newly synonymised species			
32	*Euprotomus bulla (E. bulla + E. aurora)*	Madagascar, Mozambique, Papua New Guinea, Philippines, Vanuatu	*E. aratrum + E. aurisdianae*
	Euprotomus bulla (as currently defined)	*Papua New Guinea, Philippines, Vanuatu*	*NA*
	Euprotomus aurora	*Madagascar, Mozambique*	*NA*
36	*Strombus pugilis (S. pugilis + S. alatus)*	Florida (USA), French Guiana, Guadeloupe, Martinique, Panama	*S. gracilior*
	Strombus pugilis	*French Guiana, Guadeloupe, Martinique, Panama*	*NA*
	Strombus alatus	*Florida (USA)*	*NA*
73	*Dolomena labiosa (D. labiosa + D. abbotti)*	Madagascar, Philippines	*D. wienekei*
	Dolomena labiosa	Madagascar	*NA*
	Dolomena abbotti	Philippines	*NA*
72	*Dolomena vittata (D. vittata + D. operosus)*	Singapore, China, Australia	*D. campbelli*
	Dolomena vittata	Australia	*NA*
	Dolomena operosus	Singapore, China	*NA*
3. Previously synonymised species			
27	*Rimellopsis powisii*	Philippines	*R. laurenti*
28	*Rimellopsis laurenti*	Vanuatu, New Caledonia	*R. powisii*
4. Changes to taxonomic rank—subspecies raised to species			
56	*Harpago chiragra*	Papua New Guinea, Japan, China	*H. rugosa*
57	*Harpago rugosa*	New Caledonia	*H. chiragra*
60	*Lambis truncata*	Mozambique	*L. sowerbyi*
61	*Lambis sowerbyi*	Papua New Guinea, New Caledonia, Vanuatu, China	*L. truncata*

Note: Note that for newly synonymised species, summaries for currently accepted species are given below (italic font), where relevant (single-gene reciprocal monophyly only, as these were synonymised for the concatenated BEAST phylogeny). Species are numbered (*n*) in order of clades in Figure 2, with species name, geographical range (based on genetic sequences only), sister clades/species (based on relationships in the BEAST tree; Figure 3), whether sister clades/species co-occur in at least one of the eight biogeographical regions in Figure 3 (see Section 2.7), divergence time between sister clades (nearest Myr; from Figure 3), the occurrence of fixed differences between sister clades/species for sequence from 28S (Y, yes; N, no; NA, no 28S data for this species and/or sister clade or species), average K2P distance based on COI sequence data within each ESU, and between the ESU listed and the sister clade/species separated by the smallest genetic distance using COI sequence only (NA, no COI data for this species and/or sister clade or species), reciprocal monophyly (rec. mon.) of clades/species in MrBayes (12S, 16S, 28S; Supplementary Material S8) or BEAST (COI; Figure 2; Supplementary Material S5) gene trees (Y, yes; N, no; NA, no sequence data), with posterior probability support values given in brackets.

Co-occurrence in ecoregion	Divergence time (Myr)	Fixed diffs 28S	% K2P inter COI	% K2P intra COI	COI rec. mon.	12S rec. mon.	16S rec. mon.	28S rec. mon.
Y	27	NA	7.8	NA	NA	NA	NA	NA
Y	27	NA	7.8	0.6	Y (1)	Y (1)	Y (1)	Y (0.94)
Y	34	Y	12.1	NA	NA	NA	NA	NA
Y	39	Y	12.1	2.3	Y (1)	Y (1)	Y (1)	Y (0.96)
Y	8	Y	5.2	<0.1	Y (1)	Y (1)	Y (0.99)	N
N	5	NA	4.7	0.3	Y (1)	Y (1)	Y (0.58)	N
N	5	NA	4.7	0.3	Y (1)	NA	NA	NA
N	21	NA	9.6	0.9	Y (1)	NA	NA	NA
N	21	NA	9.6	NA	NA	NA	NA	NA
Y	19	N	8.2	0.3	Y (1)	Y (1)	Y (1)	N
Y	19	N	8.2	0.6	Y (1)	Y (1)	Y (0.99)	N
N	7	N	4.6	1.4	Y (1)	N	N	N
N	7	N	4.6	0.9	Y (0.98)	Y (0.95)	Y (0.98)	N
Y	22	Y	5.7	0.4	Y	Y	Y	N
NA	*NA*	*NA*	*NA*	*NA*	*N*	*NA*	*NA*	*NA*
NA	*NA*	*NA*	*NA*	*NA*	*N*	*NA*	*NA*	*NA*
Y	23	NA	12.3	1.3	Y (1)	Y (1)	Y (0.99)	Y (1)
NA	*NA*	*NA*	*NA*	*NA*	*Y (0.93)*	*Y (0.99)*	*Y (1)*	*N*
NA	*NA*	*NA*	*NA*	*NA*	*Y (0.99)*	*Y (0.55)*	*Y (0.66)*	*N*
Y	6	Y	NA	0.9	Y (1)	Y (0.91)	N	N
NA	*NA*	*NA*	*NA*	*NA*	*N*	*N*	*N*	*N*
NA	*NA*	*NA*	*NA*	*NA*	*N*	*N*	*N*	*N*
Y	9	NA	8	1.7	Y (1)	Y (0.79)	Y (0.83)	NA
NA	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*	*NA*
NA	*NA*	*NA*	*NA*	*NA*	*N*	*NA*	*NA*	*NA*
Y	14	Y	7.7	0.3	Y	Y	Y	N
Y	14	Y	7.7	0.4	Y	Y	Y	N
Y	17	N	9.5	0.5	Y	Y	Y	N
Y	17	N	9.5	NA	NA	NA	NA	NA
N	6	N	3.7	NA	NA	NA	NA	NA
N	6	N	3.7	0.3	Y	N	Y	N



