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Neogene lake systems of Central and South-Eastern Europe: Faunal diversity, gradients and interrelations

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Abstract

The gastropod γ-diversity of 12 Neogene lake systems is evaluated. In total, 1184 gastropod taxa from 119 localities are recorded deriving from the Early Miocene *Rzehakia* Lake System, the Early to Middle Miocene Dinarid Lake System, Lake Skopje, the Paratethyan Sarmatian lakes and the South German lakes, the Late Miocene Lake Pannon, the Pliocene lakes Dacia, Transylvania, Slavonia, Kosovo and Šoštanj as well as the Holocene Lake Petea. Each lake system is characterised according to its faunistic inventory and endemism. According to their gastropod faunas the lakes may be divided into pyrgulid-, hydrobiid-, viviparid- and planorbid-dominated ones. The generally high endemism rate is between 60 and 98%. Species diversity and generic diversity are strongly correlated. In contrast, neither endemism nor lake size are tightly linked with γ-diversity. Outstandingly high diversities such as observed for Lake Pannon are rather a result of the combined effect of autochthonous evolution in a long-lived system and accumulation of inherited elements. Examples of parallel evolution in lymnaeids and planorbids are presented.

Keywords: Gastropods; Freshwater molluscs; Endemism; Ancient lakes; Evolution

1. Introduction

The Central and South-Eastern European freshwater and brackish systems of the Neogene are often characterised by outstanding endemisms. Despite the enormous amount of systematic papers dealing with local faunas, the relations between these lake systems in space and time are still unexplored. The most important biogeographic entities are the Early Miocene Rzehakia Lake System, the Early to Middle Miocene Dinarid Lake System, Lake Skopje, the Paratethyan Sarmatian lakes and the South German lakes, the Late Miocene Lake Pannon, the Pliocene lakes Dacia, Transylvania, Slavonia and Kosovo, as well as the Pleistocene and Holocene lakes Šoštanj and Petea (Fig. 1). The main obstacle for taxonomists working with the Neogene lake faunas of Central and South-Eastern Europe is the complex paleogeographic situation. Some areas have been repeatedly covered by different lake systems and therefore a single literature-based locality name might represent completely different faunas. Moreover, several classical monographs intermingled faunas from several lake systems and very different stratigraphic levels (e.g. Neumayr 1869, 1880; Brusina 1897, 1902a). Especially, the separation of Lake Pannon faunas from those of the older Dinarid Lake System was completely obscure for most taxonomists (e.g. Nuttall, 1990). Molluscs of some ancient Balkan lakes such as the Early Miocene Lake Sumadija or the early Middle Miocene Lake Serbia (Krstić et al., 2001, 2003, 2007) are still insufficiently documented and therefore excluded from present analysis.

2. Methods and limitations

The dataset is based on a compilation of published gastropod faunas from Central and South-Eastern European Neogene lake systems. The results of more than 120 systematic papers have been integrated; details and references are given below in section 4. In addition, material from the collection of the Natural History Museum Vienna (NHM) has been included. The full

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dataset with detailed locality information is available online: http://www.nhm-wien.ac.at/Content.Node/forschung/geologie/mitarbeiter/pdfs/Harzhauser-Mandic-freshwater.xls. The recorded species-level taxa have been systematically arranged and listed according to localities. In a next step, localities have been grouped into geographic and stratigraphic units. Hierarchical cluster analysis and non-metric multidimensional scaling (nMDS) were performed using the statistic software packages PAST (Hammer et al., 2001) and PRIMER (Clarke and Warwick, 1994). The groupings achieved by means of hierarchical cluster analysis were tested for robustness by using different available algorithms and were additionally compared to results from nMDS. The similarity measures providing the best interpretable groupings were the Euclidean distance (between rows) for the percentage contribution data and the Simpson index and Bray–Curtis measure for the presence/absence data.

Generally, we follow the systematic groupings of Wenz (1923–1930, 1938–1944), Falkner et al. (2001), Bank et al. (2001) and Harzhauser et al. (2002). Nevertheless, the herein presented affiliation of several genera (e.g. *Staja* Brusina, 1897, Q1 *Bania* Brusina, 1896, *Gyromelania* Wenz, 1939, *Scalimelania* Wenz, 1939) to higher taxa is problematic and may change after a modern revision. Moreover, it has to be kept in mind that the number of described species in the literature is too high for many genera as modern revisions are missing for most groups. A taxonomic revision, however, is beyond the scope of this study. Despite these limitations and "taxonomic noise", we think that this dataset is a serious first approximation.

