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Oligocene to Pleistocene mudwhelks (Gastropoda: Potamididae, Batillariidae) of the Eurasian Paratethys Sea – Diversity, origins and mangroves

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ABSTRACT

Potamidids (Potamididae, Batillariidae) are today typical inhabitants of coastal mudflats in tropical and warm temperate seas. From the Oligocene to the Early Pleistocene, the Eurasian Paratethys Sea harbored a striking diversity of mudwhelks as well. Based on occurrences from 466 localities covering an area of about 3 million km^2 we trace range expansions of potamidids from the Western Tethys and the Proto-Mediterranean Sea into the Eurasian Paratethys Sea, coinciding with global warming trends, such as the Miocene Climate Optimum, the Tortonian Thermal Maximum and the Mid-Pliocene Warm Period. For several species and genera, the stratigraphically oldest occurrences are documented from Rupelian localities south of the Paratethys, which indicates a northward migration over time. A hypothetical refuge along western Africa is hypothesized to explain the 9 Myr long gap between Oligocene and Sarmatian occurrences of *Potamides* in Europe. Highest potamidid diversities in the Central Paratethys coincided with the Miocene Climate Optimum. The second diversity peak is observed during the Sarmatian when the Volhynian flooding united the Central and Eastern Paratethys in a "Mega-Paratethys". This event appears to have boosted potamidid diversity at least in the western part of the Paratethyan basin. About 25% of the species belong to Paratethyan lineages, which partly passed the Badenian/Sarmatian Extinction Event.

A close relation with mangrove environments is documented for *Mesohalina, Ptychopotamides* and *Terebralia* and is assumed for *Tiarapirenella*. The retreat of mangroves from the Paratethys following the Miocene Climate Optimum is reflected by the loss of large species. Latest Middle Miocene to Late Miocene (Sarmatian) potamidid faunas were dominated by species of *Tiaracerithium* and *Potamides*, which were adapted to mudflats devoid of mangroves. Maeotian and Akchagylian potamidid faunas were low diverse, comparatively small and indicate two last phases of immigrations from the Mediterranean region. An influx from the Arctic region during the "Akchagylian marine incursion" can be excluded as explanation for the exotic occurrence of Akchagylian potamidids.

1. Introduction

Potamidids and batillariids are gregarious animals, usually confined to the littoral zone in mudflats, mangroves, saltmarshes, subtidal ponds, coastal lagoons and saline lakes in warm temperate and tropical regions (Kowalke, 2001; Reid et al., 2008; Ozawa et al., 2009, 2015; Reid and Ozawa, 2016).

Some Potamididae are known to be extremely euryhaline occurring

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in a wide range of salinities. For example, *Pirenella conica* (Blainville, 1829) is reported to occur at salinities from 5 to 280‰ (Reid et al., 2008). Extant Batillariidae are also euryhaline and abundant on sandy mudflats (Ozawa et al., 2009). Batillariidae may co-occur with Potamididae (Wells, 1985) but seem to be separated by sediment type preference (Maki et al., 2002) and feeding strategy (Kamimura and Tsuchiya, 2004). ***Lampanella*** Mörch, 1876 lives in large populations on mud in the intertidal zone tolerating brackish waters (Bequaert, 1942). The genus occurs in mangroves, but may also settle sand and rock platforms in sheltered environments (Plaziat, 1984; Ozawa et al., 2009).

Batillariidae appeared during the Late Cretaceous and Potamididae originated during the Middle Eocene in the Tethyan Realm (Reid et al., 2008; Ozawa et al., 2009). Both families became ubiquitous and widespread during the Eocene, Oligocene and Miocene in the Western Tethys, northeastern Atlantic and Proto-Mediterranean Sea (Lozouet, 1986; Reid et al., 2008; Dominici and Kowalke, 2014). Similarly, potamidids and batillariids were among the most abundant and widespread molluscs in the epicontinental Paratethys Sea. This sea developed around the Eocene/Oligocene boundary when it became geodynamically separated from the Western Tethys (Rögl, 1998; Popov et al., 2004; Sachsenhofer et al., 2017; Palcu and Krijgsman, 2022). This sea was divided during most of the Oligocene and Miocene into a western part, ranging from the Rhône Basin to the Carpathian Foreland Basin (Western and Central Paratethys), and a larger Eastern Paratethys, ranging from the Dacian Basin to the Caspian Basin. Therefore, the geographic area covered herein spans from Switzerland in the west to Kazakhstan in the east (Fig. 1). Both seas were only temporarily connected, which led to complex biogeographic patterns. Whereas the Central Paratethys was strongly influenced by range expansions from the Proto-Mediterranean Sea, the Eastern Paratethys gave rise to an endemic evolution of a comparatively less diverse mollusc fauna (Iljina et al., 1976; Nevesskaja et al., 1986; Studencka et al., 1998; Harzhauser and Piller, 2007). The marine faunas of the Central Paratethys became extinct at the boundary of the regional Sarmatian and Pannonian stages around 11.6 Ma, coinciding with the formation of the huge brackish Lake Pannon (Magyar et al., 1999; Neubauer et al., 2016) (Figs. 2, 3). In the Eastern Paratethys, marine faunas persisted to the Late Miocene and re-appeared during the latest Pliocene to Early Pleistocene (Akchagylian). See Rögl (1998), Popov et al. (2004) and Kováč et al. (2017) for an overview of the complex palaeogeographic history of the Paratethys Sea (Fig. 2). The regional climatic development of the Central and Eastern Paratethys Sea was discussed in a plethora of papers (Kranner et al., 2021a; Kranner

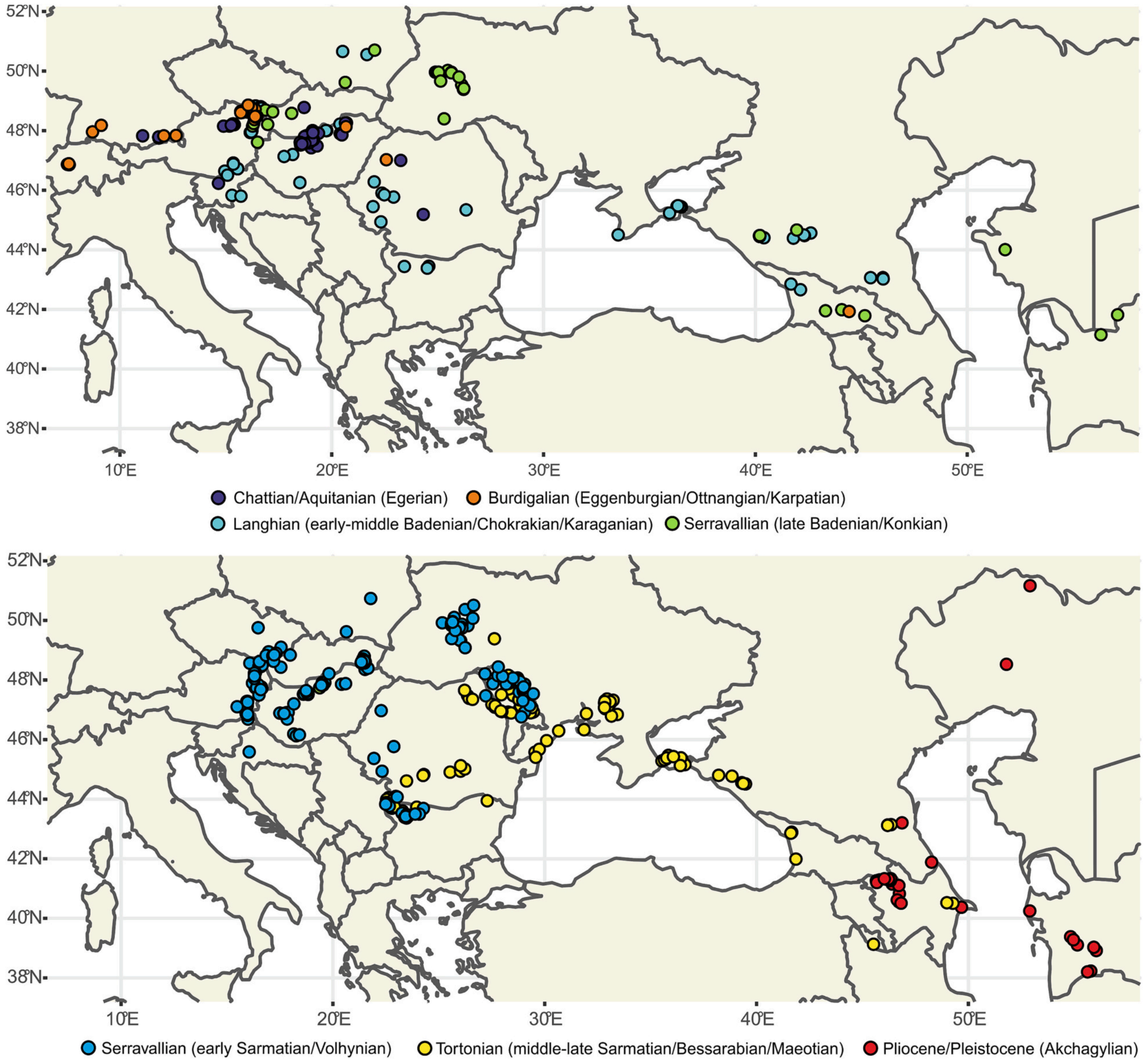

Fig. 1. Map showing the geographic spread of the localities considered in this study (see Supplementary Table 1 for names and coordinates).

