Journal of
Molluscan Studies

The Malacological Society of London

Journal of Molluscan Studies (2023) **89**: eyad016. https://doi.org/10.1093/mollus/eyad016
Published online 25 September 2023

Molecular phylogeny and biogeography of the living Pleurotomariidae (Vetigastropoda), with the description of a new genus

M. G. Harasewych[1], Patrick Anseeuw[2], Dario Zuccon[3] and Nicolas Puillandre[3]

[1]*Department of Invertebrate Zoology, Smithsonian Institution, National Museum of Natural History, PO Box 37012, MRC-163, Washington, DC 20013-7012, USA;*
[2]*Mispelstraat, 18, 9820 Merelbeke, Belgium; and*
[3]*Institut Systématique Evolution Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier, CP 26, 75005 Paris, France*

Correspondence: M.G. Harasewych; e-mail: Harasewych@si.edu

urn:lsid:zoobank.org:pub:D9DF368A-3ADF-41D5-888C-EB6FB2D6E2BB

(Received 23 December 2022; editorial decision 24 May 2023)

ABSTRACT

The once diverse family Pleurotomariidae had a widespread global distribution spanning shallow-water faunas throughout the Mesozoic but is presently known only from bathyal habitats along the western margins of the Atlantic and Indo-Pacific Oceans at temperate and tropical latitudes. We evaluate the relationships among surviving lineages of Pleurotomariidae using partial sequences of two mitochondrial genes and three nuclear genes for 22 of the 45 named Recent species-level taxa for which sequence data were available for two or more genes. Phylogenetic analyses partition these species among five lineages, including the new genus *Bouchetitrochus* n. gen. that is described herein. Of the five lineages, two are present in both the western Atlantic and the western Indo-Pacific Oceans, one is endemic to the western Atlantic and two are endemic to the western Indo-Pacific.

INTRODUCTION

The family Pleurotomariidae Swainson, 1840, among the oldest surviving lineages within Gastropoda, was a common component of the global shallow-water fauna throughout the Mesozoic but was thought to be extinct until the first living specimens were discovered at bathyal depths in the second half of the 19th century (Fischer & Bernardi, 1856). The transition from continental shelf to bathyal environments occurred during the late Paleogene (Jablonski *et al.*, 1983), possibly as a consequence of increased predation pressure in shallower waters (Vermeij, 1977). The increased sampling of deep-sea habitats by commercial fisheries as well as by biological surveys has resulted in the discovery of additional pleurotomariid taxa. A total of 45 extant species and subspecies, partitioned among four genera, have thus far been named within the family Pleurotomariidae, although not all are currently accepted (Molluscabase eds, 2023). Continued exploration of deep-sea habitats will undoubtedly result in the discovery of additional species as well as a better understanding of the ranges of presently known species.

To date, the majority of pleurotomariid species have been described primarily on the basis of shell morphology, with descriptions published in the last decade including details of anatomical features, such as radular morphology as well as molecular data, usually partial sequences of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene used by the International Barcode of Life (https://ibol.org; e.g. Anseeuw *et al.*, 2015; Zhang, Zhang & Wei, 2016; Anseeuw, Bell & Harasewych, 2017). Over the past several decades, there have been a number of studies investigating the evolutionary relationships among the basal taxa within Gastropoda using anatomical as well as molecular data. Despite multiple efforts, the relationships of Pleurotomariidae have not yet been robustly resolved. Most analyses based on morphological data (e.g. Haszprunar, 1988; Ponder & Lindberg, 1996; Sasaki, 1998) and some based on molecular data (e.g. Cunha & Giribet, 2019; Lee *et al.*, 2019; Uribe, Sei & Harasewych, 2022) include Pleurotomariidae within the order Vetigastropoda, while other molecular studies (e.g. McArthur & Harasewych, 2003; Aktipis & Giribet, 2012; Uribe *et al.*, 2022) place Pleurotomariidae outside of Vetigastropoda, or as an outgroup to a paraphyletic Vetigastropoda.

In the present study, we evaluate the relationships among living Pleurotomariidae based on selected individual exemplars of 22 of the 45 named species-level taxa for which sequence data are available for two or more of the five genes (two mitochondrial and three nuclear) that have been regularly used alone or in combination in previous studies of gastropod phylogeny. We evaluate the results in terms of the geographic distributions of the resulting clades and describe one of the main clades as a new genus.

MATERIAL AND METHODS

Sampling

Most of the newly sequenced samples were collected during several expeditions organized by the Muséum national d'Histoire naturelle, Paris (MNHN). These are: EBISCO, CONCALIS, NORFOLK 2, TERRASSES, KANADEEP and KANACONO in New Caledonia; PAPUA NIGINI, MADEEP and BIOPAPUA in Papua New Guinea; SALOMON 1 in the Solomons; ZhongSha 2015 and NanHai 2014 in Taiwan; MAINBAZA and BIOMAGLO in the Mozambique Channel; MIRIKY in Madagascar; GUYANE 2014 in French Guyana; and KARUBENTHOS 2 in Guadeloupe. Also sequenced were samples of pleurotomariids in the collections of the National Museum of Natural History, Smithsonian Institution (USNM), which were collected by the senior author during dives aboard the research submersibles *R/S Johnson-Sea-Link I and II*, *R/S Clelia*, R/S *Nekton Delta*, *R/S Idabel* and *R/S Curasub* throughout the tropical western Atlantic over a period of three decades. Additional samples were provided by amateur malacologists. The outgroups are *Cyathermia naticoides* Warén & Bouchet, 1989 (Neomphaliones: Neomphalidae) and *Turbo castanea* Gmelin, 1791 (Vetigastropoda: Turbinidae). All specimens included in the analysis, together with the outgroups, are listed in Table 1.

DNA sequencing

Newly produced sequences were generated by two labs, using slightly different protocols: the Service de Systémtaique Moléculare (UMS2700), MNHN and the Laboratories of Analytical Biology at USNM.

