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# Whelks, rock-snails, and allied: a new phylogenetic framework for the family Muricidae (Mollusca: Gastropoda)

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## Abstract

The worldwide distributed neogastropod family Muricidae comprises more than 1800 extant species of whelks, rock-shells, murex-shells, drill-shells, and coral-shells. Despite several attempts at a taxonomic revision based on morphological characters, the systematics of this family is still largely debated. Here, we present a molecular revision of the family Muricidae based on the largest dataset analysed so far, which comprises 384 specimens representing 360 species and includes, for the first time, all the currently recognised subfamilies. A molecular dataset of *cox1*, *12S rRNA*, *16S rRNA*, and *28S rRNA* genetic markers and six fossil-based calibration points were used to produce time-calibrated phylogenetic reconstructions, using a Maximum Likelihood approach. Our results confirmed the monophyly of most of the accepted subfamilies, suggested a revision of the taxonomic composition of Muricopsinae and Muricinae, and highlighted some lineages not immediately comprised in any of the recognised subfamilies. The origin and early diversification of the subfamilies of Muricidae occurred between 32 and 60 million years ago.

**Keywords:** *Muricidae*, *phylogeny*, *diversity*, *molluscs*, *tree dating*

## Introduction

The neogastropod family Muricidae is one of the most species-rich families of Gastropoda, with an estimate of more than 1800 extant species of whelks, rock-shells, murex-shells, drill-shells, and coral-shells (MolluscaBase eds. 2023). The family is distributed worldwide in all oceans, from the lower intertidal down to more than 6000 m (Sysoev 1992) and all its members are carnivores, mostly predators with a varying degree of trophic specialisation, from generalists to highly specialised. Muricids have been known to man since ancient times: Mediterranean species were used

by the Phoenicians to produce their Tyrian purple dye, and Greeks, Arabians, and Chinese employed muricid species for pharmacological use (Benkendorff et al. 2015). Nowadays, some rock shells have economic relevance, either since they are consumed as food (e.g. species of *Murex*, *Concholepas*, *Hexaplex*, *Bolinus*, and *Chicoreus*) or being pests of commercial oyster farms (Buhle & Ruesink 2009).

The classification of the family was repeatedly revised in the last century based on conchological features of extant and fossil taxa and on radular

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characters (Cossmann 1903; Thiele 1929; Keen 1971; Radwin & D’Attilio 1971; Ponder & Warén 1988; Vokes 1996; Bouchet & Rocroi 2005), while only a single comprehensive attempt at building a molecular phylogenetic framework has been performed to date (Barco et al. 2010), along with a few other works at the subfamily level that almost invariably resulted in significant changes (Oliverio & Mariottini 2001; Claremont et al. 2008, 2013; Barco et al. 2012, 2015, 2016). More recently, muricid mitogenomes have been used to address phylogenetic relationships among muricid subfamilies, by Harasewych and Sei (2022) with nine mitogenomes representing six subfamilies, and Yu et al. (2023) with 24 mitogenomes representing five subfamilies.

The classification of muricids is therefore still debated, especially regarding the familial or subfamilial ranking of some groups. A first endeavour by Cossmann (1903) divided the superfamily Muricoidea (as “cénacle” Muricacea) into three families based on shell morphology (Muricidae, Purpuridae, and Coralliophilidae), and recognized five subfamilies of Muricidae based on opercular differences (Muricinae: apical nucleus; Ocenebrinae: lateral nucleus; Trophoninae: sublateral nucleus; Typhinae: apical nucleus, shell with anal tube; Rapaninae: purpurid operculum, muricid-like shell). In recent time, modern recognition of muricid subfamilies (e.g. Bouchet & Rocroi 2005) is still largely based on radular differences, identifying a single family, Muricidae, containing 11 subfamilies: Muricinae Rafinesque, 1815, Muricopsinae Radwin & D’Attilio, 1971, Ocenebrinae Cossmann, 1903, Trophoninae Cossmann, 1903, Typhinae Cossmann, 1903, Tripterotyphinae D’Attilio & C. M. Hertz, 1988, Ergalataxinae Kuroda, Habe & Oyama, 1971, Rapaninae Gray, 1853, Haustriinae K. S. Tan, 2003, Aspellinae Keen, 1971, and Coralliophilinae Chenu, 1859. One additional subfamily was more recently recognised: Pagodulinae Barco, Schiaparelli, Houart, Oliverio, 2012 (Barco et al. 2010, 2012). This 12-subfamilies scheme was recently adopted by Houart (2018) and Merle et al. (2022).

In the present study, we investigated the phylogeny of the family Muricidae based on the largest dataset analysed so far, including, for the first time, all the currently recognised subfamilies. The phylogenetic reconstructions were also time-calibrated with several fossil records to produce a robust framework for further studies of the biology and the evolution of this family.

## Materials and methods

### Dataset

The molecular analysis was based on sequences of four molecular markers: one nuclear (*28S rDNA*) and three mitochondrial (*cox1*, *12S rDNA*, *16S rDNA*), including sequences newly produced for this work as well as sequences retrieved from the GenBank (Supplementary Materials Table S2).

