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Phylogeny of the longest existing gastropod clade (Pleurotomariida) reconstructed with Bayesian and parsimony methods and its implications on gastropod shell characters

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Evolutionary relationships of fossil gastropods have largely been inferred using taxonomic systematics. Phylogenetic relationships between extinct gastropod groups and their relationship to extant groups are largely unresolved. Here we reconstruct the phylogeny of Pleurotomariida, which has the longest fossil record among extant gastropod clades and represents one of the most diverse Palaeozoic gastropod groups. Bayesian (fossilized birth–death [FBD] model) and parsimony analyses were performed using 93 morphological shell characters comprising 109 pleurotomariidan species representing 80 genera/subgenera ranging from the Ordovician to Recent. Parsimony analysis failed to reconstruct stratigraphically congruent trees and many nodes have poor support. The FBD model incorporates the stratigraphical ages of taxa for tree reconstruction and therefore better fits the stratigraphical record. According to the FBD phylogeny, Pleurotomariida was represented by three distinct lineages during the Palaeozoic: Eotomariini, Wortheniellini and Pleurotomariini. Pleurotomariini and Wortheniellini survived the end-Permian mass extinction. Although Wortheniellini showed a higher diversification during the Triassic recovery period, only Pleurotomariini survived until the present day, suggesting that resilience to extinction was not dependent on diversification dynamics in this clade. The FBD analysis indicates that groups that have an exclusively Triassic fossil record originated during the Permian and that the origination and extinction rates increased from the Ordovician to the Jurassic and dropped subsequently. Sampling standardized diversity analysis of Pleurotomariida corroborates that they were one of the most diverse gastropod groups in the late Palaeozoic and that their diversity significantly dropped after the end-Permian mass extinction. Early ontogenetic shell characters are more conservative (phylogenetically more informative) compared to late ontogenetic shell characters. In contrast to previous assumptions, axial characters are not more homoplastic than spiral shell characters, as indicated by higher consistency index values. The data further revealed that adult gastropod shell size depends significantly on the protoconch size and the initial whorl size.

Keywords: Vetigastropoda; Bayesian; fossilized birth–death; diversity; Permian–Triassic mass extinction

Introduction

Gastropoda is the largest molluscan class (73,377 extant species, MolluscaBase, retrieved 28 September 2023) and one of the most diverse animal clades in recent and past marine ecosystems (e.g. Bouchet et al., 2002; Roden et al., 2020, fig. 4; Sepkoski, 1981). Gastropods have increased in diversity since their origin in the Cambrian (Alroy, 2010a; Erwin & Signor, 1990), but the clade composition changed significantly throughout the Phanerozoic. The dominant gastropod groups in the early evolutionary history of Gastropoda (e.g. Bellerophontida, Murchisonioidea) became extinct and were eventually replaced by groups that are alive today (e.g.

Caenogastropoda) (Frýda et al., 2008; Koken, 1889; Tracey et al., 1993). Most of the putative fossil record of the extant gastropod groups (e.g. the basal gastropod clade Patellogastropoda) extends not further back than the Triassic (e.g. Frýda, 2012). Most Palaeozoic gastropod groups became extinct either at the end-Permian mass extinction or shortly afterwards (Erwin, 1990; Nützel, 2005; Tracey et al., 1993).

The phylogenetic relationships between the Palaeozoic and Mesozoic lineages and their relationship to extant groups are largely unresolved (e.g. Frýda et al., 2008). No comprehensive quantitative phylogenetic analysis involving a wide range of gastropods throughout the entire Phanerozoic has been conducted so far. There are

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only few phylogenetic analyses of fossil gastropods, either from the early Palaeozoic (Lophospiridae: Wagner, 1999; anisostrophically coiled gastropods: Wagner, 2002), the late Palaeozoic (*Byzantia* [Neritopsidae]: Kosnik, 1997; Subulitoidea: Nützel *et al.*, 2000) or the Jurassic (*Calliotropis* [Seguenziida]: Pérez *et al.*, 2022). The present contribution is the first phylogenetic analysis covering Palaeozoic and Mesozoic gastropods and the first attempt to reconstruct the phylogeny of the entire Pleurotomariida with phylogenetic methods.

Pleurotomariida is the only extant gastropod clade with a fossil record extending back to the Ordovician or the Cambrian period (e.g. Knight *et al.*, 1960; Wagner, 2002). Pleurotomariida attained its peak generic diversity during the middle to late Palaeozoic (Hickman, 1984), reaching more than 50 genera within-stage and at stage boundary (Karapunar & Nützel, 2021). The group became one of the most diverse and abundant gastropod groups in the late Palaeozoic and early Mesozoic (Erwin, 1990; Karapunar & Nützel, 2021; Karapunar *et al.*, 2022). From the Middle Jurassic onwards, Pleurotomariida was represented almost exclusively by Pleurotomariidae, the only extant family within Pleurotomariida, except for a single representative of Stuoirellidae in the Cretaceous (Karapunar & Nützel, 2021; Kiel & Bandel, 2000). The within-stage diversity of Pleurotomariida decreased to 4–10 genera from the Middle Jurassic to Recent (Bose *et al.*, 2021; Harasewych & Kiel, 2007).

The position of Pleurotomariida within gastropod phylogeny depends on the target time interval and hence the clades included in a phylogenetic analysis. In molecular phylogenies, Pleurotomariida is recovered as sister group to all other Vetigastropoda and as basal offshoot of extant Gastropoda (e.g. Cunha *et al.*, 2022; Harasewych *et al.*, 1997; Uribe *et al.*, 2022; Williams & Ozawa, 2006; Zapata *et al.*, 2014). A phylogenetic analysis of early Palaeozoic gastropods suggests, however, that Pleurotomariida is a derived clade (Wagner, 2002). The lack of phylogenetic analyses covering early Palaeozoic to Recent members of Pleurotomariida and Gastropoda hinders our understanding of the phylogenetic relationship between different gastropod groups through time.

The evolutionary relationship of fossil Pleurotomariida to other groups is inferred based on their characteristic shell features and in Recent taxa also on anatomy. The pleurotomariidan shell is characterized by a shell slit in the outer labrum, the presence of an inner nacreous layer, and a larval shell of one whorl matching the so-called trochoid condition and reflecting non-planktotrophic larval development (Bandel, 1982; Kaim, 2004; Geiger *et al.*, 2008; Nützel, 2014). The slit reflects the soft body organization (Hickman, 1984). It serves for the

ventilation of the mantle cavity and can be regarded as a synapomorphy of the clade Pleurotomariida. The shell slit is considered a derived character in Gastropoda (e.g. Lindberg & Ponder, 2001) and plesiomorphic in living Vetigastropoda (Haszprunar, 1988). Sinus and slit in the early Palaeozoic archaeogastropods are regarded as homologous (Knight, 1941; Wagner, 2002; Yochelson, 1984). Accordingly, the slit was derived gradually from a sinus during the course of gastropod evolution (Knight, 1941; Yochelson, 1984). The phylogenetic analysis by Wagner (2002) suggests that the slit evolved multiple times in early gastropod evolution (in Pleurotomariida, Bellerophonitida and Euomphaloidea). Whether the slit reflects a similar soft body organization in these slit-bearing groups is under debate since some are extinct (e.g. Bellerophonitida, see Frýda *et al.*, 2008). However, the slit and trema/tremata (i.e. ‘a single hole’/‘a row of holes’ formed by modification of a slit) can be homologous among the slit- and tremata-bearing vetigastropods with paired mantle organs including gills (i.e. Pleurotomariida, Haliotidae, Scissurellidae, Fissurellidae), considering that the condition of having paired mantle organs and a slit are regarded ancestral in Vetigastropoda (Haszprunar, 1988; Lindberg & Ponder, 2001; Ponder & Lindberg, 1997). The evolution of the slit implies the deepening of the mantle cavity during the course of gastropod evolution (Lindberg & Ponder, 2001). With the acquisition of a slit, the animal could control water flow in the mantle cavity (Lindberg & Ponder, 2001; Yonge, 1947). Thus, the acquisition of a slit in vetigastropods can be considered as an evolutionary novelty and might have provided an advantage long before the evolution of siphonal canals in gastropods.

The knowledge of evolutionary relationships within the clade Pleurotomariida is largely based on systematic and taxonomic studies. The last comprehensive compilations of pleurotomariidan genera were published by Wenz (1938–1944) and Knight *et al.* (1960). Wagner (2002) reconstructed the phylogeny of early Palaeozoic anisostrophically coiled gastropods (i.e. excluding bellerophonitids) including the oldest pleurotomariidan taxa based on teleoconch characters. For most early Palaeozoic gastropods, the early ontogenetic shells including protoconchs are unknown. Wagner’s (2002) analysis suggested a revision of the classification scheme proposed by Knight *et al.* (1960). Since the publication of the *Treatise* (Knight *et al.*, 1960), numerous new genera have been described and family-level classifications were modified (e.g. Bandel, 2009; Gordon & Yochelson, 1987; Karapunar & Nützel, 2021; Karapunar *et al.*, 2022). Bandel and Geldmacher (1996) published a hypothetical phylogeny summarizing their opinion on the evolutionary relationship between several Palaeozoic

to Mesozoic pleurotomariid genera. Harasewych (2002, fig. 9) provided phylogenetic hypotheses depicting experts' opinions on the relationship between genera within the family Pleurotomariidae. Bouchet et al. (2017) published a family-level classification reflecting the last consensus view on phylogenetic and systematic relationships between pleurotomariidan families. Although the phylogeny of living genera and species of the family Pleurotomariidae is resolved with molecular data (Anseeuw et al., 2015, 2017; Harasewych et al., 2023), the relationship between fossil pleurotomariidan genera and families are still largely based on experts' taxonomic opinions, due to a lack of phylogenetic analyses covering the entire group.

The information to reconstruct the phylogeny of fossil gastropods relies mostly on the preserved shell characters and partly on their stratigraphical position in the fossil record. Understanding the function of the shell characters and their biological significance (the degree to which shell characters reflect the animal's anatomy) are therefore crucial for the identification of phylogenetically informative characters.

Function of shell

The gastropod shell has two primary functions: protection from predators and providing a space that is isolated from the external environment, in which the animal can regulate its metabolism. Shell morphology can provide information about underlying soft body anatomy (for instance an elongated aperture may indicate a single gill: Linsley, 1977; McNair et al., 1981), direction of inhalant and exhalant currents (slits, tremata and siphonal canals), physiology (high expansion rate may indicate higher metabolism: Vermeij, 2002), and life habit (sedentary lifestyle can be inferred from radial aperture, open coiling or shell form: Linsley, 1977; Signor, 1982; ratchet sculpture indicates burrowing habit either within sediment: Signor, 1982, 1994, or intrusion in soft sponges for feeding: Nützel, 2021). The shell is formed by different regions of mantle epithelium and the shell formation is controlled by genes and proteins (Kocot et al., 2016; McDougall & Degnan, 2018); therefore, the shell reflects the underlying genetic tool kit.

Protoconch

Similar to the systematics of extinct gastropods, the systematics of extant gastropod species and genera is still mostly based on shell characters, mainly due to the easy availability of shell characters compared to anatomical and molecular data. Indeed, a high portion of all described extant and extinct gastropod species are only known from their shells.

The gastropod shell consists of the protoconch (embryonic or larval shell) and the teleoconch (post metamorphic shell) (e.g. Nützel, 2014). Protoconch characters and characters associated with soft body anatomy are considered more informative than teleoconch characters in inferring phylogenetic relationships above the generic level (Fryda et al., 2008). A good example is larval heterostrophy (heterostrophic protoconch), which is an autapomorphy of the subclass Heterobranchia. All living vetigastropods including Pleurotomariida lack larval planktotrophy. Hence their protoconchs have a larval shell reflecting non-planktotrophic larval development consisting of about one whorl (e.g. Bandel, 1982; Nützel, 2014). A few Palaeozoic gastropods with vetigastropod adult shell morphology and a protoconch reflecting larval planktotrophy have been reported (e.g. Dzik, 1978; Kaim, 2004), but it is under debate if those truly are members of Vetigastropoda (Nützel, 2014). Thus presence/absence of potential larval planktotrophy is not phylogenetically informative within Vetigastropoda. However, the absence of plankton-feeding larvae is diagnostic for the subclass Vetigastropoda.

Shell slit

The slit and its by-product the selenizone reflect the soft anatomy of Pleurotomariida. Pleurotomariida possess paired mantle organs including ctenidia, auricles and kidneys (e.g. Harasewych, 2002; Yonge, 1947). These organs are positioned bilaterally symmetrically on either side of the shell slit, and the anus is situated at the proximal (abapertural) end of the slit (Harasewych, 2002; Hickman, 1984). The shell slit has a vital function: it facilitates the ventilation of the deep mantle cavity for respiration and disposal of excretory products (Voltzow et al., 2004; Yonge, 1947). Slit and selenizone characters (e.g. position, shape, width and depth) have been widely used in the traditional classification of Pleurotomariida (e.g. Bayer, 1965; Harasewych & Kiel, 2007; Knight et al., 1960) and these characters are considered more conservative compared to other shell characters (Batten, 1967; Karapınar & Nützel, 2021; Karapınar et al., 2022). Phylogenetic analyses with slit-bearing early Palaeozoic gastropods also suggest that the characters associated with the presence of a sinus or slit show a low rate of change compared to other characters (Wagner, 2001).

Whorl sectors

The whorl of a gastropod shell can be divided into shell sectors (Vermeij, 2002). These sectors can be inferred from the growth lines and the change in ornamentation pattern. The pleurotomariidan whorl can be divided into

two main sectors: whorl face and base, as is also the case in other gastropods. In descriptive terminology, the whorl face is defined as the region between the adapical and abapical sutures and in a strict sense is only applicable to spire whorls. Hence, the base of the whorls reflects the shell region on which the succeeding whorl embraces the previous one. Although ‘base’ in this sense is a useful term for shell descriptions, this definition may not correspond to homologous regions, because the boundary between the whorl regions does not always correspond to the position of the suture line. In most taxa, the abapical (lower) suture represents the boundary between whorl face and base. However, in some taxa, the base is seen as the shell portion below a shell angulation, and the suture line is situated above this boundary between whorl face and base (e.g. in *Glabrocingulum*). Hence, the position of the suture might be misleading to infer the boundary between the two sectors. If present, the basal angulation indicates the boundary between whorl face and base, which is commonly the case. The base can be defined as the region between the suture (or basal angulation) and the umbilicus or abapical termination/centre of the shell. In spire whorls, the base is the contact surface to the succeeding whorl; hence, it affects the shape of the succeeding whorl at the contact surface. Therefore, the ornament type or the strength of ornament usually differs between base and whorl face. All nacreous gastropods (most vetigastropods, including Pleurotomariida) restrict prominent ornaments to the whorl face including the whorl angulation and do not form prominent ornaments on their base (e.g. *Schizogonium*, *Bolma*). However, there are many exceptions in other gastropod groups. For example, members of the caenogastropod family Muricidae can remodel the shell and resorb prominent ornaments such as long spines on their base (Carriker, 1972). Formation of a thick inner lip or reduction of whorl overlap (e.g. *Epitonium*) are other strategies shown by gastropods with prominent basal ornament (Vermeij, 1977). The whorl face sector can be further divided into three subsectors in Pleurotomariida: the slit, and the subsectors above and below the slit, the upper whorl face and the lower whorl face (right and left ramps *sensu* Wagner, 2002).