In the MNHN, DNA was extracted from ethanol-preserved tissue samples using the NucleoSpin 96 Tissue Core Kit (Macherey-Nagel), following the manufacturer's recommendations, and in combination with the epMotion 5075 robot (Eppendorf). Fragments of the mitochondrial genes COI and 16S rRNA and the nuclear genes 28S rRNA and histone 3 (H3) were amplified using the universal primers LCO1490/HCO2198 (Folmer *et al.*, 1994), 16SH/16SLC (Palumbi, 1996), C1/D2 (Dayrat *et al.*, 2001; Jovelin & Justine, 2001) and H3F/H3R (Colgan, Ponder & Eggler, 2000), respectively. Amplification consisted of an initial denaturation step at 94 °C for 4 min, followed by 35/40 cycles of denaturation at 94 °C for 30 s, annealing at 48 °C for COI, 55 °C for 16S rRNA and 28S rRNA and 53 °C for H3 for 30 s, followed by extension at 72 °C for 1 min. The final extension was at 72 °C for 5 min. PCR products were purified and sequenced by the Eurofins sequencing facility, Ebersberg, Germany.

At USNM, DNA was extracted from frozen or ethanol-preserved tissue samples (*c.* 25 mg buccal muscle) using the DNeasy Tissue Kit (Qiagen) following the manufacturer's animal tissue protocol. Fragments of COI, 16S rRNA and 18S rRNA were amplified using the universal primers LCO1490/HCO2198 (Folmer *et al.*, 1994), 16SH/16SLC (Palumbi, 1996) and 18S rRNA primers (Holland, Hacker & Williams, 1991; Harasewych *et al.*, 1997), respectively. PCR amplifications used the Promega GoTaq hot start master mix (Promega M7132) according to the manufacturer's instructions but modified to reduce the reaction volume to 20 μl. The cycling parameters were: initial denaturation at 95 °C for 3 min, followed by 45 cycles of denaturation at 94 °C for 30 s, annealing at 48 °C for 45 s and extension at 72 °C for 2 min, with final extension at 72 °C for 5 min. Resulting PCR products were visualized by agarose gel electrophoresis (1.5% agarose), purified with ExoSAP-IT (Affymetrix) and sequenced using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Reactions were purified using Millipore Sephadex plates and sequenced on an ABI 3730XL automated DNA analyzer. Sequencher v. 4.7 (Gene Codes) was used to visualize, trim and assemble contigs from forward and reverse electropherograms.

All new sequences have been deposited in GenBank and/or the Barcode of Life Data System (https://www.boldsystems.org/) (Table 1). Additional sequences were downloaded from GenBank, as noted in Table 1.

Phylogenetic reconstruction

Individual exemplars were selected to represent 22 species for which sequence data were available for the highest number of genes to reduce the proportion of missing data (Table 1). In some cases, chimeric sequences were produced by concatenating sequences for different genes from different specimens of the same species. In these cases, the conspecificity of the samples was confirmed morphologically or by comparing COI sequences of the different specimens. Sequences were automatically aligned using the Clustal algorithm in BioEdit v. 7.0.5.3 (Hall, 1999). The five genes were combined into a single dataset of 3,026 bp (COI: 658 bp; 16S rRNA: 557 bp; 18S rRNA: 549 bp; 28S rRNA: 936 bp; H3: 326 bp).

Phylogenetic reconstructions were performed using maximum likelihood (ML) and Bayesian inference (BI), and the software packages were, respectively, RAxML (Stamatakis, 2006) and MrBayes (Huelsenbeck & Ronquist, 2001). For the ML analyses, the robustness of the nodes was assessed using bootstrapping, with 1,000 iterations. The BI consisted of two runs of eight Markov chains, each 30,000,000 generations long, with a sampling frequency of one tree every 3,000 generations.

We partitioned our five-gene dataset into nine partitions: three unlinked partitions (i.e. by codon positions) each for CI and H3, and single partitions for the other three genes. For the BI, each partition followed a GTR model, with a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites. For the ML analysis, each partition followed a GTR model. For the BI, convergence of each run was evaluated using Tracer v. 1.7 (Rambaut *et al.*, 2018) to check that ESS values were all greater than 200. A consensus tree was then calculated after omitting the first 25% of trees as burnin. All the analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2), using the tools MrBayes 3.2.3 on XSEDE and RAXML-HPC2 on XSEDE (8.1.11). Branch support was evaluated using Bayesian posterior probability (PP) and bootstrap support (BS) values.

RESULTS

Phylogenetic analyses of the concatenated dataset using BI and ML each produced a tree with identical topology and with most branches well supported (Fig. 1). In both trees, the two species of *Entemnotrochus* P. Fischer, 1885, *E. adansonianus* (Crosse & Fischer, 1861) and *E. rumphii* (Schepman, 1879), form a maximally supported clade that diverges from all remaining Pleurotomariidae (the '*Perotrochus* lineage') that comprise a similarly well-supported clade (PP = 1; BS = 98%). This '*Perotrochus* lineage' is composed of three highly supported clades. Seven Western Atlantic species in the genus *Perotrochus* P. Fischer, 1885 form a clade (PP = 1; BS = 88%) that includes *Perotrochus quoyanus* (Fischer & Bernardi, 1856), the type species of *Perotrochus*. In both trees, five western Pacific species that had been originally described in the genus *Perotrochus* form another maximally supported clade for which the new genus *Bouchetitrochus* n. gen. [type species *B. pseudogranulosus* (Anseeuw *et al.*, 2015)] is here proposed. The remaining pleurotomariids are included in a third well-supported clade (PP = 0.99; BS = 98%) that includes *Bayerotrochus midas* (Bayer, 1965), the only western Atlantic species, *Bayerotrochus africanus* (Tomlin, 1848), from the western Indian Ocean, a well-supported clade (PP = 1; BS = 91%) containing four western Pacific species of *Bayerotrochus*, and a clade comprising three species of *Mikadotrochus* Lindholm, 1927 (PP = 1; BS = 98%). Although the monophyly of each of these three clades is strongly