tree recovered Rostellariidae as monophyletic with low support (PP = 0.65), contrary to the *BEAST tree which recovered *Varicospira* as sister to the remaining Rostellariidae + Seraphsidae, with variable support (PP = 0.55–0.84) (Figure 1; Supplementary Material S7). Individual gene trees differed in topology,

FIGURE 2 Bayesian analysis of COI sequences implemented in BEAST and evolutionarily significant units (ESUs) delimited by five DNA species delimitation methods (Section 3.2). Results of delimitation methods are depicted via block colour (black, accepted ESUs; red, unaccepted splits; orange, unaccepted lumps), with putative species (green) on the right with names listed (black font). Unless any delimitation method proposed new splits or accepted lumps, species with multiple specimens were collapsed at tips (indicated by triangles; see Supplementary Material S5 for complete tree with all tips annotated), and relevant topologies were enlarged to the right (grey branches), with specimen number and country of collection given at tips, and all support values on branches (Supplementary Material S2). If primary species hypotheses lumped taxa, nominal species are listed in grey to the right; other species names are in red. Support values are posterior probabilities (PP); intraspecific PP and low PP (<0.5) were removed for legibility in the full tree (see Supplementary Material S5 for all support values).

including with respect to Rostellariidae; only 12S recovered Rostellariidae (PP = 0.98) (Figure 2; Supplementary Material S5–S8).

Within Strombidae, several genera were not monophyletic. For *Dolomena*, this was due to the inclusion of a well-supported clade of all *Laevistrombus* species sampled, the type species of *Doxander* (*D. vittatus*), and the monospecific *Labiostrombus* with maximum support (Figure 3). *Dolomena* has priority, so *Laevistrombus*, *Labiostrombus* and *Doxander* are no longer considered valid (Figure 3; Supplementary Material S7). Species currently assigned to *Canarium* formed four, well-supported, polyphyletic clades, as follows. (1) *Canarium scalariformis* (for which we can use the available name, *Hawaiistrombus scalariformis*) was sister to *Fusistrombus fusiformis*, which together are sister to the clade here assigned to *Dolomena*, as described above, with good support (PP = 0.91–1) (Figure 3). (2) A clade containing species formerly synonymised with the type species of *Canarium* (*C. urceus*, not included in this study) was recovered as sister to *Tridentarius* + *Terestrombus* with moderate to maximal support (PP = 0.88–1) (Figure 3). Based on morphological similarities between *C. urceus* and *C. mantinveldi*, *C. incisum* and *C. darwinense*, we believe this clade corresponds to 'true' *Canarium*. (3) Three species (*C. microurceus* and *C. mutabilis* A + B) were recovered in a clade with maximal support with the type species of *Maculastrombus* (*M. maculatus*), and are now referred to *Maculastrombus* (Figure 3). (4) two cryptic species of *"Canarium" wilsonorum*, which are currently not assigned to a genus, were resolved as sister to all species currently assigned to *Canarium*, plus *Ministrombus*, *Maculastrombus*, *Terestrombus*, *Tridentarius*, *Dolomena*, *Labiostrombus*, *Laevistrombus*, *Doxander*, and *Fusistrombus* (Figure 3; Supplementary Material S7). All concatenated and COI analyses rejected the monophyly of *Lentigo* due to the inclusion of the type species of *Thersistrombus*, resolving *L. pipus* + (*L. lentiginosus* + *L. thersites*) with high to maximal support (PP = 0.98–1; BS = 98–100). As *Lentigo* has priority, *Thersistrombus* is no longer considered valid (Figures 1g and 3; Supplementary Material S7). Analyses also rejected the monophyly of xenophorids *Xenophora* and *Onustus*; however, this is not the focus of this study (Figures 2 and 3; Supplementary Material S5–S8) and will be discussed in a separate study.