3. The lakes: geography, geological settings and stratigraphic framework

3.1. Rzehakia Lake System (RLS, ~17.5–17.2 Ma; S. Germany, Austria, Moravia)

The oldest lake system treated herein is the Early Miocene *Rzehakia* Lake System (Fig. 2). Its name is derived from the endemic bivalve genus *Rzehakia* (Korobkov, 1954). The geographic extension of the RLS reaches from Bavaria to Moravia, covering an area about 650 km long (W–E) and 150 km wide (N–S) (Senes, 1973). It had formed along the northern shoreline of the Paratethys Sea in the North-Alpine Foreland Basin and, in its Moravian prolongation, in the Carpathian Foredeep. The lakes developed during the Early Miocene (mid-Burdigalian) and reflect the sea-level lowstand TB 2.1 of Haq et al. (1988) (Rögl, 1998). This event caused the Central Paratethys Sea to disintegrate into several basins and allowed the development of strongly structured coastal plains with extensive brackish-water lakes. Little is known about the geochemistry of these lakes. Traditionally, they are considered as marine-derived brackish lakes (Rögl, 1998; Popov et al., 2004). This assumption is supported by the occurrence of endemic cardiids such as *Limnopagetia* (Schlickum, 1963) and *Limnopappia* (Schlickum, 1962) and taxa such as *Siliqua* (Megerle von Mühlfeld, 1811), which all have marine ancestors. The origin of the RLS fauna is partly rooted in the Eastern Paratethys (Popov et al., 1993; Rögl, 1998; 1999). Several endemic genera apparently originated in the faunas of the Kozakhurian Stage (e.g. *Limnopagetia*) and subsequently settled the western and central Paratethyan shores.

Based on considerable differences of the mollusc faunas of the western (Bavarian) and eastern (Austrian–Moravian) part, Harzhauser and Mandic (2008) and Mandic and Corić (2007) proposed the existence of at least two disconnected lakes. A further separation into smaller lakes in the western part of the RLS is indicated by slight faunistic differences between the Lower Bavarian Oncophora Basin and the Upper Bavarian Kirchberg Basin (Kowalke and Reichenbacher, 2005). The paleobiogeographic relations within the RLS are based on the high degree of endemics on the generic level. All lakes of that system have in common taxa such as the bivalves *Rzehakia, Limnopagetia*, and *Limnopappia* and the gastropod *Ctyrokia* (Schlickum, 1965). On the species-level, however, hardly any faunistic relation is represented aside from the ubiquist *Melanopsis impressa* (Krauss, 1852) along with the theodoxid *Theodoxus cyrtocelis* (Krauss, 1852) and the planorbid *Gyraulus applantus* (Thomae, 1845). The absence of RLS bivalves in the probably partly synchronous Dinaride Lake System suggests a distinct paleobiogeographic boundary between these lake systems.

3.2. Dinarid Lake System (DLS, ~17–15 Ma; Croatia, Bosnia and Herzegovina, Montenegro, Serbia, Hungary and Slovenia)

The Dinarid Lake System (DLS) formed during the late Oligocene and Miocene in today NW–SE trending intramountain basins parallel to the slowly rising Dinarid mountain chains (Pavelić, 2001). Extensional tectonics generated enhanced subsidence of elongated depressions during the Early to Late Miocene. The comparatively low terrigeneous input supported the diversification of lacustrine environments, including both deep- and shallow-water habitats. This habitat diversification sparked the spectacular Miocene radiation of the benthic fauna. Geographically, the deposits of the DLS cover parts of Croatia, Bosnia and Herzegovina, Montenegro, Serbia, Hungary and Slovenia (Krstić et al., 2001, 2003). During its maximum extent, the lake system covered an area of c. 75,000 km^2. Subsequent rifting in the Pannonian Basin System triggered the marine flooding of the northern DLS and considerably reduced it.

The stratigraphic correlation and paleogeographic extension of that shrunken DLS, termed Lake Herzegovina by Vujnović et al. (2000), are still under discussion. The younger deposits, however, lack DLS endemics such as *Clivunella* Katzer, 1918

Fig. 1. Geographic setting of the investigated lake systems. 1: Rzehakia Lake System (RLS, ~17.5–17.2 Ma), 2: Dinarid Lake System (DLS, ~17–15 Ma), 3: Lake Skopje (LSK, ~15 Ma), 4: Paratethyan Sarmatian Lakes (PSL, 12.4–11.8 Ma), 5: South German lakes (incl. Lake Steinheim) (SGL, 14.3– ~12 Ma), 6: Lake Pannon (LP, 11.6–5.8 Ma) 7: Lake Slavonia (LS, ~4–3 Ma), 8: Lake Transylvania (LT, ~4.5–3 Ma), 9: Lake Dacia (LD, ~5–3 Ma), 10: Lake Kosovo (LK, ~3–2 Ma), 11: Lake Šoštanj (LSO, 2.5 Ma), 12: Lake Petea (P, 0.1–0 Ma). The outlines of the Early and Middle Miocene lakes reflect only the modern sediment distribution, whilst the outlines of the Late Miocene and Pliocene lakes roughly coincide with their former extent.