Stratigraphical information in phylogenetic analyses

Stratigraphical information is important in palaeontological studies to understand evolutionary relationships and the tempo of evolution but has rarely been incorporated in phylogenetic analyses. Few phylogenetic studies on gastropods directly included stratigraphical information as a character in parsimony analyses (Kosnik, 1997;

Nützel *et al.*, 2000). The stratocladistic method was introduced to select the best tree based on the principle of parsimony not only based on characters but also on ages (Fisher, 2008). Similarly, stratigraphical information was used in tree inference within a maximum likelihood approach (Wagner, 1998). The fossilized birth–death (FBD) model is a recent development to incorporate stratigraphical ages (sampling age including the uncertainty) for phylogenetic tree estimation within a Bayesian framework (Warnock & Wright, 2020; Wright *et al.*, 2022). Various metrics and tools have been developed to measure stratigraphical congruence, that is the match between the order of appearance of clades along the tree and the order of their appearance in the stratigraphical record (e.g. Bell & Lloyd, 2015; Wright & Lloyd, 2020). Because the FBD model incorporates stratigraphical ages into tree estimation, it reconstructs trees with a better fit to the stratigraphical record (King, 2021). The FBD model was previously used to infer phylogenies based solely on morphological datasets (e.g. fossil echinoderms: Wright, 2017; Wright *et al.*, 2021; fossil cephalopods: Pohle *et al.*, 2022) but it has hitherto never been used to infer a phylogeny of gastropods.

Material and methods

Taxon sampling

Pleurotomariida is composed of 283 genera/subgenera (excluding Cirridae; [Supplemental material, Appendix 6](#)). However, not all of these genera are included in the present phylogenetic analyses. This is largely because many of them are based on insufficiently known type species or include only poorly documented species. In these cases, too many character states are unknown to include them in a meaningful way. As preparation for our analyses, we revised the mostly exceptionally well-preserved Pleurotomariida from the Triassic St. Cassian Formation (Karapınar & Nützel, 2021) and studied exceptionally well-preserved specimens from the Pennsylvanian (Carboniferous) of the USA (Karapınar *et al.*, 2022). These studies helped to clarify the state of characters for many genera that had previously been unknown or insufficiently known, especially for characters concerning the early ontogenetic shells (protoconch and early teleoconch). Moreover, we included data from our taxonomic studies on gastropods from the Mississippian of Scotland (Karapınar *et al.*, 2024), the Permian of Thailand (Ketwetsuriya *et al.*, 2020), the Lower Jurassic of Germany (Gründel & Nützel, 1998; Nützel & Gründel, 2015) and the Triassic Marmolada Limestone, Italy (Nützel, 2017). We also studied specimens housed in the Bayerische Staatssammlung für Paläontologie und

Geologie, Munich (BSPG), Naturhistorisches Museum Wien (NHMW), Geologische Bundesanstalt, Vienna (GBA) and the Natural History Museum, London (NHMUK). Among 110 species included in the analyses, only five species were not directly examined by the authors and their information was gathered from the literature (Bayer, 1965; Knight, 1941; Mazaev, 2015, 2019). The inventory numbers of the studied specimens and the literature used in character scoring can be found in [Supplemental material, Appendix 1](#).

We carefully assigned specimens from the museum collections to previously described genera and species. If a specimen did not represent a previously described species, it was left in open nomenclature. Such specimens will be described in a separate future publication. A total of 109 pleurotomariidan species representing 80 genera/subgenera were included in the present analysis.

Information regarding the geological ages of the specimens was retrieved from the specimen labels and the publications where they were described. Out-of-date or regional stratigraphical ages were assigned to the modern standard international geological ages according to the Geological Time Scale 2018 (Walker et al., 2018). The specimens were assigned to geochronological time units, at the highest resolution representing a geological age (e.g. Carnian) and the lowest resolution representing a geological period (e.g. Triassic). The minimum and maximum ages of the species occurrences (FAD, LAD) basically represent the upper or lower boundary of these time units, during which the species occurred. The geological ages of the specimens are given in the Supplementary Code and Data (available on Zenodo (<https://zenodo.org/records/13313306>)).

Shell characters

The shell characters that have been used in the traditional classification of the family Pleurotomariidae (e.g. Bayer, 1965; Harasewych & Kiel, 2007) and the characters that were previously used in morphological phylogenetic analyses of early Palaeozoic gastropods (Wagner, 2002) were taken into consideration for the construction of the character list and many new (not used hitherto) characters were added. The character list comprises 93 characters ([Supplemental material, Appendix 2](#)). All characters are discrete, 22 of them have binary states and 71 of them are multistate. Seventy-five characters are unordered and 18 are ordered (chs 0, 4–6, 8, 25–26, 28, 37, 39, 42, 44, 52, 54, 56, 81, 90–91).

Characters were coded for four discrete shell sectors: upper whorl face, slit, lower whorl face and base (see introduction for descriptions of sectors). Approximately 31% of the characters used in the analysis are related to

the slit (29 out of 93; chs 0–24, 32–34, 37), 32 characters are related to the upper whorl face (chs 26–36, 53–54, 59–70, 71–77), 21 characters are related to the lower whorl face (chs 38–42, 55–56, 59–70, 77–78), 8 characters are used to code the base (chs 46–49, 57–58, 79–80). Characters 25, 43–45, 50–52, 81–92 are not regarded as part of the shell sectors. Characters 32–34 are considered to belong to both the selenizone and upper whorl face sectors. Characters 59–70, 77 are considered to belong to both the upper and lower whorl face sectors.

Gastropod shells keep records of shell morphology at all different ontogenetic growth stages due to being formed by accretionary shell growth. This feature allows study of early ontogenetic shell characters and ontogenetic change of the different shell characters in gastropods. Previously, early ontogenetic shell characters (e.g. ornamentation, formation of selenizone) were used in classification because members of the same genus show the same character states in the early ontogenetic shell (Karapınar & Nützel, 2021; Karapınar et al., 2022). Characters related to ontogeny (e.g. change in coiling direction) were previously also used in the phylogenetic analysis of gastropods (e.g. Wagner, 2002). In the present character list, 63 characters are related to late ontogeny (chs 4–8, 10–14, 16, 18–22, 24–26, 28, 30, 32–33, 35, 37–40, 42–58, 64–71, 73, 75, 77–80, 85, 87, 89, 92), 21 characters are related to early ontogeny (chs 0, 1, 2, 15, 17, 23, 31, 34, 36, 59–63, 72, 74, 76, 83–84, 90–91) and nine characters code ontogenetic change (chs 3, 9, 27, 29, 41, 81–82, 86, 88). Among the characters, 45 are related to axial sculpture (chs 0, 1, 5, 6, 15–22, 26–29, 31, 34, 36, 37, 39–41, 46, 48–49, 51–58, 60–62, 69–76) and 31 code spiral elements (chs 2, 3, 4, 7–14, 23–24, 30, 32–33, 35, 38, 42–45, 47, 63, 66–68, 77–80).

The character matrix (given in the Supplementary Code and Data) was initially composed in Morphobank (<https://morphobank.org/>) and later modified in Mesquite (Maddison & Maddison, 2021).

Parsimony analysis

Parsimony analysis was performed in TNT v. 1.5 (Goloboff & Catalano, 2016) by using different algorithms. *Sinuopea sweeti* (upper Cambrian) was selected as the outgroup taxon because it was recovered as a sister taxon of other early Palaeozoic pleurotomariidan taxa in the phylogenetic analysis conducted by Wagner (2002). The initial trees were produced by using the following values for the algorithms Sectorial search: RSS (minimum sector size 5, maximum sector size 54, that is the 50% of the number of ingroup taxa), CSS (100 rounds, minimum sector size 5); XSS (100 rounds);

Ratchet (100 iterations); Drift (100 cycles); Tree fusing (100 rounds) with 1000 random additional sequences. After obtaining the initial trees, suboptimality criteria were set to retain trees with less than 10 steps with relative fit difference 0.1. Additional trees were searched with the traditional search algorithm by using the initial trees (with the command “bbreak”). Bremer supports were calculated with all trees (optimal trees, that is the most parsimonious trees [MPTs], and suboptimal trees, that is the trees having a maximum of 10 more steps than the MPTs). The strict consensus tree was calculated with the MPTs among all trees. The character matrix was resampled by using 1000 iterations for bootstrap supports. All trees are provided in the Supplementary Code and Data. The apomorphies are given in [Supplemental material, Appendix 3](#).

Bayesian analysis

We performed a Bayesian tip-dating analysis with the FBD process, which incorporates stratigraphical data (occurrence dates including uncertainty) into the analysis. The Bayesian tip-dating analysis includes three models: a morphological evolution model (=character transition model including the rate of evolution of character states; and site rate model for incorporating among character rate variation), an evolutionary clock model (=branch rate model, that is the rate of evolution along the tree) and a tree model (speciation, extinction, fossilization and extant sampling rates) (Warnock & Wright, 2020; Wright *et al.*, 2021). Extant sampling rate is the rate at which extant taxa are sampled and the fossilization rate is the sampling rate of fossils along lineages of a complete FBD tree.

The FBD method was implemented in RevBayes v. 1.2.1 (Höhna *et al.*, 2016) using several morphological evolution and clock models. First, the Mk Model (Lewis, 2001) was used as a substitution model, which assumes that the change from one state to another is equally probable for all character states. Two invariable characters (chs 36 and 76) were excluded to prevent ascertainment bias. It is noteworthy that the inclusion of these characters in the parsimony analysis did not have an impact on tree estimation, and so they were retained in that analysis. Second, the character state frequencies were modelled by a discretized beta distribution. In both morphological substitution models, the coding was set as ‘variable’. In all analyses, a gamma distribution with four rate categories was used to model among-character rate variation (the site rate model). As a clock model, first, we used a strict clock model, which assumes no evolutionary rate difference among branches. Additionally, we used an uncorrelated lognormal relaxed evolutionary clock to model the character rate variation

along the tree. For the tree model, speciation, extinction and fossilization rates were drawn from exponential prior distributions. We tested the FBD model both with constant speciation, extinction and fossilization rates and allowing different speciation, extinction and fossilization rates at a priori determined time intervals (skyline model). For the skyline model, we defined five time intervals: 509.0–485.4 Ma (origin time to Ordovician), 485.4–358.9 Ma (Ordovician–Devonian); 358.9–251.9 Ma (Carboniferous–Permian); 251.9–145 Ma (Triassic–Jurassic); 145–0 Ma (Cretaceous–Recent).

The oldest fossils belonging to Pleurotomariida range from the upper Cambrian (e.g. *Taenioospira*; Knight *et al.*, 1960; Batten, 1967; see also Wagner, 2002) to the lower Ordovician (e.g. *Clathrospira*; Wagner, 2002). The oldest occurrences of *Sinuopea* (the sister taxon to Pleurotomariida; see Wagner, 2002) is from the upper Trempealeauan (~501.0–485.4 Ma), which corresponds approximately to the Furongian Epoch. Therefore, the origin time for the clade Pleurotomariida (i.e. split from *Sinuopea* lineage) can be estimated to be at least around 501 Ma. Hence, we set the origin time estimation between 460–509 Ma (slightly earlier than the appearance of the first observed taxon *Clathrospira trochiformis* and the lowermost boundary of Cambrian Epoch 3 [Miaolingian]). The sampling rate of extant taxa (ρ) was set to 0.023 because only one extant species (out of 44, MolluscaBase) was included in the analysis.

The analysis was run for 100,000 generations, 25% of which were discarded as burn-in. We carried out four separate runs for each model and checked for convergence of posterior probabilities using the R package Convenience (Fabreti & Höhna, 2022). Posterior trees from these four runs were used to calculate posterior clade probabilities, which is the proportion of the appearance of a clade in sampled posterior trees. The summary of the trees is given as the maximum a posteriori (MAP) tree, that is the tree with the highest posterior probability. The node ages were estimated by using the 95% highest posterior density (HPD) interval, which covers 95% of the posterior distribution of node ages. In addition to the Markov Chain Monte Carlo (MCMC) analyses, we ran power posterior analyses to compute marginal likelihoods using the Stepping Stone and Path Sampling approaches (Höhna *et al.*, 2021). The marginal likelihoods were then used to compute Bayes Factors to select between the models.

Morphological evolutionary rates along branches and the diversification rate figures were produced with the R package RevGadgets (Tribble *et al.*, 2022).

The RevBayes scripts are provided in the Supplementary Code and Data. Icytree was used for visualization of the Bayesian tree (Vaughan, 2017).

The apomorphy list of the Bayesian tree ([Supplemental material, Appendix 4](#)) was produced in TNT.

Stratigraphical congruence analysis

There are several metrics to measure whether a phylogeny is congruent with stratigraphical information or not. The Stratigraphic Consistency Index (SCI, Huelsenbeck, 1994) is the ratio of the number of stratigraphically consistent nodes (i.e. the oldest descendant of that node is the same age or younger than the oldest descendant of the sister taxon) to the number of all nodes (excluding the root node). The Relative Completeness Index (RCI, Benton & Storrs, 1994) is the ratio between the sum of the observed ranges of taxa to the sum of the total ghost ranges (minimum implied gap, MIG). The corrected Manhattan Stratigraphic Measure (MSM*, Pol & Norell, 2001) is the ratio between the minimum possible sum of ghost ranges (G_{\min}) to the minimum implied gap (the sum of the total ghost ranges) [G_{\min}/MIG]. The Gap Excess Ratio (GER, Wills, 1999) is the ratio of the difference between the maximum possible sum of ghost ranges (G_{\max}) and minimum implied gap to the difference between maximum and minimum possible sums of ghost ranges [$(G_{\max} - \text{MIG})/(G_{\max} - G_{\min})$].

The metrics were calculated with the R package ‘strap’ (Bell & Lloyd, 2015). The R code used in the analysis is provided in the Supplementary Code and Data.