3.4 | Taxonomic changes

We hereby recognise the following new combinations (see Supplementary Material S2): *Lentigo thersites* (Swainson, 1823) (previously *Thersistrombus*), *Dolomena robusta* (G. B. Sowerby III) (previously *Neodilatilabrum*), *Dolomena epidromis* (Linnaeus, 1758) (previously *Labiostrombus*), *Dolomena vittata* (Linnaeus, 1758) (previously *Doxander* Wenz, 1940), *Dolomena turturella* (Röding, 1798), *Dolomena taeniata* (Quoy & Gaimard, 1834), *Dolomena vanikorensis* (Quoy & Gaimard, 1834) (all previously *Laevistrombus*), *"Canarium" wilsonorum* (Abbott, 1967), *Hawaiistrombus scalariformis* (Duclos, 1833), *Maculastrombus mutabilis* (Swainson, 1821), *M. microurceus* Kira, 1959 (all four previously *Canarium*). These changes to generic assignments render *Lentigo*, *Dolomena*, and *Canarium* monophyletic. Two taxa hitherto ranked as subspecies are now recognised as distinct species: *Harpago rugosus* (G. B. Sowerby II, 1842) (previously *H. chiragra rugosus*) and *Lambis sowerbyi* (Mörch, 1872) (previously *L. truncata sowerbyi*); also, we reinstate *Rimellopsis laurenti* (Duchamps, 1992) as a species (previously synonymised with *Rimellopsis powisii* (Petit de la Saussaye, 1840)) (Figure 1c; Supplementary Material S2). We also synonymise *Euprotomus aurora* Kronenberg 2002 with *Euprotomus bulla* (Röding, 1798), *Strombus alatus* Gmelin, 1791 with *Strombus pugilis* Linnaeus, 1758, *Dolomena abbotti* Dekkers & Liverani, 2011 with *Dolomena labiosa* (W. Wood, 1828), and *Dolomena operosa* (Röding, 1798) with *Dolomena vittata* (Linnaeus, 1758) (Supplementary Material S2). We synonymise *Eustrombus* Wenz, 1940 with *Aliger* Thiele, 1929, synonymise *Millepes* Mörch, 1852 with *Lambis* Röding, 1798 as is supported by Kronenberg (1993), and confirm the synonymy of *Macrostrombus* Petuch, 1994 with *Aliger* as defined in Dekkers (2008). Finally, we confirm the placement of *Ministrombus variabilis* (Swainson, 1820) in *Dolomena* as established by Liverani (2014).