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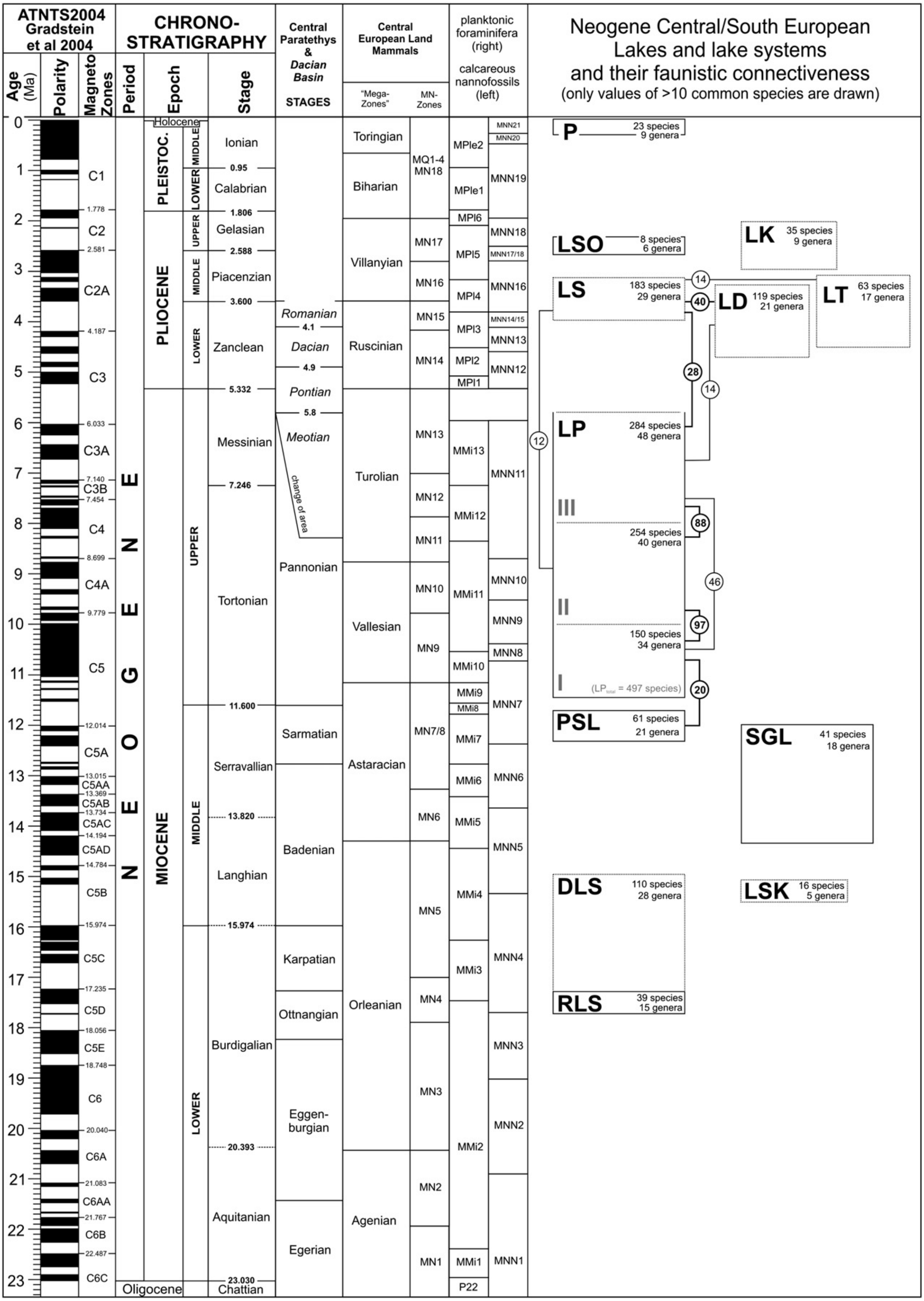

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and *Delmiella* Kochansky-Devidé and Slišković, 1972 (Kochansky-Devidé and Slišković, 1978, 1980). A typical fauna of the late DLS is recorded from the Sinj Basin in south-eastern Croatia, It represents the best investigated record of the DLS and yields an extraordinarily high species diversity (e.g. Neumayr, 1869; Brusina, 1874, 1897, 1902a).

3.3. Lake Skopje (LSK, ~15 Ma; Macedonia)

The data on that lake are extremely poor. The investigated mollusc fauna was first described more than a century ago (Burgerstein, 1877; Pavlovic, 1903) and is known so far only from Skopje. Following the current paleogeographic reconstructions, those deposits could represent the southern part of the Serbian Lake of Krstić et al. (2001, 2003, 2007) dated as early Middle Miocene (c. 16–14 Ma). The Serbian Lake extended via a 200 km wide, NNW–SSE striking depression between the Dinaride and Carpathian orogenes from Belgrade (N Serbia) to Serres (N Greece). Its molluscs, including *Kosovia* (Pavlovic, 1903), are insufficiently documented — mainly in unpublished reports and theses. Apparently, based on a synopsis by Krstić et al. (2007), they differ not only from synchronous DLS faunas but also from those of Lake Skopje. Consequently, Lake Skopje is treated herein as an independent paleogeographic unit.

3.4. Paratethyan Sarmatian Lakes (PSL, 12.4–11.8 Ma; Romania, Austria, Hungary)

During the late Middle Miocene, the isolated Paratethys Sea developed a conspicuous endemic marine mollusc fauna (Harzhauser and Piller, 2007). The coastal flats of this sea were fringed by several freshwater systems. The paleogeography of these coastal lakes is unclear and our knowledge on the fauna might be incomplete. Only few localities yield rich assemblages, whereas most other occurrences are rather out-of-habitat findings in marine deposits. Important Sarmatian wetland faunas are known from Soceni in Romania (Jekelius, 1944) and the Austrian Eisenstadt-Sopron Basin (Harzhauser and Kowalke 2002). Răcăştie (formerly Rákosd) in the Deva region in Romania is another important Sarmatian locality described by Gaál (1911) and Szalai (1928). In addition, Szalai (1928) and Boda (1959) described species from various Hungarian localities in the Bakony region and the Bükk Mountains.