Diversity analyses

BK compiled a list of all genera previously regarded as Pleurotomariida (c. 480 genera) from the published literature (e.g. Knight, 1941; Knight et al., 1960) and revised their attribution based on the most recent published opinions on Pleurotomariida (e.g. Bouchet et al., 2017; Karapınar & Nützel, 2021; Karapınar et al., 2022; Wagner, 2002). Sinuopeidae, Raphistomatidae and Trochonematoidea (Lophospiridae and Trochonematidae) were previously regarded as Pleurotomariida (e.g. Knight et al., 1960) but were not recovered within Pleurotomariida in the phylogenetic analysis of Wagner (2002); therefore, they are not considered Pleurotomariida (Bouchet et al., 2017) and were not included in the list of pleurotomariidan genera. Bouchet et al. (2017) included Murchisonioidea and Cirridae within Pleurotomariida. Murchisonioidea consists of slit-bearing high-spired gastropods with either a vetigastropod-type protoconch (e.g. Frýda & Manda, 1997: *Murchisonia*) or a caenogastropod-type protoconch (Mazaev, 2011; Nützel & Bandel, 2000; Nützel & Pan, 2005; Pan & Erwin, 2002). Based on shell microstructure (i.e. the absence of a nacreous shell layer; Bandel et al., 2002) and the presence of a caenogastropod-type

protoconch, slit-band gastropods with planktotrophic protoconchs are placed in the caenogastropod family Goniasmatidae (e.g. Karapınar et al., 2022; Nützel & Bandel, 2000; Nützel & Karapınar, 2023). Apart from a few examples (e.g. Frýda & Manda, 1997), most members of Murchisonioidea with known protoconchs (mainly from the late Palaeozoic) have protoconchs reflecting planktotrophic larval development (Bandel et al., 2002; Karapınar et al., 2024; Mazaev, 2011; Nützel & Bandel, 2000; Nützel & Pan, 2005), suggesting that most of them are members of Caenogastropoda. However, nacre (a shell microstructure known only in the vetigastropod shell among extant gastropods) was reported in an Ordovician member of Murchisonioidea (Mutvei, 1983). Since Murchisonioidea is probably a polyphyletic group and many of them represent Caenogastropoda, its members were not included in the analysed list of pleurotomariidan genera. Similarly, the high-spired slit bearing superfamily Sinuspiroidea Mazaev, 2011 was also excluded from the pleurotomariidan generic list. Based on the change in coiling direction during ontogeny, Bandel (1993) united slit-less Cirridae and slit-bearing Porcellioidea in the superfamily Cirroidea (=Porcellioidea). It is debated whether Cirridae is related to Porcellioidea or Eucyclidae (see Conti & Monari, 2001; Karapınar & Nützel, 2021; Szabó et al., 2019); therefore, the family Cirridae was excluded from the list of pleurotomariidan genera. As a result of a revision, the current list consists of 283 pleurotomariidan genera (see [Supplemental material, Appendix 6](#) for the complete list).

The Phanerozoic gastropod occurrences were downloaded from the Paleobiology Database (PBDB) (www.paleobiodb.org; 16 January 2023). The non-marine occurrences were excluded from the dataset. Determinations above genus rank and uncertain genus attributions (i.e. cf., ?, aff., “”, ex gr., *sensu lato*, informal) were also excluded from the dataset. The occurrence dataset was subsetted for 283 pleurotomariidan genera for analysing the diversity of Pleurotomariida. For diversity analyses, the shareholder quorum subsampling method (SQS) of Alroy (2010b) was used to overcome potential sampling biases across different geological ages. SQS was conducted in the R package *divDyn* version 0.8.2 (Kocsis et al., 2019) and the quorum was set as 0.6. The PBDB data and the R code used for the diversity analysis are provided in the Supplementary Code and Data.

Homoplasy analysis

Homoplasy can be inferred by comparing the number of character state changes of different characters along a tree. The characters with fewer character state changes can be regarded as being less homoplastic. However, the number of state changes are related to the number

of character states; hence, the characters with higher number of states show more state changes. To calculate homoplasy, we used the Consistency Index (CI), which is the division of the number of observed state changes by the minimum possible number of state changes of a character (i.e. the number of character states minus one). The consistency index of characters was calculated with TNT by using ‘statsall.run’ code (provided in the Supplementary Code and Data). The consensus tree of the parsimony analysis and the maximum a posteriori tree of the Bayesian tip-dating analysis were used to calculate CI values. Median CI values of different character sets (early ontogenetic characters vs late ontogenetic characters; axial vs spiral characters; upper whorl face, selenizone, lower whorl face, basal characters) were compared with Mann–Whitney and Kruskal–Wallis tests to assess if some groups of characters were more homoplastic than the other groups. A Spearman Rank Correlation test was used to test the relationship of protoconch size and first whorl size to adult shell size.

Results

Parsimony analysis

In the initial search, 322 trees of different scores were obtained, nine of them representing the most parsimonious trees (MPTs) with tree lengths of 1601 steps, CI of 0.130 and Retention Index (RI) of 0.521. In the second search, which was done based on the initial trees, 99,999 trees were obtained, 60 of them representing MPTs with tree lengths of 1601 steps, CI of 0.130 and RI of 0.521. A strict consensus tree of 60 MPTs is given in Fig. 1.

Twelve groups are defined (using the ending -ides herein, unassigned to Linnean categories) in the most parsimonious tree considering the taxonomic systematics of Pleurotomariida. Overall group compositions indicate that compositions of pleurotomariidan families suggested by taxonomists are largely para- or polyphyletic. The clades (the monophyletic groups, underlined and indicated with *), paraphyletic groups (underlined) and their family compositions (in parentheses) are as follows:

Euryzonines* (subfamily Euryzoniinae)
Kittlidiscides* (family Kittlidiscidae, family Lancedellidae in part)
Zygitides (family Zygitidae), paraphyletic
Porcelliides (family Porcelliidae), paraphyletic
Mourloniides (family Eotomariidae in part, family Luciellidae in part, family Phymatopleuridae in part), paraphyletic

Ptychomphalides (family Ptychomphalidae, subfamily Liospirinae, family Trochotomidae, family Temnotropidae), paraphyletic
Gosseletinides (family Gosseletinidae in part, family Rhaphistomellidae in part, family Portlockiellidae in part), paraphyletic
Wortheniellides (family Wortheniellidae, family Schizogoniidae, family Eotomariidae in part, family Rhaphistomellidae in part, family Lancedellidae in part), paraphyletic
Glabrocingulini* (family Eotomariidae in part)
Clathrospirides* (family Eotomariidae in part, subfamily Ruedemanninae)
Phymatopleurides (family Phymatopleuridae in part, family Portlockiellidae in part, family Eotomariidae in part, family Stuorellidae) paraphyletic
Pleurotomariides* (family Pleurotomariidae, family Phymatopleuridae in part)

Bayesian analysis

Model selection is an important component of Bayesian phylogenetic analysis, since recovered trees and branch lengths vary depending on the initial model and model parameters. We used stepping stone sampling (i.e. calculation of marginal likelihoods of each model) as done in previous studies with morphological phylogenies (Wright *et al.*, 2021). Stepping stone sampling in RevBayes favoured the uncorrelated lognormal (UCLN) clock model over strict clock model (Table 1). Among different models, the highest marginal likelihood was found for the model with UCLN clock model, unequal character state frequencies and constant speciation, extinction and fossilization rates (Table 1). Therefore, this model was selected and the maximum a posteriori (MAP) tree of this model is presented herein (Fig. 2). The second most probable model was the UCLN clock model with discrete character state frequencies and 5-skyline intervals. Note that stepping stone sampling has been criticized (May & Rothfels, 2023) and the skyline model might truly give a better fit to the data. The recovered MAP tree of the 5-skyline model is provided in the Supplementary Code and Data and different speciation, extinction and fossilization rates at different skyline intervals are presented in Figure 8.

Eleven groups (underlined below) are recovered in the MAP tree (Fig. 2). Except for Euryzonines and Porcelliides, all monophyletic and paraphyletic groups recovered in the parsimony analysis are present in the Bayesian phylogeny. However, their compositions are different than the composition of the same named groups in the most parsimonious tree. An additional clade, Ptychomphalines, is defined in the Bayesian

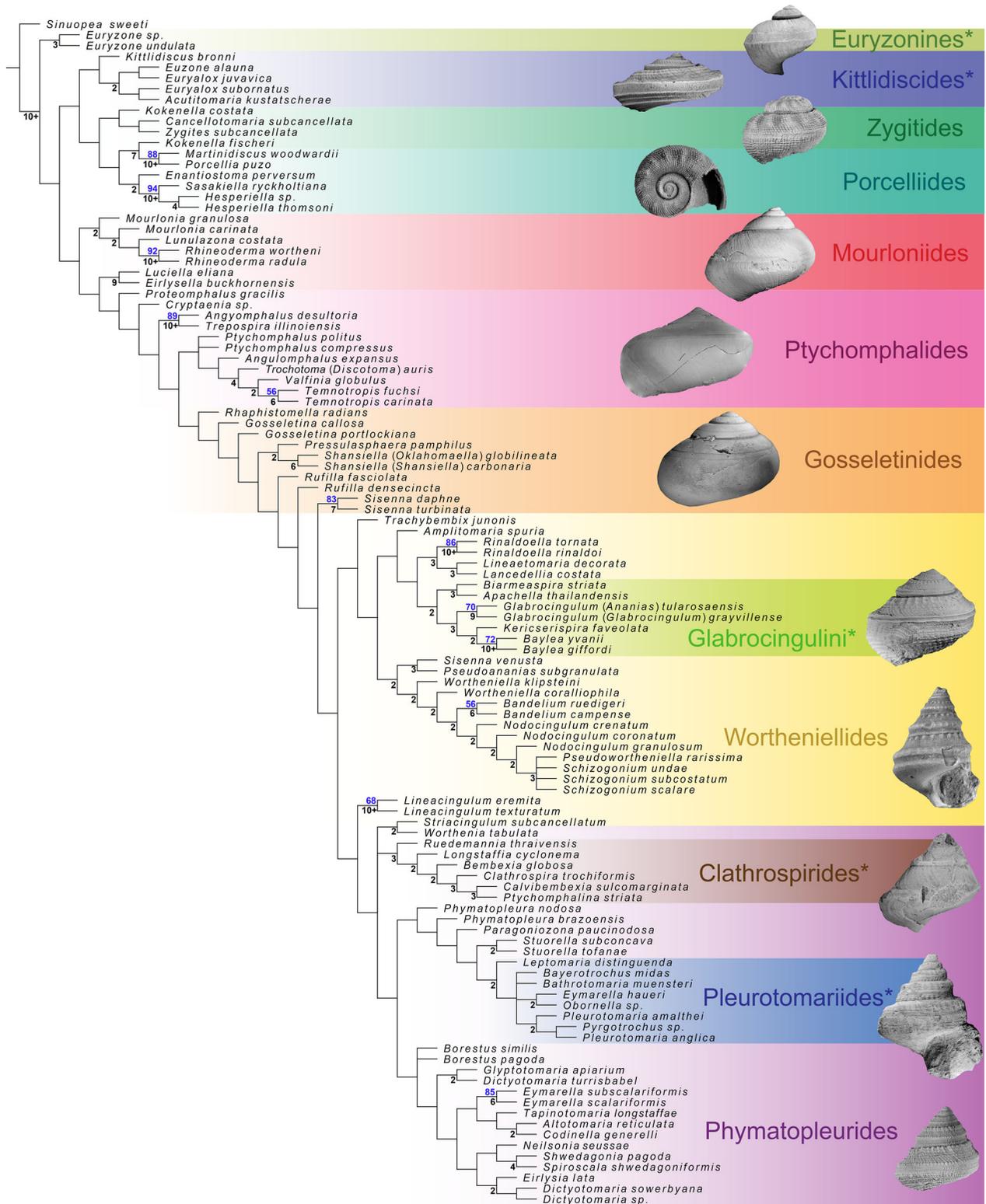


Figure 1. The strict consensus tree of 60 most parsimonious trees (MPTs) (1601 steps, CI: 0.130, RI: 0.521), reconstructed with parsimony. Bootstrap values >50% are indicated in blue above the nodes. Bremer support values >1 are indicated in black below the nodes. Clades are denoted by an asterisk (*), all other groups are paraphyletic.

Table 1. Marginal likelihoods (logarithm) of the Bayesian models.

	Constant		Skyline	
	Mk	Discretized	Mk	Discretized
Strict clock	-6897.944	-6874.242	-6866.347	-6861.913
UCLN	-6834.551	-6822.926	-6837.589	-6829.381

Note: UCLN model has the highest marginal likelihood (in bold).

tree. The group compositions (monophyletic groups are indicated with *) partly reflect the current taxonomic systematics of Pleurotomariida:

Clathrospirides (family Eotomariidae in part), paraphyletic

Ptychomphalines* (family Eotomariidae in part, family Porcellidae in part)

Gosseletinides (family Gosseletinidae in part, subfamily Liospirinae, subfamily Euryzoniinae, family Eotomariidae in part, family Luciellidae in part), paraphyletic

Mourloniides (family Eotomariidae in part, family Phymatopleuridae in part, family Porcellidae in part), paraphyletic

Pleurotomariides* (family Pleurotomariidae, family Phymatopleuridae in part)

Glabrocingulini (family Eotomariidae in part, family Phymatopleuridae in part), paraphyletic

Phymatopleurides (family Phymatopleuridae, family Portlockiellidae, family Luciellidae in part, family Eotomariidae in part), paraphyletic

Zygitides (family Zygitidae, family Porcellidae in part), paraphyletic

Kittlidiscides* (family Kittlidiscidae, family Lancedellidae in part)

Wortheniellides (family Wortheniellidae, family Stuorellidae, family Schizogoniidae, family Eotomariidae in part, family Lancedellidae in part, family Rhabdostomellidae in part), paraphyletic

Ptychomphalides* (family Ptychomphalidae, family Temnotropidae, family Rhabdostomellidae in part, family Trochotomidae)

Additionally, Glabrocingulini, Wortheniellides and Ptychomphalides are collectively representing the clade Wortheniellini. Phymatopleurides, Kittlidiscides, Zygitides and Pleurotomariides are representing the clade Pleurotomariini. Clathrospirides, Ptychomphalines, Gosseletinides and Mourloniides are together representing the clade Eotomariini.

The family classifications of the analysed genera and their clade/group assignments in the Bayesian and parsimony analyses are given in [Supplemental material, Appendix 7](#).

Stratigraphical congruence analysis

The stratigraphical congruence indices indicate that, compared to the FBD tree, the most parsimonious trees are stratigraphically more inconsistent (i.e. the number of daughter lineages with occurrences older than their ancestral lineages is higher) and have more ghost ranges (measured with different metrics as presented in [Table 2](#); [Supplemental material, Appendix 5](#)). The most parsimonious phylogeny plotted against geological ages can be found in the [Supplemental material, Supplementary Figure 1](#).