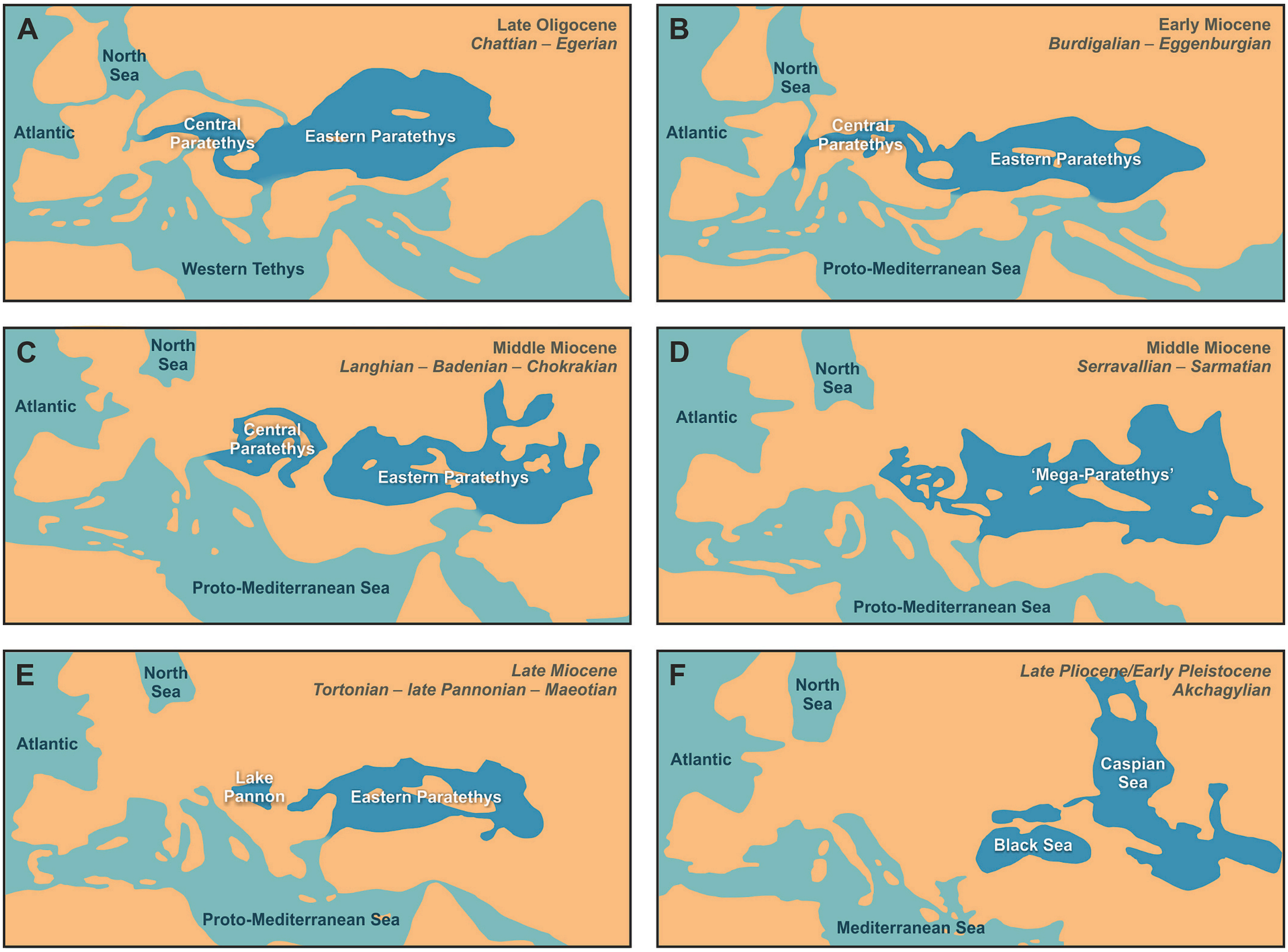

Fig. 2. Paleogeographic maps depicting the development form the Late Oligocene to the Late Pliocene/Pleistocene; modified from Popov et al. (2004) and Lazarev et al. (2021).

et al., 2021b; Popov et al., 2022; Kopecká et al., 2022; Scheiner et al., 2023 and references therein). All authors recognized that the global climatic evolution is strongly reflected in the Paratethyan paleoenvironments. Therefore, we compare our paleontological data especially with major climatic events as defined by Zachos et al. (2008) and Westerhold et al. (2020).

Recently, Harzhauser et al. (2023a) provided an in-depth revision of the taxonomy of the Oligocene to Pleistocene Paratethyan mudwhelk faunas. These authors documented 17 species of Potamididae (Fig. 4) and 11 species of Batillariidae (including *Lampanella* Mörch, 1876, which represents a yet undescribed family; Ozawa et al., 2009) (Fig. 5). These three potamidid groups (Potamididae, Batillariidae, *Lampanella*) are paraphyletic, because *Lampanella* is sister to Planaxidae in the molecular phylogeny of Ozawa et al. (2009).

Although Paratethyan mudwhelks are thus represented by three families, herein we refer generally to 'potamidids' for the sake of simplicity. The 28 species are placed into ten genera: Potamididae: *Potamides* Brongniart, 1810, *Theodisca* Harzhauser et al., 2023a, *Terebralia* Swainson, 1840, *Ptychopotamides* Sacco, 1895, *Mesohalina* Wittibschlager, 1983, *Lampanella* Mörch, 1876; Batillariidae: *Granulolabium* Cossmann, 1889, *Tiarapirenella* Sacco, 1895, *Tiaracerithium* Sacco, 1895, *Pustulosia* Harzhauser et al., 2023a. Of these, only *Terebralia* and *Lampanella* are still existing.

The aim of this study is to assess the diversity of potamidids in the Paratethys Sea through time, analyze the similarities between Central and Eastern Paratethyan assemblages and discuss the origin of the species. In addition, we discuss which species can be reliably used as indicators for mangroves.

2. Material and methods

Twenty-seven Paratethyan potamidid species are included herein based on data in Harzhauser et al. (2023a), from where also the geographic occurrences and stratigraphic ranges are taken (Supplementary Table 1).

The species are: *Potamides caspius* Andrussow, 1902, *Potamides disjunctus* (Sowerby, 1832), *Potamides fraterculus* (Mayer, 1878), *Potamides galidzgensis* (Iljina et al., 1976), *Potamides taitboutii* (d'Orbigny, 1844), *Potamides* sp. 1, *Theodisca azerbajdjanica* (Ali-Zade, 1940), *Theodisca biseriata* (Friedberg, 1914), *Theodisca cicur* (Zhizhchenko, 1934), *Theodisca theodisca* (Rolle, 1856), *Terebralia duboisi* (Hörnes, 1855), *Terebralia lignitarum* (Eichwald, 1830), *Terebralia menestrieri* (d'Orbigny, 1844), *Terebralia prolignitarum* (Sacco, 1887), *Terebralia subcorrugata* (d'Orbigny, 1852), *Ptychopotamides cinctus* (Bruguière, 1792), *Mesohalina margaritacea* (Brocchi, 1814), *Lampanella maeotica* (Karlov, 1932), *Lampanella obliquistoma* (Seguenza, 1880), *Lampanella volhynica* (Friedberg, 1914), *Granulolabium moravicum* (Hörnes, 1855), *Granulolabium plicatum* (Bruguière, 1792), *Granulolabium pseudoplicatum* (Friedberg, 1914), *Tiarapirenella bicincta* (Brocchi, 1814), *Tiarapirenella tabulata* (Hörnes, 1855), *Tiaracerithium pictum* (de Basterot, 1825), *Pustulosia hornensis* (Schaffer, 1912) and *Pustulosia submitralis* (Eichwald, 1851). Geography: Paratethyan potamidids are documented from 466 geo-