3.5. South German lakes (incl. Lake Steinheim) (SGL, 14.3 to ~12 Ma; Germany)

During the late Middle Miocene several freshwater systems developed in southern Germany in the area between Munich, Nürnberg and Stuttgart. The most important of these are the Steinheim Lake in the Swabian Alb and the Ries Lake at the border between the Swabian and Franconian Alb. Both formed by a simultaneous meteorite impact during the middle Miocene (~14.3 Ma; Tütken et al., 2006). The crater basins became filled by freshwater, and long-lived lakes became established. The smaller Steinheim Lake had a diameter of c. 3.5 km, whilst the Nördliger Ries impact structure was c. 25 km in diameter. Aside from endemics, the mollusc fauna is closely related to the assemblages of the coeval wetland faunas of the so-called Silvana Beds in the adjacent North-Alpine Foreland Basin. Representative localities are Hohenememmingen (26 km SSE of Nördlingen) and Zwiefaltendorf (70 km SE of Steinheim). Little is known about the paleogeography and paleolimnology of the associated small lakes. Especially at Zwiefaltendorf, the mollusc fauna was described from reworked lithoclasts outcropping in Pleistocene deposits (Schlickum, 1976). Despite the earlier impact age of 14.3 Ma, most of the assemblages are correlated with the mammal zone MN 7 (Tütken et al., 2006), pointing to an age between c. 13.5–12 Ma.

3.6. Lake Pannon (LP, 11.6–5.8 Ma; Austria, Czech Republic, Slovakia, Hungary, Romania, Croatia, Slovenia, Bosnia, Serbia)

At about 11.6 Ma a glacioeustatic sea-level drop caused the final disintegration of the Paratethys Sea, and Lake Pannon arose in the Pannonian basin system (Magyar et al., 1999; Harzhauser et al., 2004). The benthic ecosystem collapsed at that point and marine life completely vanished. The lake was initially brackish, slowly freshening and slightly alkaline (Harzhauser et al., 2007). A very detailed paleogeographic development throughout the late Miocene is provided by Magyar et al. (1999). Accordingly, Lake Pannon attained a maximum length of 860 km (from the Karlovac Basin close to Zagreb in the west to the Transylvanian Basin in Romania in the east) and a width of 550 km (from the Vienna Basin in the north to Belgrade in the south). It covered an area of c. 290,000 km^2 and is the largest aquatic system considered in this study. The lake was highly structured by numerous islands and mountain ranges. Its maximum water depth may have reached 800 m in its central part but less than 200 m elsewhere (Magyar et al., 1999).

At around 9 Ma the lake began to shrink. Its north-western part turned into fluvial plains and, in the east, the Transylvanian Basin became dry land, reducing the area to c. 180,000 km^2. Finally, in the latest Miocene, a comparably small lake of c. 480 km width remained, covering only the southern basins of the Pannonian basin system. Herein, the succession is separated into 3 time slices: LP, Phase I: 11.6–10.0 Ma, Phase II: 10.0–8.0 Ma, Phase III: 8.0–5.8 Ma. These units roughly represent the build-up phase of Lake Pannon (Lower Pannonian), its maximum extent (Middle Pannonian, *C. subglobosae* Zone) and its gradual retreat (Upper Pannonian = "Pontian" sensu Stevanović, 1990a,b,c).

Fig. 2. Chronostratigraphic and biostratigraphic correlation scheme for the Mediterranean and Paratethyan areas (after Gradstein et al., 2004 and Piller et al., 2007). The stratigraphic range and the number of documented species and genera of each lake system are indicated in the right column (see text for abbreviations). Numbers in circles represent species that occur in two lakes.