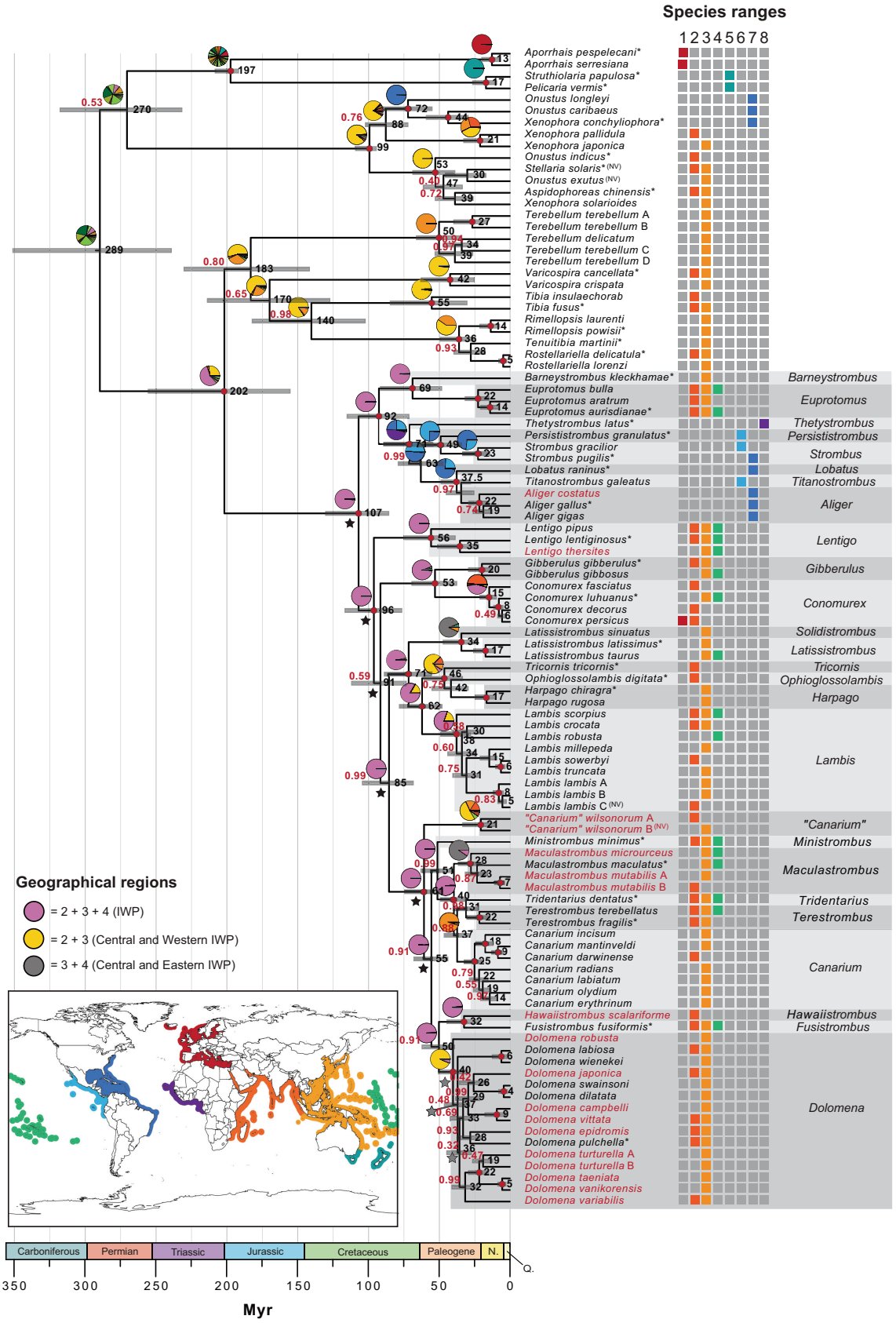


FIGURE 3 Time-calibrated Bayesian analysis of COI, 12S, 16S, and 28S data as implemented in BEAST. Scale is given below with geologic age; Q: Quaternary. Grey bars at nodes are 95% highest posterior density intervals for node ages; mean node ages (black) are rounded to the nearest Myr. Posterior probability (PP) values (red) are on branches (red circles, PP = 1). Pie charts show probabilities of ancestral ranges for major clades, estimated via BioGeoBEARS (regions 1–8; see map and Section 2.7), including ranges overlapping regions (1) 2 + 3 + 4, (2) 2 + 3, and (3) 3 + 4 (see key). Stars indicate relative cladogenesis significance levels (black, $p < .05$; grey, $p < .01$). Asterisks (*) mark putative type taxa (except for *Terebellum terebellum* and *Lambis lambis* where the 'real' type is a species complex); species with changed generic assignments are in red font. NV, GenBank sequences lacking voucher data. Strombid genera are marked for ease of discussion.