Homoplasy analysis

The CI values among different character sets were compared for both the most parsimonious tree and the Bayesian tree. The early ontogenetic shell characters have higher CI values than the late ontogenetic shell characters ([Fig. 3](#) for Bayesian tree, Mann–Whitney test for medians $p = 0.019$; [Supplemental material, Supplementary Figure 3](#) for parsimony tree). Although not significantly, the CI values of characters related to ontogenetic change are also higher than late ontogenetic characters ([Fig. 3](#) for Bayesian tree, Mann–Whitney test for medians $p = 0.145$; [Supplemental material, Supplementary Figure 3](#) for parsimony tree). Axial characters have higher CI values than spiral characters, but the difference is not significant ([Fig. 4](#) for Bayesian tree, Mann–Whitney test for medians $p = 0.197$; [Supplemental material, Supplementary Figure 4](#) for parsimony tree). The median CI values do not differ significantly among the sets of characters related to different shell sectors ([Fig. 5](#) for Bayesian tree, Kruskal–Wallis test, $p = 0.335$; [Supplemental material, Supplementary Figure 5](#) for parsimony tree).

Correlation between larval and adult shell size

The data further revealed that the larval shell size and first whorl width (including larval shell and early part of teleoconch) are positively correlated with adult shell size ([Fig. 6](#); Spearman rank correlation test, $r_s=0.43$, $p < 0.05$; Kruskal–Wallis test for equality of medians $p = 0.001$).

Morphological evolutionary rates along branches

According to the best model (uncorrelated log normal clock with discrete character state frequencies), morphological evolutionary rate does not show significant differences among branches or in the early evolutionary history of any clade ([Fig. 7](#)).

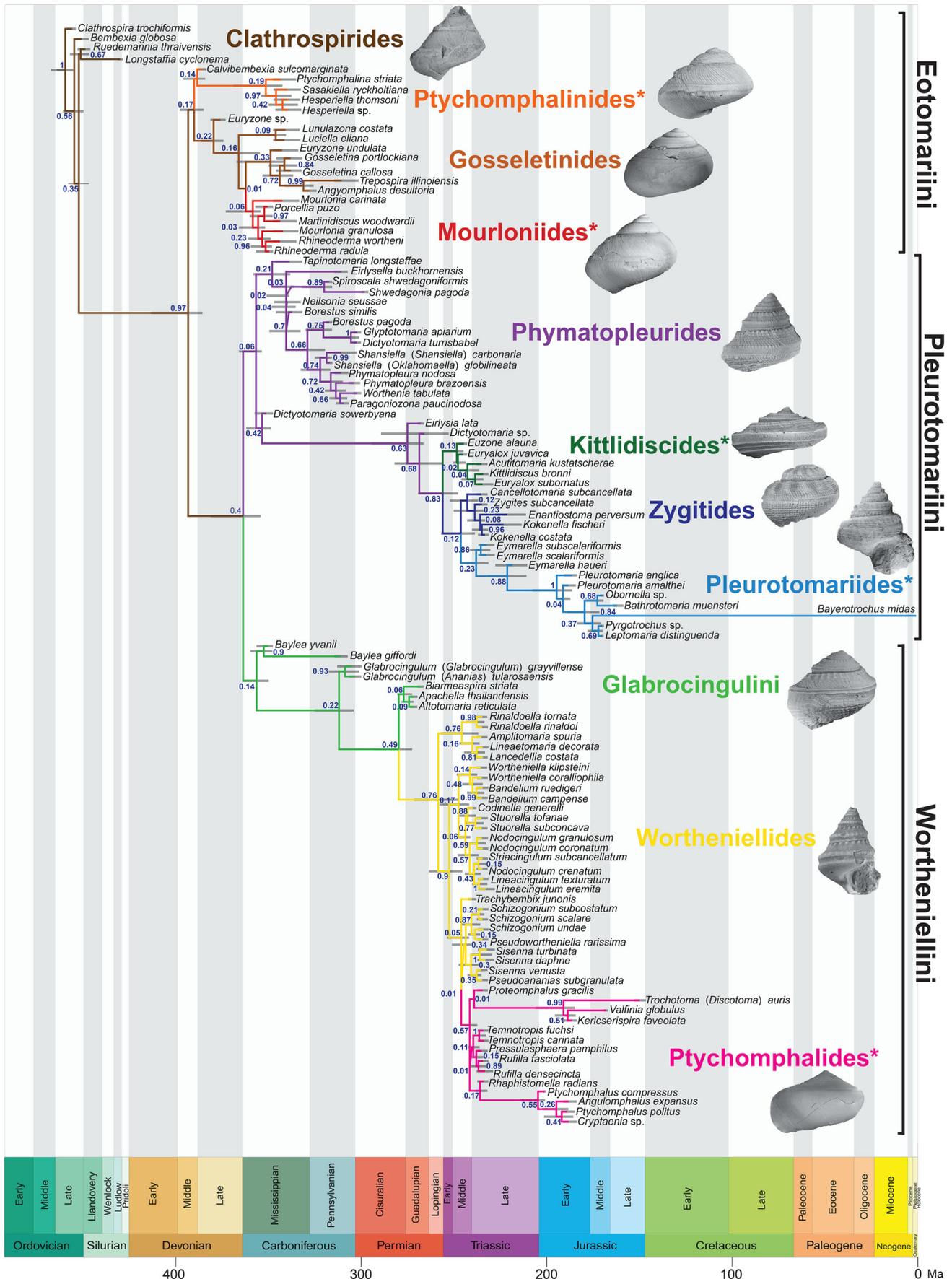


Figure 2. The maximum a posteriori (MAP) tree of the uncorrelated lognormal (UCLN) clock model, reconstructed with the fossilized birth–death model. The numbers at nodes indicate the posterior probabilities of clades. The error bars indicate the 95% highest posterior density (HPD) interval for divergence times. Clades are denoted by an asterisk (*), all other groups are paraphyletic.

Table 2. Stratigraphical congruence metrics for the consensus tree of the 60 most parsimonious trees (MPTs) and the maximum a posteriori (MAP) tree (see Supplemental material, [Supplementary Figs 1 and 2](#) for the time scaled trees). **Abbreviation:** MIG: Minimum Implied Gap; G_{Max} : maximum possible sum of ghost ranges; G_{Min} : minimum possible sum of ghost ranges; SCI: Stratigraphic Consistency Index; RCI: Relative Completeness Index; GER: Gap Excess Ratio; MSM*: corrected Manhattan Stratigraphic Measure.

	MIG	G_{Max}	G_{Min}	SCI	RCI	GER	MSM*
Parsimonious tree	6324.79	24895.49	500.99	0.68	-546.77	0.76	0.08
FBD tree	1239.64	20252.09	458.39	0.70	-28.82	0.96	0.37

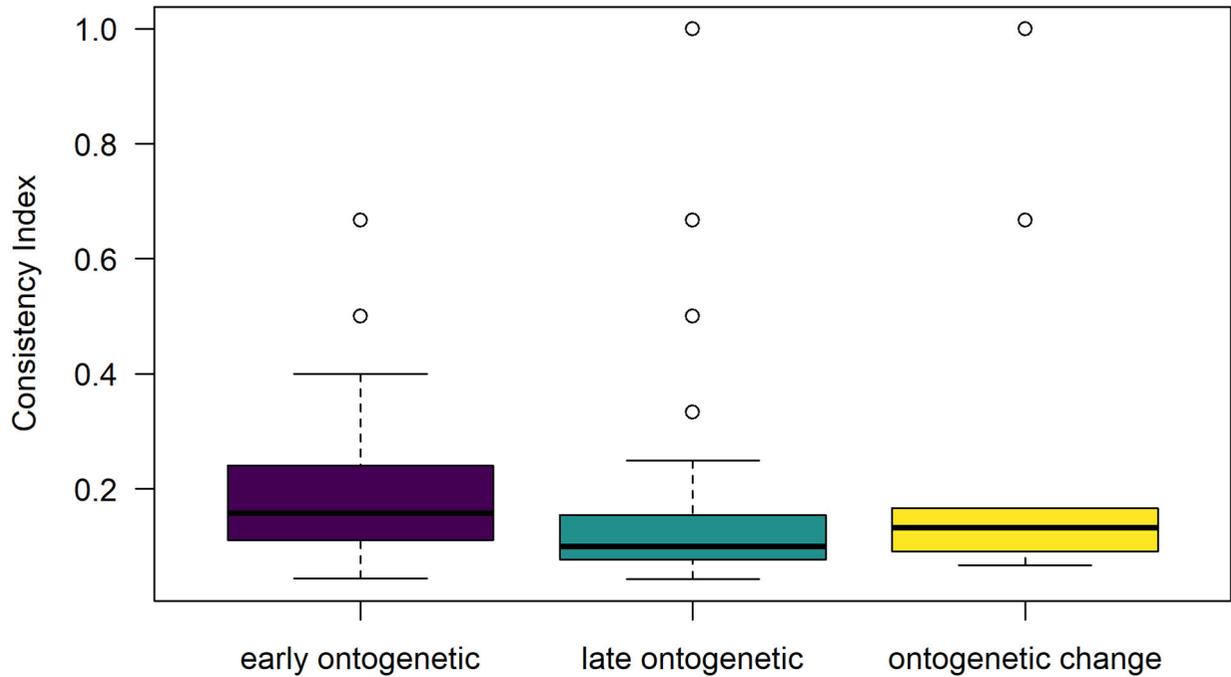


Figure 3. Box plot of consistency index (CI) values of the character sets that are related to the early ontogenetic shell, the late ontogenetic shell and the ontogenetic change. The CI values were calculated with the maximum a posteriori tree of the Bayesian tip-dating analysis.

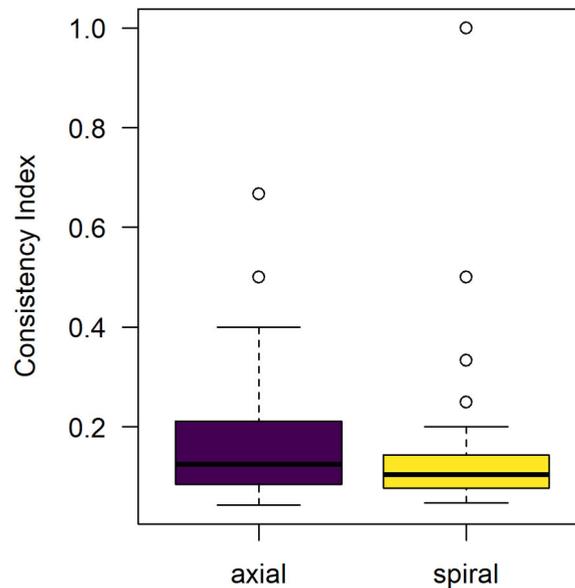


Figure 4. Box plot of consistency index (CI) values of the character sets that are related to the axial characters and the spiral characters. The CI values were calculated with the maximum a posteriori tree of the Bayesian tip-dating analysis.

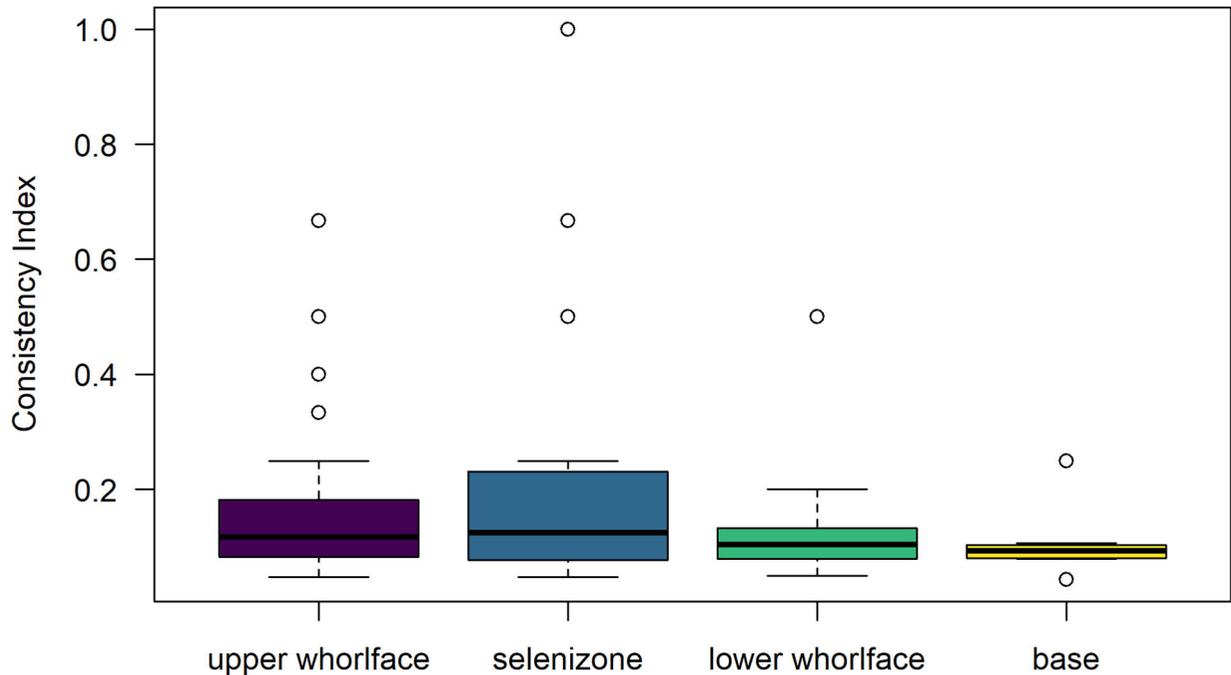


Figure 5. Box plot of consistency index (CI) values of the character sets that are related to different shell sectors. The CI values were calculated with the maximum a posteriori tree of the Bayesian tip-dating analysis.

Speciation, extinction and fossilization rates through time

The Bayesian analysis with 5-skyline model reconstructed significantly different speciation and extinction rates at different skyline intervals (Fig. 8): an increase in speciation and extinction rate from the Ordovician–Devonian interval to the Triassic–Jurassic interval, with an abrupt drop in the Cretaceous–Recent interval. It also reconstructed a slight increase in fossilization rate from the Mesozoic onwards.