Table 1. List of taxa and genes used in phylogenetic analyses (GenBank sequences first reported in this study are indicated in bold font)

Taxon	Voucher	Location	Depth (m)	No. of genes	GenBank acc. nos					Bold ID no.
					COI	16S rRNA	18S rRNA	28S rRNA	H3	
Cyathermia naticoides Warén & Bouchet, 1989	MCZ:Mala:378348	East Pacific Rise		5[1]	DQ093518	DQ093472	AY923888	FJ977685	DQ093498	
Turbo castanea Gmelin, 1791	MCZ:Mala:378777	Abaco, Bahamas		5[2]	FJ977763	FJ977713	FJ977650	AM404008	FJ977742	
Entemnotrochus adansonianus (Crosse & Fischer, 1861)	MNMN-IM-2013-61163	Guadeloupe	210–240	5[3]	**OQ075929**	**OQ075937**	**ON563470**	**OQ075949**	**OQ075959**	**PLERO065-22**
Entemnotrochus rumphii (Schepman, 1879)	USNM 888698	Amami-O-Shima, Japan	120	2	L78911		L78889			
Perotrochus pyramus Bayer, 1967	MNHN-IM-2013-60460	Guadeloupe	432–482	4	**OQ075928**	**OQ075936**		**OQ075947**	**OQ075958**	**PLERO064-22**
Perotrochus charlestonensis Askew, 1988	USNM 1080831	Marathon, FL, USA	180–299	3	MK559363*	MK559363*	**ON563483**			
Perotrochus amabilis (Bayer, 1963)	USNM 1080832	Marathon, FL, USA	178–181	3[4]	KY432519		**ON563481**		AY923965	
Perotrochus maureri Harasewych & Askew, 1993	USNM 888662	Charleston, SC, USA		2	L78914		L78892			
Perotrochus lucaya Bayer, 1965	USNM 888619	San Salvador, Bahamas	520	3[5]	L78916	KY671216	L78891			
Perotrochus quoyanus (P. Fischer & Bernardi, 1856)	MNHN-IM-2013-60292	Guadeloupe	323–347	5[6]	**OQ075933**	**OQ075943**	L78890	**OQ075955**	**OQ075966**	**PLERO066-22**
Perotrochus sunderlandorum (Petuch & Berschauer, 2017)	USNM 1153967	Curaçao	168	2	**ON586603**	KY671222				
Bouchetitrochus pseudogranulosus (Anseeuw *et al.*, 2015)	MNHN-IM-2009-7495	Chesterfield Islands	348–354	4	KR087196	**OQ075942**		**OQ075954**	**OQ075965**	**PLERO033-15**
Bouchetitrochus gotoi	USNM 894500	Amami-O-Shima, Japan	180–200	2	KY432520	KY671205				
Bouchetitrochus caledonicus (Bouchet & Métivier, 1982)	MNHN-IM-2007-36302	New Caledonia	270	4	KR087189	**OQ075941**		**OQ075953**	**OQ075963**	**PLERO041-15**
Bouchetitrochus deforgesi (Métivier, 1990)	MNHN-IM-2007-32086	Chesterfield Islands	300–323	4[7]	**OQ075934**	**OQ075945**		**OQ075948**	**OQ075968**	**PLERO062-22**

Table 1. Continued

Taxon	Voucher	Location	Depth (m)	No. of genes	GenBank acc. nos					Bold ID no.
					COI	16S rRNA	18S rRNA	28S rRNA	H3	
Bouchetitrochus wareni (Anseeuw et al., 2015)	MNHN-IM-2007-34685	New Caledonia	380–430	4	KR087222	**OQ075938**		**OQ075950**	**OQ075960**	**PLERO020-15**
Bayerotrochus midas (Bayer, 1965)	SBMNH uncat. tissue			5[8]	AY923930	KY671212	AY923892	FJ977668	AY923966	
Bayerotrochus africanus (Tomlin, 1848)	MNHN-IM-2007-38002	Madagascar	244–300	4	**OQ075930**	**OQ075939**		**OQ075951**	**OQ075951**	**PLERO063-22**
Bayerotrochus belauensis Anseeuw et al., 2017	USNM 905393	Palau	212	2	KY432527	KY671232				
Bayerotrochus boucheti boucheti (Anseeuw & Poppe, 2001)	MNHN-IM-2007-34676	New Caledonia	450–495	5	KU693174 = KY432525	**OQ075944**	**ON563471**	**OQ075956**	**OQ075967**	**PLERO060-15**
Bayerotrochus boucheti mirificus Anseeuw, 2016	MNHN-IM-2009-7484	Chesterfield Islands	543–544	4	KU693173	**OQ075935**		**OQ075946**	**OQ075957**	**PLERO061-15**
Mikadotrochus vicdani (Kosuge, 1980)	Toba Aquarium	Bohol, Philippines		4	**OQ075931**	**OQ075940**		**OQ075952**	**OQ075962**	**PLERO068-22**
Mikadotrochus beyrichi (Hilgendorf, 1877)	Not available	Boso Peninsula, Japan		3	AM049331		AM048636	AM048695		
Mikadotrochus hirasei (Pilsbry, 1903)	MNHN-IM-2013-43545	Japan	150	3[9]	**OQ075932**		AF417117		**OQ075964**	**PLERO067-22**

An asterisk indicates an appropriate gene portion taken from a complete mitochondrial genome sequence. The superscript numbers indicate composite gene sequences: 1, 18S rRNA sequence is from a different specimen; 2, 28S rRNA sequence is from a different specimen; 3, 18S rRNA sequence is from a specimen from Marathon, FL, USA (voucher: USNM 1080839); 4, H3 sequence is from a specimen from Louisiana, USA (voucher: LACM152930); 5, 16S rRNA sequence is from a specimen from Grand Bahama Island, Bahamas (voucher: USNM 880236); 6, 18S rRNA sequence is from a specimen from Guadeloupe (voucher: USNM 888646); 7, 28S rRNA sequence is from a different specimen (MNHN-IM-2009-7486); 8, 28S RNA sequence is from MCZ: Mala:378259; and 16S RNA sequence is from a specimen from Roatan, Honduras DNR; 9, 18S rRNA sequence is from a different specimen, also from Japan.