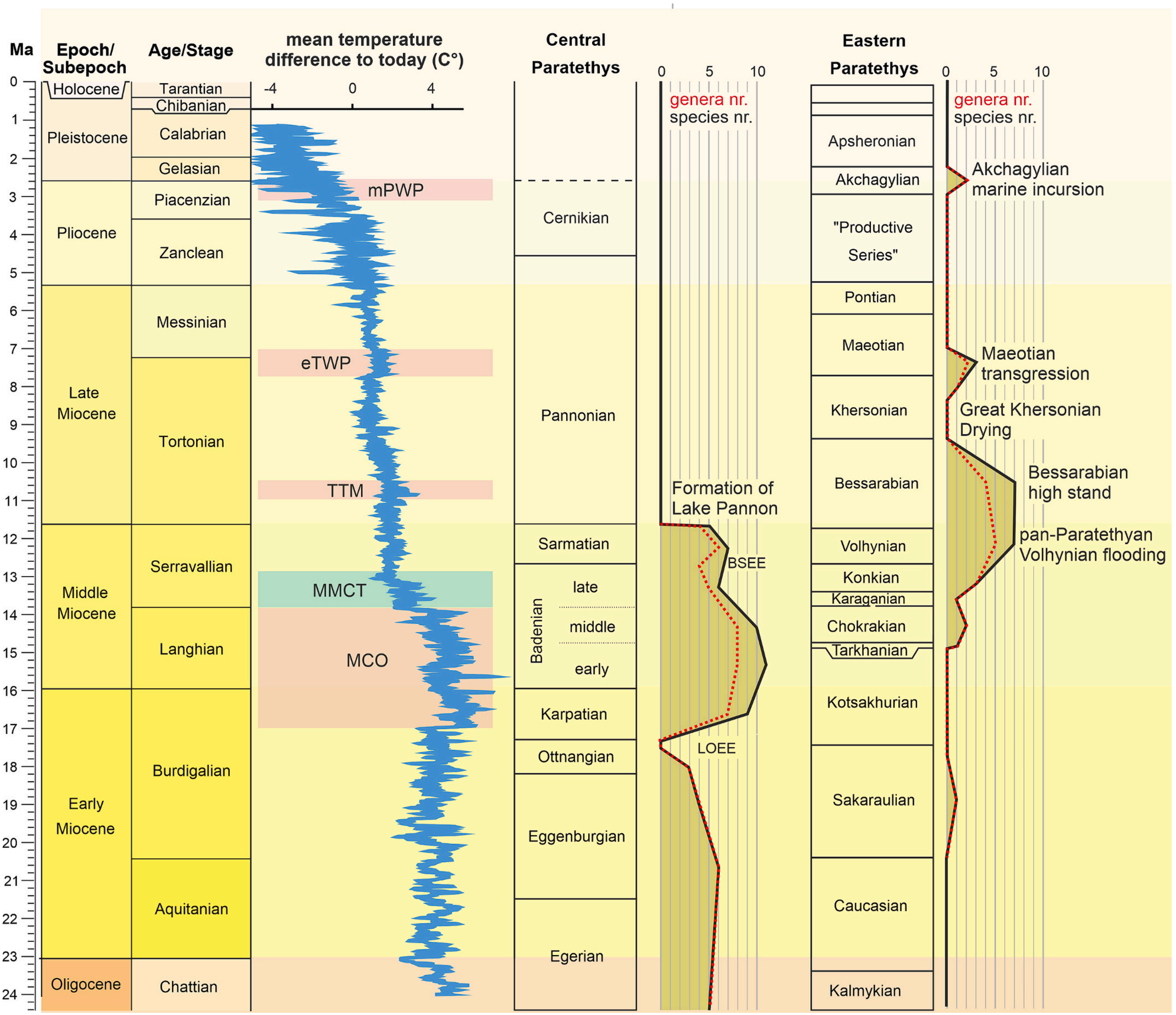

Fig. 3. Diversity of Paratethyan potamidids compared to the global climate record after Westerhold et al. (2020). Regional stratigraphic stages modified from Mandic et al. (2015), Neubauer et al. (2015), Palcu et al. (2015), Gradstein et al. (2020), Speijer et al. (2020) and Lazarev et al. (2021). MCO: Miocene Climate Optimum, MMCT: Middle Miocene Climate Transition, TTM: Tortonian Thermal Maximum, eTWP: End-Tortonian Warm Period, mPWP: Mid-Pliocene Warm Period, LOEE: Late Ottnangian Extinction Event, BSEE: Badenian-Sarmatian Extinction Event.

referenced localities (Supplementary Table 1, Fig. 1). In most cases it was not possible to find the exact position of the outcrops from where the fossils have been described. Therefore, the coordinates usually represent only the region of the findings (e.g., center of village). The information on the geographic occurrences was deduced from hundreds of taxonomic papers, and we refer to Harzhauser et al. (2023a) for a full list of these references. In total, the localities span nearly 4000 km from west to east and cover about 3 million km^2 (Fig. 1).

Stratigraphy: The occurrences of Paratethyan mudwhelk faunas were grouped into stratigraphic bins, which correspond to the regional stages (Fig. 3). This is the highest resolution possible to include all occurrences. Stage boundaries are taken from Harzhauser et al. (2020) for the Central Paratethys and from Lazarev et al. (2020, 2021), Jorissen et al. (2018), Palcu et al. (2019), Popov et al. (2019, 2022) and Speijer et al. (2020) for the Eastern Paratethys. Central Paratethyan occurrences derive from Switzerland, Germany, Austria, Czechia, Slovakia, Hungary, Poland, western Ukraine, Romania, Slovenia and Bulgaria. Eastern Paratethyan occurrences are located in eastern Ukraine, Romania (Moldavian Platform), Moldova, Bulgaria (Dacian Basin), Crimea, Russia, Azerbaijan, Georgia, Armenia, Kazakhstan and Uzbekistan.

Sampling quality: Rarefaction was applied to assess if the sampling per time bin is sufficient to capture potamidid diversities realistically (Krebs, 1989). The analysis was computed in PAST 4.05 (Hammer et al., 2001). The localities listed in the Supplementary Table 1 represent samples, which were grouped into 12 time-bins: Egerian, Eggenburgian, Ottnangian, Karpatian, early Badenian, middle Badenian, late Badenian, Konkian, Volhynian, Bessarabian, Maeotian, Akchagylian. See Colwell et al. (2012) for an in-depth discussion on the method.

Biogeography: The Jaccard similarity index (JI) was calculated for each stage bin and region as measure for the faunal similarity and connectivity between the Central and Eastern Paratethys using the vegdist function of the package vegan vs. 2.5–7 (Oksanen et al., 2020) for R vs. 4.1.2 (R Core Team, 2021). Herein, species numbers per time-bin as used for rarefaction have been compared.

Size: To estimate the average size of adult specimens of the analyzed species, the shell height of at least ten fully grown specimens of each

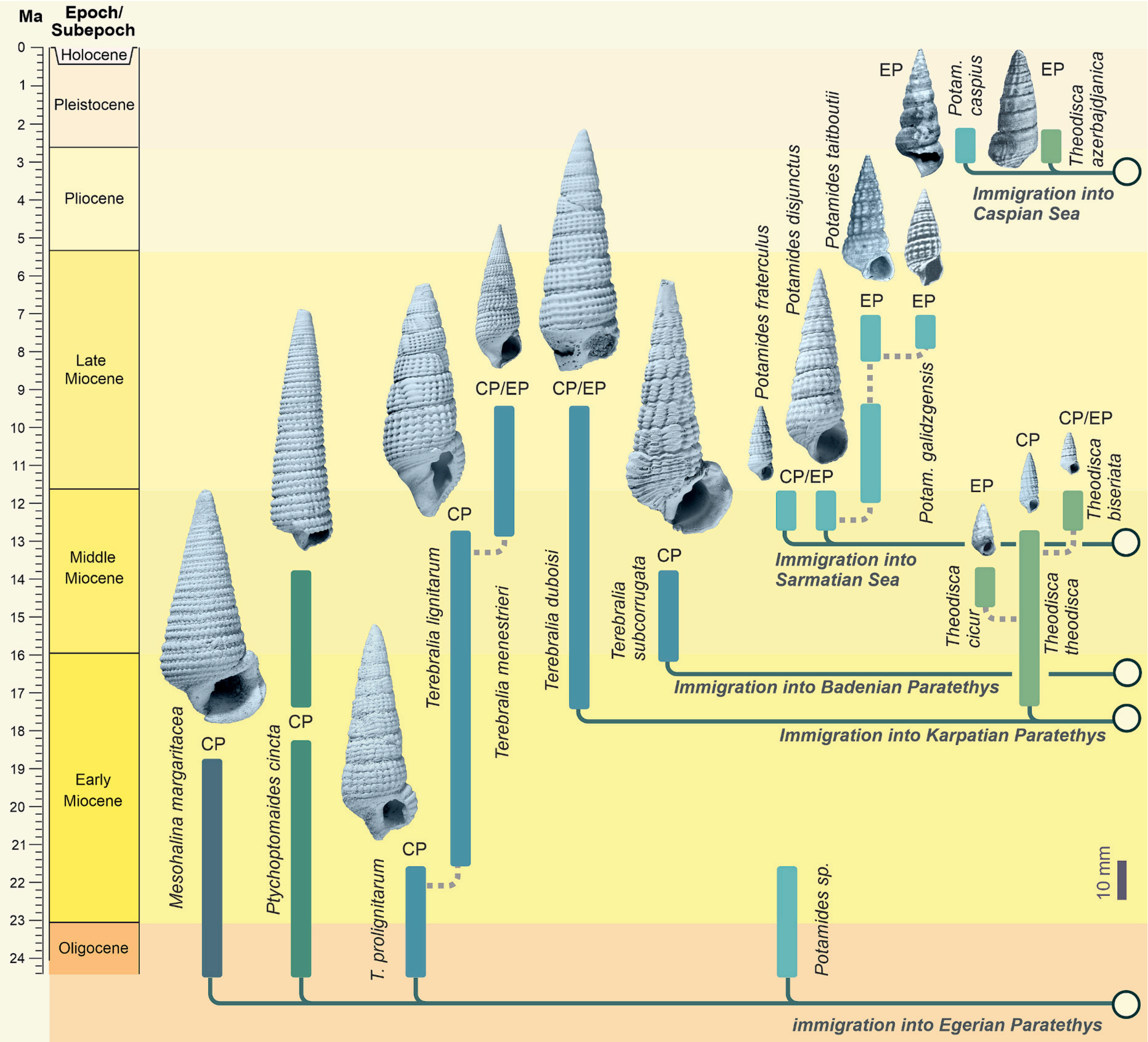

Fig. 4. Stratigraphic occurrences of Paratethyan Potamididae. Assumed lineages are connected by dotted gray lines. Circles to the right and green lines mark phases of range expansions from the Proto-Mediterranean Sea. CP = Central Paratethys, EP = Eastern Paratethys. Colors of bars represent genera. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species was used for each time bin (Supplementary Table 2); adult specimens were randomly selected from the lots; note that we included 40 specimens of *Potamides caspius*, because this species comprises populations, which differ in size and sculpture and might represent distinct taxonomic units (but it is beyond the scope of this study to clarify the status of these morphotypes). This selection does not qualify for a detailed analysis of shell size evolution but allows for a rough estimate of size classes represented by the various species. Herein we distinguish between small (<20 mm), medium sized (20–50 mm) and large species (>50 mm). Because many of the species are confined either to the Central Paratethys or to the Eastern Paratethys, we did not analyze differences in size between these regions.

Limitations: All localities represent coastal-marine settings and for all occurrences major reworking or transport as discussed by Dominici and Danise (2022) is unlikely. Nevertheless, we admit that no detailed information on the sedimentary facies of the 466 localities is available. A second limitation is that no information on the sampling efforts for the various localities is available. Most of the localities are 'classical' localities, which have been visited by geologists for decades. Therefore, we assume that the species-level diversity of most localities is fairly well recovered.