For the newly produced sequences (170), DNA was extracted from tissue samples at the Service de Systématique Moléculaire (UAR 2AD, MNHN, Paris) using the Epmotion 5075 robot (Eppendorf), following the manufacturer’s recommendations, or at the Department of Biology and Biotechnologies “Charles Darwin” of Sapienza University of Rome, with standard phenol/chloroform (Oliverio & Mariottini 2001) or “salting out” protocols (Fassio et al. 2022). Polymerase chain reactions (PCR) were performed with 1–3 µL of DNA template in a 25 µL reaction volume, including 2.5–3 µL of 10 × NH<sub>4</sub> reaction buffer, 2.5–3 µL of 50 mM MgCl<sub>2</sub> solution, 0.15–0.2 µL of BIOTAQ DNA polymerase, 0.4 µL of each 25 pM primer solution, 1 µL of 10% bovine serum albumin solution, and 0.5 µL of 10 mM nucleotide mix solution (Fassio et al. 2022). The PCR conditions were as follows: initial denaturation (4 min at 94°C); 35 cycles of denaturation (30 s at 94°C), annealing (40 s at 48–52°C for *cox1* and *16S*; 40 s at 58–62°C for *28S*; 60 s at 58–66°C for *12S*) and extension (1 min at 72°C); and final extension (10 min at 72°C). Primers used to amplify the selected markers are reported in Table S1. The PCR products were purified using ExoSAP-IT (USB Corporation) and sequenced at Macrogen, Inc. or by the Eurofins sequencing facility.

Additionally, 3,980 sequences of the barcode markers *cox1*, 911 of the *16S*, 806 of the *12S*, and 832 of the *28S*, were retrieved from the GenBank.

Sequences were aligned either using the Geneious R7 algorithm (Kearse et al. 2012) (*cox1*) or with the software MAFFT (Kuraku et al. 2013; Katoh et al. 2019), choosing the Q-INS-I algorithm (*12S*, *16S*, and *28S*). The hypervariable regions of the *12S*, *16S*, and *28S* alignments were excluded from the analysis after identification through the software Gblocks (v. 0.91b, Castresana 2000 – all options set for the least stringent selection). A concatenated dataset was assembled with SequenceMatrix (Vaidya et al. 2011).

Taxonomic identification of every specimen was based on morphological examination of each voucher, where available. The identity of those specimens for which that was not possible was checked – as far as possible – by their position in the *cox1* single-gene trees (see below for methods details) preferably in relation to pedigreed sequenced vouchers from publicly available collections included in the dataset. Single gene trees were used to discard contaminations, sequencing artefacts and redundant identical sequences, to have a single or few representatives for each species.

Thereafter, the final dataset was defined through a selection of sequences that maximised the taxonomic coverage of the family and the gene coverage of each species, removing redundancy. Four species of Buccinoidea (Oliverio & Modica 2010) were included in the dataset as an outgroup for rooting the trees: *Buccinum undatum* Linnaeus, 1758, *Kelletia lischkei* Kuroda, 1938, *Penion ormesi* (Powell, 1927), *Serratifusus lineatus* Harasewych, 1991.

#### Phylogenetic analyses and temporal calibration

The substitution model for each partition (12S, 16S, 28S, and 1st, 2nd, and 3rd codon positions of *cox1*) was chosen with PartitionFinder 2 (Lanfear et al. 2016). Uncalibrated phylogenetic analyses were performed by ML on single gene datasets with IQTree v2.0.3 (Nguyen et al. 2014).

The concatenated dataset along with six calibration points were used to produce time-calibrated trees to estimate the node ages of each clade of the family Muricidae using a Maximum Likelihood (ML) approach. We identified the six calibration points for the phylogenetic trees of Muricidae, based on the most reliable fossil data (Table I). The first appearance of the family is witnessed in the Upper Cretaceous of Texas (Merle et al. 2011) with the earliest known species attributed to **Muricidae (1)**, *Paziella (Flexopteron) cretacea* (Garvie, 1991) from the Maastrichtian (c. 70 million years ago, mya); the family was certainly

Table I. Date intervals (95% confidence range in mya) obtained from least-squares ML analyses (by IQTree) for selected major nodes, along with fossil records used as calibration points. \*based on Douglas et al. (2014); samples from Seymour Island suggested to be older (45.8–58.4 mya) based on Montes et al. (2019).

| Node                     | Old(est) fossil records  | Used calibration point | ML results  |
|--------------------------|--|------------------------|-------------|
| Muricidae                | In the interval 70–112 mya according to Merle et al. (2011). Oldest undisputable muricid, <i>Flexopteron cretacea</i> from the Upper Cretaceous (Maastrichtian=c. 70 mya) (Merle et al., 2022)   | (1) 70–112 mya         | 80          |
| Typhinae                 | <i>Laevityphis muticus</i> from the lower Ypresian (48.6–55.8 mya) of England and France (Merle et al., 2022)  | (2) 48.6–55.8 mya      | 39.49–48.35 |
| Ocenebrinae              | <i>Ocenebrina varisulcata</i> from the Middle Eocene (Bartonian, 37.8–41.2 mya) (Merle et al., 2022)   | (3) 37.8–41.2 mya      | 20.94–30.24 |
| Trophoninae              | <i>Gemixystus nyxii</i> from the the Ypresian of France (48–56 mya), or <i>Trophon disparoides</i> from the Late Eocene of Antarctica (34–45 mya*) (Griffin & Pastorino, 2005)   |                        |             |
| Ocenebrinae+ Trophoninae |  |                        | 34.26–44.37 |
| <i>Nucella</i>           | (Collins, 1996)  | (4) 20.4–23 mya        | 10.57–15.42 |
| <i>Murex trapa</i>       | Plio-Pleistocene (MNHN collection)   | (5) 0.01–5.3 mya       | 0–0.49      |
| <i>Timbellus</i>         | Danian 61.6–66 (Merle 2022)  | (6) 61–66 mya          | 24.19–35.82 |
| Muricinae s.s.           |  |                        | 30.38–38.75 |
| Muricopsinae             | <i>Eofavaria</i> sp. 1 from lowermost early Eocene of Alabama (47.8–56 mya: Vokes, 1994)<br>From the Priabonian of France ( <i>Murexsul primigenius</i> ) and of S Australia ( <i>M. prionotus</i> ) (33.8–37.8 mya: Merle et al., 2022) |                        | 46.22–54.86 |
| Pagodulinae              |  |                        | 30.37–39.44 |
| Haustrinae               | <i>Haustrum intermedium</i> from the early Miocene (Aquitainian) of NZ (Merle et al., 2022) 20.4–23  |                        | 27.79–36.02 |
| Ergalataxinae            | <i>Taurasia sacyi</i> from the Early Oligocene of France (Rupoelian, 28.4–33.9), or <i>Orania fischeri</i> from the Late Oligocene of Aquitaine (Chatian, 23.3–27.8) (Merle et al., 2022)  |                        | 41.05–52.93 |
| Coralliophilinae         | <i>Timotia aldrichi</i> from the Middle Eocene (Bartonian = 37.8–41.2 mya) of Mississippi and Louisiana  |                        | 73.06–79.60 |
| Rapaninae                | <i>Cymia berryi</i> Olsson, 1931, from the Late Eocene (37.2–33.9 mya) of Peru (Vermeij & Carlson, 2000)   |                        | 55.69–65.42 |

