



Molecular phylogenetics of Hastrinae and Pagodulinae (Neogastropoda: Muricidae) with a focus on New Zealand species

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(Received 20 January 2015; accepted 20 April 2015)

ABSTRACT

We investigated the relationships of the muricid subfamilies Hastrinae, Pagodulinae and the genus *Poirieria* using a molecular phylogenetic approach on a dataset of three mitochondrial genes (12S, 16S and COI). These taxa form a well-supported clade within Muricidae. The phylogenetic analysis suggests that *Poirieria* is the sister group of Pagodulinae and that *Axymene*, *Comptella*, *Pagodula*, *Paratrophon*, *Trophonella*, *Trophonopsis*, *Xymene*, *Xymenella*, *Xymenopsis* and *Zeatrophon* are all worthy of genus-level rank within this subfamily. We propose the use of *Enixotrophon* for a group of species currently classified in *Pagodula*. The results also support a new taxonomic arrangement in Hastrinae.

INTRODUCTION

The family Muricidae is among the most species-rich and morphologically diverse groups of marine gastropods, with over 1,600 extant named species and a rich fossil record. Muricids are active predators of a wide range of benthic invertebrates, with feeding adaptations including drilling (Carriker, 1981), scavenging (Morton, 2006) and ectoparasitism (Devarajen *et al.*, 2004). The predatory pressure imposed by these snails has an important role in shaping the structure of marine benthic communities (Morton, 1999, 2004; Peharda & Morton, 2006; Harding *et al.*, 2007).

Historically, muricid taxonomy and systematics have been based on shell morphology and, to a small degree, on radular and anatomical characters (for a short review see Barco *et al.*, 2010). Recent molecular studies have tested this traditional classification and resulted in significant changes (Claremont, Reid & Williams, 2008; Barco *et al.*, 2010, 2012; Claremont *et al.*, 2013a, 2013b). Several genera, however, remain doubtfully assigned within recognized subfamilies, while parallel evolution of similar shell morphologies in living (Bouchet & Houart, 1994) and fossil genera (Herbert & Del Río, 2005) has resulted in unstable classification.

The two most recently defined muricid subfamilies, Hastrinae Tan, 2003 and Pagodulinae Barco, Schiaparelli, Houart & Oliverio, 2012, represent two closely-related lineages of Muricidae, predominantly distributed in New Zealand, Australian and South American waters. The most recent phylogenetic analyses of Muricidae indicate that Hastrinae and Pagodulinae form a clade and that Typhinae are the most closely related subfamily (Barco *et al.*, 2010, 2012).

The subfamily Hastrinae was based on a cladistic analysis, principally of anatomical characters, of muricids endemic to New Zealand and Australia (Tan, 2003). Hastrinae were distinguished from the species of Rapaninae and Trophoninae analysed by Tan (2003) and were assigned subfamilial rank based on a unique combination of characters of the operculum, radula, accessory salivary gland, oesophagus, paraspermatozoa (in males) and bursa copulatrix (in females). Tan (2003) assigned species of *Lepsiella* Iredale, 1912, *Lepsithais* Finlay, 1928 and *Haustrum* Perry, 1811 to Hastrinae and treated *Bedevea* Iredale, 1924 as a subgenus of *Lepsiella*, a classification accepted by Barco *et al.* (2010). *Lepsiella* and *Lepsithais* are now considered to be synonyms of *Haustrum* (Beu, 2004) and the subfamily currently includes two genera and up to 10 species (depending on the author), geographically restricted to New Zealand and southern Australia, with the sole exception of *Bedevea paivae* (Crosse, 1864), which has been introduced by human agency to South Africa (Kilburn & Rippey, 1982), the Canary Islands and Madeira (Houart & Abreu, 1994).

Barco *et al.* (2012) analysed the phylogenetic relationships of Southern Ocean muricids traditionally assigned to Trophoninae and investigated differences in radular and penial morphology of 12 genera. Evidence was found for a new subfamily, Pagodulinae, comprising seven genera, four of which were based on molecular data: *Pagodula* Monterosato, 1884, *Trophonella* Harasewych & Pastorino, 2010, *Xymenopsis* Powell, 1951 and *Xymene* Iredale, 1915. A further three genera, *Boreotrophon* Fischer, 1884, *Paratrophon* Finlay, 1926 and *Trophonopsis* Bucquoy & Dautzenberg, 1882 were assigned on the basis of radular and penial morphology. Additionally, *Axymene* Finlay, 1926, *Lenitrophon* Finlay, 1926, *Xymenella* Finlay, 1926 and *Zeatrophon* Finlay, 1926 were treated as subgenera of

Xymene pending further evidence, while a further 16 genera of uncertain affinities were listed as *incertae sedis*.

Thus some uncertainty remained with respect to phylogenetic relationships and taxonomic level of some genera assigned to Pagodulinae, in particular for the genera *Pagodula* and *Xymene* and its subgenera. We include among these the genus *Poirieria* Jousseaume, 1880, with species morphologically close to some pagodulines, but with an uncertain phylogenetic position within the Muricidae.

Pagodula was treated as a full genus by Marshall & Houart (2011), but as a subgenus of *Poirieria* by Merle, Garrigues & Pointier (2011). Taxonomic uncertainty was largely due to the convergent ‘pagodiform’ shell morphologies of *Pagodula* and *Poirieria* species. *Pagodula* currently includes 47 named living species with a global distribution in high to low latitudes (Marshall & Houart, 2011). Phylogenetic information is currently restricted to few species: the type species *P. echinata* (Kiener, 1840) from the northeastern Atlantic; *P. eos* Marshall & Houart, 2011 and *P. lata* Marshall & Houart, 2011 from New Zealand; and *P. cuspidarioides* (Powell, 1951) from the Scott sea-mounts in the Ross Sea, Antarctica.

Finlay (1926) proposed a classification of several New Zealand muricids based on shell and protoconch morphology, recognizing the genera *Axymene*, *Comptella* Finlay, 1926, *Paratrophon*, *Terefundus* Finlay, 1926, *Xymene*, *Xymenella* and *Zeatrophon*, with subgenera *Axymene* (*Lenitrophon*) and *Terefundus* (*Minotrophon*) both of Finlay, 1926. Ponder (1972) found no convincing morphological distinctions between Finlay’s genera and synonymized *Axymene*, *Lenitrophon*, *Xymenella* and *Zeatrophon* with *Xymene*. Beu (2011) recently resurrected Finlay’s earlier classification.

The genus *Poirieria* was discussed by Barco *et al.* (2012) in connection with Pagodulinae, because of general similarity in radular morphology between its type species (see Marshall & Houart, 1995) and species of *Pagodula*, but its phylogenetic position within the Muricidae is currently unknown. *Poirieria* is one of the oldest known muricid genera and is traditionally classified in the subfamily Muricinae. Merle *et al.* (2011) suggested that this and other ancient genera with similar simple shell morphologies do not in fact belong in Muricinae, but are more likely to represent ‘basal’ muricids, i.e. sister lineages of other more recent subfamilial clades. *Poirieria* is currently perceived as comprising three subgenera distinguished by their shell morphology: *Poirieria* (*Poirieria*), *Poirieria* (*Actinotrophon*) Dall, 1902 and *Poirieria* (*Caelobassus*) Stilwell & Zinsmeister, 1992. The subgenus *Poirieria* comprises three living New Zealand species and apparently the Early Paleocene fossils from the western Atlantic, Europe and the Indo-Pacific. The subgenus *Actinotrophon* includes three living species from the northeastern and western Atlantic as well as the Indo-West Pacific, and fossil species from the Pliocene of Central America. The subgenus *Caelobassus* is a monotypic taxon represented by the Late Eocene species *Caelobassus radwimi* from Seymour Island, Antarctica (Stilwell & Zinsmeister, 1992).