3. Results

3.1. Mudwhelks diversity

The generic and species-level diversity of Paratethyan potamidids varies considerably through time (Fig. 3). Generally, the generic diversity and the species-level diversity display roughly parallel trends, due to the low number of species per genus.

Central Paratethys Sea: The oldest potamidid faunas of the Central Paratethys derive from the Egerian stage (26.9–21.5 Ma) (Figs. 2, 3, 4, 5). This stage spans parts of the Chattian and the Aquitanian. The dataset includes 49 localities of Egerian age mostly from Hungary along with occurrences from Germany, Austria, Slovakia, Slovenia and Romania. In total, the Egerian faunas comprise five species and five genera. Data from the Eggenburgian stage (21.5–18.1 Ma) included herein are mainly from Austria along with two occurrences from Germany and one from Romania. Six species and six genera are documented from this interval. The Ottnangian stage (18.1–17.2 Ma) is represented by only five localities from Germany and Switzerland and yielded only three species. The Karpatian stage (17.2–15.97 Ma) is represented by 16 localities from Austria, Czechia and Hungary and nine species and seven genera. Highest potamidid diversities in the Central Paratethys were attained

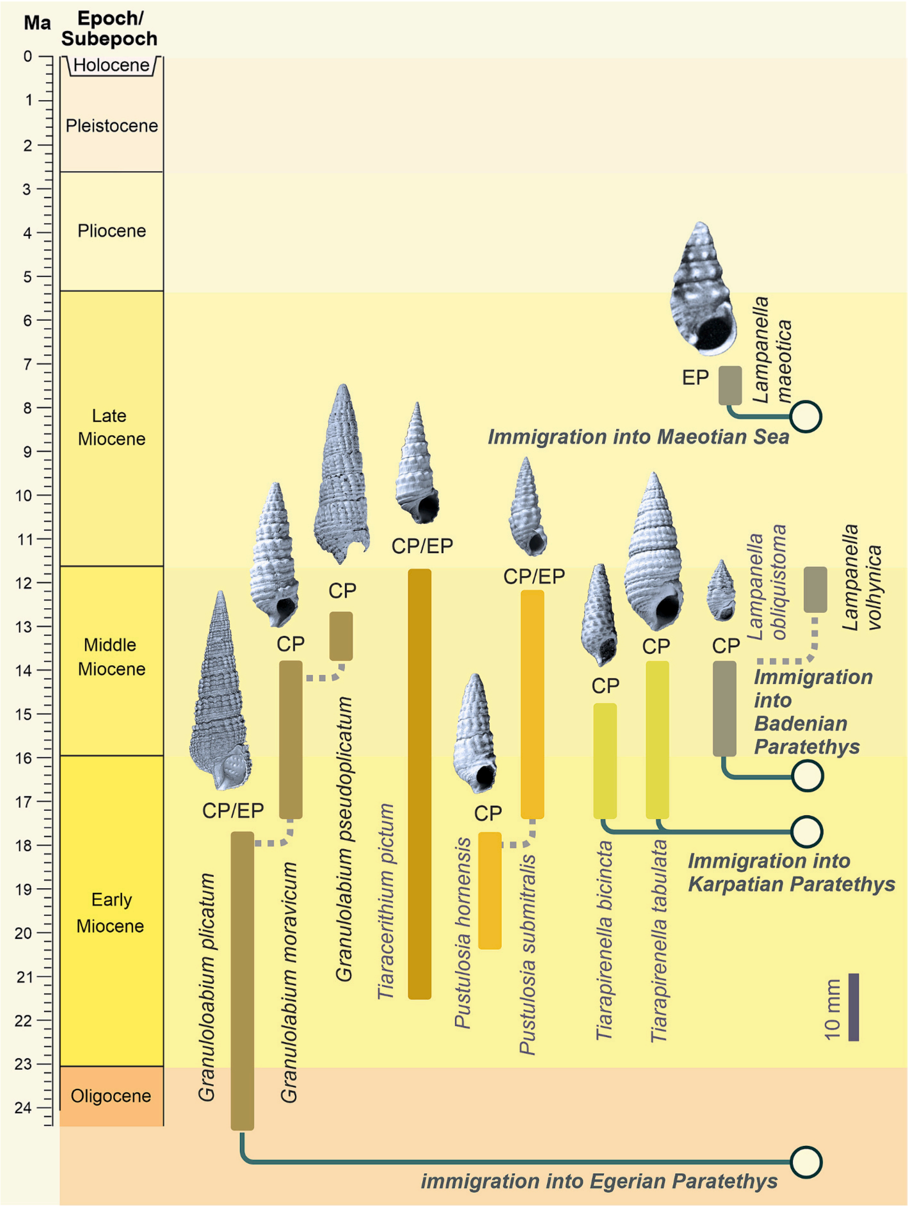

Fig. 5. Stratigraphic occurrences of Paratethyan Batillariidae. For details see caption of Fig. 4.

during the Badenian stage (15.92–12.7 Ma), which can be divided into three phases. Eleven species and eight genera are documented from nine localities from Austria and Hungary covering the lower Badenian (lower Langhian). The middle Badenian (upper Langhian) is represented by 40 localities in Austria, Bulgaria, Croatia, Czechia, Hungary, Poland, Romania and Slovenia, which contained ten species and eight genera. The upper Badenian is represented by 23 localities in Austria, Poland, Slovakia and Ukraine and witnesses a decline of diversity with six species and five genera. Seven species and six genera are documented from the lower Sarmatian (= Volhynian; 12.7–~11.8 Ma; Fig. 2) from 110 localities in Austria, Croatia, Hungary, Poland, Slovakia and Ukraine. Five species and four genera are found during the middle Sarmatian (= Bessarabian; ~11.8–~9.4 Ma), which is represented by four localities in Austria, Hungary and Ukraine.

Eastern Paratethys Sea: mudwhelk assemblages from the Oligocene to Lower Miocene are limited to a single species (*Granulolabium plicatum*) reported from three localities in Georgia from the Rupelian and Sakaraulian (~20.4–~17.4 Ma). Middle Miocene faunas of the Eastern Paratethys show continued low diversity. A single species is documented from a single Russian locality of the Tarkhanian (~15.0–~14.8 Ma). The lower Chokrakian (~14.8–~13.8 Ma) is much better sampled with 19 localities in Russia and Georgia. Nevertheless, still only one species is documented from these Chokrakian outcrops. A single locality in the Russia contained a single species from the Karaganian (~13.8–~13.4 Ma). The Konkian (~13.4–~12.7 Ma) is represented by seven localities from Georgia, Kazakhstan, Turkmenistan and Russia, which yielded three species and three genera. Seven species and five genera are recorded from the Volhynian (12.7–~11.8 Ma), from 42 localities in Bulgaria, Moldova, Romania and Azerbaijan. The Bessarabian (~11.8–~9.4 Ma) is represented by 54 localities from Bulgaria, Moldova and Romania, which yielded seven species and four genera. The Khersonian (~9.4–7.65 Ma) saw a distinct drop in diversity; only a single species is documented from the upper Khersonian of Romania, Moldova and Ukraine. The Maeotian (7.65–6.1 Ma) is represented by 51 localities in Azerbaijan, Bulgaria, Georgia, Russia and Ukraine. Lower Maeotian mollusc faunas yielded three mudwhelk species of two genera. After a gap of nearly 4 Myr, potamidid faunas appeared again at about 2.75 Ma during the Akchagylian (2.95–2.15 Ma), which is represented by 27 localities in the Caspian Sea Basin (Armenia, Azerbaijan, Georgia, Kazakhstan, Russia and Turkmenistan). Two species and two genera are documented from the Akchagylian, which occur in both the uppermost Pliocene and the Lower Pleistocene part of the Akchagylian (Lazarev et al., 2021).

3.2. Sampling quality

The rarefaction curves for the Ottnangian, Karpatian, middle Badenian, Konkian, Volhynian, Bessarabian, Maeotian and Akchagylian faunas level off asymptotically, indicating that the sampled localities mirror the respective diversities with high fidelity (Fig. 6). Ascending graphs, which imply insufficient sampling, are drawn for the Eggenburgian and especially for the early Badenian. The rarefaction curves of the Egerian and the late Badenian are intermediate with very shallow growth rates without levelling off. Rarefaction analysis was not possible for time bins containing only a single species (Tarkhanian, Chokrakian and Karaganian). The high number of Chokrakian localities, however, suggests that the Chokrakian potamidid fauna is indeed represented only by one species. Thus, the data are sufficient to discuss the development of potamidid diversities for most of the time bins but are too sparse for clear interpretations concerning the Early Miocene of the Eastern Paratethys.

3.3. Size classes

The size classes of Paratethyan potamidid faunas represent a bimodal pattern: most species are small or in the lower range of the medium sized class (below 40 mm). The second group comprises large species of >50 mm in shell height. The medians of the pooled data for each time bin are highest for the Egerian and Eggenburgian (Fig. 7). For the Eggenburgian, the insufficient sampling might lead to an underestimation of medium sized species. The median shell height drops significantly after the Eggenburgian. The low median shell height, however, persists during the Karpatian and the early–middle Badenian. The decline of large Potamididae started during the late Badenian/Konkian. Small and medium sized species occur during the Maeotian and Akchagylian (Fig. 7).