not present before the Albian (Lower Cretaceous, 112 Mya), which was set as the lower bound (Barco et al. 2012). The fossil record of **Typhinae (2)** places the first certain appearance of the subfamily (quite typical morphologically) in the Lower Eocene (Ypresian) (MHNH collection) based on the occurrence of *Typhis tubifer* (Bruguière, 1792) and on *Laevityphis muticus* from the lower Ypresian of England and France (Merle et al. 2022). Fossils belonging to the subfamily **Ocenebrinae (3)** are common in the lower Miocene, and the earliest known species is *Ocenebrina rarisulcata* from the Middle Eocene (Bartonian, 37.8–41.2 mya) (Merle et al. 2022). The genus *Nucella* (Ocenebrinae) **(4)**, has its first documented record in the lower Miocene (Aquitanian, c. 22.5 mya) (Collins et al. 1996). For the genus *Murex*, fossil records of *Murex trapa* **(5)** appeared during the Pliocene of Java (Ponder & Vokes 1988). The genus *Timbellus* **(6)** has the first documented appearance in the Lower Eocene (Danian, 61.6–66 mya) (Merle et al. 2022).

A Bayesian inference approach was attempted using the software BEAST 1.8.0 (Drummond et al. 2012) but, despite numerous and long runs, none of the analyses reached convergence. ML time calibrated analyses were performed with the software IQTree v2.0.3 (Nguyen et al. 2014) and LSD21 (To et al. 2016) implemented in R (version 4.2.1, R Core Team 2022). We estimated divergence times with this distance-based calibration method implementing the least-squares dating criterion (–date). We set tips to the present time (–date-tip 0) and calculated a confidence interval based on 100 iterations (–date-ci 100), using the same dataset partition of the not-dated phylogenetic analysis. The default settings employed a birth-death tree prior in combination with a clock.rate = 0 and a ucl.d.mean value of 0.05. Ultrafast bootstraps (Ufb: 10000 replicates; Hoang et al. 2017) were performed, with 25% samples of burn-in, to evaluate the support of tree branches.

Phylogenetic trees were drawn using FigTree v. 1.4.4 (Rambaut 2018). For all the phylogenetic analyses, nodes with ultrafast Bootstraps (Ufb)  $\geq 95\%$  were considered as statistically supported.

Phylogenetic analyses were run on the Plateforme de Calcul Intensif et Algorithmique PCIA (UAR2700 2AD, MNHN), on the CIPRES Science Gateway (Miller et al. 2010), and on Terastat2 (Department of Statistical Science, Sapienza University of Rome; Bompiani et al. 2020).

## Results

After quality testing all the sequences, checking for consistency and redundancy, and assessing

a taxonomic ID to each sequence, we eventually selected the final dataset to maximise the number of represented species. The final dataset was composed of 384 muricid specimens, representative of 360 species, 80 of which type species (Supplementary Material Table S2 and Figure S1), and included 170 newly produced sequences. The final combined alignment after Gblocks was 3179 bp long, of which 455 bp for the *12S*, 649 bp for the *16S*, 1417 bp for the *28S* and 658 bp for the *cox1*.

The substitution models found by Partition Finder 2 for each partition of our dataset are shown in Table S3.

### Phylogenetic reconstruction

The single gene (Supplementary Material Figures S1–S4) and combined dataset (Figures 1 and 2) phylogenetic analyses yielded broadly congruent trees for the major supported nodes.

Fully supported nodes corresponding to subfamilies were as follows: Coralliophilinae (Ufb 100%), Rapaninae (Ufb 100%), Ocenebrinae (Ufb 100%), Haustrinae (Ufb 100%), Typhinae (Ufb 99%), and Pagodulinae (Ufb 100%).

The subfamily Ergalataxinae was recovered as monophyletic (Ufb 100%) with two exceptions: *Daphnellopsis lamellosa*, which was the sister taxon to the clade of *Pterynotus* (Ufb 85%), formerly ascribed to Muricinae; and *Orania nodosa* that ended up inside the rapanine clade (Ufb 100%).

A large clade of core Muricinae (Ufb 100%) was defined, which included species of the type genus *Murex*, as well as of the genera *Chicoreus*, *Muricanthus*, *Haustellum*, *Hexaplex*, *Naquetia*, *Chicomurex*, *Phyllonotus*, *Siratus*, *Bolinus*, *Vokesimurex*. The genera *Timbellus* (Ufb 100%) and *Pterynotus* (Ufb 100%) and the species *Flexopteron poppei* and *Ponderia magna*, traditionally in Muricinae, resulted in four distinct lineages, even if their relationships with other nearby clades were not supported, with the exception of *Ponderia magna* that was the sister lineage to the clade Haustrinae + Pagodulinae (Ufb 100%).