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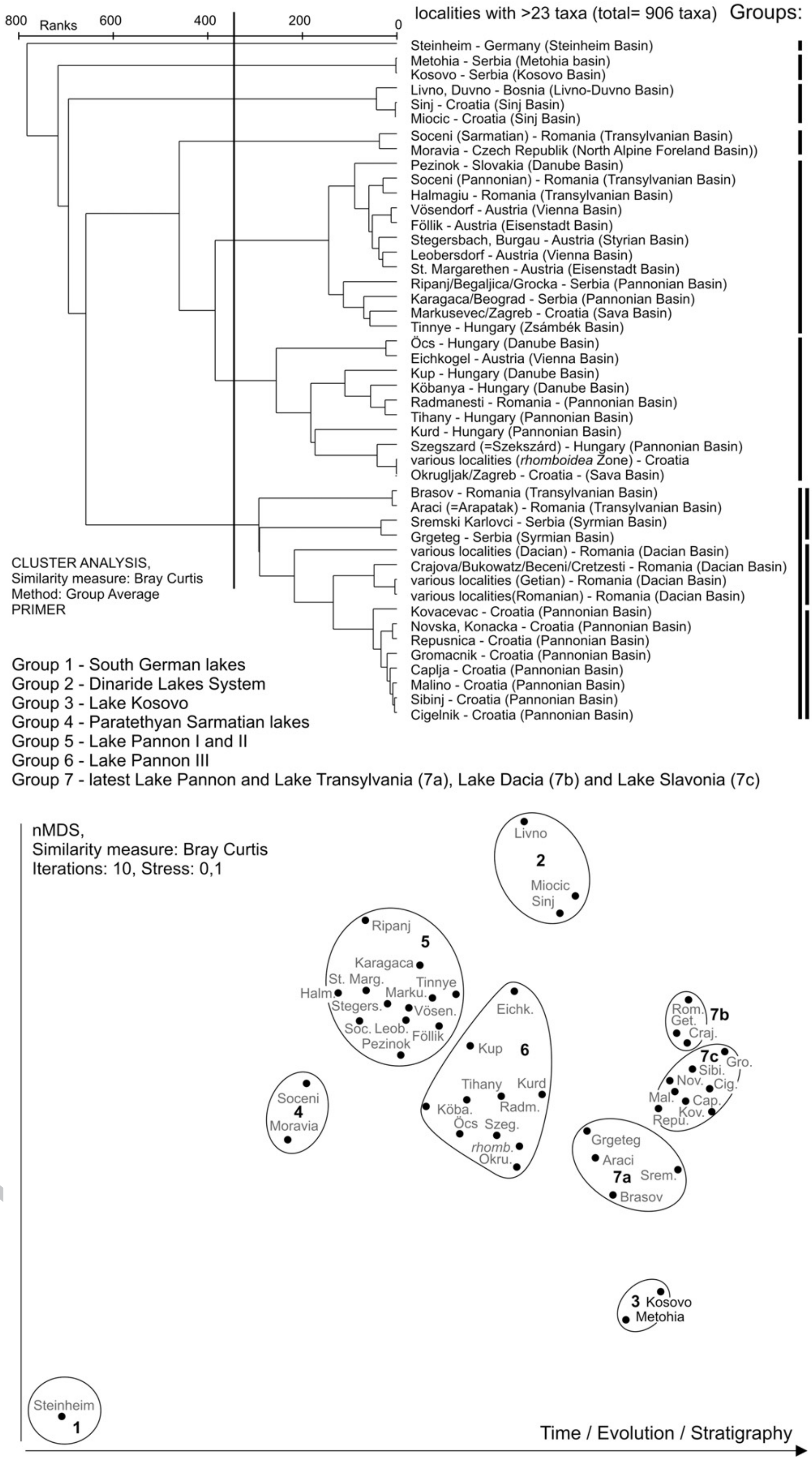

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3.7. Lake Dacia (LD, ~5–3 Ma; Romania, Bulgaria)

Lake Dacia formed in Pliocene times in place of the former Eastern Paratethys Sea. It filled the name-giving Dacian Basin and had a W–E extension of roughly 500 km and less than 200 km width, covering an area of c. 78,000 km^2. It was delimited in the north and west by the Carpathian Mountains and by the Balkanids and the Moesian platform in the south and extended into the area of the modern Black Sea. The age of the herein considered deposits is Dacian to Romanian (Snel et al., 2006).

3.8. Lake Transylvania (LT, ~4.5–3 Ma; Romania)

This elongate U-shaped lake was situated on the SE-Carpathians and covered the Brasov Basin complex, the Ciuc Basin and the Gheorgheni Graben (see Fielitz and Seghedi, 2005 for tectonic setting). It had a length of about 180 km (N–S) and was rather narrow, attaining a maximum width of 20–30 km. This only c. 4500 km^2 large lake was not a relic of Lake Pannon, but formed independently during the late Dacian and Romanian (László, 2005) within the Carpathian nappe system.

3.9. Lake Slavonia (LS, ~4–3 Ma; Croatia, Bosnia, Serbia, Romania)

This lake is also known as *Paludina Lake*, referring to the conspicuous diversity and endemic evolution of viviparid gastropods. It's a small Pliocene lake about 290 km long and 120 km wide, covering the southernmost basins of the Pannonian basin system over about 28,000 km^2. Its geographic extension is similar to that of the latest phase of Lake Pannon. Therefore, it is discussed by some authors as being a direct descendent of lake Pannon (e.g. Magyar et al., 1999). This relation remains somewhat questionable because reliable geological data and modern datings are missing.

3.10. Lake Kosovo (LK, ~3–2 Ma; Serbia, Kosovo)

Lake Kosovo was a roughly circular lake of about 50 km diameter covering an area of c. 8000 km^2. Its deposits are restricted to the larger Metohia Basin in the west and the elongated Kosovo Basin in the east (Atanacković, 1990). The stratigraphy of the basin is described by Milosević (1966). Accordingly, mollusc faunas occur in the Kosovo Basin in Middle Miocene, Upper Miocene and Pliocene deposits. The oldest fauna is part of Lake Serbia and is not considered herein. The Miocene and Pliocene faunas have been revised by Krstić et al. (2001), who treat Lake Kosovo as part of the Macedonian-Drim System (Marović et al., 1999). The latter lake system covered southern Serbia, Macedonia, southern Bulgaria and central Greece during the Late Pliocene. Its endemic mollusc fauna of Akchagylian age, however, is known so far only from the Metohia and Kosovo Basins (Atanacković, 1985; Krstić et al., 2001).

3.11. Lake Šoštanj (LSO, 2.5 Ma; Slovenia)

The investigated fauna derives from Pliocene lignite-bearing lacustrine deposits at Šoštanj near Velenje in Slovenia. Geologically, these deposits are part of the Velenje Basin and are dated as Villafranchian (Brezigar et al., 1985). Three small lakes are still present in the depression along a length of c. 4 km; the extent of the Pliocene lake is unknown. The locality is also referred to as Schönstein in the old literature (Rolle, 1860, 1861).