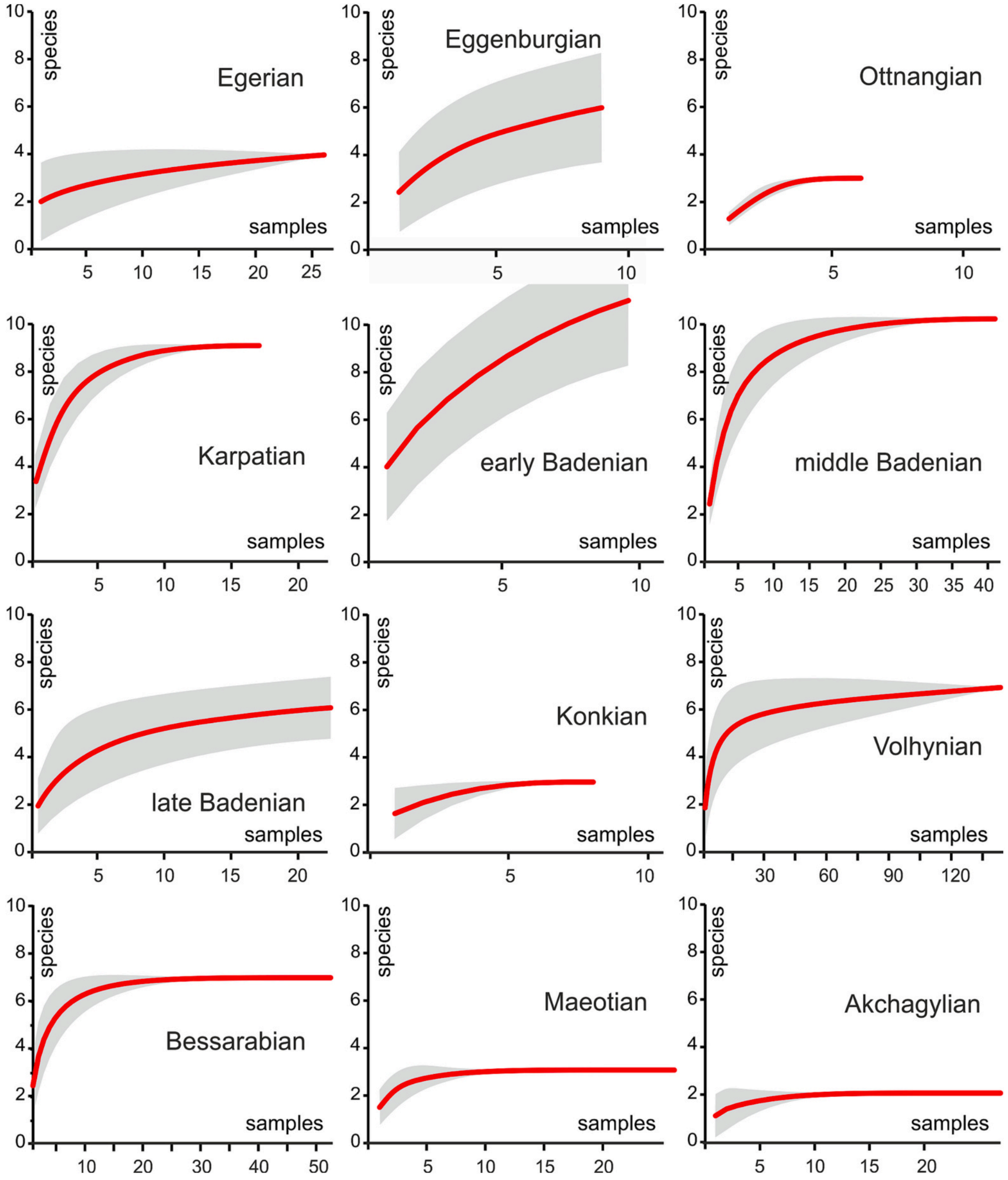

Fig. 6. Rarefaction curves per stage. Gray areas indicate 95% confidence intervals.

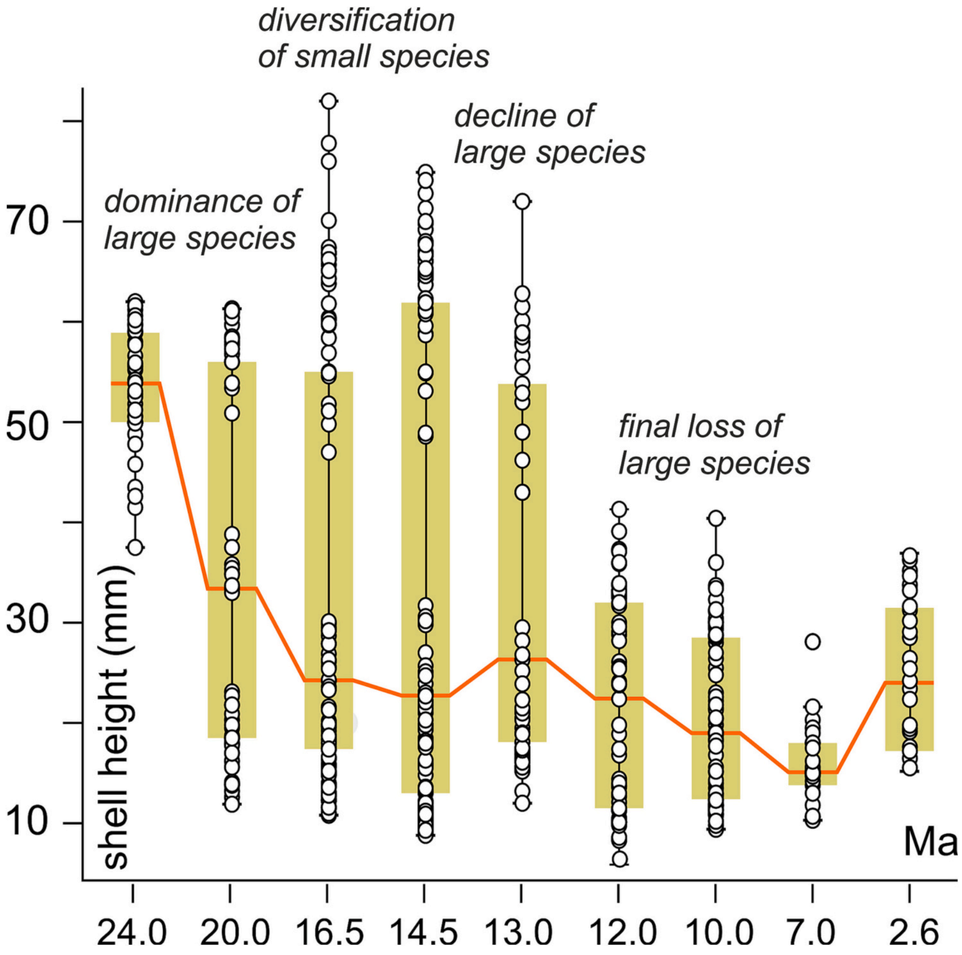

Fig. 7. Boxplots of mean shell height of potamidid species through time. Dots represent individual specimens; orange line represents mean of pooled data (see Supplementary Table 2 for data and Supplementary Fig. 1 for box plots depicting each species separately).

3.4. Connectivity of faunas in time and space

Within the Central Paratethys, the Jaccard similarity index (JI) between Egerian and Eggenburgian faunas is low (JI = 0.38) (Fig. 8), although some emblematic species like *Mesohalina margaritacea*, *Ptychopotamides cinctus* and *Granulolabium plicatum* occurred in both stages in considerable numbers. The JI increases to 0.5 at the Eggenburgian/Ottnangian boundary but drops to zero during the late Ottnangian, due to the extirpation of all potamidids at that time (= Late Ottnangian Extinction Event sensu Harzhauser and Piller, 2007); at that time marine species declined distinctly due to the changing water chemistry following tectonic isolation (Popov et al., 2004; Kováč et al., 2017). Consequently, the comparison between lower Ottnangian and Karpatian faunas reveals a very low JI of 0.2, which is maintained by the occurrence of ubiquitous species, such as *Terebralia lignitarum* and *Tiaracerithium pictum.* The JI increases distinctly between Karpatian and lower Badenian faunas (JI = 0.82) and peaks at the early/middle Badenian boundary with a JI of 0.91 (Fig. 8). Subsequently, the JI decreases to 0.46 at the middle/late Badenian and drops to 0.3 at the transition from the late Badenian to the Volhynian (early Sarmatian). Within the Sarmatian, however, the mudwhelk faunas become quite uniform, with no turnover observed between Volhynian and Bessarabian faunas (JI = 1.0).

Within the Eastern Paratethys, the poor Tarkhanian record causes a moderate JI at the Tarkhanian/Chokrakian boundary of 0.3. The faunistic similarity between Chokrakian+Karaganian and Konkian faunas increased to 0.5 but dropped again down to 0.25 at the Konkian/Volhynian boundary. Subsequently, the JI increases distinctly to 0.75 between Volhynian and Bessarabian faunas. Afterwards the faunistic relations diminished and attained only a JI of 0.14 between Bessarabian and Maeotian faunas and dropped to zero between Maeotian and Akchagylian faunas.

The comparison between both seas shows very limited connectivity between lower to middle Badenian faunas and their coeval Eastern Paratethyan pendants, ranging from only 0.1 during the early Badenian to 0.25 during the middle Badenian (Fig. 8). During the late Badenian/Konkian, the faunistic similarities increased to a JI of 0.5 and culminated during the Sarmatian–Volhynian and onset of the Bessarabian (JI = 0.85).