In this study we treat genera of particular relevance to the systematics of Haustriinae and Pagodulinae, and in particular we test: (1) the monophyly and phylogenetic relationships of the species-rich genus *Pagodula* within the Pagodulinae; (2) the taxonomic ranking of the genus *Xymene* and related subgenera and (3) the phylogenetic position of *Poirieria* within the Muricidae with respect to Pagodulinae and Haustriinae. Additionally, we test the morphology-based assignment of the genera *Paratrophon* and *Trophonopsis* to the Pagodulinae, as well as the position of *Comptella*, which is currently *incertae sedis*.

MATERIAL AND METHODS

Taxon sampling and outgroup selection

We include original data for five type species and nine nominal genera from the working classification proposed by Barco *et al.*

(2012). Taxonomic assignments follow the classification accepted in the World Register of Marine Species (www.marinespecies.org) at the time of submission. New arrangements based on the outcomes of the molecular results are proposed. Voucher data, references and accession numbers are included in Table 1. We used the Typhinae as outgroup, represented by sequences of six species from Barco *et al.* (2010).

DNA sequencing and alignment

Each specimen was identified based on shell morphology upon collection, fixed in 96–100 % ethanol and a piece of tissue was dissected for DNA extraction. We extracted the total genomic DNA from a tissue digestion using proteinase K and a phenol-chloroform protocol (Hillis, Moritz & Mable, 1996). Fragments of the mitochondrial cytochrome oxidase I (COI) and the ribosomal genes 12S and 16S were obtained with the same primers, PCR mix and cycles as used by Barco *et al.* (2010, 2012).

PCR products were sequenced by Macrogen Inc. (Seoul, South Korea) using an automatic sequencer AB3730XL (Applied Biosystems). Forward and reverse sequences were assembled and reciprocally edited with Sequencher v. 4.1.4 (Gene Codes Corporation, Ann Arbor, MI). The COI dataset was aligned manually and translated to amino acids to check for the presence of stop codons. 16S and 12S datasets were aligned with MAFFT (Katoh *et al.*, 2002) using the Q-INS-i algorithm (Katoh & Toh, 2008). We selected gene-specific substitution models using jModelTest (Posada, 2008), applying the Bayesian information criterion (Schwarz, 1978). The alignments of 12S and 16S included some gap-rich regions that were excluded using Gblocks v. 0.91b (Castresana, 2000) with the same settings used by Barco *et al.* (2010).

Phylogenetic analysis

We analysed our dataset using maximum likelihood (ML) and Bayesian (BA) approaches. We constructed ML phylogenies with PhyML v. 3.0 (Guindon *et al.*, 2010) as implemented in the ATGC bioinformatics platform (www.atgc-montpellier.fr). We used a neighbour joining starting tree optimized with nearest neighbour interchanges and we estimated node support with 1000 bootstrap replicates. In the ML consensus tree, nodes found in more than 75 % of bootstrap replicates were considered well supported, those found between 75 and 50 % were considered moderately supported and those below 50 % were considered unsupported.

For the BA inference we used MrBayes (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), running two analyses with four chains each for 2×10^7 generations sampled every 2×10^4 . We evaluated chain convergence using a plot of the standard deviation of average split frequencies and the potential scale of reduction factor (Gelman & Rubin, 1992). A consensus tree was obtained after summarizing the resulting topologies and discarding the ‘burnin’. In analysing the BA consensus tree, clades recovered with posterior probability (PP) between 0.95 and 1 were considered well supported, those with PP between 0.90 and 0.94 were considered moderately supported and those with lower PP were considered unsupported.

The phylogenetic position of *Poirieria* within the Muricidae is unknown. We tested our hypothesis that the genus is closely related to the Pagodulinae by running a preliminary analysis with a reduced dataset (one or two species per genus from the present dataset) and included sequences available from recent work (Barco *et al.*, 2012). For this analysis we used the same settings and analytical framework described by Barco *et al.* (2012).

In the main analysis we used our complete dataset for the phylogenetic reconstruction of Haustriinae, Pagodulinae and *Poirieria*. We first analysed each gene separately with ML and

Table 1. Specimens of Muricidae used in this study, with sampling localities, museum registration numbers and sequence accession numbers.

Species	Voucher reg. no.	Locality	GenBank acc. nos		
			COI	12S	16S
Haustrinae					
<i>Bedeva paivae</i> *	AMS C458273	Australia, Tasmania, Bruny I., Isthmus Bay.	FN677412	FN677387	FN677437
<i>Bedeva vinosa</i>	AMS C458268	Australia, Tasmania, Diana's Beach, NE of Scamander.	FN677413	FN677385	FN677435
<i>Haustrum albomarginatum</i>	M.301488/1	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844980		
	M.301488/2	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844979	KP845114	
	M.301488/3	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844978	KP845113	
	M.301488/4	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844977	KP845112	
	M.301488/5	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844976	KP845111	
	M.301488/6	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844975	KP845110	
	M.301488/7	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844981	KP845115	
	M.301488/8	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844974	KP845109	
<i>Haustrum haustorium</i> *	UO HH-PB	New Zealand, Pukerua Bay.	FN677410	FN677389	FN677443
<i>Haustrum lacunosum</i>	UO LL2-SC	New Zealand, St Clair, Dunedin, intertidal.	FN677411	FN677388	FN677442
	M.285283/1	New Zealand, Stewart Island, Ringaringa, 46°55'S, 168°09'E, intertidal.	KP844983	KP845117	KP845072
	M.285283/2	New Zealand, Stewart Island, Ringaringa, 46°55'S, 168°09'E, intertidal.	KP844982	KP845116	KP845071
	M.285283/3	New Zealand, Stewart Island, Ringaringa, 46°55'S, 168°09'E, intertidal.	KP844984	KP845118	KP845073
<i>Haustrum scobina</i>	M.301489/1	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844991	KP845125	
	M.301489/2	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844990	KP845124	
	M.301489/3	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844989	KP845123	
	M.301489/4	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844988	KP845122	
	M.301489/5	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844985	KP845119	
	M.301489/6	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844992	KP845126	
	M.301489/7	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844986	KP845120	
	M.301489/8	New Zealand, SW of Hawera, 39°36.4'S, 174°14.5'E, intertidal.	KP844987	KP845121	KP845074
Pagodulinae					
<i>Axymene aucklandicus</i> *	M.290404/3	New Zealand, Marfells Beach, Clifford Bay, intertidal.	KP844957	KP845097	KP845061
	M.285287	New Zealand, Stewart Island, Lonnekens Bay, 46°54.3'S, 168°8.3'E, intertidal.	KP844958	KP845098	KP845062
<i>Axymene traversi</i>	M.290404/1	New Zealand, Marfells Beach, Clifford Bay, intertidal.	KP844963	KP845103	KP845067
	M.290404/2	New Zealand, Marfells Beach, Clifford Bay, intertidal.	KP844959	KP845099	KP845063
	M.290404/4	New Zealand, Marfells Beach, Clifford Bay, intertidal.	KP844962	KP845102	KP845066
	M.290404/5	New Zealand, Marfells Beach, Clifford Bay, intertidal.	KP844961	KP845101	KP845065
	M.303366/1	New Zealand, Hicks Bay, near wharf, 37°34.1'S, 178°18.0'E, intertidal.	KP844960	KP845100	KP845064
	M.303366/2	New Zealand, Hicks Bay, near wharf, 37°34.1'S, 178°18.0'E, intertidal.	KP844965	KP845105	KP845069
	M.305190	New Zealand, Mahia Peninsula, Oraka Beach, 34°04.0'S, 177°54.2'E, intertidal.	KP844964	KP845104	KP845068
<i>Comptella curta</i> *	M.305597	New Zealand, off Snares Islands, 48°01.2'S, 166°36.8'E, 73 m.	KP844966		
<i>Enixotrophon cuspidarioides</i>	NIWA3817a	Antarctica, Ross Sea, 68°07.2'S, 179°14.8'E, 879 m.	HM887946		
	NIWA3817b	Antarctica, Ross Sea, 68°07.2'S, 179°14.8'E, 879 m.	HM887932		
	NIWA3361	Antarctica, Ross Sea, 67°43.4'S, 179°42.7'E, 1145 m.	HM887934		
<i>Enixotrophon eos</i>	NIWA30162	New Zealand, Chatham Rise, 42°39.3'S, 177°12.8'E, 1377–1402 m.	HE804834		HE804815
<i>Enixotrophon lata</i>	M.284123	New Zealand, Challenger Plateau, 36°54.8'S, 167°31.9'E, 1211–1216 m.	HE804835		
	M.284040	New Zealand, Challenger Plateau, 38°34.9'S, 167°08.9'E, 974 m.	HE804836		HE804816
<i>Enixotrophon maxwelli</i>	M.301808/1	New Zealand, E of Cape Palliser, 41°43.3'S, 175°39.8'E, 1486–1473 m.	KP844969	KP845108	
	M.301808/2	New Zealand, E of Cape Palliser, 41°43.3'S, 175°39.8'E, 1486	KP844968	KP845107	
	M.301808/3	New Zealand, E of Cape Palliser, 41°43.3'S, 175°39.8'E, 1486	KP844967	KP845106	