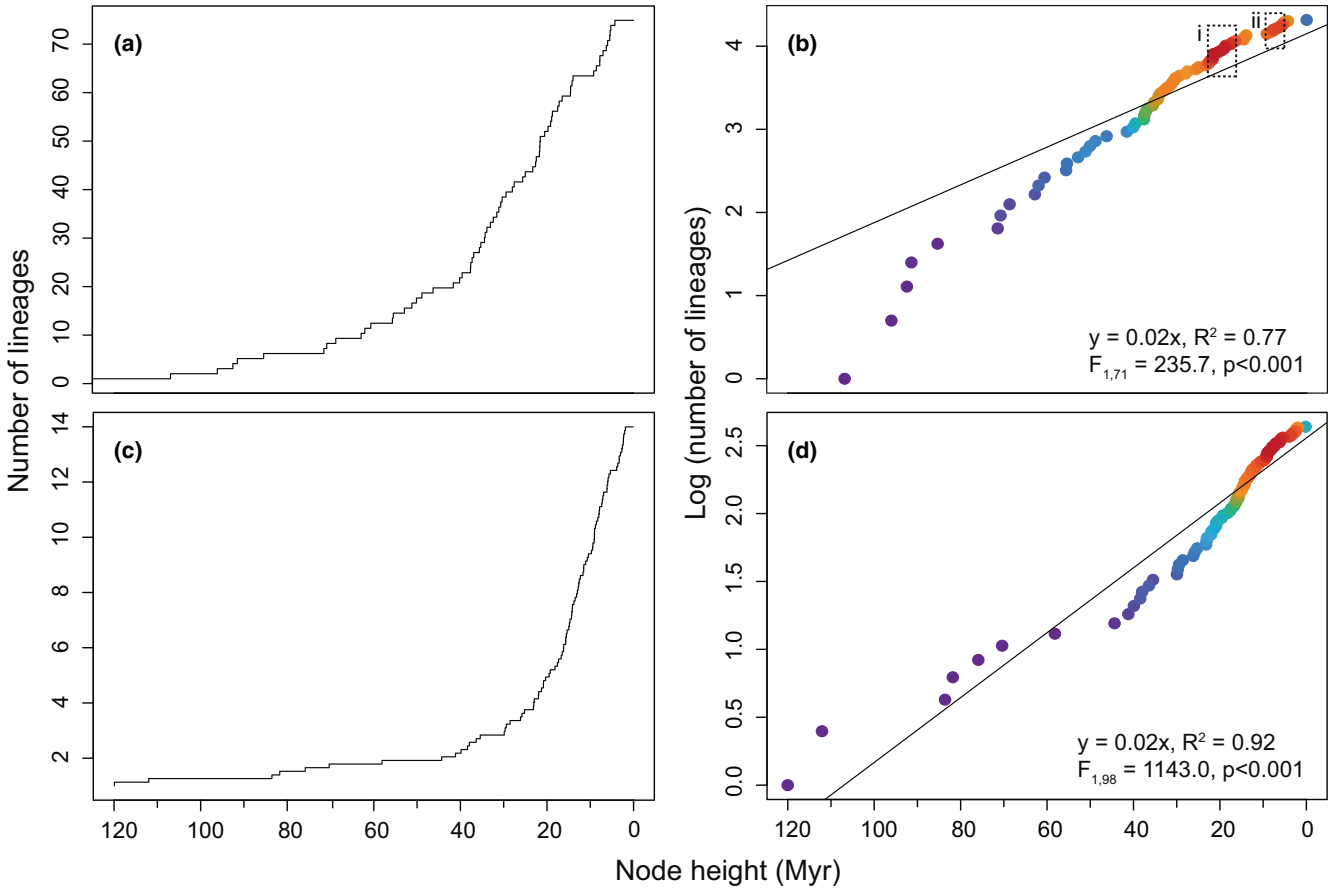


FIGURE 4 Lineage through time plots for (a, b) Strombidae only and (c, d) Stromboidea: (a, c), number of observed lineages through time; (b, d), log-transformed observed lineages through time, coloured by density (red = high density, purple = low density). The BEAST tree used was a chronogram; therefore, node heights on the x-axis correspond to time (Myr). A linear model (black line) was fit using R; adjusted R^2 values, *F*-statistic, degrees of freedom and *p*-value of the linear model are reported. Periods of highest increase in cladogenesis marked by boxes (dashed black lines): I, ca. 17–23 Mya (Early Miocene); ii, ca. 6–9 Mya (Late Miocene).

3.5 | Diversification and dispersal through time

The BEAST chronogram suggests that Struthiolariidae and Aporrhaidae diverged 197 Mya (95% highest probability density interval, HPD: 192–208 Mya), and that Xenophoridae diverged from lineages giving rise to Struthiolariidae and Aporrhaidae 270 Mya (95% HPD: 232–317 Mya), radiating around 99 Mya (95% HPD: 95–109 Mya) (Table 1; Figure 3). These results suggest Seraphsidae diverged from Rostellariidae 183 Mya (95% HPD: 142–230 Mya) and radiated 50 Mya (95% HPD: 35–66 Mya) (Table 1; Figure 3). An older radiation was suggested for Strombidae and Rostellariidae than is known from the fossil record: 107 Mya (95% HPD: 86–130 Mya) and 183 Mya (95% HPD: 127–213 Mya), respectively (Table 1; Figure 3). Significant increases in diversification rate were identified in the strombid lineage (RC, $p < .01$–0.05); six occurred at nodes with moderate to maximal support (PP = 0.91–1), and three at younger nodes lacking support (PP <0.50–0.59) (Figure 3). LTT plots suggested two younger diversification events in Strombidae, at approximately 17–23 and 6–9 Mya (Figure 4b). Both LTT plots were convex, suggesting decreasing speciation rates

through time (Harvey et al., 1994); this was supported for Strombidae by a significant negative γ-value ($\gamma = -3.13$, $p < .01$), implying an early burst in diversification (Pybus & Harvey, 2000), but not for Stromboidea ($\gamma = -0.06$, $p = .95$) (Figure 4). Ancestral ranges of Stromboidea and the clades containing (1) Xenophoridae + Struthiolariida e + Aporrhaidae and (2) Strombidae + Rostellariidae + S eraphsidae were all unresolved (Figure 3). The ancestral ranges of Xenophoridae and Strombidae were resolved with moderate and high probability, respectively (Central and Western Pacific, $p = .87$; IWP, $p = .99$) (Figure 3).

4 | DISCUSSION

4.1 | Phylogenetic analysis

The rapidly changing systematics of Stromboidea, and Strombidae in particular, is driven by a substantial scientific interest and a large morphological diversity of shells within the groups (Figure 1). Since the first molecular phylogeny of Strombidae (Latiolais et al., 2006), the number of strombid genera has increased dramatically (e.g., Bandel, 2007; Dekkers, 2012a; Dekkers & Maxwell, 2020; Liverani et al., 2021); yet sparse molecular sampling has hindered discussions of relationships. This more taxonomically comprehensive phylogenetic study is therefore a much-needed step in shaping our understanding of strombid systematics and highlights the need for both molecular and morphological data to robustly test taxonomic and phylogenetic hypotheses. Using molecular data, this study shows that several stromboidean groups require systematic revision. Here, all relationships among strombid genera as defined in this study were recovered with moderate to maximal support, except for the clade sister to *Lentigo*, which was recovered with low support (PP = 0.59) (Figure 3). These results differ from the strombid phylogenies containing fewer taxa but produced with mitogenome data (Irwin et al., 2021; Machkour-M'Rabet et al., 2021), which resolved (*Strombus* + *Aliger*) + (*Con omurex* + ((*Harpago* + *Lambis*) + (*Tridentarius* + *Dolom ena*))) with varied support. Additional mitogenome sequences in Li, Gu, et al. (2022) resulted in the same topology, plus with *Lentigo* as sister to all other strombids, and *Euprotomus* Gill, 1870 as sister to *Strombus* + *Aliger*.