4. Discussion

4.1. Global climate and regional events and the Paratethyan potamidid record

The first Paratethyan potamidids appeared during the Late Oligocene Warming (De Man and Van Simaeys, 2004; O'Brien et al., 2020), which seems to have provided favorable environmental conditions because at that time mudflat environments became widespread (Harzhauser and Mandic, 2002). Their diversity remained rather stable during the Early Miocene until the late Ottnangian break-down. This drop of potamidid diversity during times of continued warm temperatures is clearly unrelated to climate trends but was very likely primarily triggered by regional geodynamic events, which led to the Late Ottnangian Extinction Event (Harzhauser and Piller, 2007). This event was caused by tectonic isolation of large parts of the Paratethys Sea, which resulted in

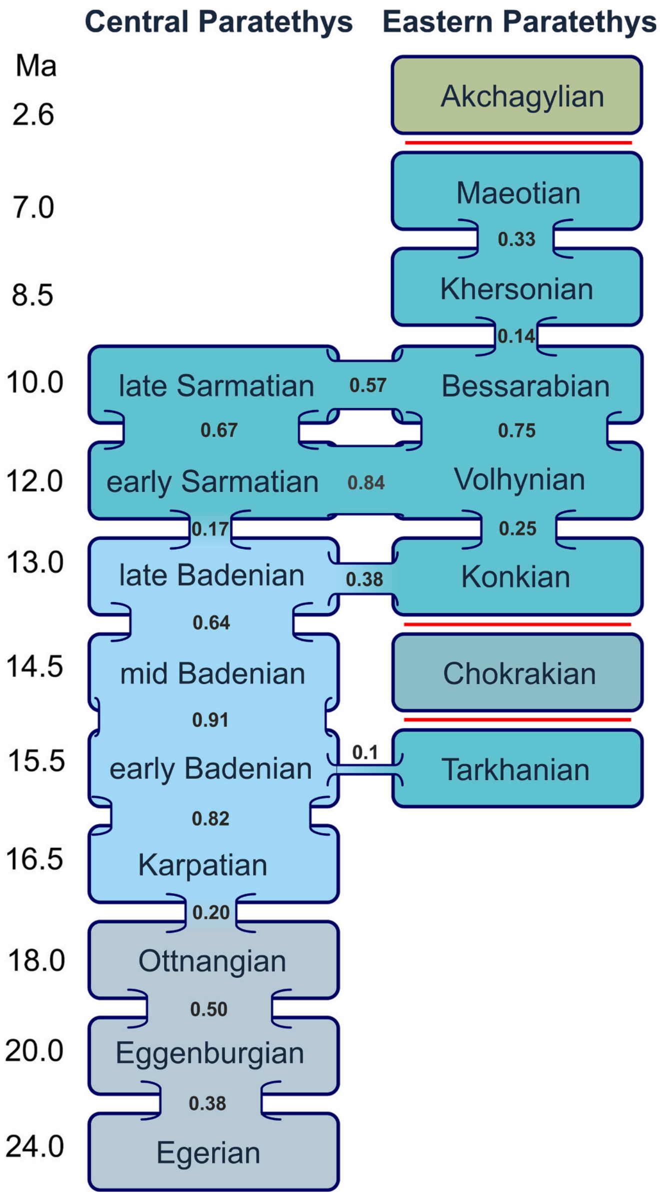

Fig. 8. Biogeographic connectivity within and between the Central and Eastern Paratethys based on the Jaccard Index of the potamidid faunas.

severe changes in water chemistry and a strong loss in marine diversity (Rögl, 1998; Popov et al., 2004; Harzhauser and Piller, 2007). The increased diversity during the following Karpatian coincided strikingly with the beginning of the Miocene Climatic Optimum (Zachos et al., 2008; Westerhold et al., 2020; Steinthorsdottir et al., 2021), with highest temperatures during the early and middle Badenian (Langhian) (Fig. 3). This warming led to range expansions of numerous thermophilic molluscs from the Proto-Mediterranean Sea into the Central Paratethys (Harzhauser et al., 2003b) and many gastropod families experienced a peak in diversity: e.g., Ranellidae (Landau et al., 2009), Clavatulidae (Harzhauser et al., 2022a), Conidae (Harzhauser and Landau, 2017), Turritellidae (Harzhauser and Landau, 2019). The decline of potamidid diversity in the late Badenian coincided with the Middle Miocene Climate Transition (Shevenell et al., 2004; Hamon et al., 2013; Westerhold et al., 2020) in the Serravallian. A comparable pattern of declining diversities was previously documented by Harzhauser and Piller (2007) and Harzhauser et al. (2018, 2023a) for various other gastropod families in the Central Paratethys. Comparable data for the Eastern Paratethys, however, were missing so far. The unstable hydrological condition (e.g., changes in salinity, Popov et al., 2022) in the Eastern Paratethys were more important for changes in its biotic composition than the climatic events. This hypothesis, however, will need proof from new faunistic data.

The high potamidid diversity of the Sarmatian Sea is not directly linked to global climate trends. Instead, it correlates with the formation of a "Mega-Paratethys" following the Pan-Paratethyan Volhynian Flooding around 12.7 Ma (Figs. 2, 3). At that time, the Central and Eastern Paratethys became fully connected (Palcu et al., 2015). The large size of this sea and the broad intertidal zone in the shallow basins (Kranner et al., 2021a, 2021b) might have supported the high mudwhelk diversity. We note however, that faunistic information on the Sarmatian Paratethys is biased towards western occurrences and especially Eastern Paratethyan occurrences are situated mainly west of the modern Black Sea, whereas information on its eastern part is sparse.

Marine environments became replaced by near-freshwater conditions and potamidids disappeared from the Central Paratethys region with the geodynamically triggered formation of Lake Pannon around 11.6 Ma (Magyar et al., 1999; Neubauer et al., 2016). The Eastern Paratethys was not affected by this event and therefore a high diversity was maintained in the Eastern Paratethys during the stable Bessarabian sea level highstand (Palcu et al., 2019), which coincided with the global Tortonian Thermal Maximum (Westerhold et al., 2020; Holbourn et al., 2021; Harzhauser et al., 2022b). The abrupt disappearance of potamidids from the Eastern Paratethys after the Bessarabian coincides with an extreme sea level drop of about 300 m with the onset of the Khersonian. In addition, a severe drop in salinity down to 5 ‰ occurred (Iljina et al., 1976). These events were followed by a phase of intensely dry conditions in Central Eurasia, termed "Great Khersonian Drying" by Palcu et al. (2019), which might have been the final cause for the temporary extirpation of potamidids in the Paratethys.

The short-term return of potamidids afterwards coincides with the Maeotian transgression (Rögl, 1998; Palcu et al., 2019), which in turn matches a negative isotope excursion during the latest Tortonian and early Messinian (Westerhold et al., 2020), termed herein End-Tortonian Warm Period (Fig. 3). A connection of the Eastern Paratethys with the Proto-Mediterranean Sea was proposed by Palcu et al. (2019) for this timespan, which would fit to our biogeographic data and explain the re-immigration.

The last phase of Paratethyan potamidid faunas coincided with the Mid-Pliocene Warm Period (or Mid-Piacenzian Warm Period) of Raymo et al. (1996), Haywood & Valdes (2004), Westerhold et al. (2020), Williams et al. (2021) and Dominici and Danise (2022) and correlates with the Akchagylian sea level rise in the Caspian Basin. The initial Akchagylian transgression around 2.95 Ma was explained by Lazarev et al. (2021) by increased freshwater runoff, which seems to have hampered the spread of potamidids, although some species are known to withstand strongly lowered salinities (Reid et al., 2008). The second phase, termed "Akchagylian marine incursion" by Lazarev et al. (2021), led to marine conditions between 2.75 and 2.45 Ma and is witnessed by the occurrence of potamidids in the Caspian Basin. Lazarev et al. (2021) assumed a connection with the Arctic Ocean to explain the sudden influx of seawater. No potamidids, however, can exist in the Arctic region because they are thermophilic. Instead, our data point to a connection with the Mediterranean Sea, which is supported by the occurrence of *Potamides* in the Romanian (Pliocene) of the Dardanelles Basin (Taner, 1997) (note that this hypothetical connection is not drawn in Fig. 2, because the distribution could also be explained by transport by birds).

Kováč et al. (2017) pointed out the importance for changing water circulation patterns in the Central Paratethys with anti-estuarine circulation leading to good deep-water connections with the Proto-Mediterranean Sea and increased isolation during phases of estuarine circulation. The change in circulation regimes, however, is not reflected in the potamidid faunas.

4.2. Range expansions and exotic occurrences

Mudwhelks are gregarious animals, which occur in large numbers and possess thick carbonatic shells (Reid et al., 2008). Therefore, their fossil record is very good. The rarefaction curves support this interpretation and suggest that the faunas of most stages are well sampled except for the Eggenburgian and lower Badenian, which might contain more species than detected so far. This makes mudwhelks excellent tools to trace shifts in faunal composition and to detect arrivals of species from adjacent biogeographic regions. The stratigraphic ranges of Paratethyan Potamididae (Fig. 4) and Batillariidae (Fig. 5) suggest six phases of range expansions, which alternate with phases of autochthonous diversifications. For the Oligocene and Early Miocene our data are best for the Central Paratethys. For the Middle Miocene to Pleistocene our data cover also the Eastern Paratethys reliably.

The Egerian immigration: Egerian assemblages comprise Paleogene species with common Western Tethyan origin. These are *Mesohalina margaritacea, Ptychopotamides cinctus*, *Granulolabium plicatum* and *Terebralia prolignitarum.* These species were all present already during the Rupelian in the Western Tethys [e.g., Italy (Sacco, 1888, 1895), Greece (Harzhauser, 2004) and Turkey (Harzhauser et al., 2016)] and were documented partly also from the northeastern Atlantic (Lozouet, 1986; Lozouet et al., 2001). The initial formation of the Paratethys Sea coincided with an isolation event, which caused wide-spread anoxia (Sachsenhofer et al., 2017; Palcu and Krijgsman, 2022). The respective mollusc faunas of the lower Oligocene Kiscellian stage are highly endemic and our knowledge on these faunas is biased towards offshore environments (Noszky, 1940; Báldi, 1986). No information on mudwhelk faunas from the Kiscellian stage is available. Therefore, we do not know if the Egerian mudwhelks have persisted along the Paratethyan coasts since the Early Oligocene or if these species invaded the Central Paratethys during the Egerian from the Proto-Mediterranean Sea. In respect to the high endemicity of the Kiscellian faunas and because the Egerian coincided with the global Late Oligocene warming (De Man and Van Simaeys, 2004; O'Brien et al., 2020), we consider the latter scenario more likely.