3.12. Lake Petea (P, 0.1–0 Ma; Romania)

Lake Petea, situated about 9 km SE of Oradea in W. Romania, is the only still existing lake in the herein utilised dataset. It is a very small (>1 km^2) thermal-spring-fed freshwater rivulet and lake with constant water temperature of c. 30 °C. The area is now protected because of the occurrence of the endemic water lily *Nymphaea lotus thermalis* (de Candolle, 1821), the rudd *Scardinus erithrophtalmus racovitzai* (Müller, 1958) and the gastropod *Melanopsis parreyssi* (Pauca, 1933). Lake Petea is a very young, mainly Holocene, aquatic system which did not originate before Pleistocene times (pers. com. Marton Venczel). Due to the complex history of the region, the locality is referred to in the literature also as Bischofsbad (German) and as Püspökfürdö (Hungarian). It is included herein because of its diversity of melanopsids and its Mio-Pliocene "flair", whilst other Pleistocene and Holocene lakes are excluded.

4. Results

In total, 1184 gastropod species and (chrono- or morpho-) subspecies from 119 localities have been compiled from the extensive literature on Miocene to Pleistocene Central and South European lakes and lake systems. This surprisingly high diversity is even comparable with marine gastropod diversity for the same geographic area during the Miocene (c. 1300 taxa in Harzhauser and Piller, 2007). In a first step a cluster analysis was performed to group localities in evolutionary entities. The number of taxa in single localities differed strongly, ranging

Fig. 3. Plots of cluster analysis using Bray–Curtis similarity measure and Group Average method and non-metric Multidimensional Scaling (MDS) of Miocene to Pliocene lake-fauna bearing localities with more than 23 taxa. The cluster analysis demonstrates the presence of 7 taxonomically constrained paleogeographic, paleobiogeographic and stratigraphic units (Groups 1 to 7). The peri-Paratethys units (Groups 1 to 3) are strictly divided from units of the Central Paratethys/Lake Pannon region, forming a coherent but internally hierarchically ordered group. The hierarchical ordering of localities of that latter group follows a stratigraphic pattern, which is also evident in the non-metric MDS plot. The hierarchical/stratigraphical ordinance starts with the Middle Miocene Sarmatian Lakes (Group 4), goes through early Late Miocene (Group 5) and late Late Miocene (Group 6) Lake Pannon up to the latest Miocene and Pliocene residual lakes (Group 7). The subgroups within Group 7 reflect paleogeographic units. The full dataset with all localities is available online: http://www.nhm-wien.ac.at/Content.Node/forschung/geologie/mitarbeiter/pdfs/Harzhauser-Mandic-freshwater.xls.

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from one to maximally 97 recorded species. Prior to analysis the dataset was therefore filtered to records containing sufficient taxa for a reasonable comparison. The best results were achieved from the species diversity of 24 upwards and using the Bray Curtis Similarity measure. The resulting grouping was used as test for a priori assumptions about paleogeographic units.

The ordering of localities coincided with their paleogeographic and stratigraphic patterns. Thus, seven paleobiogeographic units were clearly distinguished (Fig. 3): the Dinaride Lake System, the Paratethyan Sarmatian Lakes, the South German Lakes, Lake Kosovo, Lake Pannon I & II and Lake Pannon III, and a cluster representing the faunas of the latest Lake Pannon, Lake Slavonia, Lake Dacia and Lake Transylvania. Within the area of the former Paratethys Sea, the hierarchical ordering showed a clear stratigraphic pattern, with the oldest lake systems at the base and the Pliocene lakes at the top of the line-up. The peri-Paratethys systems (Dinaride Lake System, South German Lakes and Lake Kosovo), although principally following a similar stratigraphic pattern, ordered strictly separately from the Central Paratethys line-up, underlining their autochthonous evolutionary and paleoecological status.

4.1. Faunistic inventories and sources

The groupings in Fig. 3 represent ancient lake systems with fairly consistent faunas. In the next step the faunas were merged for each lake to provide a synopsis of the faunistic composition of each lake (Fig. 4). This dataset allows estimation of the γ-diversities (sensu Whittaker, 1972) and outlines the dominant taxa. There are, however, clear limitations to this approach. Especially the phenotypic plasticity of several freshwater gastropod species (e.g. within *Melanopsis* Férussac, 1823) is difficult to handle and might result in over-splitting in some genera (Geary 1990). Hybridisation effects as discussed by Geary (1992) and Bandel (2000) for Lake Pannon melanopsids will also increase the inventory. As this phenomenon cannot be solved based solely on conchological data, we maintain several of these critical morpho-species. Another drawback is the time-averaging that is inevitable in such datasets. Therefore, at least for the extremely long-lived Lake Pannon, we tried to separate the faunas into 3 time slices. Taxonomic remarks: Pyrgulidae are maintained as a family although molecular data hint at a subfamily level (Szarowska et al., 2005). The thiarid *Tinnyea* (Hantken, 1887) is counted to the Melanopsidae.