4.1.1 | Systematics

Results suggest that six stromboid genera are not monophyletic using current generic assignments. As Strombidae was the focus of the sampling effort, changes to generic boundaries are only proposed for this family. *Canarium*, *Dolomena* and *Doxander* were polyphyletic in all analyses (Figures 2 and 3; Supplementary Material S5–S8). The most parsimonious solution to this, based on the BEAST chromogram, is to recognise the following groups (listed here as A–G) at the genus level; however, we are unable to propose strong characters in support of *Canarium* and *Dolomena* as redefined here. (A) As the clade sister to *"C." wilsonorum* had only moderate support (PP = 0.91) and *"C". wilsonorum* bears a morphological similarity to the type of *Canarium*, this species may belong to *Canarium*. Further molecular work may help to resolve this; thus, *"C". wilsonorum* is assigned to *"Canarium"* as a conservative measure instead of introducing a new genus-group name (Table 2). Note that these results do not support the former assignment of *"C". wilsonorum* to *Conundrum* (Liverani et al., 2021) (Figure 3). (B, C) The clade sister to *Fusistrombus fusiformis* + *Hawaiistrombus scalariformis* received only moderate support (PP = 0.91). As these generic names already exist, *Fusistrombus* is retained as valid (with *Neostrombus* as a junior objective synonym) and *Hawaiistrombus* (type: *Strombus hellii*) is accepted, given the morphological disparity between these taxa (Table 2). (D, E) *Ministrombus* (excluding *Dolomena variabilis*) and *Maculastrombus* (including *M. microurceus* and *M. mutabilis*) are retained (Table 2). (F) Thus, *Canarium* is restricted to the remaining currently assigned species. (G) Due to the polyphyly of *Dolomena* and the low resolution of relationships in the clade containing *Neodilatilabrum*, *Dolomena*, *Doxander*, *Labiostrombus* and *Laevistrombus*, this clade is redefined as *Dolomena*, resolved with maximal support (Figure 3; Supplementary Material S2). The relationships of the type species, *Dolomena pulchella*, are unsupported; thus, the true name-bearing clade comprising *Dolomena* is uncertain.

Here, we redefine *Aliger* to include *Macrostrombus* and *Eustrombus*, based on short internodal distances among these genera, although the three genera are reciprocally monophyletic (Table 2). The clade including these genera was recovered with maximal support (Figure 3) and shares general morphological characters with nearly all species from the Tropical Eastern Pacific and Tropical West Atlantic (e.g., expanded outer lip, glazed parietal area). Analyses did not recover the monophyly of *Lentigo* (Figures 2 and 3; Supplementary Material S5–S8); thus, we recognise *Thersistrombus* Bandel, 2007 as a synonym of *Lentigo* (Table 2). This is a morphologically diverse clade, and we could find no shared characters between *Thersistrombus* and *Lentigo* except for a columellar callus that is extended on the ventral side of the shell. As such, this grouping is a conservative measure based on the paraphyly of *Lentigo*, and exploration of further characters, including anatomical and shell microsculpture characters, is needed.

Several species boundaries differ from current species concepts (Figure 2; Supplementary Material S4 and S5); however, further work is required, as discussed below. Nevertheless, we raise *Lambis sowerbyi*, *Harpago rugosus*, and *Rimellopsis laurenti* (formerly *L. truncata sowerbyi*, *H. chiragra rugosus* and *R. powisii*, respectively), to species level based on species delimitation analyses (Figure 2; Supplementary Material S3, S4, S5). These species, as well as all other newly recognised species in this study, were recovered as monophyletic in at least one of the single-gene trees (where data were available) (Table 2).

4.1.2 | Hybrids in Strombidae

The literature contains several references to strombid specimens possessing intermediate shell morphologies, interpreted as putative intrageneric (e.g., Dekkers, 2012b; Kronenberg, 2013; Liverani & Wieneke, 2016) and intergeneric hybrids, though none were tested with molecular data. While claims of intrageneric hybrids are plausible, intergeneric hybrids (*Latissistrombus latissimus* × *L. lambis*, *Conomurex decorus* × *Gibberulus gibberulus*, *L. latissimus* × *H. chiragra*; Dekkers & Maxwell, 2018; Kronenberg, 2008; Maxwell & Ocean, 2022) are less likely, as these occur between lineages separated for substantial periods, according to the chronogram: *Latissistrombus* × *Lambis* or *Harpago*, 71 Mya (95% HPD: 56–88 Mya); *Conomurex* × *Gibberulus*, 53 Mya (95% HPD: 38–69 Mya) (Figure 3). As far as we are aware, intergeneric hybrids are unknown in natural molluscan populations and appear in very few other groups (e.g., Franco-Trecu et al., 2016). Molecular data will be informative for understanding these taxa.