Continued

PHYLOGENY OF PAGODULINAE AND HAUSTRINAE

Table 1. Continued

Species	Voucher reg. no.	Locality	GenBank acc. nos		
			COI	12S	16S
<i>Enixotrophon tangaroa</i>	M.301825	New Zealand, SE of Cape Campbell, 42°08.1'S, 174°32.3'E, 1169–1213 m.	KP844971		
	M.301835	New Zealand, Chatham Rise, Headstone Seamount, 42°40.5'S, 179°57.4'W, 1020–1120 m.	KP844970		
<i>Enixotrophon venustus</i>	M.306209	New Zealand, southern Kermadec Ridge, Rumble II West chimney field, 35°20.9'S, 178°32.6'E, 1180–1306 m.	KP844972		KP845070
	M.306255	New Zealand, southern Kermadec Ridge, Tangaroa Seamount, 36°19.8'S, 178°02.1'E, 847–866 m.	KP844973		
<i>Pagodula echinata*</i>	BAU01114.3	Spain, Banco Algarrobo, 36°21.1'N, 03°58.1'W, 365 m.	KP844993		
	BAU01114.4	Spain, Banco Algarrobo, 36°21.1'N, 03°58.1'W, 365 m.	KP844994		
<i>Paratrophon exsculptus</i>	M.297885	New Zealand, S of Waitotara, Waiinui Beach, 39°52.2'S, 174°44.6'E, intertidal.	KP844996	KP845128	KP845076
	M.298790/1	New Zealand, S of Waitotara, Waiinui Beach, 39°52.2'S, 174°44.6'E, intertidal.	KP844997	KP845129	KP845077
	M.298790/2	New Zealand, S of Waitotara, Waiinui Beach, 39°52.2'S, 174°44.6'E, intertidal.	KP844995	KP845127	KP845075
<i>Paratrophon patens</i>	M.285284/1	New Zealand, Stewart Island, Ringaringa, 46°55'S, 168°09'E, intertidal.	KP844998	KP845130	KP845078
	M.285284/2	New Zealand, Stewart Island, Ringaringa, 46°55'S, 168°09'E, intertidal.	KP844999	KP845131	KP845079
<i>Paratrophon quoyi</i>	M.280406	New Zealand, Bland Bay, 35°21.1'S, 174°22.3'E, intertidal.	KP845000	KP845132	KP845080
	M.305192	New Zealand, Spirits Bay, Pananehe Island, 34°25.2'S, 172°51.2'E, intertidal.	KP845001	KP845133	KP845081
<i>Poirieria syrinx</i>	M.301834	New Zealand, S of Castlepoint, Kaiwahata Seamount, 41°20.2'S, 176°10.9'E, 687–730 m.		KP845135	
	M.301837	New Zealand, ENE of Cape Palliser, 41°31.2'S, 175°48.4'E, 723–746 m.	KP845003	KP845136	
	M.314529	New Zealand, SE of Cape Campbell, 41°59.1'S, 174°41.9'E, 685–730 m.	KP845002	KP845134	KP845082
<i>Poirieria zelandica*</i>	M.303377/1	New Zealand, Tasman Bay, off Kaiteriteri, 41°00.9'S, 173°02.2'E, 16 m.	KP845005	KP845138	
	M.303377/2	New Zealand, Tasman Bay, off Kaiteriteri, 41°00.9'S, 173°02.2'E, 16 m.	KP845006	KP845139	KP845083
	M.303377/3	New Zealand, Tasman Bay, off Kaiteriteri, 41°00.9'S, 173°2.2'E, 16 m.	KP845007	KP845140	
	M.303377/4	New Zealand, , Tasman Bay, off Kaiteriteri, 41°00.9'S, 173°02.2'E, 16 m.	KP845004	KP845137	
<i>Trophonella echinolamellata</i>	M.305194	New Zealand, off Nelson, 20–30 m.	KP845008	KP845141	
	MNA2713	Antarctica, Bellingshausen Sea, Skua shelter, 65°09'S, 064°09.6'W, diving depth.	JX110857		HE804819
<i>Trophonella longstaffi</i>	BAU00949	Antarctica, Ross Sea, Tethys Bay, 74°41'S, 164°01'E, 29 m.	FN651950	FN651882	FN651927
	MNA42	Antarctica, Ross Sea, Tethys Bay, 74°24.6'S, 164°03'E, 10 m.	JX110858		HE804821
	NIWA38623b	Antarctica, Ross Sea, 67°24.7'S, 179°56.5'E, 300 m.	HM431868		
<i>Trophonella scotiana*</i>	MNA4	Antarctica, Ross Sea, 71°45.3'S, 171°08.9'E, 250 m.	JX110861		HE804820
<i>Trophonella shackletoni</i>	MNA5	Antarctica, Ross Sea, 71°45.3'S, 171°25.0'E, 282 m.	JX110860		HE804817
	MNA40	Antarctica, Ross Sea, 78°S, 164°E, 18 m.	JX110859		HE804818
<i>Trophonopsis muricatus*</i>	BAU01111.1	Spain, Calahonda, 36°41.6'N, 03°21.1'W, 67 m.	KP845010		
	BAU01111.2	Spain, Calahonda, 36°41.6'N, 03°21.1'W, 67 m.	KP845011		
	BAU001111.3	Spain, Calahonda, 36°41.6'N, 03°21.1'W, 67 m.	KP845012		
	BAU01112.1	Spain, Calahonda, 36°42.9'N, 03°18.3'W, 76 m.	KP845009		
	BAU01112.2	Spain, Calahonda, 36°42.9'N, 03°18.3'W, 76 m.	KP845013		