Diversity analysis

The Shareholder Quorum Subsampling analysis of PBDB data confirms that Pleurotomariida was a major component of global gastropod diversity from the Silurian to the Permian (Fig. 9). The group represents up to 40% of the total generic gastropod diversity in the Palaeozoic (Supplemental material, Supplementary Figure 6). After the end-Permian mass extinction, the diversity of the group drastically dropped and it represented only 10% and below of gastropod generic diversity. After an initial recovery of the group, the re-diversification was interrupted in the Carnian (Fig. 9). The present sampling standardized analysis of the PBDB occurrence data results in a diversity curve for the Permian–Triassic interval that is very similar to that presented previously based on range through data without sample standardization by Karapınar & Nützel

(2021). The analysis further indicates that the Permian–Triassic interval was highly determinant in the Mesozoic–Recent evolutionary history of the group.

Discussion

The clade and group compositions recovered by our phylogenetic analyses are not in agreement with the current taxonomic systematics of Pleurotomariida. Therefore, the current systematic arrangement of Pleurotomariida needs to be revised. However, there are inconsistencies between tree topologies reconstructed with different methodologies (Bayesian *vs* parsimony) and models (skyline *vs* no skyline). Tree topologies are also susceptible to changes in the taxon/character matrix, i.e. inclusion/exclusion of characters/taxa. As the traditional taxonomic works on which the current systematics is largely based, the present phylogenetic trees are hypotheses that are subject to further testing. Our results show that different phylogenetic approaches suggest different evolutionary relationships among taxa, perhaps because they are based on different model assumptions. In addition to testing evolutionary hypotheses proposed in taxonomic systematics, the analyses allow for testing previous hypotheses about homoplasy among the shell characters (axial *vs* spiral; early ontogeny *vs* late ontogeny; selenizone *vs* other shell

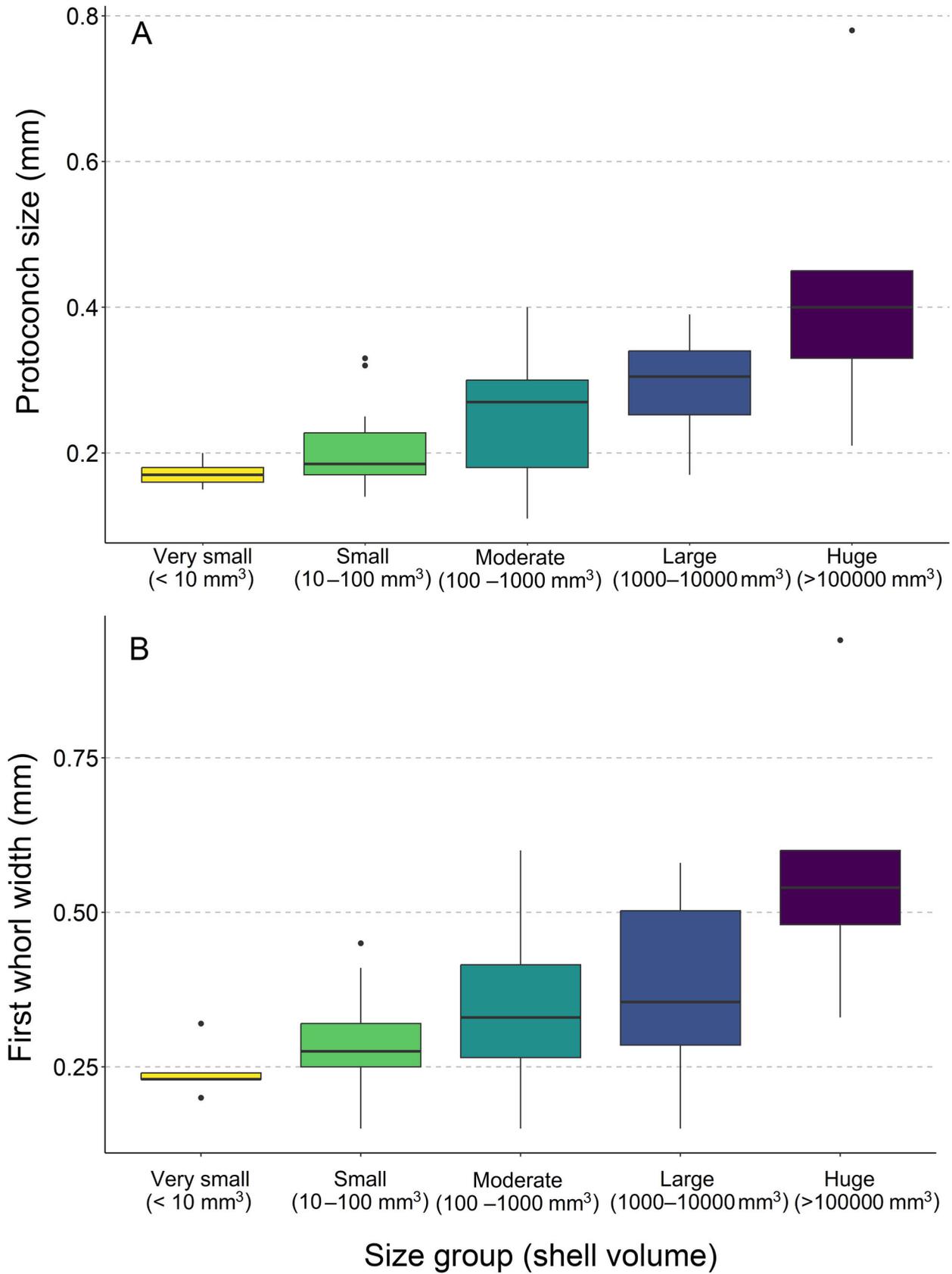


Figure 6. Box plots of **A**, protoconch size and **B**, first whorl width of gastropods belonging to different size groups.

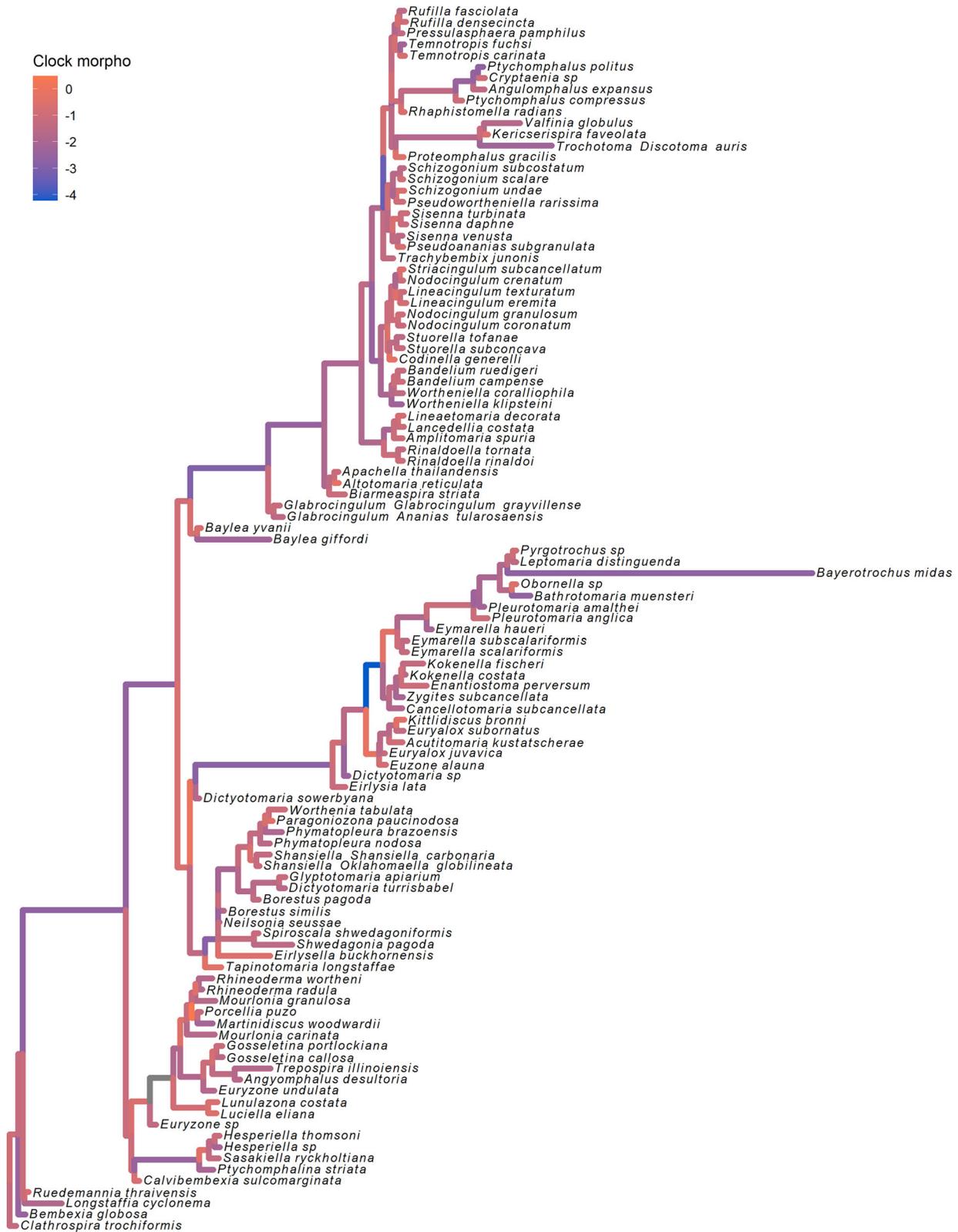


Figure 7. Maximum a posteriori (MAP) tree with uncorrelated lognormal (UCLN) clock model, coloured according to the posterior-mean estimates of the morphological evolutionary rate along branches. The figure was produced after taking the decimal logarithm of the original morphological evolutionary rates.

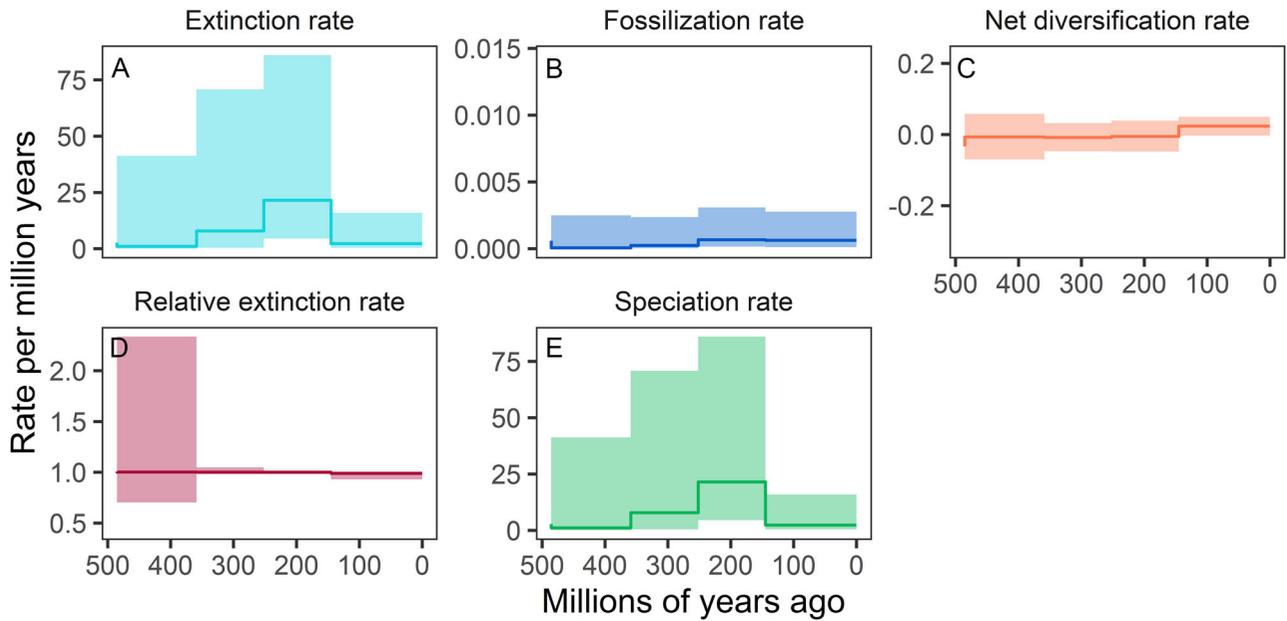


Figure 8. Diversification rates estimated according to the 5-skyline model. **A**, the extinction rate. **B**, the fossilization rate. **C**, the net diversification rate (speciation minus extinction). **D**, the relative extinction rate (extinction divided by speciation). **E**, the speciation rate. Dark lines denote the posterior-mean estimates, shaded areas correspond to the 95% credible intervals. See the Supplementary Code and Data for the maximum a posteriori (MAP) tree of the 5-skyline model.

sectors), which have important implications for the usage of shell characters in gastropod phylogenetic analyses.

Implications for classification

Both trees (parsimony and Bayesian) suggest that many of the current systematic arrangements are not monophyletic. The parsimony method produced a tree that is not congruent with stratigraphical data (Supplemental material, [Supplementary Figure 1](#)). The CI and RI of the MPTs are relatively low and indicate that the characters show a high rate of transformation. The relatively high number of character states per character might be a reason for the high number of character states changes (or low CI and RI values). However, high transformation rates can also indicate that the characters used in the analysis are highly variable and hence phylogenetically less informative. Both in the Bayesian tree and in the most parsimonious tree, clade supports are very low apart from a few small clades. Low clade support is a common issue in morphological datasets due to the low number of characters compared to molecular datasets. The taxonomic systematics of the analysed taxa and their group/clade affinity recovered in the parsimony and Bayesian trees are presented in the [Supplemental material, Appendix 7](#). A revision of the current classification is suggested based on the reconstructed phylogenies for taxa that are recovered in the same groups in both trees ([Table 3](#)). Accordingly, we herein raise the

rank of Wortheniellidae [Bandel, 2009](#) to superfamily Worthenielloidea.

Parsimony analysis. Parsimony analysis indicates that the generic composition of the families Porcellidae (*Porcellia*, *Hesperiella*, *Enantiostoma*, *Martinidiscus*, *Sasakiella*), Luciellidae (*Luciella*, *Eirlysella*), Schizogoniidae (*Schizogonium*, *Pseudowortheniella*) and Pleurotomariidae (*Pleurotomaria*, *Leptomaria*, *Bayerotrochus*, *Bathrotomaria*, *Obornella*, *Pyrgotrochus*) are monophyletic. The current systematic composition of the family Trochotomidae is paraphyletic. The tree topology ([Fig. 1](#)) suggests that the families Eotomariidae, Ptychomphalidae, Wortheniellidae, Phymatopleuridae, Zygitidae, Rhaphistomellidae, Lancedellidae, Stuorellidae are polyphyletic in their current generic composition.