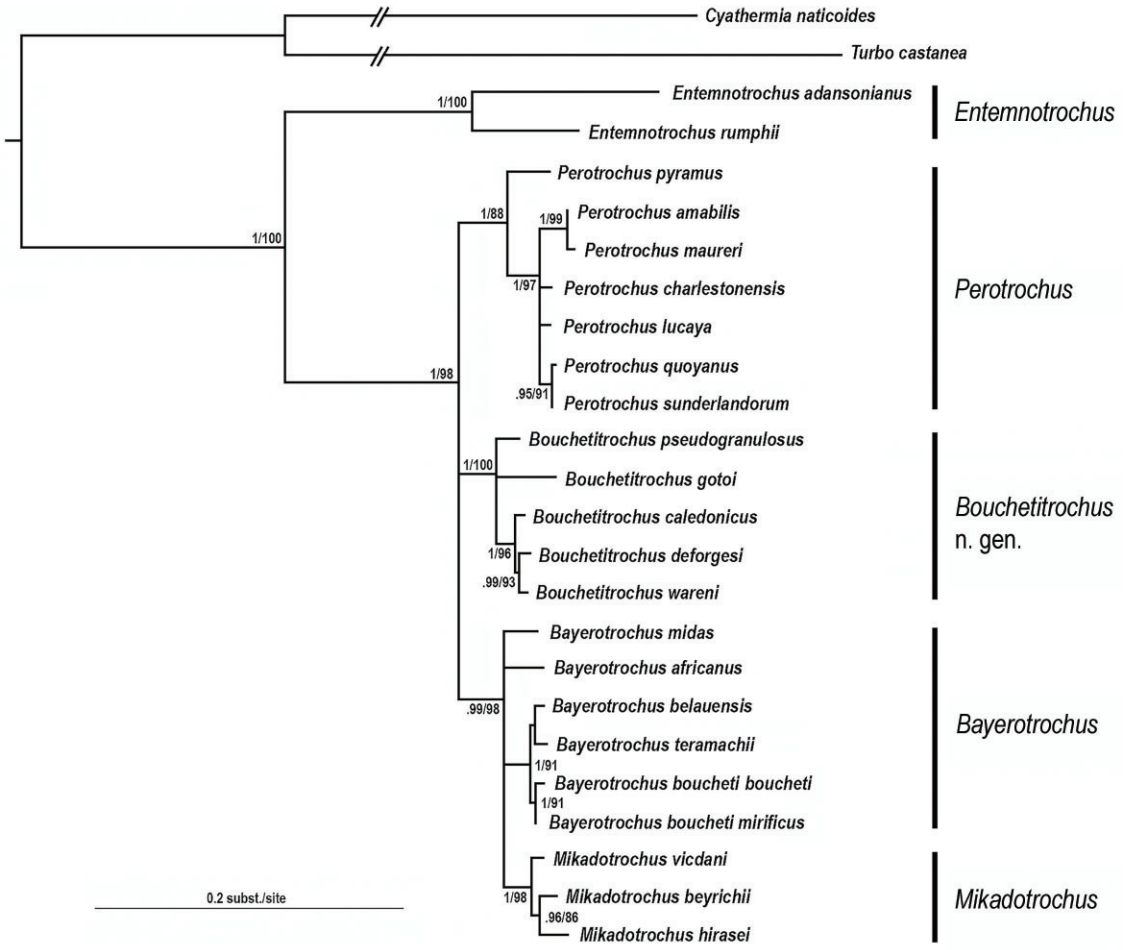

Figure 1. BI tree based on the five-gene dataset. PP >0.95 and BS values >80% are provided for relevant nodes.

supported, relationships among them in the five-gene tree are not resolved with significant support.

DISCUSSION

Relationships among the genus-level groups in the five-gene tree are less well resolved than those reported in several previously published single gene trees (e.g. Harasewych *et al.*, 1997; Harasewych, 2002; Anseeuw *et al.*, 2015, 2017; Zhang e*t al.*, 2016), although the number of species-level taxa and relationships among them may vary in some instances. *Perotrochus pyramus* Bayer, 1967, originally described in the genus *Perotrochus*, had been transferred to *Bayerotrochus* (Harasewych, 2002) but appears as a member of *Perotrochus* in our tree. The species *P. gotoi* Anseeuw, 1990 had been transferred to *Mikadotrochus* (Molluscabase eds, 2023, based on Anseeuw, 2010) but emerges as a member of the new genus *Bouchetitrochus* in this study, as do the species originally proposed as *P. caledonicu*s Bouchet & Métivier, 1982, *P. deforgesi* Métivier, 1990, *P. wareni* Anseeuw *et al.*, 2015 and *P. pseudogranulosus*. *Perotrochus vicdani* Kosuge, 1980 is here shown to be referrable to the genus *Mikadotrochus* with strong support. Generic assignments of the remaining species in our tree are concordant with those reported in Molluscabase (Molluscabase eds, 2023). The genus *Bayerotrochus* is not recovered as monophyletic in our five-gene tree because it includes *Mikadotrochus*. However, *Bayerotrochus* and *Mikadotrochus* were previously recovered as sister taxa with strong support in published trees based on partial COI gene sequences (e.g. Anseeuw *et al.*, 2015, 2017). Additional data to complete the five-gene data matrix may improve resolution of these nodes in the five-gene tree.