Continued

Table 1. Continued

Species	Voucher reg. no.	Locality	GenBank acc. nos		
			COI	12S	16S
<i>Xymene plebeius</i> *	M.285282/2	New Zealand, Stewart Island, Deep Bay, 46°54.8'S, 168°8.0'E, intertidal.	KP845027	KP845144	KP845088
	M.305138/1	New Zealand, Whangaruru Harbour, Admirals Bay, 35°22.2'S, 174°21.4'E, 3 m.	KP845028		KP845089
	M.305138/3	New Zealand, Whangaruru Harbour, Admirals Bay, 35°22.2'S, 174°21.4'E, 3 m.	KP845029		KP845090
	M.302931/1	New Zealand, Wellington, N of Miramar Wharf, 41°18.6'S, 174°48.8'E, intertidal.	KP845030	KP845145	KP845091
	M.302931/2	New Zealand, Wellington, N of Miramar Wharf, 41°18.6'S, 174°48.8'E, intertidal.	KP845031		KP845092
	M.302931/3	New Zealand, Wellington, N of Miramar Wharf, 41°18.6'S, 174°48.8'E, intertidal.	KP845032		KP845093
	M.302931/4	New Zealand, Wellington, N of Miramar Wharf, 41°18.6'S, 174°48.8'E, intertidal.	KP845033		KP845094
	M.302931/5	New Zealand, Wellington, N of Miramar Wharf, 41°18.6'S, 174°48.8'E, intertidal.	KP845022	KP845143	
	M.302931/6	New Zealand, Wellington, N of Miramar Wharf, 41°18.6'S, 174°48.8'E, intertidal.	KP845023		KP845084
	M.302931/7	New Zealand, Wellington, N of Miramar Wharf, 41°18.6'S, 174°48.8'E, intertidal.	KP845024		KP845085
	M.302931/8	New Zealand, Wellington, N of Miramar Wharf, 41°18.6'S, 174°48.8'E, intertidal.	KP845025		KP845086
M.302931/9	New Zealand, Wellington, N of Miramar Wharf, 41°18.6'S, 174°48.8'E, intertidal.	KP845026		KP845087	
<i>Xymenella pusilla</i> *	M.305852/1	New Zealand, Golden Bay, Tukurua, 40°44.0'S, 172°42.1'E, intertidal.	KP845015		
	M.305852/2	New Zealand, Golden Bay, Tukurua, 40°44.0'S, 172°42.1'E, intertidal.	KP845016		
	M.305852/3	New Zealand, Golden Bay, Tukurua, 40°44.0'S, 172°42.1'E, intertidal.	KP845017		
	M.305852/4	New Zealand, Golden Bay, Tukurua, 40°44.0'S, 172°42.1'E, intertidal.	KP845018		
	M.305852/5	New Zealand, Golden Bay, Tukurua, 40°44.0'S, 172°42.1'E, intertidal.	KP845019		
	M.305852/6	New Zealand, Golden Bay, Tukurua, 40°44.0'S, 172°42.1'E, intertidal.	KP845020		
	M.305852/7	New Zealand, Golden Bay, Tukurua, 40°44.0'S, 172°42.1'E, intertidal.	KP845021		
M.305394	New Zealand, Lyall Bay, 41°20.0'S, 174°47.5'E, intertidal.	KP845014	KP845142		
<i>Xymenopsis muriciformis</i> *	BAU00913	Chile, Tierra del Fuego, Pueblo Porvenir.	JX033993		HE804813
<i>Zeatrophon ambiguus</i> *	M.305193	New Zealand, Stewart Island, Port William, 46°50.4'S, 168°06.1'E, 20–30 m.	KP845035	KP845147	
	M.285274/1	New Zealand, Stewart Island, Vaila Voe, Paterson Inlet, 46°54.5'S, 168°06.5'E, intertidal.	KP845036	KP845148	KP845095
	M.285274/2	New Zealand, Stewart Island, Vaila Voe, Paterson Inlet, 46°54.5'S, 168°06.5'E, intertidal.	KP845037	KP845149	
	M.285274/3	New Zealand, Stewart Island, Vaila Voe, Paterson Inlet, 46°54.5'S, 168°06.5'E, intertidal.	KP845034	KP845146	
<i>Zeatrophon pulcherrimus</i>	M.284120	New Zealand, Challenger Plateau, 38°01'S, 168°27'E, 570–575 m.		KP845150	
Outgroup					
<i>Siphonochelus boucheti</i>	MNHN-IM-2009-5041	New Caledonia, NORFOLK2 2003, Norfolk Ridge, Sponge Bank, 25°54'S, 168°22'E, 500–505 m.	GU575387	FN651883	FN651928
<i>Siphonochelus pavlova</i>	MNHN-IM-2009-8590	Coral Sea, EBISCO 2005, Lansdowne Plateau, 21°05'S, 160°45'E, 297–378 m.	GU575388	FN651884	FN651929
<i>Monstrotyphis imperialis</i>	MNHN-IM-2009-8449	New Caledonia, EBISCO 2005, S of Nova Bank, 22°49'S, 159°23'E, 320–345 m.	GU575389	FN651888	FN651933
<i>Typhisopsis coronatus</i>	BAU00396	Panama, Isla San José, 08°18'N, 079°3'W, 30.5 m.	FN651951	FN651885	FN651930
<i>Typhisala grandis</i>	BAU00376	Panama, Isla San José, 08°18'N, 079°3'W, 30.5 m.	FN651952	FN651886	FN651931
<i>Typhinellus labiatus</i>	BAU00181	Tunisia, Borj el Mussar,	FN651953	FN651887	FN651932

Abbreviations: BAU, Department of Biology and Biotechnologies 'Charles Darwin', Rome; M, Museum of New Zealand Te Papa Tongarewa, Wellington; MNHN, Muséum National d'Histoire Naturelle, Paris; AMS, Australian Museum, Sydney; UO, University of Otago; MNA, National Museum of Antarctica, Genoa; NIWA, National Institute of Water and Atmospheric Research, Wellington. Type species are marked with an asterisk.

BA approaches, and the resulting trees were compared to test for incongruence among genes. The presence of divergent, highly-supported clades among gene trees would be considered evidence for gene incongruence. In the absence of incongruence we analysed the combined three-gene matrix both with ML and BA methods and missing sequences were coded as unknown data. In the BA partitioned analysis each partition (COI, 12S and 16S) was unlinked; base frequencies, alpha parameter and proportion of invariable sites were estimated separately for each partition during the phylogenetic reconstruction. For the ML analysis, a single substitution model was used, because PhyML does not allow partitioning.

We evaluated some taxonomic assignments by comparing specimen identifications and Kimura 2-parameter (K2P) distance values obtained from the COI alignment using MEGA v. 6 (Tamura *et al.*, 2013). We used the distance value of 0.03 as a threshold between intra- and interspecific distances among muricid species; this value is consistent with previous studies (Castelin *et al.*, 2010; Claremont *et al.*, 2011; Zou *et al.*, 2012; Crocetta *et al.*, 2012; Barco, Corso & Oliverio, 2013a; Barco *et al.*, 2013b).