The family Eotomariidae is a large group comprising more than 90 genera. The evolutionary relationships between these genera are not clear (see [Karapunar et al., 2022](#)). In the current analysis, members of Eotomariidae are recovered as members of five distinct groups: Mourloniides, Ptychomphalides, Wortheniellides, Clathrospirides and Phymatopleurides. It is noteworthy that *Mourlonia* and *Ptychomphalina* are distantly placed in the tree (Mourloniides and Clathrospirides), despite the fact that they were once regarded as synonyms due to their morphological similarity ([Knight et al., 1960](#)). The current phylogeny supports the view of [Gordon and Yochelson \(1987\)](#), who considered the two genera

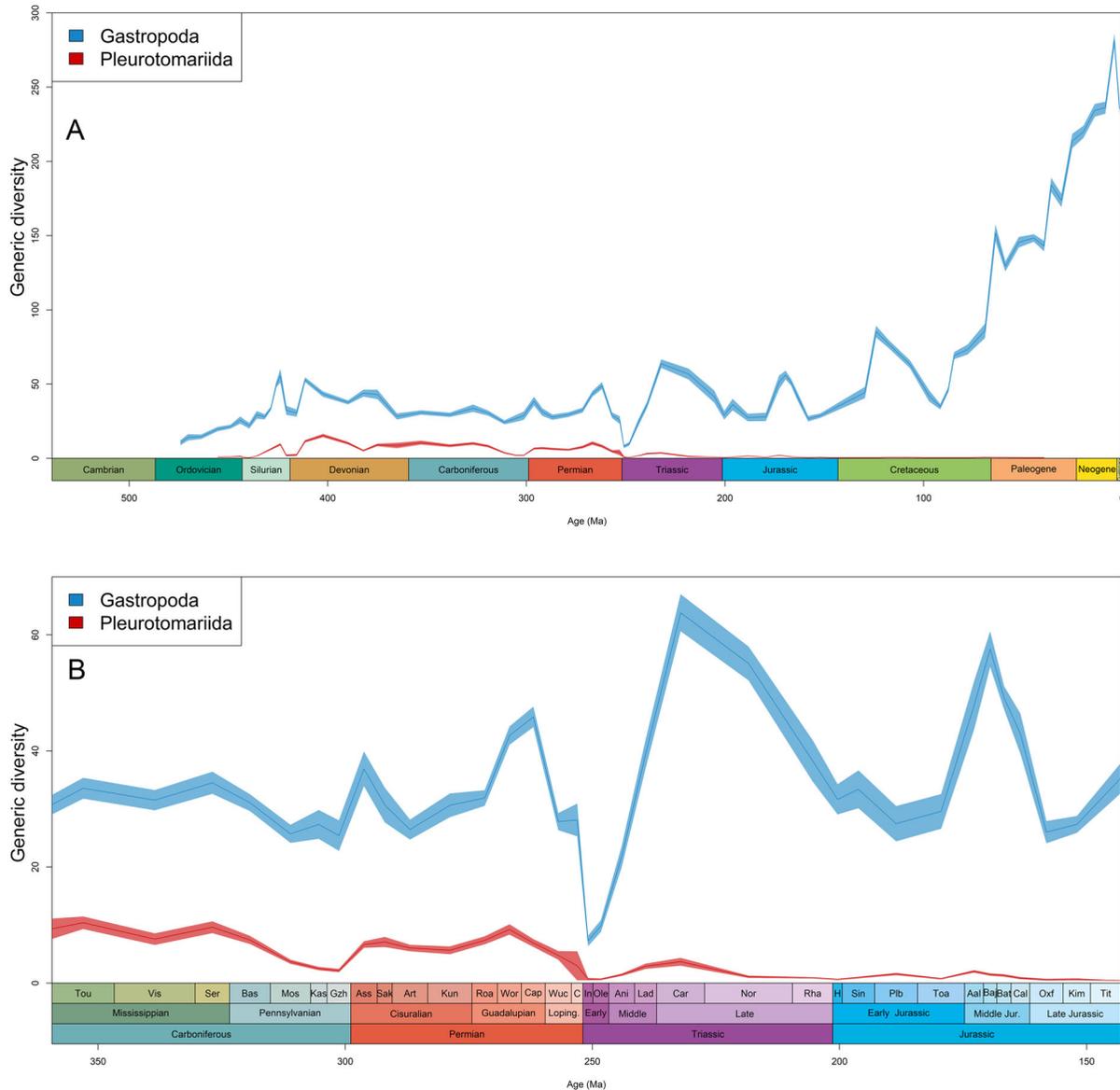


Figure 9. Generic diversity of Gastropoda (blue) and Pleurotomariida (red) **A**, through the Phanerozoic and **B**, from the Carboniferous to the Jurassic. Dark lines denote the mean values of 100 replicates with Shareholder Quorum Sampling of the data from the Paleobiology Database, shaded areas correspond to the 95% confidence intervals.

separate and placed them in separate tribes (Mourloniini and Ptychomphalini). However, *Mourlonia* was recovered as sister group of *Lunulazona*, which is in contrast to the view of Gordon and Yochelson (1987). *Baylea*, *Glabrocingulum* (*Ananias*) and *Glabrocingulum* (*Glabrocingulum*) are the most species-rich and globally distributed upper Palaeozoic eotomariid genera. They can be united under the tribe Glabrocingulini Gordon & Yochelson, 1987. *Biarmeaspira* was considered to be derived from *Baylea* (Karapınar et al., 2024; Ketwetsuriya et al., 2020; Mazaev, 2015). In the parsimony analysis, both genera were recovered in Glabrocingulides, with *Biarmeaspira* being distant from

Baylea. The position of Glabrocingulini within the group Wortheniellides suggests a close relationship between the upper Palaeozoic Glabrocingulini and the Triassic Wortheniellidae. Wortheniellidae might represent a surviving lineage of Glabrocingulini after the end-Permian mass extinction event. The upper Palaeozoic eotomariid genera *Neilsonia*, *Shwedagonia* and *Spiroskala* are recovered within Phymatopleurides, suggesting an affinity of the tribe Neilsoniini Gordon & Yochelson, 1987 to Phymatopleuridae.

The members of Phymatopleuridae are recovered in Mourloniides and Pleurotomariides, in addition to Phymatopleurides. *Rhinoedermia* and *Eirlysia* were

Table 3. Revised classification of Pleurotomariida.**Clade Eotomariini**

- Superfamily Eotomarioidea Wenz, 1938
 Family Eotomariidae Wenz, 1938
 Subfamily Eotomariinae Wenz, 1938
 ?Subfamily Nelsoniinae Knight, 1956
 Subfamily Ruedemanniinae Knight, 1956
 Family Mourloniidae Gordon & Yochelson, 1987 (includes *Rhineoderma*)
 Family Porcellidae Zittel, 1895
 Family Ptychomphalidae Wenz, 1938
 Family Gosseletinae Wenz, 1938
 Subfamily Euryzoninae Wagner, 2002
 Subfamily Liospirininae Knight, 1956
 Family Luciellidae Knight, 1956

Clade Wortheniellini

- Superfamily Worthenielloidea Bandel, 2009
 Tribe Glabrocingulini Gordon & Yochelson, 1987 (includes *Glabrocingulum*, *Baylea*, *Biarmeaspira*, *Apachella*)
 Family Wortheniellidae Bandel, 2009
 Family Schizogoniidae Cox in Knight et al., 1960 (=Pseudowortheniellidae Bandel, 2009)
 Family Lancedellidae Bandel, 2009 (includes only *Lancedellia* and *Lineaetomaria*)
 Family Stuorellidae Bandel, 2009
 Superfamily Ptychomphaloidea Wenz, 1938
 Family Ptychomphalidae Wenz, 1938
 ?Family Rhabhistomellidae Bandel, 2009
 Family Temnotropidae Cox in Knight et al., 1960
 Family Trochotomidae Cox in Knight et al., 1960 (includes *Kericserispira*)

Clade Pleurotomariini

- Superfamily Pleurotomarioidea Swainson, 1840
 Family Pleurotomariidae Swainson, 1840 (includes *Eymarella*)
 Family Zygitidae Cox in Knight et al., 1960 (includes *Enantiostoma*)
 Family Kittlidiscidae Cox in Knight et al., 1960 (includes *Euryalox*, *Euzone*, *Acutitomaria*)
 Family Phymatopleuridae Batten, 1956
 Family Portlockiellidae Batten, 1956

Note: The following pleurotomariidan families were not analysed: Family Phanerotrematidae Knight, 1956; Family Rhabdichismatidae Knight, 1956; Family Polytremaeidae Wenz, 1938; Family Catantostomatidae Wenz, 1938. As discussed in the Material and methods section, the family Cirridae and superfamily Murchisonioidea were not included in the analysis.

previously considered as eotomariid genera but are now placed in Phymatopleuridae (Karapınar et al., 2022). However, *Rhinoederma* was recovered within the Mourloniidae, in agreement with the older classification by Knight et al. (1960). *Worthenia* was previously placed in Ruedemanninae (Knight et al., 1960), which was doubted by Karapınar et al. (2022) in the light of new information on early ontogeny and it was placed in Phymatopleuridae. However, in the analysis *Worthenia tabulata* was recovered between *Ruedemannia* (Clathrospiridae) and Wortheniellidae, supporting the earlier opinions. *Tapinotomaria* was removed from Portlockiellidae and assigned to Phymatopleuridae by Karapınar et al. (2022). The present analysis supports this placement, but the members of Portlockiellidae are placed in Gosseletinae far from Phymatopleuridae, in contrast to the view presented by Karapınar et al. (2022).

Bandel (2009) erected Rhabhistomellidae and included only *Rhabhistomella*. Karapınar and Nützel (2021) included *Rhabhistomella*, *Sisenna* and *Rufilla* in

Rhabhistomellidae. The present parsimony analysis supports a close relationship between *Sisenna* and *Rufilla* and a close affinity of *Rhabhistomella*, *Sisenna* and *Rufilla* to *Gosseletina*.

Kittlidiscidae and Temnotropidae are composed of a single genus each and their relationships to other groups were not resolved. The tree reveals the relationship of these families to other genera and families. *Euzone*, *Euryalox* and *Acutitomaria* seem to be closely related to *Kittlidiscus*, and hence Kittlidiscidae. These three genera were previously also considered closely related and were placed tentatively in Lancedelliidae (Karapınar & Nützel, 2021). The tree indicates a placement of *Euzone*, *Euryalox* and *Acutitomaria* within Kittlidiscidae. *Rinaldoella* is recovered as a sister taxon of the two members of the family Lancedelliidae (*Lancedellia* and *Lineaetomaria*). As previously discussed by Karapınar and Nützel (2021), *Lancedellia* and *Rinaldoella* might represent synonyms, but *Rinaldoella* has a very small adult shell size with few whorls and information on comparable initial whorls of

Lancedellia is unknown. *Rinaldoella* resembles Scissurellidae (e.g. Geiger, 2012) with its overall small size, position of the selenizone, planispirally coiled early whorls, sudden appearance of the selenizone, and prominent selenizone borders (Karapınar & Nützel, 2021); therefore, *Rinaldoella* might belong to Scissurellidae. If so, the most parsimonious tree suggests that Scissurellidae might be a living representative of Wortheniellides.

Previously Temnotropidae was placed in Haliotoidea, which was refuted by Karapınar and Nützel (2021), who argued for a possible derivation of Haliotidae from Trochotomidae. The parsimony analysis reconstructed Temnotropidae as sister group of Trochotomidae. Although Haliotidae was not analysed in the present study, it is likely that it was derived from these closely related groups.

Although the Triassic families Stuoirellidae and Schizogoniidae are recognized as distinct families, their relationships to other families have been unknown (Karapınar & Nützel, 2021). The most parsimonious phylogeny suggests that Stuoirellidae (*Stuoirella*, *Codinella*) is polyphyletic and both genera have close relationships to Pleurotomariidae, as was suggested by Knight et al. (1960). Schizogoniidae is closely related to the Triassic family Wortheniellidae. The phylogenetic analysis also indicates that Wortheniellides was the most diversified group of Pleurotomariida within the Triassic.

Kokenella fischeri (Zygitidae) was recovered as sister taxon of the Palaeozoic genus *Porcellia* (Porcellidae), while *Kokenella costata* was recovered as sister to all other Zygitides. *Kokenella* and *Porcellia* are quite similar to each other in general whorl morphology but differ in selenizone characters and the morphology of the early whorls: planispiral in *Kokenella* and trochospiral in *Porcellia*. They were placed in the same family by Knight et al. (1960) but have no longer been considered as closely related due to differences in the morphology of the early whorls (see Karapınar & Nützel, 2021).

Trepsira and *Angyomphalus* were recovered within Ptychomphalides, indicating a close relationship between the Palaeozoic subfamily Liospirinae and the Mesozoic family Ptychomphalidae, as also previously suggested by Karapınar and Nützel (2021) based on a taxonomic analysis. The composition of Ptychomphalides as found with the parsimony analysis corroborates Gründel's (2011) opinion on the systematics of Ptychomphaloidea.

Pleurotomariides is recovered as crown group within Phymatopleurides. Pleurotomariides represents a lineage that survived the end-Permian mass extinction among the Palaeozoic Phymatopleurides stock and has persisted

until today. Representatives of the Triassic genus *Eymarella* were recovered both within Phymatopleurides and Pleurotomariides.

The present tree suggests that the shift of the position of the selenizone towards the abapical portion of the whorl face occurred independently three times in the families Porcelliidae (Porcellides), Luciellidae (Mourloniides) and Portlockiellidae (Gosseletinides).

The present parsimony analysis reconstructed the members of the same genera distantly suggesting polyphyly of these genera in their current composition (i.e. *Eymarella*, *Sisenna*, *Kokenella*).

It is expected that the pleurotomariidan taxa from older geological ages (early Palaeozoic) are more basally situated within the tree and the younger taxa are reconstructed as more distant from the root. However, in the present most parsimonious tree, the stratigraphical order of the taxa is not congruent with their position along the tree (e.g. the early Palaeozoic group Clathrospirides is placed in a more derived position than the Mesozoic groups Zygitides, Ptychomphalides and Wortheniellides). Parsimony analysis does not consider the ages when constructing phylogenies, although it is important information that helps to decipher relationships between taxa. On the other hand, the FBD method incorporates age information into the analysis. The stratigraphical congruence metrics indicate that maximum parsimonious trees are stratigraphically less consistent and have more ghost ranges than the Bayesian tree (Table 2).