4.2 | Divergence and dispersal within the evolutionary history of Stromboidea

Divergence time estimation using molecular data can offer a new perspective on the evolutionary history of a group, although conflicts with the fossil record often add uncertainty to results. Here, Strombidae is estimated to have originated during the Cretaceous, which predates the oldest undisputed strombid fossil by at least 59 Myr (Figure 3; Table 1). This could be attributed to inadequacy of the model (Brown & Smith, 2018) and/or incompleteness of the fossil record; for example, the fossil record in the Indo-West Pacific (IWP) is poorly studied (Harzhauser et al., 2018), despite being the modern global biodiversity hotspot. Preservation is also often poor in these gastropod fossils due to the instability of aragonitic shells (by contrast, calcite preserves well; James et al., 2005; Cherns & Wright, 2009), which is particularly problematic when the oldest fossils lack distinctive characteristics. Furthermore, the role of volcanism and erosion in the formation/disappearance of oceanic islands generally prevent burial of sediment and associated fauna, in contrast to the more complete fossil records of continental islands (Soja, 1992), although few oceanic islands were present in the central IWP prior to ca. 20 Mya (Leprieur et al., 2016). With these caveats in mind, the following discussion on historical biogeography and diversification is tentative and warrants further exploration.

4.2.1 | Timing and causes of diversification

Time-calibrated phylogenies facilitate discussion of changes in the rate of cladogenesis relative to other periods in time. However, note that lineages through time (LTT) plots, while useful, are based on extant taxa and do not consider 95% highest probability density intervals—problematic for reconstructing evolutionary histories (Figures 3 and 4) (Helmstetter et al., 2022; Louca & Pennell, 2020). In the fossil record, the number of strombid genera increases during the Miocene (Kronenberg & Harzhauser, 2012); similarly, our results suggest increases in cladogenesis rate in the Early and Late Miocene (Figure 4b). Increased cladogenesis of other shallow-water gastropods in the Miocene (Kohn, 1990; Meyer, 2003; Reid et al., 2010; Vermeij, 1996; Williams, 2007; Williams & Duda Jr., 2008) are often associated with the eastward shift of the global biodiversity hotspot from the Tethys to its current position in the central IWP (Briggs, 2007; Leprieur et al., 2016; Renema et al., 2008; Wilson et al., 1998). This shift is attributed to tectonic events, including the Early Miocene formation of the Gomphotherium land bridge, which limited Tethys-IWP faunal exchange (Harzhauser et al., 2007), and the collision of the Australia and New Guinea plate with Pacific arcs and the southeast Asian plate margin ca. 25 Mya, which led to the creation of shallow-water habitats and extended coastlines (Kohn, 1990; Meyer, 2003; Williams & Duda Jr., 2008; Wilson et al., 1998). These events facilitated the expansion of seagrass habitats and diversification of zooxanthellate corals ca. 20–25 Mya, increasing habitat complexity and the rate of cladogenesis of many benthic groups (Brasier, 1975; Reuter et al., 2011). As strombids are predominately associated with seagrass beds and coral rubble (Stoner & Waite, 1991), this event also may have driven cladogenesis within Strombidae, approximately 23 Mya (Figure 4).

By contrast, relative cladogenesis analyses suggested several earlier increases in diversification rate in the Middle Eocene ($p < .01$) (Figure 3). This supports the progressive increase in taxonomic diversity suggested in the

fossil record, from the Early Cenozoic to a Middle Eocene maximum in the western Tethys (Crame & McGowan, 2022). A pulse of diversification is particularly evident within the Anglo-Paris Basin; for example, the wide range of molluscs found within the Calcaire Grossier Formation is similar in biodiversity to the present day IWP hotspot (Cossmann & Pissarro, 1904–1913; Merle, 2008). By contrast, aporrhaid diversity and geographic distribution gradually declined during the Early Cenozoic, after the K/Pg mass extinction (Roy, 1994). Roy (1996) suggested that this coincided with the reciprocal rise in strombid and rostellariid genera during the Palaeocene and Eocene and may reflect a biotic replacement event and/or different responses to the same environmental change.