RESULTS

DNA sequences

We sequenced 76 specimens and obtained 55 sequences of 12S, 34 of 16S and 74 of COI (GenBank accession numbers are listed in Table 1). Sequences of COI were all 658 bp long; no gaps were required for the alignment and no stop codons were detected. Sequences of 12S (542 to 548 bp) and 16S (742 to 754 bp) were reduced to 532 bp and 716 bp, respectively, after using Gblocks. The final alignment was 557 bp long for 12S and 806 bp long for 16S. The substitution models selected by jModelTest were GTR + I + Γ for all three genes.

Phylogenetic analysis

The preliminary analysis generated a well-supported clade comprising Typhinae, Haustriinae, Pagodulinae and *Poirieria*, confirming our hypothesis that *Poirieria* is closely related to these three subfamilies. Monophyly of each of the three subfamilies, as well as the position of *Poirieria* as sister group of the Pagodulinae, all received high support value (Supplementary material, Fig. S1).

The trees obtained from ML analyses were annotated with bootstrap support values and compared with those from MrBayes analyses. In the phylogenetic analyses performed with MrBayes all chains reached convergence, with an average standard deviation of split frequencies lower than 0.01 and PSRF values of each parameter approaching 1.00. We obtained a consensus tree after excluding 25 % of the sampled trees from the initial 'burnin' phase.

Single-gene trees from ML and BA analyses were almost identical. Differences in branching patterns received low support both in bootstrap and PP values (Supplementary material, Fig. S2). Clades recovered with high support in each topology were congruent, suggesting no divergent evolutionary histories among genes.

After combining the datasets we obtained the consensus topology shown in Figure 1. No incongruence was found between ML and BA analysis, with the exception of slightly different, but unsupported, branching patterns within the Pagodulinae (marked in Fig. 1). We recovered a monophyletic clade comprising Pagodulinae, Haustriinae and *Poirieria*. Haustriinae formed a well-supported clade, and both *Bedevea* and *Hautrum* were monophyletic and strongly supported. We also recovered a well-

supported clade for *Poirieria zelandica* and *P. syrinx*, and high support for their position as sister group to all the Pagodulinae.

Paratrophon was recovered at the base of the remaining Pagodulinae, while the other genera formed three unresolved groups: a weakly supported clade for *Zeatrophon*; one well-supported clade comprising *Xymenella* and *Xymene*; and a third group with an unresolved node including *Comptella*, *Xymenopsis*, *Pagodula*, *Trophonopsis*, *Axymene*, *Trophonella* and *Enixotrophon*. In the latter group, all genera represented by more than one species received strong support. Two species were not monophyletic in this topology: *Trophonella shackletoni* and *Axymene aucklandicus*.

K2P distances were calculated in the COI dataset (Table 2). High K2P intraspecific distances were found between the two specimens morphologically identified as *Trophonella shackletoni* (0.038) and between the two identified as *Axymene aucklandicus* (0.073). Interspecific K2P genetic distances were almost all above 0.03. The only exception was the specimens identified as *Paratrophon patens* and *P. exculptus*, which were not reciprocally monophyletic and had a low interspecific distance (0.012).

DISCUSSION

Relationships among muricid subfamilies are yet incompletely understood due to lack of robust support at the basal nodes of their molecular phylogeny (Barco *et al.*, 2010). The subfamilies discussed here, however, belong to a well-defined clade: Pagodulinae and Haustriinae are monophyletic and form a highly-supported clade with the Typhinae as sister group; the genus *Poirieria* is shown here to belong in this clade, as sister group of the Pagodulinae.

Phylogenetic position of *Poirieria* and related taxa

We raise *Poirieria*, *Actinotrophon* and *Caelobassus* to full generic rank; we include *Poirieria* in the Pagodulinae and interpret the latter two groups as Muricidae *incertae sedis* pending further studies.

Two species of *Poirieria* were included in our dataset, both belonging to *Poirieria* s. s. according to the classification of Merle *et al.* (2011). These two species were recovered as a sister group of the Pagodulinae and both have a radular morphology (illustrated by Marshall & Houart, 1995) corresponding to the diagnosis proposed for the Pagodulinae (Barco *et al.*, 2012). The radulae of *Poirieria zelandica*, *P. syrinx* and *P. kopua* share with other pagodulines a rachidian tooth with three major cusps, a larger central cusp with a smaller lateral cusp on each side, two intermediate denticles independent from the central and lateral cusps, and a lack of marginal cusps.

The distinction of *Poirieria*, *Actinotrophon* and *Caelobassus*, as well as their relationship with *Pagodula*, is traditionally defined by shell sculpture, but characters are shared to varying degrees across these genera, specifically: (1) shape of the P1 spine, which may subtubular in *Poirieria* and *Actinotrophon* or nontubular in *Pagodula* and *Caelobassus*; (2) high spire and narrow last adult whorl in *Actinotrophon* and *Pagodula*, lower spire and larger body whorl in *Poirieria* and *Caelobassus*; and (3) presence of P2, P3 and P4 cord spines in *Poirieria* and *Pagodula* versus their absence in *Actinotrophon* and *Caelobassus*. The significance of these differences should be further evaluated in the light of our results (i.e. inclusion of *Poirieria* in Pagodulinae and distinction of *Pagodula* and *Enixotrophon*) and the intrageneric variation observed in *Poirieria* between Atlantic and Austral species (Merle *et al.*, 2011: 152). Living species of *Actinotrophon* have shell (Merle *et al.*, 2011) and radular (Bayer, 1971) morphologies congruent with their inclusion in Pagodulinae, but DNA data are not yet available to confirm this hypothesis. *Caelobassus* is known only as a fossil and resembles Early Paleocene species from Europe currently assigned to *Poirieria*. Because of the uncertainty in evaluating shell morphology in these