Bayesian analysis. The maximum a posteriori (MAP) tree suggests that the taxonomic composition of the family Eotomariidae is polyphyletic as is also suggested by parsimony analysis and was previously discussed based on taxonomic analyses (Karapınar et al., 2022). The FBD model incorporates fossil sampling ages into the analysis and FBD trees thus depict divergence times (node ages). In the early Palaeozoic, Pleurotomariida was represented by the stem group Clathrospirides. The early paraphyletic stem group within the clade Pleurotomariida is herein called Eotomariini (Fig. 2), a lineage restricted to the Palaeozoic. Two distinct clades appeared in the earliest Carboniferous: one is Wortheniellini, and the other is Pleurotomariini; both survived the end-Permian mass extinction.

The Bayesian analysis indicates that the current generic composition of the families Zygitidae (*Kokenella*, *Cancellotomaria*, *Zygitis*), Trochotomidae (*Valfinia*, *Trochotoma*), Stuoirellidae (*Stuoirella*, *Codinella*), Schizogoniidae (*Schizogonium*, *Pseudowortheniella*), Pleurotomariidae (*Pleurotomaria*, *Leptomaria*, *Bayerotrochus*, *Bathrotomaria*, *Obornella*, *Pyrgotrochus*), and Ptychomphalidae (*Ptychomphalus*,

Angulomphalus, *Cryptaenia*) are monophyletic. The composition of Wortheniellidae is found to be paraphyletic. The tree topology further suggests that the families Eotomariidae, Luciellidae, Rhabdostomellidae, Phymatopleuridae, Porcellidae, and Lancedellidae are polyphyletic in their current generic composition.

The diverse clade Eotomariini corresponds largely to Eotomariidae in the sense of Knight *et al.* (1960). The earliest offshoot of Eotomariini is the group Clathrospirides, which has the same group composition as in the most parsimonious tree except *Ptychomphalina* and *Calvibembexia*, which form the clade Ptychomphalinides. Gosseletinides is recovered as the sister group of Murloniides, and is composed of the family-groups Euryzoniinae, Luciellidae and Eotomariidae in part and the subfamily Liospirinae. In the parsimony analysis, Liospirinae is reconstructed in Ptychomphalides. In contrast, Liospirinae is placed distantly from Ptychomphalides and recovered within Gosseletinides in the Bayesian analysis. The placement of *Rhineoderma* in Murloniides in both parsimony and Bayesian trees argues against the proposal of Karapınar *et al.* (2022), who placed this genus in the family Phymatopleuridae.

The eotomariid genera *Shwedagonia*, *Neilsonia* and *Spiroscala* are recovered within Phymatopleurides. These three taxa have long been considered to be the members of Eotomariidae (Knight *et al.*, 1960). However, the recovery of these three genera within Phymatopleurides also in the parsimony analysis suggests a close affinity of these genera to the family Phymatopleuridae. The members of the family Portlockiellidae and *Tapinotomaria* are recovered again in the Phymatopleurides, corroborating the views of Karapınar *et al.* (2022) (see also discussion on parsimony analysis). Unlike in the most parsimonious tree, *Worthenia* is recovered within Phymatopleurides and this supports the placement of *Worthenia* in the family Phymatopleuridae (Karapınar *et al.*, 2022). The members of Phymatopleurides (*Dictyotomaria* and *Eiryksia*) gave rise to the groups Kittlidiscides and Zygitides. As in the parsimony analysis, Kittlidiscides and Zygitides are recovered as sister groups. The members of these groups are known only from the Triassic, but the tree suggests that Kittlidiscides originated in the Permian. A more detailed study of Permian deposits might reveal the early members of this clade. As in the parsimony analysis, the lancedellid genera *Acutitomaria*, *Euryalox* and *Euzone* were recovered within Kittlidiscides, and hence strongly supports placement of these genera in the family Kittlidiscidae. In the most parsimonious phylogeny, Zygitides and Pleurotomariides were reconstructed distant from each other. In the Bayesian

phylogeny, Zygitides represents the sister group of Pleurotomariides. *Enantiostoma*, a taxon previously considered as a member of Porcellidae, is reconstructed in Porcellidae in the parsimony analysis but is recovered within Zygitides in the Bayesian tree. *Enantiostoma* is indeed very similar to *Kokenella* in whorl and selenizone morphology. *Enantiostoma* differs from *Kokenella* in its sinistrally and trochospirally coiled late whorls, while the whorls of *Kokenella* coil planispirally through its entire ontogeny. Further, taxa that were previously considered to represent Porcellidae were recovered within Murloniides (*Porcellia*, *Martinidiscus*) and in Ptychomphalinides (*Hesperella*, *Sasakiella*). These taxa were united under the family Porcellidae based on a change in coiling direction in early ontogenetic stages (e.g. Frýda *et al.*, 2019). The change in coiling direction in early ontogeny has long been regarded as highly informative for inferring phylogeny (e.g. by Bandel, 1993, 2009; Frýda *et al.*, 2008, 2019; Schwarzd, 1992). The present Bayesian analysis indicates that a change in coiling to another direction has happened at least three times (in Ptychomphalinides, Murloniides, Zygitides): *Hesperella*, dextral to sinistral; *Martinidiscus* and *Porcellia*, dextral to planispiral; *Enantiostoma* and *Sasakiella*, planispiral to sinistral. Many taxa show changes in coiling of whorls from planispiral to dextral (e.g. *Cancellotomaria*, *Trepostira*, *Sisenna*), which seemingly originated at least 10 times independently according to the Bayesian tree. The phylogeny indicates that the change in coiling direction of the teleoconch during early ontogeny might not be as important for higher level systematics, as previously suggested (e.g. by Bandel, 1993; Frýda *et al.*, 2008).

The members of *Eymarella* were reconstructed in separate lineages in the parsimony analysis, in Pleurotomariides and Phymatopleurides. Unlike in the most parsimonious tree, all three species of *Eymarella* are recovered as sister groups in the Bayesian tree. *Eymarella* is recovered as the ancestral lineage of Pleurotomariides (family Pleurotomariidae). This suggests the placement of *Eymarella* in the family Pleurotomariidae. The tree confirms that Pleurotomariidae originated in the Triassic. The composition of Pleurotomariides supports the monophyly of the family Pleurotomariidae. Pleurotomariides is the only group within Pleurotomariini that survived the end-Triassic and end-Cretaceous mass extinctions and has persisted until today.

The eotomariid group Glabrocingulini (*Glabrocingulum*, *Baylea*, *Biarmeaspira*) is recovered as a basal group in Wortheniellini. *Biarmeaspira* is regarded to be very closely related to *Baylea* (Karapınar *et al.*, 2024; Ketwetsuriya *et al.*, 2020;

Mazaev, 2015), but *Biarmeaspira* might be polyphyletic in its current composition (Karapınar et al., 2024). The FBD tree supports the idea that the Permian *Biarmeaspira striata* is distantly related to the Carboniferous *Baylea*. Glabrocingulini gave rise to Wortheniellides and Ptychomphalides. Although the fossil record of Wortheniellides is restricted to the Mesozoic, the tree suggests that Wortheniellides originated in the Permian and, if so, this group survived the end-Permian extinction. Wortheniellides is the next group recovered within Wortheniellini. The Bayesian phylogenetic analysis suggests that the families Schizogoniidae, Stuorellidae and Lancedellidae are most closely related to Wortheniellidae. These families all together comprise the clade Wortheniellides. Wortheniellides was the most diversified pleurotomariid clade during the Triassic but could not survive the extinction at the end-Triassic despite its remarkable Triassic diversification. Similar to the parsimony analysis, the Bayesian analysis suggests a close relationship of *Rinaldoella*, *Amplitomaria*, *Lancedellia* and *Lineaetomaria*. This indicates that the composition of Lancedellidae as proposed by Karapınar and Nützel (2021) is polyphyletic. As discussed above, if *Rinaldoella* is found to be a member of Scissurellidae, this family might be the living descendant of the clade Wortheniellini.

In Ptychomphalides, the families Temnotropidae and Ptychomphalidae represent sister groups. Ptychomphalides further comprises the members of Rhabdistomellidae (*Rhabdistomella* and *Rufilla*), which supports the opinion of Gründel (2011), who considered *Rhabdistomella* to be closely related to the family Ptychomphalidae. Temnotropidae is recovered as the sister group of Ptychomphalidae in the Bayesian tree, although Temnotropidae was recovered as the sister group of Trochotomidae in the most parsimonious tree. The Bayesian analysis reconstructed *Kericserispira* as a member of Trochotomidae, while it was recovered within Glabrocingulini in the parsimony tree. *Kericserispira* shares a similar whorl and selenizone morphology with *Trochotoma* and *Glabrocingulum*, apart from that most members of *Trochotoma* have a selenizone terminating with a trema. The long time gap between Glabrocingulini (Carboniferous–Permian) and *Kericserispira* (Early Jurassic) and the recovery of *Kericserispira* next to *Valfinia* and *Trochotoma* within the Bayesian tree suggest placement in Trochotomidae. If the family Haliotidae was derived from Trochotomidae as previously proposed by Karapınar and Nützel (2021), then this lineage could be the second ancestral lineage (in addition to the Pleurotomariides) that has persisted until today.

Sisenna and *Rufilla* were considered to be sister taxa (Karapınar & Nützel, 2021); however, they were recovered in closely related but distinct clades (Ptychomphalides and Wortheniellides) in the Bayesian tree. *Pressulasphaera* was previously tentatively assigned to family Gosseletinidae by Karapınar & Nützel, (2021) but the analysis indicates a close relationship with *Rufilla*. *Eirlysella* was placed in Luciellidae by Karapınar & Nützel (in Karapınar et al. 2022) but recovered as sister to *Tapinotomaria* within Phymatopleurides.

Parsimony vs Bayesian analysis. Parsimony analysis aims to reconstruct phylogeny with the minimum amount of character state change but fails in constructing reliable phylogenies of clades if homoplasy is pervasive. The traditional taxonomic method also works with the principle of parsimony but also involves space (geography) and time (stratigraphy), which relaxes the strict assumption of parsimony. If taxa from distant geological times are recovered as being very closely related in a parsimony tree, this likely reflects morphological convergence of various lineages. Convergence (homoplasy) is an a posteriori hypothesis, but inclusion of congeneric taxa in the analyses (a priori information) allows assessment of the reliability of the most parsimonious tree and the homoplasy implied by it. The recovery of congeneric taxa in distant groups makes the phylogenetic hypothesis reflected in the most parsimonious tree doubtful.

The Bayesian tip-dating analysis allows differential evolutionary rates among characters, among lineages and through time. Most importantly, the Bayesian tip-dating analysis incorporates time, the main component of evolution. Therefore, Bayesian tip-dating approximates evolution much better than parsimony. It also resembles the method employed in traditional taxonomic systematics, which, unlike parsimony, includes stratigraphical age information. Comparing parsimony and Bayesian trees is difficult. The trees are reconstructed based on different assumptions (parsimony) or models (e.g. character evolution, clock model). Stratigraphical congruence metrics are used to compare the trees reconstructed with parsimony and Bayesian methods because they provide an independent comparison under different optimality criteria (e.g. López-Antoñanzas & Peláez-Campomanes, 2021; Sansom et al., 2018; Wright & Lloyd, 2020). The stratigraphical congruence indices (Table 2) suggest that the Bayesian tip-dating phylogeny is a better fit to the stratigraphical ages of the involved taxa, as expected, and as previously shown (King, 2021). Furthermore, congeneric taxa were not recovered in distant groups in the Bayesian tip-dating tree, unlike in the parsimony analysis. Thus, the Bayesian tip-dating

tree is favoured over parsimony for the reconstruction of the phylogeny of Pleurotomariida presented herein.

Impact of taxon sampling on phylogeny

Poor character coding with many unknown character states hampers the resolution of phylogenetic relationships; hence, we included taxa that have the least missing information. The taxon sampling for the present phylogenetic analyses was not evenly distributed through time (i.e. we did not sample the same or a similar number of taxa from each time interval). Although we included as many different groups as possible from each time interval to cover the diversity of Pleurotomariida fully, the diversity of the sampled taxa does not entirely reflect the Phanerozoic diversity of the Pleurotomariida (Fig. 9). The taxon sampling is therefore partly biased by the preservation favouring the late Palaeozoic to early Mesozoic interval over the early Palaeozoic interval, where gastropods are particularly well-preserved in a number of fossil Lagerstätten (e.g. Roden *et al.*, 2020). Improving sampling with additional early Palaeozoic and Permian taxa would allow us to test and improve the recovered trees.

Which shell characters are more homoplastic?

The shell features reflecting anatomy are probably of higher phylogenetic value (Vermeij, 2002). For instance, the shell slit of Pleurotomariida reflects the anatomy of soft parts including the mantle cavity and its organs, e.g. the position of the selenizone might reflect the proportions of the right and left part of the soft body (Bandel & Geldmacher, 1996; Ebbestad & Peel, 2001), a deep slit indicates a deep mantle cavity (Lindberg & Ponder, 2001). Characters related to the slit and selenizone have long been used in the classification of fossil Pleurotomariida. The slit-related characters are found to be more conservative at the generic level than other shell characters (e.g. Batten, 1967; Karapınar & Nützel, 2021; Karapınar *et al.*, 2022) and might be more phylogenetically informative than other shell characters such as the shell ornament. If selenizone characters are more stable than characters of other shell sectors (i.e. upper whorl face, lower whorl face, base), then they are expected to change less frequently. The comparison of CI values of different sets of characters related to separate shell sectors (Fig. 5) showed no statistically significant difference. Although the selenizone and upper whorl face have slightly higher CI values than other shell sectors, the difference is not significant. Hence, selenizone characters seem not to be of more importance in inferring phylogeny than other shell sectors. These results contradict previous opinions which considered

selenizone characters to be more conservative than other shell characters (e.g. Batten, 1967; Karapınar & Nützel, 2021) and Wagner's (2001) analysis, which suggested that characters associated with the sinus or slit show a lower rate of change compared to other shell characters.

Vermeij (2002) argued that axial shell characters could be less reliable than the spiral characters in inferring phylogeny because axial characters are temporally discontinuous while spiral characters are present throughout ontogeny. Some of the middle Palaeozoic eotomariid genera (e.g. *Ptychomphalina*, *Lunulazona*) share similar ornamentation of strong axial ribs, suggesting that axial sculpture might be conservative in early groups. If axial characters are less reliable, in other words more homoplastic, then their CI values are expected to be lower than those of spiral elements. However, the axial characters in Pleurotomariida have higher CI values than the spiral characters, indicating that they are less homoplastic. Although the difference is not statistically significant, the present result does not corroborate Vermeij's (2002) assumption. Pérez *et al.* (2022, fig. 5A, B) also could not find a significant difference between the CI of axial and spiral characters in the vetigastropod genus *Calliotropis* (Seguenziida). It should be noted that Pérez *et al.* (2022, fig. 5) used many more spiral characters in their taxon/character-matrix than in the matrix used herein (the ratio between the number of spiral characters *vs* axial characters is *c.* 2.5 in Pérez *et al.* 2022, whereas the ratio is *c.* 0.7 herein). The present result based on the clade Pleurotomariida taken together with the result presented by Pérez *et al.* (2022) indicate a lack of significant differences in homoplasy of axial *vs* spiral characters in Vetigastropoda. The relative similarity in homoplasy of these characters can be clade specific. Further studies with the inclusion of other clades (e.g. Caenogastropoda) could reveal if the present result is consistent for all Gastropoda.