4.1.1. Rzehakia Lake System (RLS, ~17.5–17.2 Ma)

In total, 39 gastropod species attributed to 15 genera (species/genera ratio = 2.6) have been described from the RLS in the papers of Rzehak (1893), Schlickum (1963, 1964a,b, 1966, 1967), Ctyroky (1972), Steininger (1973) and Kowalke and Reichenbacher (2005). The fauna is characterised by its small size, the individuals usually being less than 10 mm in height. Few exceptions, such as *Viviparus suevicus* (Wenz, 1919) or *Melanopsis impressa* (Krauss, 1852), exceed this limit. Similarly, the dreissenids are small-sized with ranges from 10–20 mm (Harzhauser and Mandic, 2008). The highest percentage of 56% is contributed by Hydrobiidae (22 species). These are represented by *Nematuerella* (Sandberger, 1874) (9), *Staliopsis* (Rzehak, 1893) (6) and *Hydrobia* (Hartmann, 1821) (2) and the endemic genus *Ctyrokia* (Schlickum, 1965) (5). All other families are represented by 5 or less species: Planorbidae (5), Neritidae (4), Melanopsidae (3), Viviparidae (2), Lymnaeidae (2), Bithyniidae (1). The most striking feature of the RLS gastropod fauna is the diversity of the hydrobiids *Ctyrokia* and *Staliopsis.* The endemicity on the species-level is high (77%).

4.1.2. Dinarid Lake System (DLS, ~17–15 Ma)

The entire gastropod fauna of the DLS is composed of 110 species and 28 genera (species/genera ratio = 3.9). The DLS literature is manifold, partly hard to get and a synopsis is completely missing up to now. The most important papers are: Brusina (1870, 1874, 1878, 1884b, 1881, 1896, 1897, 1902a), Neumayr (1869, 1880), Kittl (1895), Kochansky-Devidé and Slišković (1972), Jurišić-Polšak (1979), Jurišić-Polšak and Slišković (1988) and Olujić (1999).

Most of the species are small-sized (<1 cm); larger shells (1–3 cm) are confined to few species belonging to the genus *Melanopsis* and to the thiarid *Tinnyea* (up to 7 cm). Hydrobiidae (40) and Melanopsidae (34) are the dominant families, followed by the Planorbidae (13). Stenothyridae (6), Pyrgulidae (6), Neritidae (5), Lymnaeidae (3), Viviparidae (1), Bithyniidae (1) and Valvatidae (1) are subordinate as taxa but may be important constituents concerning individual numbers. The most eye-catching radiations are represented by the genera *Melanopsis* (29), *Prososthenia* (Neumayr, 1869) (18), and *Fossarulus* (Neumayr, 1869) (14), which develop extraordinary numbers of species. All other genera are recorded only with 5 to 1 species. Endemic DLS genera are the stenothyrid *Bania* (Brusina, 1896), the pyrgulid *Marticia* (Brusina, 1897) and the derived clivunellids *Clivunella* and *Delminiella*, which are endemic even on the family level. *Fossarulus* and *Dianella?* Gude, 1913, although recorded as rare elements from other Miocene lake systems as well, display a unique diversity in the DLS. The endemicity level is extremely high (98%).

4.1.3. Lake Skopje (LSK, ~15 Ma)

The gastropod fauna of Lake Skopje has been described in only few papers (Burgerstein, 1877; Pavlovic, 1903). Sixteen small-sized species from 5 genera are known (species/genera ratio = 3.2). These represent an unusual diversity of Pyrgulidae (7 species of *Dianella*) accompanied by Melanopsidae (3), Hydrobiidae (3), Neritidae (2) and Stenothyridae (1). There is no endemism on the genus level but a complete endemism on the species-level. The fauna is small-sized, ranging between 2 and 15 mm.

4.1.4. Paratethyan Sarmatian Lakes (PSL, 12.4–11.8 Ma)

The Sarmatian wetland systems were inhabited by 61 gastropod species attributed to 21 genera (species/genera ratio = 2.9) (Hörnes, 1856; Stoliczka, 1862; Jekelius, 1944; Boda, 1959; Harzhauser and Kowalke, 2002). The dominant families are the Hydrobiidae (15 species) and the Pyrgulidae (12) followed by the Neritidae (9), Valvatidae (8) and Stenothyridae (7). The rest is contributed by