The subfamily Muricopsinae as traditionally conceived, did not form a clade. The clade including the type genus *Muricopsis* (Ufb 99%), as well as the genera *Acanthotrophon*, *Favartia*, *Murexsul*, *Pazinotus*, *Zetecopsis*, and *Xastilia*, included also the genera *Attaliosa*, *Aspella*, and *Dermomurex* (formerly classified in the subfamily Aspellinae), and *Tripterotyphis triangularis* (formerly in the Tripterotyphinae). Conversely, the genus *Vitularia* – traditionally included in the Muricopsinae – formed a distinct lineage (Ufb



Figure 1. Maximum Likelihood phylogenetic reconstruction of the family Muricidae using IQTree. Values at nodes indicate ultrafast bootstrap support. Three letters at the end of each specimen's label along with colours (as in Figure 2) indicate the current subfamily assignment. Type species are indicated with an \* at the end of the name.

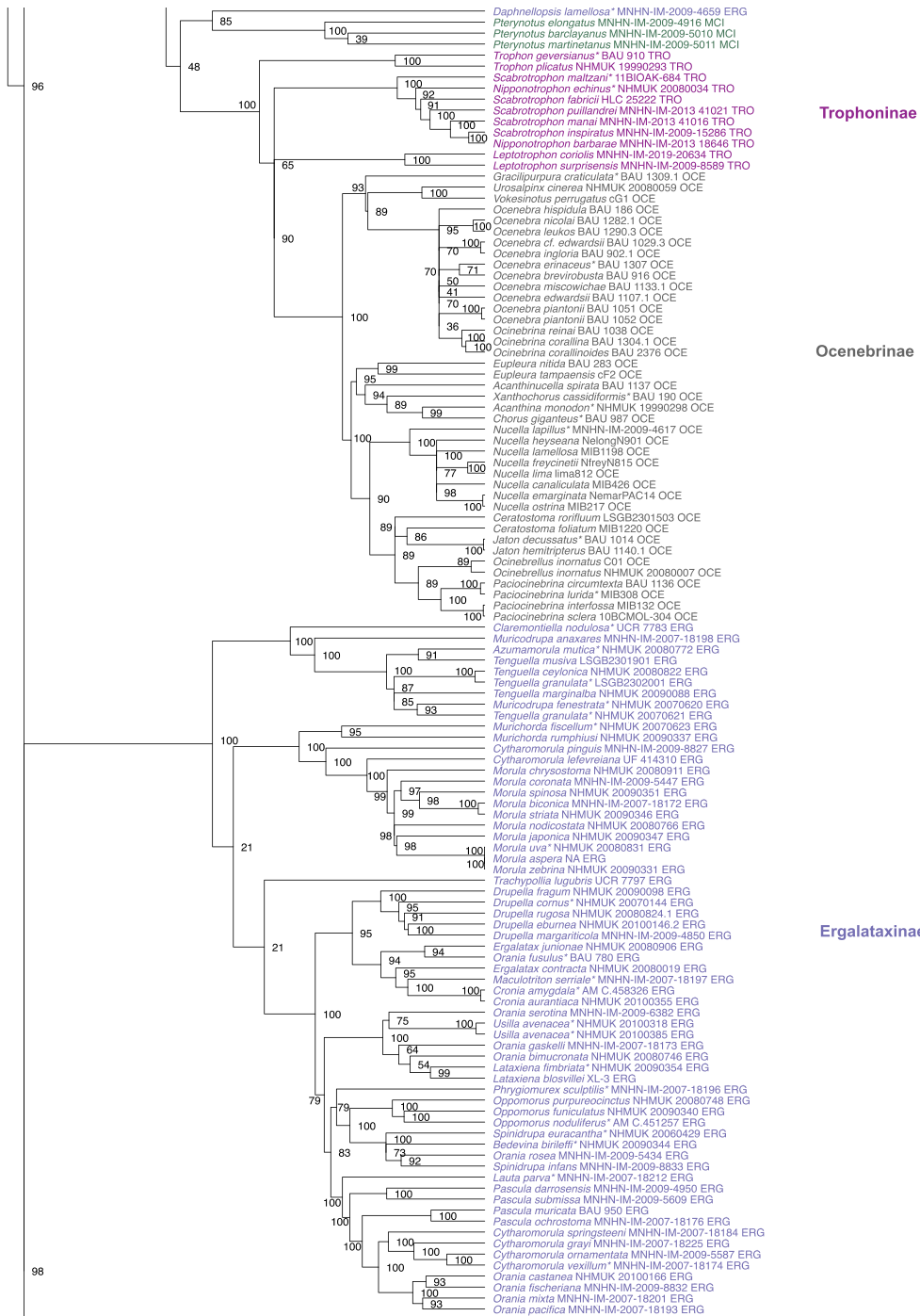


Figure 1. (Continued).