Characters related to ontogenetic change in shell morphology are used in gastropod classification and phylogenetic analyses (e.g. Bandel, 1993; Frýda *et al.*, 2008; Wagner, 2002). This refers not only to protoconch morphology but also ontogenetic changes within teleoconch morphology that can provide phylogenetic information. Based on a change in coiling direction during ontogeny, Bandel (1993) suggested a close relationship between Porcellidae and Cirridae. The change in coiling direction during ontogeny seems to not be an important character as suggested by the recovered Bayesian tree (see discussion on Bayesian tree). Vermeij (2002) argued that ontogenetic characters are phylogenetically uninformative. In our analyses, the comparison of early ontogenetic characters, late ontogenetic characters and

characters related to ontogenetic change suggest that early ontogenetic characters are significantly more conservative in comparison to late ontogenetic characters. In contrast to the assumption made by Vermeij (2002), the characters related to ontogenetic change are not of less importance than the other sets of characters.

We found that the ‘spirally continuous shell sectors’ (i.e. upper whorl face, selenizone, lower whorl face, base) do not differ from each other significantly in homoplasticity. However, early *vs* late ontogenetic shell portions (‘axially divided shell sectors’) differ significantly from each other in the degree of homoplasticity.

Correlation between larval and adult shell size

As outlined, we found a positive correlation of the size of the protoconch and the size of the early ontogenetic shell (width of the first whorl including larval shell and early part of teleoconch) with adult shell size (Fig. 6). A similar positive correlation between adult body size and egg-size (as reflected by the size of protoconch I) has been reported for planktotrophic gastropods (Collin, 2003; Rundle, et al., 2007). In late Palaeozoic neritimorph and caenogastropod species, adult and larval shells have been found to resemble each other in shape and ornamentation (Seuss et al., 2012). Apparently, the larval and adult shell features (size, ornamentation) are strongly correlated in certain gastropod groups.

Vetigastropoda including Pleurotomariida lack planktotrophic larval development; their larvae are non-feeding (e.g. Nützel, 2014). In Caenogastropoda and other groups with planktotrophic larval development, the size of the initial whorl together with the number of protoconch whorls can be used as a proxy to infer larval development: smaller initial whorls reflecting a small egg size and a high number of protoconch whorls indicating planktotrophic larval development (Nützel, 2014; Nützel et al., 2006). In Vetigastropoda, which lacks planktotrophic larval development, size variation of larval shells reflects the yolk amount and is not subject to change during ontogenetic development since they are non-feeding. The present data reveals that larger species also produce larger eggs and larvae. The amount of yolk directly affects the lifespan of the lecithotrophic larva, as do the other factors such as temperature (Padilla et al., 2018). Therefore, the size of the larva is vital and can affect the dispersal and consequently the speciation rate. The interrelationship between larval modes (planktotrophic *vs* non-planktotrophic), dispersal capacity and speciation rate has been shown before (e.g. Barroso et al., 2022; Jablonski, 1986; Jablonski & Hunt, 2006). Whether larger vetigastropod species (with larger protoconchs) have a wider geographical distribution compared to smaller vetigastropods (with smaller protoconchs) and

have a lower extinction rate needs testing with more data. Barroso et al. (2022) did not find a relationship between body size and geographical distribution in their study including all gastropod groups. Distribution is affected by other factors such as environmental tolerance of species and distribution of predators, so the relationship between larval size and distribution can be more complex than assumed.

Environmental stressors (e.g. dysoxia, abrupt temperature increase, soupy substrate) can cause a decrease in adult shell size in molluscs within species (e.g. Fürsich et al., 2020; Piazza et al., 2020) or among species of the same genus (e.g. Huang et al., 2023). However, it has not yet been studied whether this type of stunting is also associated with small larval shells and eggs. Different shell sizes might also be attained as an adaptation against predation (size refuge, e.g. Boulding et al., 2017; Vermeij, 1987). Karapınar et al. (2022) showed that Carboniferous pleurotomariid taxa with smaller larval shells have a higher juvenile/adult ratio, indicating a lower survival rate. This points to a possible trade-off between larval shell size and fecundity (small eggs, high fecundity, high mortality). Thus, environmental stressors or high predation pressure might affect adult shell size, which might in turn cause trade-offs in life history traits such as changes in larval shell and egg size.

The correlation between larval and adult shell size has implications for the origin of planktotrophy/lecithotrophy. Planktotrophy in gastropods is assumed to have evolved at the Cambrian–Ordovician transition, suggested by the decrease in initial whorl size (including the protoconch; Nützel et al., 2006, 2007). The relationship between the egg size and the developmental mode in gastropods has been known for a long time (e.g. Nützel, 2014 and citations therein; Thorson, 1950). Larval developmental mode in marine invertebrates correlates with environmental factors such as primary production and temperature (Marshall et al., 2012). Changes in larval shell size as a result of life history trade-offs imposed by environmental changes (e.g. temperature, primary productivity) might have triggered a change in larval development in the evolutionary history of gastropods. This assumption can be tested by inclusion of taxa with different larval developmental mode into phylogeny.

Adult shell size is used as proxy for estimating metabolism, and large size is considered to indicate higher metabolism in molluscs (e.g. Finnegan et al., 2011). An increase in metabolism has been inferred from an increase in body size of gastropods from the Mesozoic onwards (e.g. Finnegan et al., 2011). Taken together, the increase in body size since the Mesozoic

and the correlation between larval shell size and adult shell size, an increase in larval shell size in vetigastropods since the Mesozoic can be assumed, but that assumption needs testing through a time series analysis of vetigastropod protoconch size.

Morphological evolutionary rates and turnover rates within Pleurotomariida through time

Morphological evolutionary rates may change during the evolutionary history of a clade (for instance a boost in morphological evolutionary rates in early history within the clade). If there is a decrease in evolutionary rates, this may limit the ability of a clade to occupy new niches or adapt to new ecosystems. In the early Palaeozoic, gastropods showed higher morphological changes in the Cambrian to the Lower Ordovician than from the Middle Ordovician onwards (Wagner, 1995). The FBD model with uncorrelated clock suggests that the morphological evolutionary rate did not differ significantly through time or among pleurotomariidan lineages from the Ordovician to Recent (Fig. 7). Apparently, the evolvability (i.e. the ability to produce new morphologies) did not decrease through time in Pleurotomariida. Therefore, the demise of Pleurotomariida cannot be explained with a change in their ability to produce new morphologies. On the other hand, the decrease in morphological disparity (e.g. survival of only conical forms in the Cenozoic; Bose *et al.*, 2021) might be a stochastic consequence of their decrease in diversity.

Variations in origination/extinction rates in different time intervals might cause the observed decline of Pleurotomariida in post-Palaeozoic times. The Bayesian analysis with 5-skyline model suggests an increase in the speciation and extinction rates from the Ordovician–Devonian interval to the Triassic–Jurassic time interval and an abrupt drop in the Cretaceous–Recent interval. As mentioned above, taxon sampling is neither homogeneous through time nor in accordance with their diversity. The diversity analysis of fossil occurrences suggests a drop in generic diversity of Pleurotomariida from the Permian to the Triassic (Fig. 9; Karapınar & Nützel, 2021, figs 96–97), but the number of taxa included in the phylogenetic analysis from the Permian is much lower than taxa from the Triassic. The fossilization rate follows the same trend as the extinction and origination rates, capturing this sampling heterogeneity. Whether the heterogeneous sampling through time (coding of many taxa from the Carnian) biased the origination and extinction rate estimates of the Bayesian analysis can be tested by more homogeneous sampling in further phylogenetic analyses. An analysis of the PBDB data with the three-timers method of Alroy

(2010b) does not indicate such evolutionary rate differences through time (personal observation).

Phanerozoic diversity of Pleurotomariida

Although Pleurotomariida is a minor component in Recent marine communities, they have the longest fossil record among all extant gastropod clades and they were especially diverse and abundant in the Palaeozoic (see Introduction). The sampling standardized diversity curve (Fig. 9) corroborates previous findings that the diversity of Pleurotomariida peaked in the Devonian and Carboniferous, and it was one of the most diverse gastropod groups in the late Palaeozoic (Erwin, 1990; Hickman, 1984; Karapınar, *et al.* 2022). As previously shown by an analysis of generic diversity using the range-through method (Karapınar & Nützel, 2021), the SQS analysis also suggests that the diversity of Pleurotomariida dropped abruptly at the Permian–Triassic boundary (Fig. 9). Although the diversity of Gastropoda in the Triassic surpassed its diversity prior to the end-Permian mass extinction, Pleurotomariida could not recover completely in the Triassic (i.e. it failed to reach pre-extinction diversity) and showed a decline after the Carnian peak in diversity. During the mid-Carnian, climate change and the associated environmental change, the so-called Carnian Pluvial Episode, triggered a biotic crisis, by which the gastropods were most affected (Dal Corso *et al.*, 2020). The present SQS analysis and the previous diversity analysis (by Karapınar & Nützel, 2021) indicate that the recovery of Pleurotomariida was interrupted in the Carnian and the group experienced a more severe extinction than other gastropod clades during the Carnian biotic crisis. Hence, Pleurotomariida did not contribute to the post-Palaeozoic expansion of Gastropoda.

Overall, Gastropoda has been considered to belong to the Modern Evolutionary Fauna (Sepkoski, 1981). However, the diversity trend of Pleurotomariida resembles that of the Palaeozoic Evolutionary Fauna (cf. Alroy, 2010a; Rojas *et al.*, 2021; Sepkoski, 1981), which suffered heavily at the end-Permian mass extinction and remained subsequently diminished due to a failure to recover. We consider Pleurotomariida therefore to be a member of the Palaeozoic Evolutionary Fauna and suggest that different clades within a phylum can have an affinity to different evolutionary faunas. Pleurotomariida were well adapted to environments and communities during the late Palaeozoic but could not be a major part of newly established post-Palaeozoic communities although they were present with a considerable number of genera and species in the Late Triassic (Karapınar & Nützel, 2021). As previously discussed by Karapınar and Nützel (2021), the newly evolved

genera in the Triassic were distributed in the tropical zone within the Tethys. Geographical distribution is known to be one of the factors in extinction selectivity (Finnegan et al., 2023; Payne & Finnegan, 2007). Poor geographical distribution or narrow niches might have played a role in the decline of Pleurotomariida. The slit weakens their shell to durophagous predation, and the increase of durophagous predators through time (the Mesozoic Marine Revolution) might have caused their decline (Harasewych, 2002; Lindström & Peel, 2005, 2010; Vermeij, 1977). The reason why some groups such as Pleurotomariida failed to diversify compared to other groups in the evolutionary history of Gastropoda still needs investigation. Together with the Triassic extinction of Bellerophonitida (Kaim & Nützel, 2011) and high-spired slit-bearing caenogastropods ('Murchisonioidea') (Nützel & Karapınar, 2023), the dwindling of Pleurotomariida indicates a strong pressure on the character shell slit and its associated anatomy. Only the little slit shells (scissurellids, fissurellids) have a considerable diversity in modern seas (e.g. Geiger, 2012).

The Bayesian tree suggests that Wortheniellini was more diversified during the Triassic recovery period compared to Pleurotomariini. Both clades persisted into the Jurassic. Pleurotomariini was represented in the Jurassic and Cretaceous by the family Pleurotomariidae. Wortheniellini was represented by Rhabdistomatidae (*Sisenna*), Ptychomphalidae, Trochotomidae, and Stuoirellidae (*Ramusatomaria*: Szabó et al., 2019) in the Jurassic, and only by a single taxon of Stuoirellidae in the Cretaceous (*Stuoirella*: Kiel & Bandel, 2000). However, among these two clades, only Pleurotomariini could survive the end-Cretaceous mass extinction and has persisted until today. Given the fact that Wortheniellini diversified more than Pleurotomariini in the Triassic but only Pleurotomariini survived until today, the resistance to extinction did not depend on the diversification dynamics.

Conclusions

Although the group compositions and within-group relationships between the analysed pleurotomariidan genera are somewhat similar in the trees reconstructed with parsimony and Bayesian methods, the inferred phylogenetic relationships between the groups differ considerably in both analyses. In the tree reconstructed with parsimony analysis, members of the same genus are recovered distantly from each other in three cases. Moreover, the positions of genera and groups in the most parsimonious tree do not fit with their stratigraphical record. Generally, the support values of the parsimony tree are low, and the

composition of many families suggested by traditional taxonomy appears to be paraphyletic. The phylogeny reproduced with Bayesian analysis is more consistent with the traditional classification because members of the same genus appear to be closely related to each other along the tree, and the position of lineages is congruent with their appearance in the fossil record. Both methods produce sister-group relationships between genera that are not congruent with the current systematics and hence we propose a new classification scheme for Pleurotomariida. The Bayesian phylogeny suggests that the groups that are only known from the Triassic fossil record probably originated in the Permian.

The diversity analysis confirms that Pleurotomariida was one of the most diverse gastropod groups in the late Palaeozoic and indicates that the end-Permian mass extinction effectively diminished the group. Despite the origination of several genera in the Triassic and considerable diversity in the Carnian, overall Pleurotomariida failed to fully recover (i.e. their Triassic diversity is much lower than that in the Permian). By contrast, the Triassic gastropod diversity as a whole surpassed that of the Permian, indicating a selective failure to recover for Pleurotomariida. There was also a considerable decline in the Late Triassic and after the Early Jurassic. Wortheniellides, the most diversified group in the Middle–Late Triassic, diminished through time and became extinct in the Mesozoic. Pleurotomariides, which originated in the Triassic, persist until today but declined in diversity. Hence, Pleurotomariida followed the diversity pattern of the Palaeozoic evolutionary fauna. Seemingly, other factors than the diversification rates or overall diversity played a role in the differential survival of the groups.

Analyses of character transformations revealed that early ontogenetic characters are more conservative compared to late ontogenetic characters. In contrast to previous assumptions, axial and spiral shell characters and the different shell sectors (upper whorl face, selenizone, lower whorl face, base) did not differ significantly in homoplasy. The data further revealed a positive correlation between the size of the larval shell, initial whorl size, and the size of the adult shell, which are regarded as indicators of larval ecology and metabolism rate, respectively.

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