4.2.2 | Biogeographical reconstruction

Interestingly, time-calibrated analyses within this study suggest similar divergence times between East Pacific/Atlantic (EP/A) and IWP sister groups in the shallow-water Strombidae (92 Mya) and largely offshore Xenophoridae (88 Mya) (Figure 3). Some biogeographic barriers to dispersal likely had a significant impact on both offshore and shallow-water groups, such as the rise of the Isthmus of Panama (Macpherson et al., 2010). In Strombidae and Xenophoridae, divergence between EP/A and IWP sister groups followed the initiation of the widening of the Atlantic (110–65 Mya), which constituted a significant oceanic barrier to larval dispersal (Hou & Li, 2018). For larvae crossing the modern Atlantic via one of the main surface currents, the journey is estimated to take 40–60 days at 14–90 cm s^{-1} (Scheltema, 1971). The pelagic larval duration of *Aliger gigas* is ca. 60 days (Stoner, 2003), making larval drift more likely before the Atlantic opening was at its widest.

Previous molecular studies supported a monophyletic EP/A strombid clade derived from a paraphyletic IWP clade (Irwin et al., 2021; Latiolais et al., 2006; Machkour-M'Rabet et al., 2021). By contrast, our results for Strombidae and Xenophoridae resolve an IWP clade sister to an EP/A clade, together sister to a second, more diverse IWP clade (Figure 3), supporting Irwin et al. (2024) with lower taxon sampling. Ancestral range reconstructions based on the phylogeny recovered in this study suggest an IWP origin for strombids (Figure 3), which is consistent with the Tethyan origin supported by the oldest definitive strombid fossil (Bayan, 1870; Wieneke et al., 2023; Table 1). In the IWP, the strombid fossil record extends only to the Miocene (e.g. Bose et al., 2023), except for one incomplete specimen assigned to Strombidae from the Middle Eocene of Indonesia (*Jogjacartanus sultani*; Leloux & Wesselingh, 2009, p. 657, pl. 235, figures 6, 7). Although this paucity is attributed to the Miocene shift in biodiversity toward the IWP, there is still much about the pre-Miocene IWP that remains unknown.

4.3 | Future work

It is crucial to recognise that putative species discussed here as cryptic require further exploration within an integrative taxonomic framework (Puillandre et al., 2012, 2021). In all instances where "cryptic lineages" were identified, we were unable to confidently assign any to the typical form. Both *Lambis lambis* and *Maculastrombus mutabilis* have several historical synonyms that might be appropriate for some of the cryptic species revealed by these results. Also, sequence data for two putative cryptic species, *"C". wilsonorum* B and *L. lambis* C, have no voucher data (Supplementary Material S2). We note that the *L. lambis* cryptic species reported by Li, Zheng, et al. (2022) are here identified as *L. sowerbyi* and *L. lambis* B; nevertheless, our results suggest a species complex within *L. lambis* that requires further attention. We also note that the geographic range of *Dolomena variabilis* (formerly *Ministrombus*) extends to New Caledonia (Figure 2; Supplementary Material S2 and S5), which Maxwell (2022) restricts to *M. caledonicus*, indicating the species may have been oversplit taxonomically. We strongly recommend further investigation into the species complex of *T. terebellum*; while four cryptic species were identified (*T. terebellum* A–D), some were only represented by juveniles within this study. This, together with highly variable shell patterns and overlapping geographic regions (Table 2), means that we could not exclude the possibility that one or two of these species could represent *T. hubrechti* Poppe and Tagaro, 2016 or *T. simoni* Dekkers, S. J. Maxwell and Congdon, 2019. Furthermore, the shell colour pattern on the type specimen of *T. terebellum* is faded (Jung & Abbott, 1967, pp. 445–454, pl. 323), which complicates identification of the type species. It is also worth noting that the calibration ages chosen (Table 1) likely affected recent divergences (as well as deeper stromboid nodes) by pulling inferred dates toward them (Arbogast et al., 2002); thus, divergence estimates for cryptic taxa (>5 Myr; Table 2) may be overestimated. Finally, two xenophorid genera (*Xenophora* and *Onustus*), and four strombid genera (*Lentigo*, *Canarium*, *Dolomena* and *Doxander*) are not monophyletic and these groups require further study with increased taxon sampling to resolve their relationships, particularly those of Xenophoridae; 63% of currently accepted xenophorid species currently lack molecular data, including the new genus *Ponderiana* Nappo, Bini & Santucci, 2022. In particular, *Canarium* and *Dolomena* should be revisited more fully with regards to both morphological and

molecular data, given that this study lacks the type species for *Canarium* and that the deeper nodes containing *Dolomena pulchella* (type species of *Dolomena*) are unsupported (Figure 3).

5 | CONCLUSION

This study advances our understanding of stromboidean systematics, as well as the patterns of speciation and biogeography which have shaped the evolution of the superfamily. We provide the largest phylogenetic analysis for Stromboidea so far, focusing on relationships within Strombidae. The time-calibrated analysis supports the hypothesis that changes in habitat resulting from tectonic activity at the Oligocene/Miocene boundary led to a period of rapid cladogenesis in both shallow-water and offshore in the Central IWP. Interestingly, LTT plots suggest two distinct pulses of strombid diversification within the Miocene. This radiation occurred earlier than is currently known from the fossil record; however, both ancestral range reconstructions and fossils support a Tethyan/IWP origin for Strombidae.

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