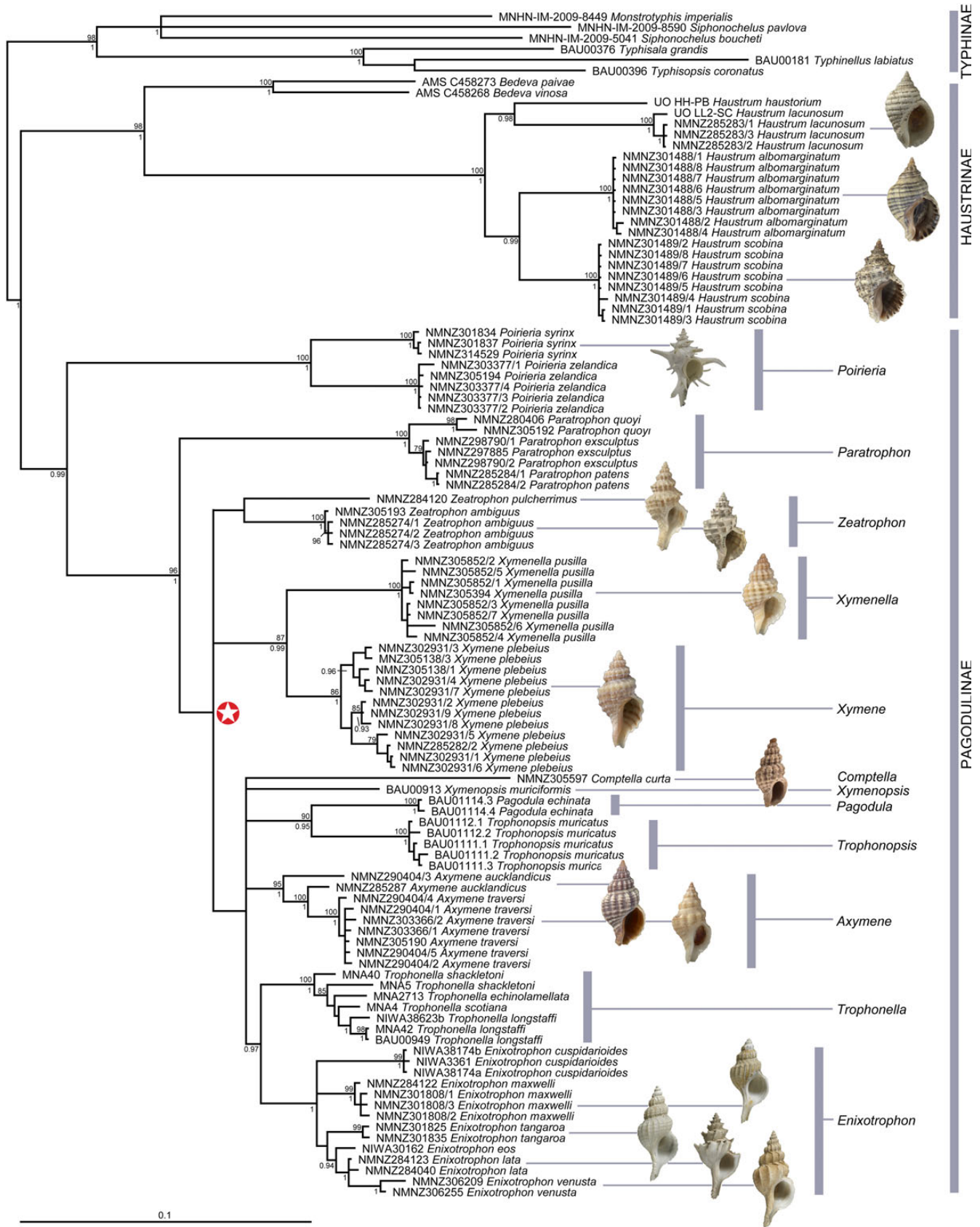


Figure 1. Results of ML and BA phylogenetic analyses of the combined dataset of the muricid subfamilies Haustrinae, Pagodulinae and the genus *Poirieria*. The nomenclature used in the tree reflects the results of the analysis. Bootstrap values (above nodes, percentage values) and posterior probabilities (below nodes, proportion value) are reported only for nodes with high support. The clade containing branching patterns that differ between ML and BA analyses (but which are unsupported) is marked with a star (see text).

early taxa, we support the original classification of *Caelobassus* at genus level in Muricidae *incertae sedis*.

Although not included in our dataset, we believe that sufficient evidence is available for comment on *Flexopteron* Shuto, 1969. Introduced for *F. philippinensis* Shuto, 1969 from Miocene beds in the Philippines, *Flexopteron* has been interpreted as a subgenus of *Paziella* (Merle *et al.*, 2011) or *Poirieria* (Vokes, 1992). The radulae of *Paziella* and living *Flexopteron* species (Harasewych, 1984; Houart, 1985) differ significantly from each other and from those of Pagodulinae. The rachidian tooth of *Paziella pazi* (Harasewych, 1984: fig. 27) has a central cusp projecting at about 90° relative to the basal plate, while the rachidian tooth of *Flexopteron primanova* (Houart, 1985: fig. 3) has central and lateral cusps with the same orientation and a narrower basal plate, but differs from that of pagodulines in having marginal cusps. Accordingly, we doubt that there is any close relationship between *Flexopteron*, *Poirieria* and *Paziella*, and therefore assign *Flexopteron* and *Paziella* at full generic rank within the Muricidae *incertae sedis*.

Haustrinae

Our phylogenetic analysis supports the distinction of *Bedevea* and *Haustrum* as discrete genera within Haustrinae, and assignment of *Haustrum vinosum* Lamarck, 1822 to *Bedevea*. Tan (2003) recovered our same *Bedevea* clade embedded within the other Haustrinae ('clade N', including *B. paivae* and *B. vinosa*, the latter species classified as *Lepsiella*), but support was provided by the sole synapomorphy of having lenticular egg capsules. According to Tan (2003) this character is equivocal because of its appearance in some rapanines and ergalataxines as well as in *Zeatrophon ambiguus*. *Bedevea paivae* and *B. vinosa* were also morphologically distinct, with the former species possessing at least five autapomorphies.

Our second clade of Haustrinae comprises *H. haustorium* (the type species of *Haustrum*), *H. lacunosa*, *H. scobina* and *H. albomarginatum*. The latter has at times been treated as a subspecies or a synonym of *H. scobina* (e.g. Powell, 1979; Tan, 2003), although we recovered them as two monophyletic clades with an average K2P interspecific distance of 0.051, indicating that they are distinct species, thus supporting the findings of Knox (1963), Kitching & Lockwood (1974) and Smith & McVeagh (1991), which have been overlooked by subsequent compilers and revisers (e.g. Powell, 1979; Tan, 2003).

The geographic distribution of Haustrinae species included in our analysis supports our two-genus classification: *Bedevea paivae* and *B. vinosa* are endemic to southern Australia, while true *Haustrum* appears to be restricted to New Zealand. According to this hypothesis, the only Haustrinae missing from our dataset [*H. baileyana* (Tenison Woods, 1881) and *H. flindersi* (A. Adams & Angas, 1863) from southern Australia (Tan, 2003)], may prove to belong in *Bedevea*. This geographic separation suggests a vicariant origin of the two lineages, consistent with the low dispersal potential of living Haustrinae species (Tan, 2003). This hypothesis, however, needs to be tested by examination not only of living but also fossil taxa, whose dispersal potential might have been different. The Quaternary species described in '*Lepsiella*' from southern South America by Gordillo & Nielsen (2013) apparently originated from Australasia by means of the Antarctic Circumpolar Current during a Quaternary glacial period; whether its relationships are with *Bedevea* or *Haustrum* is unclear.

Pagodulinae

Barco *et al.* (2012) erected Pagodulinae based on the analysis of molecular data for *Trophonella* species, *Zeatrophon pulcherrimus* and the type species of *Pagodula* and *Xymenopsis*. The New Zealand

species herein referred to *Enixotrophon*, *Trophonopsis* and *Paratrophon* were assigned to Pagodulinae on the basis of their pagoduline radula and the external morphology of the penis. In this contribution we have increased the taxonomic coverage to confirm and enhance this classification.

Barco *et al.* (2012) recovered *Pagodula echinata* and the New Zealand species assigned to *Pagodula* by Marshall & Houart (2011) as discrete clades. The use of *Pagodula* is here restricted to the clade including the type species, *P. echinata*. Marshall & Houart (2011) included *Trophon carduelis* Watson, 1883, the type species of *Enixotrophon* Iredale, 1929, in their review of *Pagodula*, and *Enixotrophon* is thus available as a genus for the southern species they assigned to *Pagodula*. Despite the clear distinction of the two genera in our tree, no evident morphological characters were found to distinguish them.