The deepest divergence among the living Pleurotomariidae is between the genus *Entemnotrochus* (Fig. 2A), easily recognized by a large, conical shell with a long, narrow slit spanning *c.* half a whorl and a wide, deep umbilicus, and all remaining living species (here referred to as the '*Perotrochus* lineage'; Figs 2B–E), which have smaller shells with more rounded whorls, a broader, shorter slit that spans less than a quarter whorl and a nacreous callus along the columella rather than a wide, open umbilicus.

The lineages leading to *Entemnotrochus* and *Perotrochus* are reported to have diverged during the Middle Triassic (Szabó, 1980) or Lower Jurassic (Benfrika, 1984) (see Harasewych, 2002: fig. 9). Bose, Das & Mondal (2021: Appendix 1) compiled a list of 149 species of Cenozoic Pleurotomariidae and apportioned them among seven genera, noting that a number of species that had originally been described as *Pleurotomaria* Defrance, 1826 could not be accurately assigned to genera due to poor preservation. Of the seven Cenozoic genera of Pleurotomariidae, *Conotomaria* Cox, 1959 became extinct at the end of the Paleocene, while *Chelotia* Fischer, 1885 and *Leptomaria* Eudes-Deslongchamps, 1864 became extinct at the end of the Eocene. Bose *et al.*'s (2021) study shows that the genera *Entemnotrochus* and *Perotrochus* both appeared in the Early Eocene, *Mikadotrochus* dates to the Middle Miocene, and *Bayerotrochus* is recorded only from the Recent fauna. Both *Entemnotrochus* and *Perotrochus* had wide distributions in the Early Cenozoic, but the closure of the Tethys Sea during the mid-Miocene blocked global equatorial currents, resulting in the isolation of the Atlantic from the Indo-West Pacific

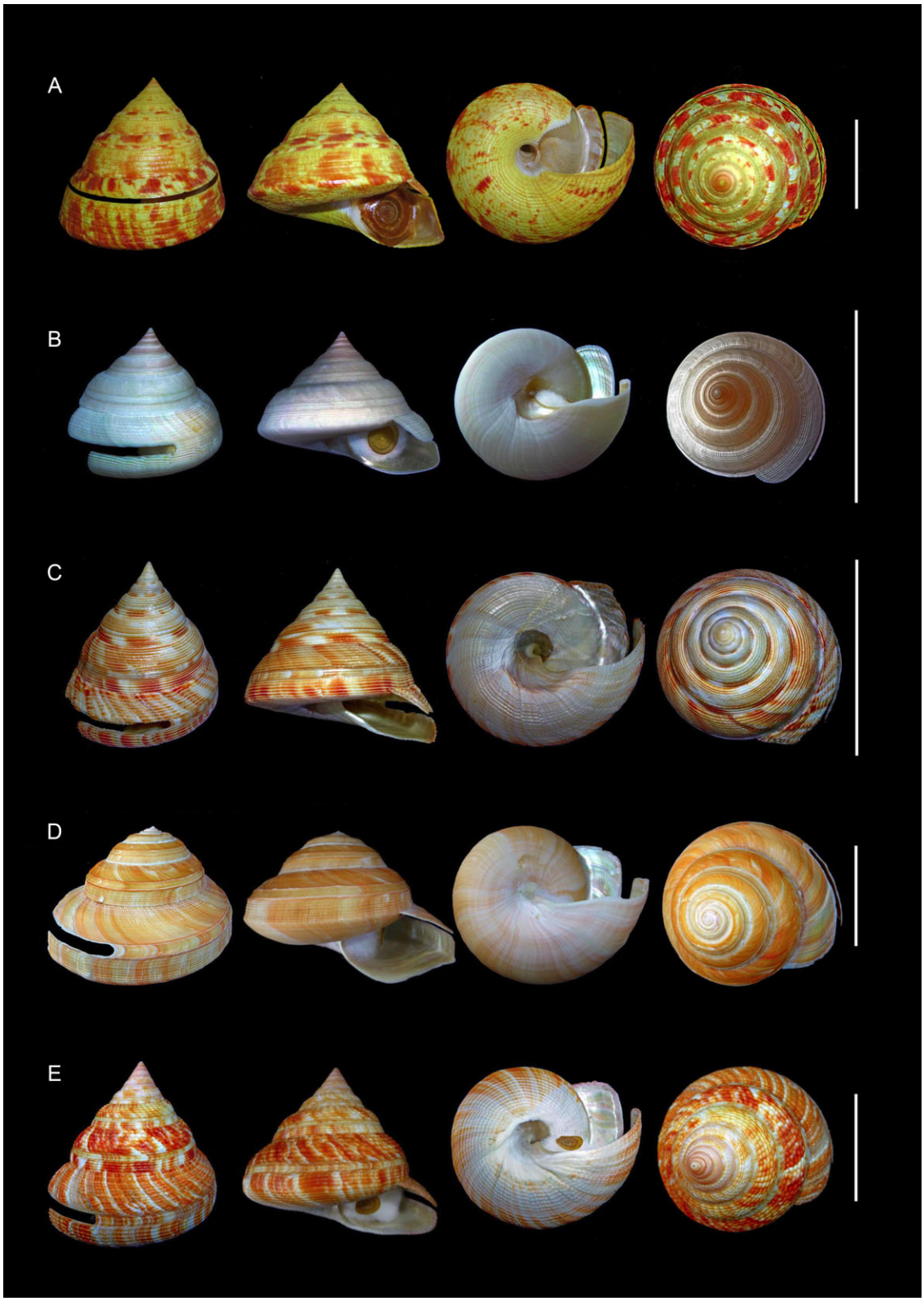

Figure 2. Type species of the genera of living Pleurotomariidae. **A.** *Entemnotrochus adansonianus*, Andros Island, Bahamas. **B.** *Perotrochus quoyanus* Roatan, Honduras. **C.** *Bouchetitrochus pseudogranulosus*, Coral Sea, New Caledonia. **D.** *Bayerotrochus midas* Roatan, Honduras. **E.** *Mikadotrochus beyrichii*, Japan. Scale bars = 5 cm for adjacent species. All specimens are from the Patrick Anseeuw collection.