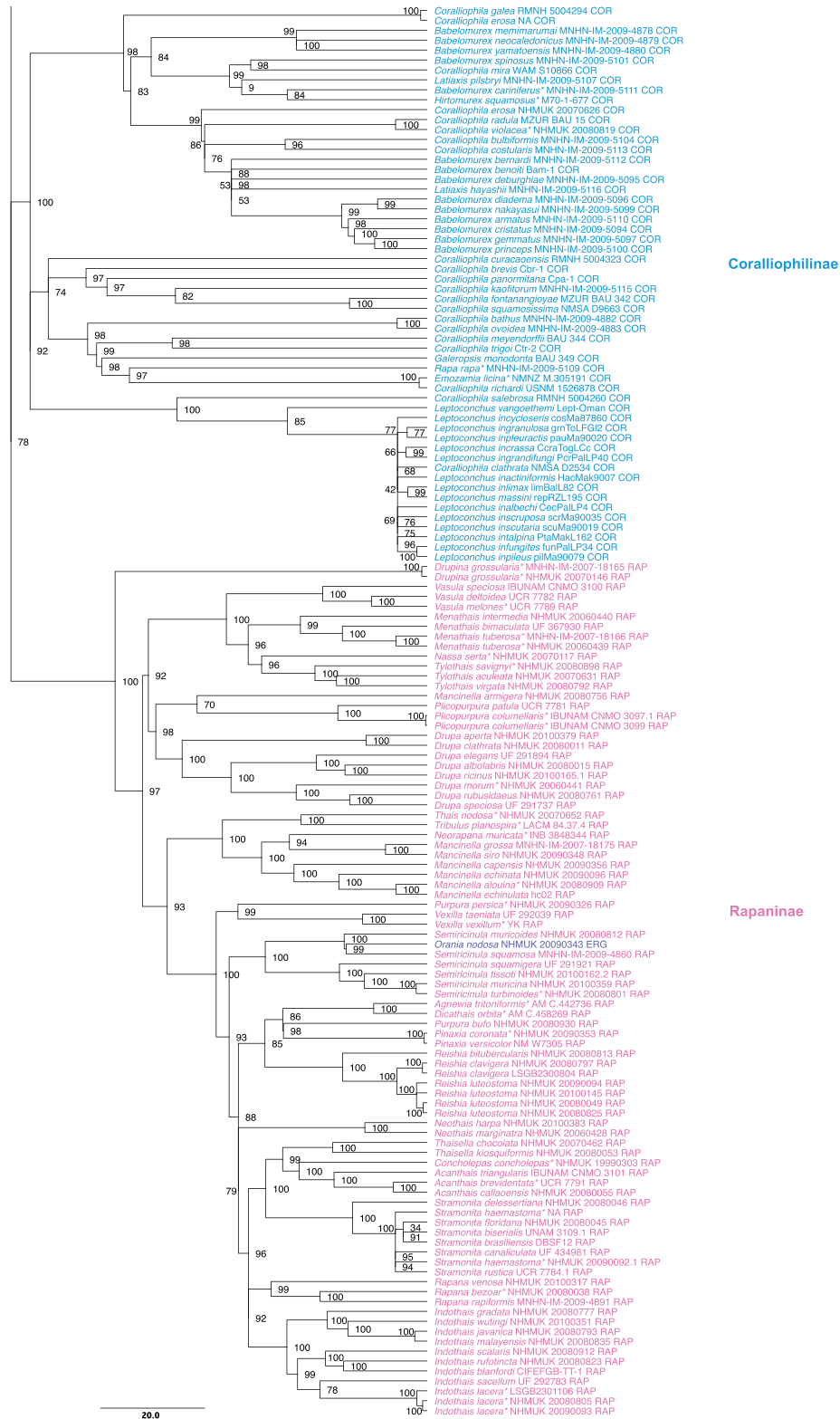


Figure 1. (Continued).