The Karpatian immigration: Vast mudflats fringed the basins of the Central Paratethys during the Karpatian (e.g., Zuschin et al., 2004, 2014), which together with the onset of the Miocene Climatic Optimum supported a high potamidid diversity. These favorable conditions allowed the arrival of *Tiarapirenella, Terebralia duboisi* and probably *Theodisca theodisca* (Figs. 4, 5). *Terebralia duboisi* appeared already during the Aquitanian and early Burdigalian in the northeastern Atlantic but arrived in the Central Paratethys not before the Karpatian. At that time, we observe also the first appearance of *Tiarapirenella*, which is represented by two species. The origin of *Tiarapirenella* remains enigmatic because Tortonian occurrences in the Proto-Mediterranean Sea postdate the occurrences in the Central Paratethys Sea. As the genus occurred abruptly with two distinct species in the Karpatian, we assume that it had evolved outside the Paratethys Sea.

The Badenian immigration: The third wave of new arrivals occurred during the early Badenian with *Terebralia subcorrugata* and *Lampanella obliquistoma*. *Terebralia subcorrugata* can be traced back to the Oligocene and Early Miocene of the Western Tethyan Region (Harzhauser, 2004; Esu and Girotti, 2010) but is unknown from coeval Paratethyan deposits. Chattian and Early Miocene roots in the Western Tethyan faunas are also documented for the genus *Lampanella* (e.g., Lozouet et al., 2001; Esu and Girotti, 2010). This immigration event coincided with a phase of reflooding of Central Paratethyan Basin (Sant et al., 2019) following a sea-level low around the Early/Middle Miocene boundary, which was amplified in some basins by strong tectonic movements (Harzhauser et al., 2020).

The Sarmatian immigration and the first* Potamides *conundrum: The Badenian/Sarmatian boundary was marked by a severe extinction of entire many marine gastropod families (Sarmatian–Badenian Extinction Event of Harzhauser and Piller, 2007), which was followed by the radiation of a highly endemic fauna throughout the Central and Eastern Paratethys. The ubiquitous *Potamides fraterculus* and *Potamides disjunctus* are enigmatic within this fauna as they lack any Paratethyan roots. No *Potamides* species are recorded from Badenian and Konkian deposits of the Paratethys and therefore, the ancestors of these species must be found somewhere else. The genus *Potamides* originated during the Middle Eocene in the northeastern Atlantic (Lozouet, 1986; Harzhauser et al., 2023a) and was represented there until the Oligocene by its type species *Potamides lamarckii.* A spotty occurrence of the genus is also known from the Egerian of the Paratethys, listed by Harzhauser et al. (2023a) as *Potamides* sp. There is no fossil *Potamides* species known from the Early and Middle Miocene of the Proto-Mediterranean Sea and the northeastern Atlantic as already pointed out by Lozouet (1986). The most logical explanation for the huge gap of about 9 Myr between the Oligocene and the Sarmatian occurrences of *Potamides* (Fig. 4) is to assume a continuous distribution along the coasts of western Africa. The faunistic relations in several Paratethyan gastropod families, such as the Turritellidae, Conidae and Clavatulidae, with modern faunas in the tropical eastern Atlantic, support this hypothesis (Lozouet, 2014; Harzhauser and Landau, 2017, 2019; Harzhauser et al., 2022a). Further examples of such assumed Miocene immigrants from the western African coasts are the enigmatic strombids *Pereiraea gervaisi* (Vézian, 1856) and *Europrotomus schroeckingeri* (Hoernes and Auinger, 1884), which display stratigraphically short-lived but distinct occurrences in the Central Paratethys (Mikuž, 1999; Harzhauser et al., 2003b; Kronenberg and Harzhauser, 2012). Lozouet (2014) even coined the term "Euro-West African Region" to emphasize the faunistic relations between the present-day African and Cenozoic European faunas. Unfortunately, this hypothesis cannot be tested due to the lack of Oligocene–Miocene deposits along western Africa. An obvious problem of our "West-Africa-hypothesis" is the lack of *Potamides* species in coeval Mediterranean strata. Yet, no plausible alternative scenarios are known at this time. Whilst the above-mentioned groups (strombids, turritellids, etc.) suggest a marine connection for the migration of larvae, for the potamidids transport by birds is a possible vector of distribution as well (Ozawa et al., 2015).

***The Maeotian immigration*:** The occurrence of *Lampanella maeotica* cannot be explained by Paratethyan ancestors. *Lampanella obliquistoma* had never entered the Eastern Paratethys and was restricted in the Central Paratethys to the Middle Miocene (Fig. 4). *Lampanella volhynica* was restricted to the early Sarmatian of the Carpathian Foredeep. The genus most probably arrived in the Maeotian Eastern Paratethys from the Proto-Mediterranean Sea, where *Lampanella obliquistoma* is documented from coeval Tortonian and Messinian strata (D'Amico et al., 2012; Harzhauser et al., 2013). Therefore, we hypothesize that L. *maeotica* is an Eastern Paratethyan offshoot of Proto-Mediterranean populations of L. *obliquistoma*. This interpretation is in line with the Proto-Mediterranean origin of several other early Maeotian molluscs as documented by Popov and Nevesskaya (2000).

The Maeotian occurrence of *Potamides taitboutii* documents a direct relation with the Bessarabian faunas. This is striking, because the freshwater conditions during parts of the Khersonian (Lazarev et al., 2020) would not sustain marine faunas. Findings of *Potamides* from the Khersonian of the Moldavian Platform and the Black Sea Lowland Basin by Muratov and Nevesskaja (1986) and from the Dacian Basin by Lazarev et al. (2020), however, bridge the gap between the Bessarabian and Maeotian occurrences. During the Tortonian and Messinian, *Potamides* was not restricted to the Paratethys but is also documented from the Proto-Mediterranean Sea (*Potamides tuberculiferus* (Cocconi, 1873) and *Potamides disjunctus* sensu Davoli, 1990) (Davoli, 1990; Dominici et al., 2020). Both species are morphologically close to the Sarmatian/Maeotian *Potamides taitboutii*. A revision of these species is necessary to evaluate their relationship with the Paratethyan species.

The Akchagylian immigration and the second* Potamides *conundrum: The potamidid fauna of the Akchagylian cannot be directly derived from Paratethyan ancestors because of the about 4-Myr-long gap between the last Maeotian potamidids and the re-appearance of mudwhelks in the Caspian Basin (Fig. 3). Thus, *Potamides caspius* and *Theodisca azerbajdjanica* must be rooted in Mediterranean ancestors. As both genera are presented in the Pliocene and Early to Middle Pleistocene of the Mediterranean Sea by *Theodisca graeca* (Deshayes, 1835) and *Potamides granosus* (Borson, 1821) (see Brunetti, 2013), this relation would not be surprising. Whilst this hypothesis works well for *Theodisca graeca* – *T. azerbajdjanica*, it is less convincing for *Potamides caspius*. The Mediterranean Pliocene-Pleistocene *Potamides granosus* does not seem to be closely related with *Potamides caspius* based on its sculpture, which is closer to the *Potamides fraterculus*-lineage (see Harzhauser et al., 2023a). *Potamides* was documented by Taner (1997) also from the Pliocene of the Dardanelles Basin, representing a potential geographic steppingstone.

Therefore, the Akchagylian *Potamides* likely migrated into the Caspian Basin from the Mediterranean Sea, but its direct ancestor remains enigmatic. An immigration from the Arctic Ocean, following the model of Lazarev et al. (2021), can be excluded for all Potamididae based on climatic restraints (Reid et al., 2008).

4.3. Paratethyan lineages and species groups

A close phylogenetic relation and direct evolution within the Paratethys can be hypothesized for several species basing on morphological similarities. Such species groups are *Pustulosia hornensis* and *Pustulosia submitralis* (Fig. 5), of which *P. hornensis* is endemic to the Central Paratethys, and the *Potamides disjunctus* – *P. taitboutii* – *P. galidzgensis* species group (Fig. 4), which is entirely endemic to the Paratethyan realm. No potential ancestors of these lineages are known from adjacent regions. Similarly, the stratigraphic succession from *Granulolabium plicatum* to *G. moravicum* and *G. pseudoplicatum* (Fig. 5) might represent another continuous succession of species from the Egerian to the late Badenian, of which the latter two are endemic to the Central Paratethys. *Terebralia lignitarum* – *T. menestrieri* (Fig. 4) and *Theodisca theodisca* – *T. biseriata* (Fig. 4) are two additional examples of endemic species-groups, which can be derived from widespread ancestors, but were later restricted to the Paratethys. Both groups pass the Badenian/Sarmatian (Konkian/Volhynian) boundary and lead to endemic species.

The origin of the Chokrakian *Theodisca cicur* is less obvious and might represent an endemic offshoot of Central Paratethyan populations of *T. theodisca* or might be derived from Proto-Mediterranean ancestors.

4.4. The trend towards small shells

We observe a general trend towards the dominance of small species from the Oligocene to the Early Pleistocene (Fig. 7). The peak in shell size during the Egerian is caused by the dominance of large Potamididae such as *Terebralia prolignitarum, Ptychopotamides cinctus* and *Mesohalina margaritacea* and the comparatively low number of small and medium sized species. The median shell height drops significantly after the Eggenburgian, which coincides with the disappearance of the large *Mesohalina* and *Ptychopotamides*. Subsequently, a shift towards low mean values resulted from the diversification of small and medium sized species, which evolved during the Karpatian. The decline of large Potamididae started during the late Badenian/Konkian and culminated in the final extinction of large Potamididae after the Bessarabian. This resulted in small to medium sized Maeotian and Akchagylian faunas (Fig. 7). The overall trend towards smaller sizes is also evident in some lineages at the species level. This includes the evolution from *Potamides disjunctus* to *P. taitboutii* during the Bessarabian with a size reduction of one third. Similarly, the development from *Terebralia lignitarum* to its assumed descendant *T. menestrieri* with the onset of the Volhynian, led to a size reduction of about 50%. This observation is interesting, because Payne and Heim (2020) documented that large sized species are generally not at greater risk of extinction than small species. In turritelline gastropods Pietsch et al. (2023) discussed small size as evolutionary advantage due to larger population size and high generational turnover. Whilst we have no information on the latter for Paratethyan potamidids, the larger population size might have been an important factor for the success of smaller species, as the small species typically occur in much larger numbers than the large sized species. This field observation, however, lacks statistical proof.