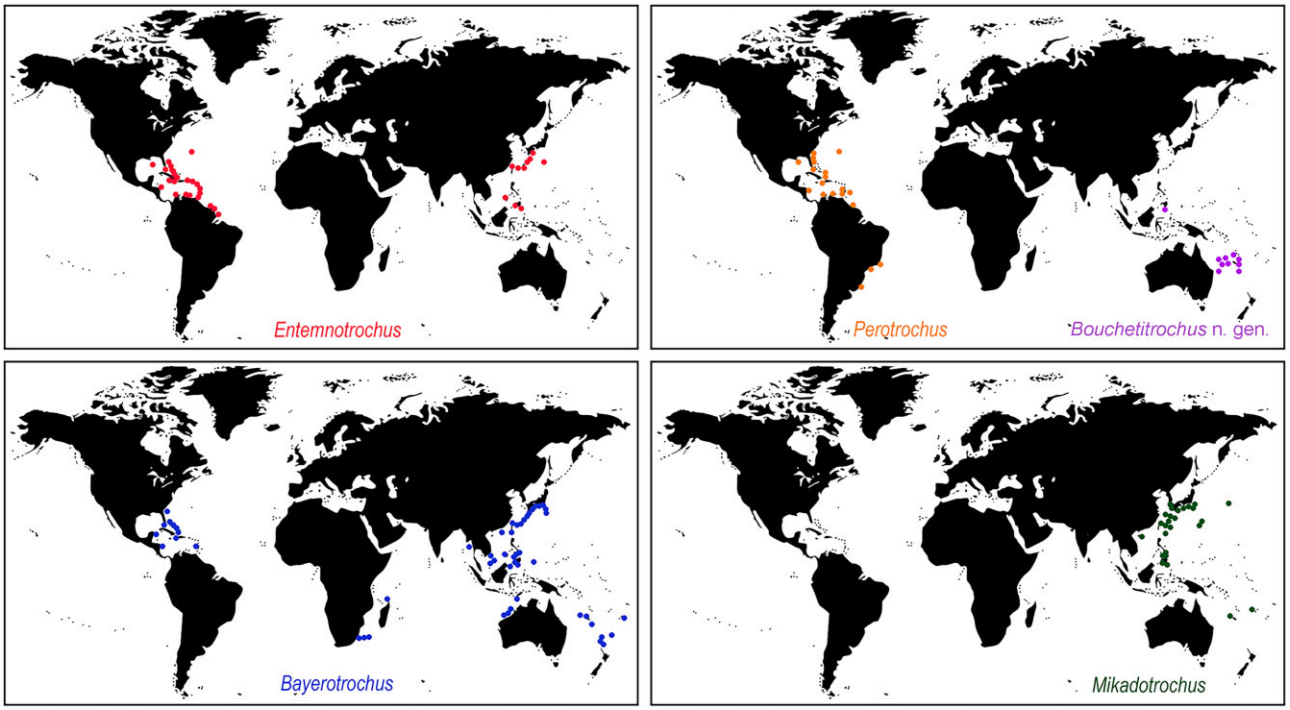

Figure 3. Maps showing the geographic distribution of living species within each of the five genera of living Pleurotomariidae. **A.** *Entemnotrochus*. **B.** *Perotrochus* and *Bouchetitrochus* n. gen. **C.** *Bayerotrochus*. **D.** *Mikadotrochus*.

faunas (Hou & Li, 2017). This resulted in a vicariant division of pleurotomariid faunas into those inhabiting the western margins of the Atlantic Ocean at temperate and tropical latitudes from those along the western margins of the Indian and Pacific Oceans at similar latitudes.

The genus *Entemnotrochus* was widespread and diverse during the Paleogene throughout and beyond the Neo-Tethys Sea, with a dozen species ranging from the west coast of North America and throughout Europe and India to Japan and Taiwan (Bose *et al.*, 2021), yet only a single Recent species, *E. rumphii*, is known to occur in the western Pacific Ocean, ranging from central Japan southward through the Philippines to Indonesia (Fig. 3A). Another species, *E. adansonianus* (with two subspecies), occurs in the western Atlantic, ranging from Bermuda southward throughout the Florida Keys and Bahamas into the Gulf of Mexico and throughout the Caribbean to Maranhao, Brazil (Rosenberg, 2009).

Over 40 species attributed on the basis of shell morphology to the genus *Perotrochus* were also widespread during the Cenozoic. However, molecular data discern two distinct clades among the Recent members of the *Perotrochus* phenotype. The clade that is endemic to the western Atlantic (Fig. 3B) retains the name *Perotrochus* as it includes the type species of the genus (Fig. 2B). The clade inhabiting the eastern part of the range (Fig. 3B), which is named *Bouchetitrochus* n. gen. herein (Fig. 2C), is presently known only from the vicinity of New Caledonia to the Central Philippines and southern Japan. The genus *Bayerotrochus* (Figs 2D, 3C), the most diverse and wide ranging pleurotomariid genus in the Indo-West Pacific region, includes a dozen species ranging from Japan southward to New Zealand and westward to South Africa. Although this genus has not been reported from fossil records (Bose *et al.*, 2021), the presence of a single species of *Bayerotrochus* in the western Atlantic fauna indicates that this genus originated prior to the closing of the Neo-Tethys Seaway. The earliest records of the genus *Mikadotrochus* (Fig. 2E), a clade that is the sister group to the Indo-West Pacific species of *Bayerotrochus* and ranges from Japan to the Philippines and the South China Sea (Fig. 3D), are from the Lower Miocene, suggesting that the two groups likely diverged from each other after the closing of the Neo-Tethys Sea.