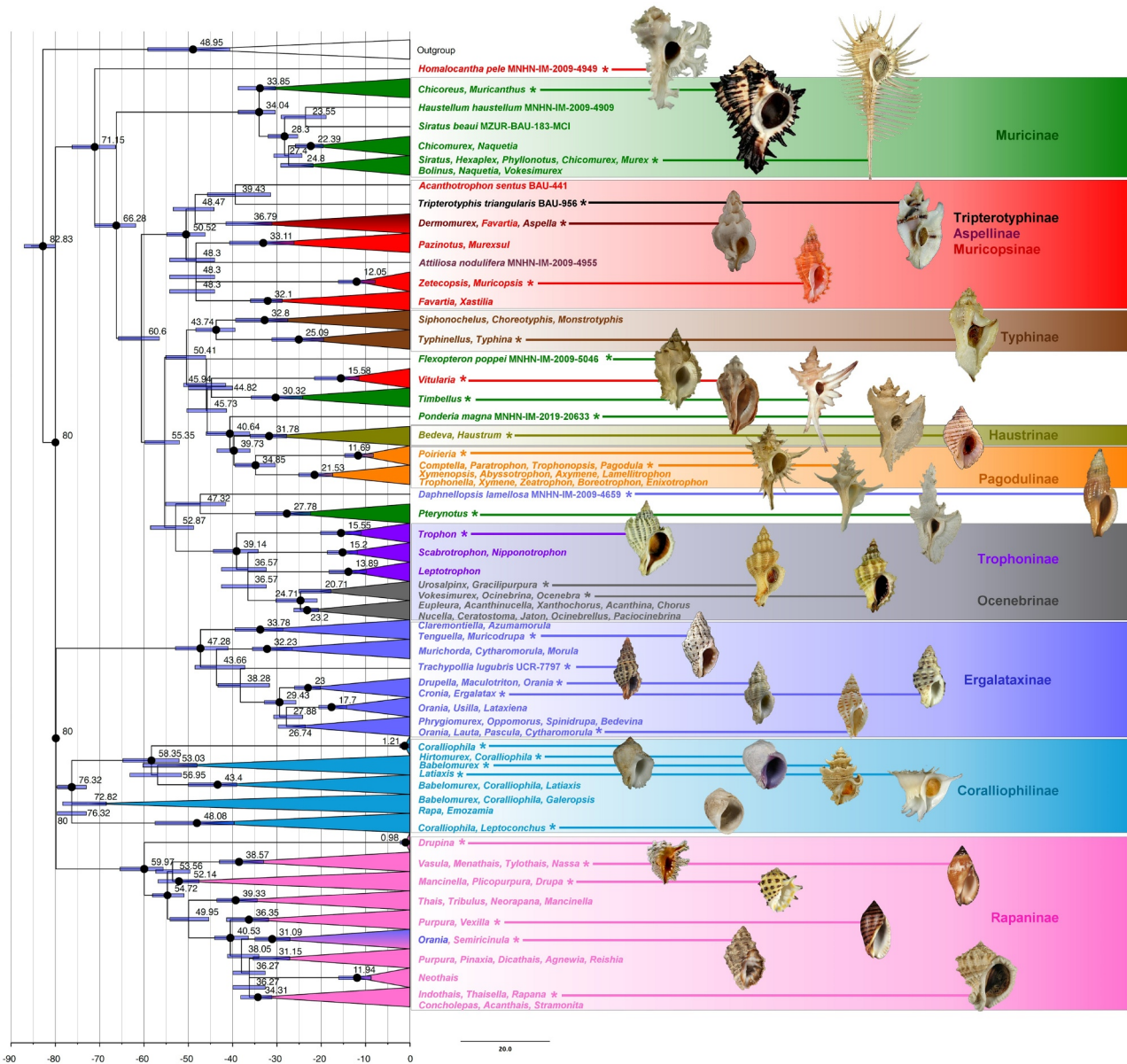


Figure 2. Maximum Likelihood time calibrated phylogenetic reconstruction of the family Muricidae using IQTree. Black dots at nodes indicate ultrafast bootstrap support values  $\geq 0.95$ . Bars at nodes indicate 95% confidence intervals of ages expressed in mya. Branches are largely collapsed (fully uncollapsed tree in Supplementary Material Figure S5). Colours of collapsed clades, taxon names, and figure-connecting lines indicate the traditional subfamilial classification of the taxa represented in the relevant lineage (as also indicated in the subfamily labelling). Shells, not to scale, of representative taxa (indicated by an asterisk), from top/left: *Homalocantha pele*; *Muricanthus radix*; *Murex pecten*; *Tripterotyphis fayae*; *Aspella producta*; *Muricopsis cristata*; *typhina coronata*; *Flexopteron poppei*; *Vitularia miliaris*; *Timbellus richeri*; *Ponderia magna*; *Haustrum lacunosum*; *Poireria zelandica*; *Pagodula echinata*; *Daphnellopsis lamellosa*; *Pterynotus elongatus*; *Trophon geversianum*; *Gracilipurpura craticulata*; *Ocenebra hispidula*; *Muricodrupa fenestrata*; *Trachypollia lugubris*; *Orania fusulus*; *Ergalatax junionae*; *Cytharomorula vexillum*; *Coralliophila galea*; *Coralliophila violacea*; *Babelomurex cariniferus*; *Latiaxis pilsbryi*; *Leptoconchus peroni*; *Drupina grossularia*; *Nassa sarta*; *Drupa ricinus*; *Vexilla vexillum*; *Semiricimula muricoides*; *Rapana bezoar*.

100%) as did also the single specimen of *Homalocantha pele*.

The subfamily Trophoninae was paraphyletic and divided into three subsequent lineages: *Trophon* (UfB 100%), *Scabrotrophon* + *Nipponotrophon* (UfB 100%), and *Leptotrophon*

(UfB 100%). The subfamily Ocenebrinae was supported as monophyletic (UfB 100%), as also was a clade including ocenebrines+trophonines (UfB 100%).

Overall, two supported major phylogenetic clades can be identified: one including Ergalataxinae,

Coralliophilinae, and Rapaninae (UfB 98%) and another including the rest of the subfamilies and lineages, with *Homalocantha pele* as the first diverging lineage (UfB 97%). Internal relationships among major lineages were generally not supported except for the clade of Ocenebrinae with the paraphyletic trophonine lineages and the pair Haustrinae + Pagodulinae (UfB 100%).

Several genera as traditionally conceived did not prove monophyletic. For example, within Ergalataxinae, the genus *Cytharomorula* resulted to be polyphyletic and split into one clade of four species including the type species *Cytharomorula vexillum* (UfB 100%), and two lineages represented by *Cytharomorula pinguis* and *Cytharomorula lefevreiana*, subsequently sisters to the genus *Morula* (both nodes UfB 100%). The genus *Orania* was split into seven clades with the type species *Orania fusulus* sister taxon to *Ergalatax junionae*, even if without full statistical support (UfB 94%). In addition, *Orania nodosa* ended up inside the rapanine clade of *Semiricimula* (UfB 100%) rather than in the ergalataxines. In the subfamily Muricinae, several genera as traditionally conceived appeared to be not monophyletic. In particular, the genus *Naquetia* resulted to be polyphyletic and split into three independent lineages: (1) *Naquetia barclayi*, (2) *Naquetia triqueter* (type species) + *Naquetia vokesae* (UfB 100%), and (3) *Naquetia cumingii*.

#### Dating major lineages

The time-calibrated phylogenies (Figure 2 and Supplementary material Figure S5; see Table I for 95% confidence interval (CI)) estimated the origin of the family **Muricidae** at 80 mya (95% CI: 80–80) during the Upper Cretaceous (Campanian). The clade of the **Muricinae** s.s. was dated at 34.04 mya (95% CI: 30.38–38.75) during the Eocene-Oligocene (Priabonian). The origin of the core **Muricopsinae** was dated at 50.52 mya (95% CI: 46.22–54.86) during the Eocene (Ypresian). The subfamily **Pagodulinae** (including the genus *Poirieria*) is estimated as having originated 34.85 mya (95% CI: 30.37–39.44) during the Eocene-Oligocene (Priabonian). The subfamily **Haustrinae** is estimated to have arisen 31.78 mya (95% CI: 27.79–36.02) in the Oligocene (Rupelian). The **Ergalataxinae** were estimated to have arisen in the Eocene (Lutetian), with the node dated at 47.28 mya (95% CI: 41.05–52.93). The **Coralliophilinae** are suggested to have originated 76.32 mya (95% CI: 73.06–79.60) during the Upper Cretaceous (Campanian). The

**Ocenebrinae** are estimated to have originated during the lower Oligocene (Chatian) 24.71 mya (95% CI: 20.94–30.24). The origin of the **Rapaninae** was estimated at 59.97 mya (95% CI: 55.69–65.42) during the Paleocene (Selandian). The origin of the **Typhinae** was dated at 43.74 mya (95% CI: 39.49–48.35) during the Eocene (Lutetian).