4.5. Mudwhelks and mangroves

The Cenozoic radiation of mudwhelks was interpreted by many authors to be closely linked to the spread of mangroves (Glaubrecht, 1997, 1999; Reid et al., 2008). However, today not all mudwhelks are indicative for an obligate mangrove association, and potamidids and batillariids are frequently found also on saltmarshes, hypersaline lagoons and in saline lakes (Kowalke, 2001; Reid et al., 2008; Reid and Ozawa, 2016). Our criteria for assuming a mangrove-relation for a certain species are: belonging to the same genus of modern gastropods living exclusively on mangroves (e.g., *Terebralia*), co-occurrence with fossil mangrove pollen and/or co-occurrence with *Ellobium*.

Modern *Terebralia* species are indeed bound to mangroves in the Indo-West Pacific Region (Ellison et al., 1999; Wells and Lalli, 2003). Mangroves and mudflats apparently were also the preferred habitat of *Terebralia* during the Paleogene and Neogene (Reid et al., 2008; Thivaiou et al., 2023). *Terebralia prolignitarum* is found at the Hungarian locality Máriahalom in assemblages with the ellobiid gastropod genus *Ellobium* (Harzhauser et al., 2023c), which is bound to mangroves (Ellison et al., 1999). Potential mangrove-associated plants from the Oligocene of Hungary are represented by the fern *Acrostichum* (Andreászky, 1954). Despite the presence of *Acrostichum* in mangrove-related habitats in the past and today, it is considered an opportunistic taxon and therefore not strictly limited to marine conditions (Moreno-Domíngues et al., 2016). In contrast, *Terebralia lignitarum* from the Karpatian of the Korneuburg Basin co-occurred with *Avicennia* mangroves, as proven by pollen records (Harzhauser et al., 2002; Kern et al., 2010). *Pustulosia* is found in mud-flat deposits, often associated with *Terebralia* (Harzhauser et al., 2023a) and therefore might have been part of the mangrove assemblage.

A direct link between mangrove fossils of the genus *Avicennia* and the genus *Ptychopotamides* is also found in the Karpatian of Austria and the Oligocene of Turkey (Harzhauser et al., 2002). Yet, the presence of *Ptychopotamides* is not limited to mangroves in these settings, where it also occupied oligohaline mudflats and swamps associated with Taxodiaceae (Latal et al., 2006; Harzhauser et al., 2015; Zuschin et al., 2014). *Mesohalina* also co-occurred with a large *Ellobium* species (Harzhauser et al., 2023a, 2023c) during the Egerian. Rupelian populations of *Mesohalina* in the Thrace Basin (Turkey) were reported by İslamoğlu et al. (2010) and Harzhauser et al. (2016) from oligohaline mangrove swamps at some distance to the sea. A close relationship between the genus *Tiarapirenella* and *Avicennia* mangroves is further evident for the Karpatian Korneuburg Basin (Austria) (Harzhauser et al., 2002). Since stable isotope data by Latal et al. (2004, 2006) suggest that *Tiarapirenella* settled brackish water environments but tolerated freshwater input, it might have preferred landward parts of mudflats and mangroves. Extant *Lampanella* lives in large populations on mud in the intertidal zone tolerating brackish waters in the Western Atlantic (Bequaert, 1942). The genus occurs in mangroves but may settle also sand and rock platforms in sheltered environments (Plaziat, 1984; Ozawa et al., 2009). Middle Miocene *Lampanella obliquistoma* could have occurred in mangroves until the Langhian/Serravallian boundary when *Avicennia* vanished from the Central Paratethys (Jiménez-Moreno et al., 2008). The Late Miocene *Lampanella maeotica* was unlikely living in mangroves, which probably did not exist in the region at that time. The latest record of alleged mangroves is a record of *Nypa* from the Pontian of Georgia, but this record remains questionable and might be the result of reworking (Shatilova et al., 2018). A Late Miocene presence of *Avicennia* is indicated for the Euxinian Basin in Bulgaria (Ivanov et al.,

2015) and the Black Sea Basin (Popescu et al., 2010), where it might have persisted in refugia until at least the Pliocene.

Paratethyan *Potamides* species are documented from various coastal marine settings, ranging from brackish water environments to hypersaline shoals (Harzhauser and Kowalke, 2002; Latal et al., 2004). A clear link to mangrove fossils can be established in none of the Sarmatian, Maeotian and Akchagylian localities.

Theodisca is documented from littoral to shallow sublittoral marine paleoenvironments and from brackish coastal mudflats. *Theodisca biseriata* preferred mixed siliciclastic–carbonatic sediments, whereas *Theodisca theodisca* was found in lignitic marls associated with *Terebralia* (Harzhauser et al., 2023a). A link to mangroves is missing. Similarly, *Theodisca cicur* occurs in clayey-sandy sediments infilling algal-bryozoan bioherms, which formed in less than few meters water depth. The species is also found as gregarious species in muddy sediments between the seashore and the bioherm zone. Another population of *Theodisca cicur* was found under lowered salinity conditions in sandy facies in the Stavropol Highland (own data A.G.). In all cases, no connection to mangroves was observed.

Oligocene and Miocene *Granulolabium* species occurred on mudflats but are often absent in mangrove associated assemblages (Harzhauser et al., 2016).

Species of *Tiaracerithium* occurred in enormous numbers in the littoral zone ranging from oligohaline mudflats to sandy littoral to shallow sublittoral marine environments (Harzhauser and Kowalke, 2002).

Thus, only *Mesohalina, Ptychopotamides, Terebralia* and *Tiarapirenella* are interpreted herein to have occurred in mangroves during the Oligocene and Early Miocene. No connection to mangroves, however, can be observed for *Granulolabium, Lampanella, Tiaracerithium, Potamides* and *Theodisca* and for late Middle to Late Miocene *Terebralia*.

5. Conclusions

About 25% of the Paratethyan Potamididae and Batillariidae species are members of autochthonous Paratethyan lineages. Such lineages partly even passed the Badenian–Sarmatian Extinction Event, which was generally less severe for potamidids compared to other gastropod families. The stratigraphically abrupt onset of the majority of the species, however, suggests immigrations from adjacent biogeographic regions. Such phases of range expansions from the (Proto)-Mediterranean Sea occurred during the Egerian, the Karpatian, the early Badenian, the early Maeotian and the early Akchagylian. In some cases, the species are documented from older strata outside the Paratethys Sea (e.g., *Terebralia prolignitarum, Terebralia subcorrugata, Lampanella*), which suggests a northward vector of migration. This is less obvious for *Theodisca, Pustulosia* and *Tiarapirenella* as older Proto-Mediterranean records are missing so far, which, however, might be due to the lack of modern revisions of Mediterranean faunas. The occurrence of Sarmatian and Akchagylian *Potamides* species is a conundrum. Although the genus has Eocene to Early Oligocene roots in Europe, the Paratethyan occurrences of the Sarmatian *Potamides disjunctus* and *P. fraterculus* cannot be linked to Proto-Mediterranean ancestors. Similarly, no ancestor is known for the Pliocene *Potamides caspius* in the Caspian Sea. We hypothesize that the "Euro-West African Region" of Lozouet (2014) along the western African coast might have acted as shelter for *Potamides* during the Neogene. Whilst this hypothesis is in line with the African 'flair' of many Miocene Paratethyan molluscs, it cannot explain the absence of *Potamides* in coeval Mediterranean deposits.

Despite their reputation as mangrove indicators (Reid et al., 2008), only *Mesohalina, Ptychopotamides*, *Terebralia* and probably *Tiarapirenella* were associated with mangroves during the Oligocene to early Middle Miocene in the Central Paratethys Sea. Consequently, none of these genera is found in the Paratethys after the Miocene Climate Transition, which coincided with the disappearance of mangroves from the Paratethys Sea (Jiménez-Moreno et al., 2008). *Tiaracerithium, Theodisca* and *Potamides*, which dominated the coasts of the Sarmatian Sea and partly re-appeared during the Maeotian and Akchagylian, were adapted to coastal environments devoid of mangroves.

The potamidid assemblages show little biogeographic connectivity between the Central and Eastern Paratethys during the Early and early Middle Miocene. The connectivity increased distinctly during the Konkian-late Badenian and peaked during the Sarmatian, with a largely uniform fauna.

Peaks in the observed diversities of Potamididae and Batillariidae coincide well with global climatic events such as the Late Oligocene Warming, the Miocene Climate Optimum, the Tortonian Thermal Maximum and the Mid-Pliocene Warm Period. Especially the Miocene Climatic Optimum is reflected by a distinct diversification of Paratethyan potamidid faunas. The Miocene Climate Transition is reflected by declining diversities and a successive loss of large species. Late Miocene, Pliocene and Pleistocene potamidids were relatively small. In the Eastern Paratethys, diversities started to raise distinctly later during the Sarmatian. But the high Sarmatian diversity is not correlated to any global climate trend. Sarmatian potamidid evolution seems to have been boosted by the formation of the "Mega-Paratethys" with the Volhynian flooding, which connected the Central and Eastern Paratethyan basins. We note, however, that this diversity peak is observed mainly in the western part of the Paratethys and will need proof by data from the east.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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