In the western Atlantic, pleurotomariid genera stratify bathymetrically (Fig. 4), while species segregate geographically, so that species occur in allopatry (Harasewych, 2002: fig. 12B). The single species of *Entemnotrochus* has the broadest geographic range and occurs at the shallowest depths (100–350 m). The genus *Perotrochus*, with multiple species, occurs at greater depths (200–550 m) than *Entemnotrochus* and spans a similar range, from Bermuda to southernmost Brazil. The greatest species diversity is on the Caribbean tectonic plate, believed to be a section of the Pacific Ocean floor that has drifted into the Atlantic since the Cretaceous (Malfait & Dinelman, 1972), although some alternative hypotheses suggest that the Caribbean evolved in place (James, Lorente & Pindel, 2009). Two species inhabiting the coast along the USA form a separate clade that is sister group to the clade inhabiting the Caribbean. When it becomes available, sequence data for *P. atlanticus* Rios & Matthews, 1968, which occurs along the coast of Brazil, will reveal if it is more closely related to its congeners from the southern Caribbean or to the species from the coast of North America, from which it may have been isolated by the intrusion of the Caribbean plate. Only a single species of *Bayerotrochus* is currently recognized in the western Atlantic fauna. Much of its geographic range overlaps with those of *Entemnotrochus* and *Perotrochus*, although it occurs at greater depths (500–800 m) than *Perotrochus*. However, it has not been reported from Bermuda, the Gulf of Mexico, the southern coast of the Caribbean Sea or off the coast of Brazil. This may be due to the absence of submersible observations or collections at appropriate depths in these areas.

Information on the bathymetric distributions of Indo-West Pacific pleurotomariids is more generalized (Fig. 4), as most records were collected by dredging or trawling, and the reported depths are within a certain range. The depths reported for *Entemnotrochus rumphii* and various species of *Mikadotrochus* largely overlap, as do the depth ranges for many species of *Bayerotrochus* and *Bouchetitrochus* (Harasewych, 2002: fig. 12A). However, *Bayerotrochus*

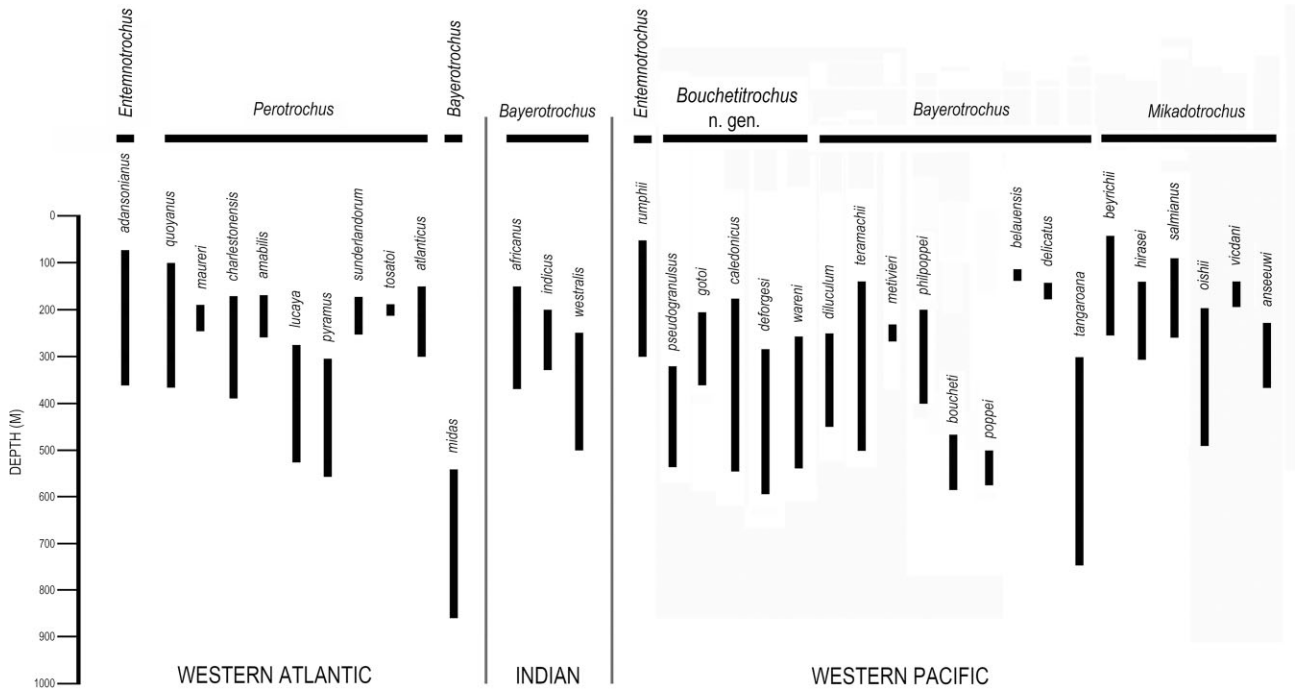

Figure 4. Distribution of living species of Pleurotomariidae by depth based on museum and literature records.

and *Bouchetitrochus* tend to occur at somewhat greater depths than *Entemnotrochus* and *Mikadotrochus*, especially in regions where their geographic distributions overlap.

Additional genetic data for species-level taxa not represented in our tree will no doubt enhance our understanding of patterns of evolution of pleurotomariids, both geographically and throughout the Cenozoic, as will more detailed population-level studies of relationships of congeneric Recent species. The development and refinement of methodologies to analyse characters of shell morphology in order to allocate fossil species into lineages that are concordant with patterns supported by molecular data is another avenue of promising research.

SYSTEMATIC DESCRIPTIONS

Class GASTROPODA Cuvier, 1795
Subclass VETIGASTROPODA Salvini-Plawen, 1980
Family PLEUROTOMARIIDAE Swainson, 1840

Genus *Bouchetitrochus* new genus

Type species: *Perotrochus pseudogranulosus* Anseeuw *et al.*, 2015.