#### Discussion

The family Muricidae is one of the largest groups of marine gastropods, and their phylogenetic systematics has always been controversial (Barco et al. 2010). In this work, we have gathered a large dataset based on the molecular information available so far, including for the first time representatives of all the currently recognised subfamilies.

Our phylogenetic hypothesis, based on the ML analyses, confirmed the monophyly of several major clades to be ranked as subfamilies. Ergalataxinae, Rapaninae, Coralliophilinae, Ocenebrinae, Typhinae, Pagodulinae, and Haustrinae were highly supported. The last two, Pagodulinae and Haustrinae, were also recovered as sister clades and share important anatomical features, such as a muricine-like radula (rachidian lacking marginal cusps, and inner denticles independent from lateral cusps), a pallial vas deferens not open to the mantle cavity across its length, the flattened, lensiform egg capsules (Tan 2003; Barco et al. 2015).

The monophyly of Trophoninae, at variance with results by Barco et al. (2015), was not recovered. The available developmental data on the trophonine and ocenebrine radulae, with adult “ocenebrine” features observed also during trophonine ontogeny (Pio et al. 2014), are fully compatible with this pattern and suggest trophonines as representing a primitive grade in an ocenebrine clade, rather than a distinct subfamily. We take this position conservatively, pending further testing with the analysis of a wider, genome-scale molecular dataset.

Relationships among the major lineages were not resolved unequivocally across the tree. A close relationship of Rapaninae, Ergalataxinae, and Coralliophilinae was supported; this was recently questioned by the results of the analysis of mitogenomes in Harasewych and Sei (2022) who recovered the coralliophiline as the sister taxon to the remaining muricids (unfortunately, Yu et al. (2023) did not include the coralliophiline mitogenome published by Harasewych and Sei (2022) in their larger dataset). However, a close relationship between Rapaninae and Ergalataxinae is also supported by morphological data (see, e.g. Herbert et al. 2007 for ontogenetic data on the radula), whereas the strong anatomical differences of Coralliophilinae may be

related to their parasitic way of life (Richter & Luque 2002, 2003).

There seem to be good reasons to restrict the concept of the subfamily Muricinae s.s. to the clade including the type genus (the core Muricinae), thus excluding from the subfamily the genera *Timbellus*, *Flexopteron*, *Ponderia*, and *Pterynotus* as in part already suggested by Barco et al. (2010) and Merle et al. (2011).

Similarly, a revision of the scope of the subfamily Muricopsinae is urged. We detected a clade that can be proposed as Muricopsinae s.s., that – along with the type species of the genus *Muricopsis* – includes the former aspellines *Aspella*, *Dermomurex*, and *Attiliosa*, and also *Tripterotyphis triangularis* (formerly in the Tripterotyphinae, that thus, quite probably represent a mere muricopsine lineage). Conversely, the genera *Homalocantha* and *Vitularia*, traditionally considered as muricopsines, should be excluded from Muricopsinae.

Several taxa were placed either independently or rather unstably in the trees and may represent independent lineages: this is the case of *Homalocantha*, *Flexopteron*, *Timbellus*, *Vitularia*, *Daphnellopsis*, and *Pterynotus*. Their actual position should be tested by a phylogenomic approach and may either end in one of the recognised subfamilies or be recognised as worthy of suprageneric taxonomic recognition. Analyses of mitogenomic datasets were not conclusive, especially with different relationships supported by either ML or BI analyses (Harasewych & Sei 2022; Yu et al. 2023). It seems reasonable to expect more resolution by phylogenomic approaches on a wider nuclear scale.

In their recent critical analysis of the fossil records, Merle et al. (2022) pointed out as the first known unquestionable muricid record is that of “*Poirieria (Paziella) cretacea*” Garvie, 1991, from the Late Cretaceous of Texas (Maastrichtian, 66–72 mya), for which they convincingly highlighted the morphological similarity with modern *Flexopteron* spp. In the Early Paleocene, other species with a shell morphology considered as “typical muricine” are known, classified in *Flexopteron*, *Poirieria*, and *Timbellus*. We agree with Merle et al. (2022) that the shell morphology of *Flexopteron* is closer to Pagodulinae than to Muricinae.

There seems to be robust evidence that the origin and early diversification of the subfamilies of Muricidae occurred between 32 and 60 mya (95% intervals ranging from 28 to 65 mya) which largely agrees with the available knowledge from the fossil records. This is broadly the same period estimated for the origin of the lineages not assigned to

a subfamily (*Flexopteron*, *Timbellus*, *Daphnellopsis*, *Pterynotus*) with the exception of *Vitularia*, which is estimated to be younger (15.58 mya, 95% CI: 11.48–21.56), and *Homalocantha* that is estimated to have diverged rather earlier (71.15 mya, 95% CI: 66.44–76.27). A remarkable exception is represented by the Coralliophilinae, for which an origin at 76 mya was estimated (95% CI: 73–79.6 mya), i.e. very close to the estimated origin of the family Muricidae; this is extremely older than any reliable fossil record for the subfamily (the oldest being from the Middle Eocene, c. 40 mya). As already suggested by Barco et al. (2010), this estimate is probably biased by the very long branches of the coralliophiline lineages, which are very likely to be produced by the “Davison-effect”, i.e. the accelerated accumulation of mutations in mitochondrial (and, to a lesser extent, nuclear) genes in protandrous hermaphrodites (Davison 2006).