We also include *Trophon cuspidarioides* in *Enixotrophon*, based on three specimens from Scott seamounts analysed previously (Barco *et al.*, 2012: fig. 6). The identification of these specimens is provisional, pending the availability of molecular-grade specimens of *Trophon cuspidarioides* from the type locality, but the 'pagodula-like' radulae and shells suggest that this and some other Antarctic and subantarctic species currently assigned to *Trophon* also belong in *Enixotrophon*. The radula of *T. geversianus* (Pallas, 1774) (type species of *Trophon*) is easily distinguished from that of pagodulines by the presence of pronounced marginal cusps on the rachidian tooth (Harasewych, 1984: fig. 25), while the Antarctic *T. cuspidarioides*, *T. emilyae*, *T. declinans*, *T. arnaudi* and *T. scolopax* have no marginal cusps (Pastorino, 2002; Barco *et al.*, 2012). The similarity of these and New Zealand *Enixotrophon* species was indicated by Marshall & Houart (2011) with respect to *T. arnaudi* and *T. declinans*. On the other hand, *T. scolopax* and *T. septus* seem more likely to belong in *Nodulotrophon* Habe & Ito, 1965, in our opinion.

Trophonopsis and *Pagodula*, the only pagoduline genera known with certainty from the northern hemisphere, are represented here by sequences obtained from their respective type species. Our tentative inclusion of *Boretrophon* in Pagodulinae is based exclusively on radula morphology of the type species (Houart, 2001; Barco *et al.*, 2012).

Relationships among the small New Zealand muricids have been variously interpreted (see Introduction). In our topology (Fig. 1) each genus is represented by a distinct monophyletic clade with high support (except *Zeatrophon*, which will be treated elsewhere). Protoconch morphology was the major criterion for discrimination of genera in the classification proposed by Finlay (1926). Beu (2011) resurrected these groups based on shell morphology and they will be further discussed elsewhere (Marshall & Houart, in prep.). Relationships of *Comptella* have been uncertain since its introduction (Barco *et al.*, 2012), but the phylogenetic analyses support its inclusion in Pagodulinae.

Terefundus, *Lenitrophon* and *Minortrophon*, the remaining genus groups with New Zealand type species, are still of doubtful classification. *Terefundus* is included in Pagodulinae because of general similarities of the shell to those of *Xymene* and *Xymenella* species. The classification of *Lenitrophon* and *Minortrophon* will be considered elsewhere (Marshall & Houart, in prep.).

Within Pagodulinae we found cases of incongruence between morphological identifications and molecular results. Specimens of *Trophonella shackletoni* and *Axymene aucklandicus* did not form monophyletic groups and had distances greater than the intra-specific threshold. In both cases, genetic structure and morphological variations should be evaluated before drawing further conclusions. The former species, however, is known to vary morphologically across its range, with two recognized subspecies, *T. s. shackletoni* and *T. s. paucilamellatus*. Specimens of *Paratrophon patens* were monophyletic but embedded within the *P. exculptus* clade, yet the average interspecific distance was particularly low (0.012). This low genetic distance suggests that

morphological differences observed between the two putative *Paratrophon* species may represent intraspecific variability within a single species.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

ACKNOWLEDGEMENTS

We thank Serge Gofas (University of Malaga, Spain) for the loan of Mediterranean specimens. This is Barcoding of Antarctic Marine Biodiversity (BAMBi) contribution no. 6; BAMBi was funded by the Italian Antarctic research programme (PNRA). Two anonymous reviewers are thanked for constructive criticisms.

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APPENDIX: CHECKLIST OF RECENT HAUSTRINAE AND PAGODULINAE

Superfamily MURICOIDEA Rafinesque, 1815 Family MURICIDAE Rafinesque, 1815 Subfamily HAUSTRINAE Tan, 2003

Genus *Bedeve* Iredale, 1924

Type species (by original designation) *Trophon hanleyi* Angas, 1867 = *T. paivae* Crosse, 1864; Recent, Australia.

Included species:

baileyana (Tenison Woods, 1881)
elongata (Tryon, 1880)
flindersi (A. Adams & Angas, 1864)
paivae (Crosse, 1864)
vinosa (Lamarck, 1822)
?sumatraensis (Thiele, 1925)

Genus *Haustrum* Perry, 1811

Type species (ICZN, 1957: Opinion 479): *Buccinum haustorium* Gmelin, 1791; Recent, New Zealand.

Included species:

albomarginatum (Deshayes, 1839)
haustorium (Gmelin, 1791)
lacunosum (Bruguière, 1789)
scobina (Quoy & Gaimard, 1833)

Subfamily PAGODULINAE Barco, Schiaparelli, Houart & Oliverio, 2012

Genus *Axymene* Finlay, 1926

Type species (by original designation): *Axymene turbator* Finlay, 1926 = *Euthria aucklandica* E.A. Smith, 1902; Recent, New Zealand.

Included species:

aucklandicus (E.A. Smith, 1902)
traversi (Hutton, 1873)

Genus *Boreotrophon* P. Fischer, 1884

Type species (by monotypy): *Murex clathratus* Linnaeus, 1767; Recent, northeastern Atlantic.

Included species:

alaskanus Dall, 1902

albus Egorov, 1992
aomoriensis (Nomura & Hatai, 1940)
apolyonis (Dall, 1919)
avalonensis Dall, 1902
bentleyi Dall, 1908
cymatus Dall, 1902
candelabrum (Reeve, 1848)
cepula (Sowerby, 1880)
clathratus (Linnaeus, 1767)
clavatus (Sars, 1878)
dabneyi (Dautzenberg, 1878)
disparilis (Dall, 1891)
egorovi Houart, 1995
elegantulus (Dall, 1907)
eucymatus (Dall, 1902)
flos (Okutani, 1964)
gaidenkoi Houart, 1995
hazardi McLean, 1996
houarti Egorov, 1994
kabati McLean, 1996
keepi (Strong & Hertlein, 1937)
macouni Dall & Bartsch, 1910
mazatlanicus Dall, 1902
multicostatus (Eschscholtz, 1829)
okhotensis Egorov, 1993
pacificus Dall, 1902
?pedroanus (Arnold, 1903)
pygmaeus Egorov, 1994
rotundatus Dall, 1902
tolomius (Dall, 1919)
triangulatus (Carpenter, 1864)
tripherus Dall, 1902
trophonis Egorov, 1993
truncatus (Ström, 1768)
xestra Dall, 1918

Genus *Comptella* Finlay, 1926

Type species (by original designation): *Trophon (Kalydon) curta*
 R. Murdoch, 1905; Recent, New Zealand.

Included species:
coronata Dell, 1956
curta (R. Murdoch, 1905)
devia (Suter, 1908)

Genus *Enixotrophon* Iredale, 1929

Type species (by original designation): *Trophon carduelis*
 Watson, 1883; Recent, eastern Australia, Tasman Sea and
 New Zealand.