Description: Shell of moderate size, with basal diameter 35–40 mm, rarely reaching over 55 mm. Shell shape trochoidal, depressed to conical, with solid shell construction for the small size. Slit narrow, forming a selenizone situated at or just below midwhorl. Shell thin but solid (*Bouchetitrochus caledonicus* and *B. pseudogranulosus*), with thicker prismatic layer in some species (*B. wareni* and *B. gotoi*). Surface sculpture with pronounced spiral cords that may appear beaded at intersections with axial ribs. A microsculptural pattern of fine radiating threads is visible between the dominant ribs in some species (*B. pseudogranulosus*). No significant differences in dominant sculpture on surface areas above and below the selenizone. Colour mottled brownish-red with a tendency to crimson patches, producing a checkerboard pattern that is more intense below the selenizone. Basal disc slightly convex to flattened, sculptured by well impressed, straight to heavily beaded spiral cords. Aperture horizontally oblong. Nacreous layer visible along the inner slit lips within the aperture, which may be either completely or only partially covered (*B. gotoi* and *B. wareni*), depending on the thickness of the prismatic layer. Operculum small, very small to absent.

Etymology: Named in honour of Professor Philippe Bouchet, who organized many expeditions throughout the Indo-Pacific, resulting in the discovery of many new species of Pleurotomariidae, including several of the species included in *Bouchetitrochus* n. gen.

Remarks: Members of the genera *Perotrochus* and *Bouchetitrochus* n. gen. are readily distinguished with significant support on the basis of their DNA sequences in single gene (e.g. Anseeuw *et al.*, 2015, 2017; Zhang e*t al.*, 2016) as well as in multi-gene phylogenetic analyses. However, both genera appear to share a plesiomorphic shell morphology that results in a lack of readily recognizable shell characteristics capable of differentiating between them. When compared to *Perotrochus quoyanus*, the type species of *Perotrochus*, the species of *Bouchetitrochus* n. gen. share many similarities in gross morphology that have led authors to initially assign these Indo-Pacific species to the genus *Perotrochus*. Morphological similarities shared by both genera include: small shell diameters; small, thin opercula; lack of an open umbilicus; presence of a callus pad; a broadly conical shell shape; weakly concave, relatively short slits (1/6th of basal diameter); and a dominant spiral sculpture and weak axial cords, producing only weakly cancellated spiral cords.

A recent analysis of the relationships among Cenozoic species of pleurotomariids (Bose *et al.*, 2021: fig. 4) using multivariate analyses of 15 shell characters included multiple Recent species of *Perotrochus* and *Bouchetitrochus* n. gen. but was not able to differentiate these genera. Positions of species of both genera overlapped in plots of principal component (PC) morphospace (both in PC1 *vs* PC2 and PC2 *vs* PC3 plots) (S. Das, personal communication).

Bouchetitrochus pseudogranulosus, the type species, differs from the other four species included in this new genus by its more regular conical shell, more flattened basal disc profile, more lustrous shell surface, a slightly longer slit length, a more intense colour pattern and microsculpture of fine radiating threads on the surface of the whorls.

Included species: *Bouchetitrochus pseudogranulosus*, *B. caledonicus*, *B. deforgesi*, *B. gotoi* and *B. wareni*.

Geographic distribution: The distributions of the five species of *Bouchetitrochus* n. gen. are limited to the western Pacific Ocean. Four species (*B. caledonicus*, *B. wareni*, *B. deforgesi* and *B. pseudogranulosus*) are restricted to areas of the New Caledonian plateau and adjacent Coral Sea, where they each occur at depths ranging from 180 to 600 m. One species (*B. gotoi*) has a broader distribution, extending from the southern Philippines towards Indonesia and further eastwards, from NW Pacific waters towards Japan, occurring at depths of 200–360 m.

ACKNOWLEDGEMENTS

MNHN specimens were obtained during research cruises and expeditions organized by the MNHN and ProNatura International as part of the Our Planet Reviewed programme, and by the MNHN and the Institut de Recherche pour le Dévelopement as part of the Tropical Deep-Sea Benthos programme: EBISCO (http://dx.doi.org/10.17600/5100080), CONCALIS (http://dx.doi.org/10.17600/8100010), NORFOLK 2 (http://dx.doi.org/10.17600/3100030), TERRASSES (http://dx.doi.org/10.17600/8100100), KANADEEP (http://dx.doi.org/10.17600/17003800) and KANACONO (http://dx.doi.org/10.17600/16003900) in New Caledonia, PAPUA NIGINI (http://dx.doi.org/10.17600/18000841), MADEEP (http://dx.doi.org/10.17600/14004000) and BIOPAPUA (http://dx.doi.org/10.17600/10100040) in Papua-New-Guinea, SALOMON 1 (http://dx.doi.org/10.17600/1100090) in the Solomons, ZhongSha 2015 and NanHai 2014 in Taiwan, MAINBAZA and BIOMAGLO (http://dx.doi.org/10.17600/17004000) in the Mozambique Channel, MIRIKY in Madagascar, GUYANE 2014 in French Guyana and KARUBENTHOS 2 (http://dx.doi.org/10.17600/15005400) in Guadeloupe. We are grateful to the numerous cruise leaders and co-PIs, in particular Philippe Bouchet, Laure Corbari and Sarah Samadi (more information can be found at https://expeditions.mnhn.fr/). These expeditions operated under the regulations then in force in the countries in question and satisfy the conditions set by the Nagoya Protocol for access to genetic resources. We are grateful to Barbara Buge, Julien Brisset, Virginie Héros and Philippe Maestrati (MNHN) for assistance in specimen curation, and to the team of SSM (UAR2700-MNHN) for support in the lab. We thank Dr Shiladri Das, of the Indian Statistical Institute, for providing additional information regarding species identities of the samples used in the previously published study of Cenozoic pleurotomariids. We thank Dr Steffen Kiel of the Swedish Museum of Natural History for his constructive review of this manuscript.

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