Taking into consideration the results from the phylogenetic analysis and the estimates of the node ages, rather than proposing a new classification of the family, we present the following annotated scheme (derived with modifications after Merle et al. 2022), with comments intended as hypotheses to be tested by further studies based on integrative approaches on anatomical and genomic data (taxa included according to results on samples assayed herein). In this scheme, the number of recognizable subfamilies is reduced to nine, but at the same time we highlighted seven lineages *incertae sedis*, which may prove worthy of subfamilial recognition.

## Family Muricidae Rafinesque, 1815

**Subfamily Muricinae Rafinesque, 1815** – To be restricted to the type genus (*Murex*) and related taxa (*Bolimus*, *Chicomurex*, *Chicoreus*, *Haustellum*, *Hexaplex*, *Muricanthus*, *Naquetia*, *Phyllonotus*, *Siratus*, *Vokesimurex*).

**Subfamily Muricopsinae Radwin & D’Attilio, 1971** – To include also former Aspellinae Keen 1971 and Tripterotyphinae D’Attilio & Hertz, 1988 (*Muricopsis*, *Acanthotrophon*, *Aspella*, *Attiliosa*, *Dermomurex*, *Favartia*, *Murexsul*, *Pazinotus*, *Tripterotyphis*, *Zetecopsis*, *Xastilia*).

**Subfamily Typhinae Cossmann, 1903** – Type genus based on a fossil (*Typhis tubifer* Bruguière, 1792). Morphologically very distinctive (*Choreotyphis*, *Monstrotyphis*, *Siphonochelus*, *Typhina*, *Typhinellus*).

**Subfamily Haustrinae** Tan, 2003 – *Haustrum*, *Bedevea*. Relative ranking with Pagodulinae to be tested.

**Subfamily Pagodulinae** Barco, Schiaparelli, Houart & Oliverio, 2012 – *Poirieria* definitely represents a plesiomorphic lineage of this subfamily (*Pagodula*, *Abyssotrophon*, *Axymene*, *Boreotrophon*, *Compiella*, *Enixotrophon*, *Lamellitrophon*, *Paratrophon*, *Trophonella*, *Trophonopsis*, *Xymene*, *Xymenopsis*, *Zeotrophon*).

**Subfamily Ocenebrinae** Cossmann, 1903 – Molecular evidence to include typical ocenebrines (*Ocenebra*, *Acanthina*, *Acanthinucella*, *Ceratostoma*, *Chorus*, *Eupleura*, *Gracilipurpura*, *Jaton*, *Nucella*, *Ocinebrellus*, *Ocinebrina*, *Paciocinebrina*, *Urosalpinx*, *Vokesinotus*, *Xanthochorus*) and also former Trophoninae (*Trophon*, *Leptotrophon*, *Nipponotrophon*, *Scabrotrophon*).

**Subfamily Ergalataxinae** Kuroda & Habe, 1971 – Monophyly of some genera as traditionally conceived to be tested (*Ergalatax*, *Azumamorula*, *Bedevena*, *Claymontiella*, *Cronia*, *Cytharomorula*, *Drupella*, *Lataxiena*, *Lauta*, *Maculotriton*, *Morula*, *Murichorda*, *Muricodrupa*, *Oppomorus*, *Orania*, *Pascula*, *Phrygiomurex*, *Spinidrupa*, *Tenguella*, *Trachypollia*, *Usilla*).

**Subfamily Coralliophilinae** Chenu, 1859 – Monophyly of several genera as traditionally conceived (including the type genus, *Coralliophila*) to be tested (*Babelomurex*, *Emozamia*, *Hirtomurex*, *Galeropsis*, *Latiaxis*, *Leptoconchus*, *Rapa*).

**Subfamily Rapaninae** Gray, 1853 – Monophyly of a few genera as traditionally conceived to be tested (*Rapana*, *Acanthais*, *Stramonita*, *Agnewia*, *Concholepas*, *Dicathais*, *Drupa*, *Drupina*, *Indothais*, *Mancinella*, *Menathais*, *Nassa*, *Neorapana*, *Neothais*, *Pinaxia*, *Plicopurpura*, *Purpura*, *Reishia*, *Semiricinula*, *Thais*, *Thaisella*, *Tribulus*, *Tylothais*, *Vasula*, *Vexilla*).

**Incertae sedis *Homalocantha*** – An odd position for a morphologically odd taxon.

**Incertae sedis *Flexopteron*** – If extant species are actually related to the upper Cretaceous and Early Paleogene lineages, it may be worthy of recognition as a separate subfamily (potentially useful to define the plesiomorphic Bauplan of Muricidae).

**Incertae sedis *Vitularia*** – Another long branch which may be biased by the Davison effect (Barco et al., 2010).

**Incertae sedis *Timbellus*** – Likely to represent an independent lineage, worthy of subfamilial rank.

**Incertae sedis *Ponderia*** – It may represent the plesiomorphic lineage at the base of the pagoduline-haustriine diversification.

**Incertae sedis *Daphnellopsis*** – Not an ergalataxine, relationships with *Pterynotus* (unsupported) to be tested.

**Incertae sedis *Pterynotus*** – Likely to represent an independent lineage (maybe with *Daphnellopsis*) worthy of subfamilial ranking.

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No potential conflict of interest was reported by the authors.

## Supplementary material

Supplemental data for this article can be accessed online at <https://doi.org/10.1080/24750263.2023.2283517>

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