Included species:
acceptans (Barnard, 1959)
araios (Houart & Engl, 2007)
arnaudi (Pastorino, 2002)
atanua (Houart & Tröndlé, 2008)
carduelis (Watson, 1882)
ceciliae (Houart, 2003)
columbarioides (Pastorino & Scarabino, 2008)
condei (Houart, 2003)
concepcionensis (Houart & Sellanes, 2006)
cuspidarioides (Powell, 1951)
declinans (Watson, 1882)
emilyae (Pastorino, 2002)
eos (Marshall & Houart, 2011)
eumorphus (Marshall & Houart, 2011)
fasciolaroides (Pastorino & Scarabino, 2008)
hastulus (Marshall & Houart, 2011)
johannthielei (Barnard, 1959)*
kosunorum (Houart & Lan, 2003)

latus (Marshall & Houart, 2011)
lochi (Marshall & Houart, 2011)
macquariensis (Powell, 1957)
maxwelli (Marshall & Houart, 2011)
multigradus (Houart, 1990)
obtusus (Marshall & Houart, 2011)
obtuseliratus (Schepman, 1911)
occiduus (Marshall & Houart, 2011)
planispinus (E.A. Smith, 1906)
plicilaminatus (Verco, 1909)
poirieria (Powell, 1951)
procerus (Houart, 2001)
pulchellus (Schepman, 1911)
pygmaeus (Marshall & Houart, 2011)
sansibaricus (Thiele, 1925)
siberutensis (Thiele, 1925)
similidroueti (Houart, 1989)
tangaroa (Marshall & Houart, 2011)
tenuirostratus (E.A. Smith, 1899)
venustus (Marshall & Houart, 2011)
veronicae (Pastorino, 1999)
vangoethemi (Houart, 2003)
ziczac (Tiba, 1981)

**Enixotrophon pulchellus* was tentatively synonymized with *Trophon johannthielei* Barnard, 1959 by Houart (1987), Houart, Kilburn & Marais (2010) and Marshall & Houart (2011). From study of additional material from Mozambique (MNHN, all juveniles, and RH) specimens from Mozambique have a much smaller and narrower protoconch than specimens from French Polynesia and Papua New Guinea (width 550–600 vs 750–800 µm). We prefer to treat *E. johannthielei* as a valid species, awaiting comparison of adult material from Mozambique, and/or DNA analysis.

Genus *Pagodula* Monterosato, 1884

Type species (by subsequent designation of Houart & Sellanes 2006: 59, by application of ICZN, 1999: Art. 70.3): *Fusus echinatus* Kiener, 1840; Recent, western Mediterranean and northeastern Atlantic.

Included species:
abyssorum (Verrill, 1885)
aculeata (Watson, 1882)
cossmanni (Locard, 1897)
echinata (Kiener, 1840)
?fraseri (Knudsen, 1956)*
golikovi (Egorov, 1992)
guineensis (Thiele, 1925)
lacunella (Dall, 1889)
limicola (Verrill, 1885)
mucrone (Houart, 1991)
parechinata Houart, 2001
verillii (Bush, 1893)

*This species was included in *Boreotrophon* by Houart (1997a: 60). The shouldered whorls and axial lamellae ending as open spines on the shoulder angulation are typical for *Pagodula*, but some forms have strongly rounded axial ribs without any lamellae, which is atypical.

Genus *Paratrophon* Finlay, 1926

Type species (by original designation): *Polytropha cheesemani*
 Hutton, 1882; Recent, New Zealand.

Included species:
cheesemani cheesemani (Hutton, 1882)
cheesemani exculptus Powell, 1933
patens (Hombron & Jacquinot, 1848)
quoyi (Reeve, 1846)

Genus *Poiriera* Jousseume, 1880

Type species (by original designation): *Murex zelandicus* Quoy & Gaimard, 1833; Recent, New Zealand.

Included species:

kopua Dell, 1956
syrinx Marshall & Houart, 1995
zelandica (Quoy & Gaimard, 1833)

Genus *Terefundus* Finlay, 1926

Type species (by original designation): *Trophon crispulatus* Suter, 1908; Recent, New Zealand.

Included species:

anomalus Dell, 1956.
?axirugosus Dell, 1956
crispulatus (Suter, 1908)
cuvierensis (Mestayer, 1919)
quadrinotus quadrinotus (Suter, 1908)
quadrinotus uncarinatus (Dell, 1956)

Genus *Trophonella* Harasewych & Pastorino 2010

Type species (by original designation): *Trophonella rugosolamellata* Harasewych & Pastorino, 2010; Recent, Antarctica.

Included species:

echinolamellata (Powell, 1951)
enderbyensis (Powell, 1958)
eversoni (Houart, 1997b)
longstaffi (E.A. Smith, 1907)
rugosolamellata Harasewych & Pastorino, 2010
scotiana (Powell, 1951)
shackletoni (Hedley, 1911)

Genus *Trophonopsis* Bucquoy & Dautzenberg, 1882

Type species (by original designation): *Murex muricatus* Montagu, 1903; Recent, Mediterranean and northeastern Atlantic.

Included species:

?aberrans (Houart, 1991)
barvicensis (Johnston, 1825)
breviata (Jeffreys, 1882)
densilamellata Golikov & Gulbin, 1977
diazii (Durham, 1942)
droueti (Dautzenberg, 1889)
?kayae Habe, 1981
?mioplectos (Barnard, 1959)
muricatus (Montagu, 1803)
nana Egorov, 1994
orpheus (Gould, 1849)
pistillum (Barnard, 1959)
polycyma Kuroda, 1953

Genus *Xymene* Iredale, 1915

Type species (by original designation): *Fusus plebeius* Hutton, 1873; Recent, New Zealand.

Included species:

huttonii (R. Murdoch, 1900)
plebeius (Hutton, 1873)

pumilus (Suter, 1899)

teres (Finlay, 1930)

warreni Ponder, 1972

Genus *Xymenella* Finlay, 1926

Type species (by original designation): *Trophon pusillus* Suter, 1907; Recent, New Zealand.

Included species:

pusilla (Suter, 1907)

Genus *Xymenopsis* Powell, 1951

Type species (by original designation): *Fusus liratus* Gould, 1849 = *Buccinum muriciformis* King, 1832; Recent, southern Chile and Tierra del Fuego.

Included species:

buccineus (Lamarck, 1816)
corrugatus (Reeve, 1845)
muriciformis (King & Broderip, 1831)
subnodosus (Gray, 1839)
?tcherniai (Gaillard, 1954)

Genus *Zeatrophon* Finlay, 1926

Type species (by original designation): *Fusus ambiguus* Philippi, 1844; Recent, New Zealand.

Included species:

ambiguus (Philippi, 1844)
mortenseni mortenseni (Odhner, 1924)
mortenseni caudatinus (Finlay, 1930)
pulcherrimus (Finlay, 1930)

MURICIDAE incertae sedis ('basal' Muricidae of Merle et al., 2011)**Genus *Actinotrophon* Dall, 1902**

Type species (by original designation): *Trophon actinophorus* Dall, 1889; Recent, Western Atlantic from Bahamas to Brazil, Panama and Colombia.

Included species:

actinophorus (Dall, 1889)
fragilis (Houart, 1996)
tenuis (Houart, 2001)

Genus *Caelobassus* Stilwell & Zinsmeister, 1992

Type species (by original designation): *Caelobassus radwini* Stilwell & Zinsmeister, 1992; Late Eocene, Seymour Island, Antarctica.

No Recent species.

Genus *Flexopteron* Shuto, 1969

Type species (by original designation): *Flexopteron philippinensis* Shuto, 1969; Late Miocene, Philippines.

Included species:

?oliverai (Kosuge, 1984)
poppei (Houart, 1993)
primanova (Houart, 1985)