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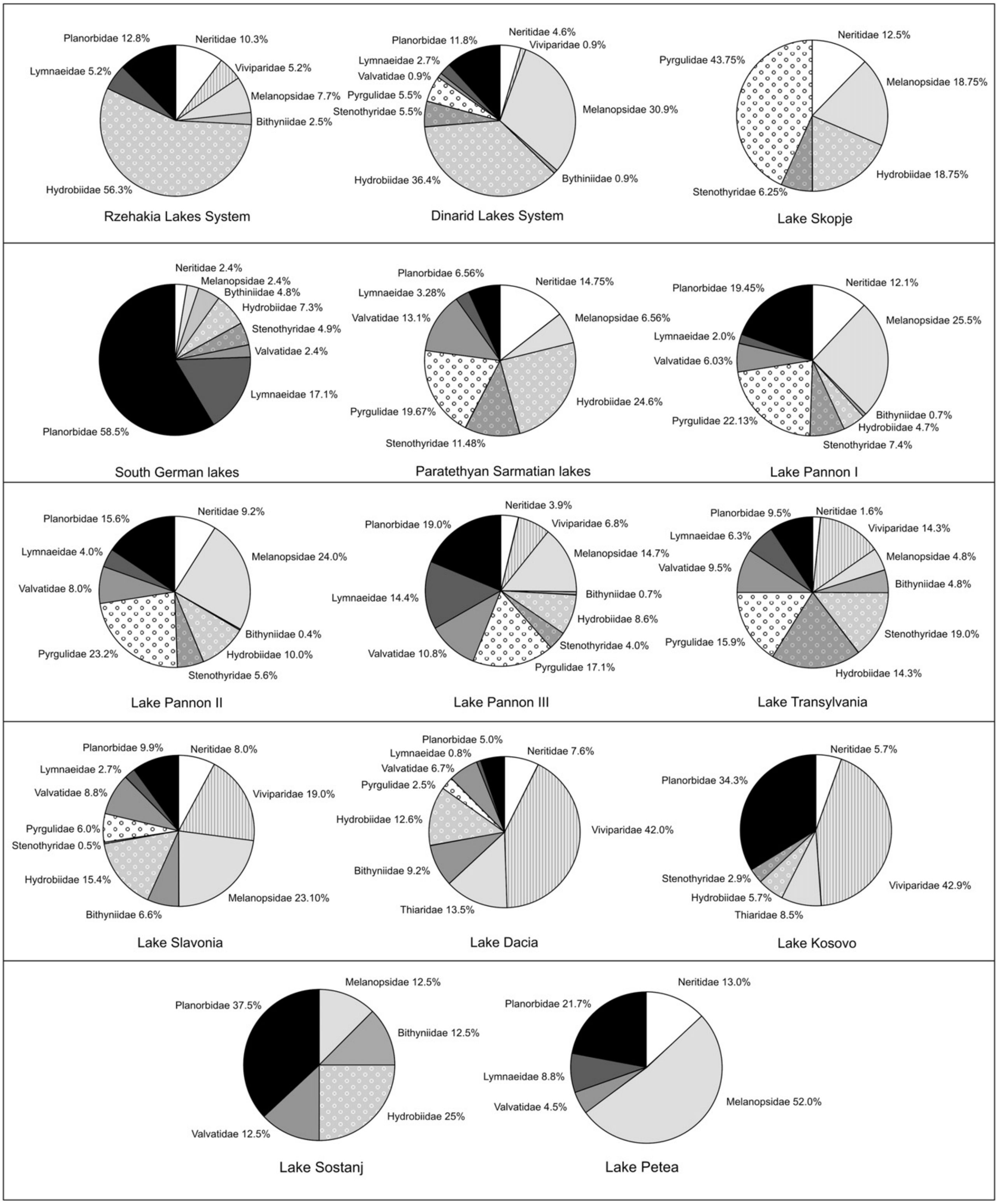

Fig. 4. Family-level analysis of the gastropod faunas (note that Pyrgulidae are treated as a family and that the thiarid *Tinnyea* is counted to the Melanopsidae). Percentages are based on species numbers and do not reflect dominance of single species in individual numbers. The corresponding species numbers are given in the text.

Melanopsidae (4), Planorbidae (4) and Lymnaeidae (2). Endemics on the genus level mainly involve stenothyrids (*Aluta* Jekelius, 1932, *Staja* Brusina, 1897) and the pyrgulids (*Socenia* Jekelius, 1944, *Baglivia* Brusina, 1892). All these genera persist into the Late Miocene and are constituents of the fauna of Lake Pannon. This faunistic relation to Lake Pannon is also present on the species-level

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and lowers the endemicity to 62%. The size of most gastropod species is rather small, ranging between 2 and 6 mm. Only the melanopsids and lymnaeids exceed the 2 cm limit.

Within the investigated time-interval, the circum-Paratethyan lakes gave rise to the first peaks of diversity within the valvatids and neritids of the European faunas.

4.1.5. South German lakes (incl. Lake Steinheim) (SGL, 14.3 to ~12 Ma)

The various small Middle Miocene lakes in southern Germany, including the famous Steinheim Lake, yield about 41 gastropod species of 18 genera (species/genera ratio = 2.3) (Klein, 1846, Gottschick, 1911, 1853, 1920; Gottschick and Wenz, 1916; Schlickum, 1976; Nützel and Bandel, 1993; Finger, 1997 and references therein).

The Steinheim Lake experienced an outstanding endemic evolution of small-sized planorbids (Hilgendorf, 1867; Nützel and Bandel, 1993). Thus, the diversity is completely dominated by the Planorbidae, which are recorded with at least 24 species. Of these, at least 17 species belong to *Gyraulus* (Charpentier, 1837). Lymnaeidae, with 7 species, are the second most species-rich group, whilst the Neritidae, Melanopsidae, Bithyniidae, Stenothyridae, Hydrobiidae and Valvatidae are represented by 1–3 species only. No endemism on the generic level has been observed so far for these lakes; a considerably endemism of c. 75% is represented by the species of the stenothyrids, hydrobiids and even more so within the planorbids. At least 10 species are also recorded from other freshwater systems such as the RLS and the PSL. Aside from *Tinnyea* and few lymnaeids, the fauna is small-sized (<5 mm).

4.1.6. Lake Pannon (LP, 11.6–5.8 Ma)

Aside from numerous monographs treating regional Lake Pannon assemblages, only Müller et al. (1999) provided a family-level synopsis of the mollusc fauna. The long history of Lake Pannon, spanning more than 6 Ma, and the large geographic extent of its deposits, is reflected in an enormous bibliography. In total, at least 497 species- and subspecies-level gastropods have been described from Lake Pannon. Only few of these species existed throughout the history of the lake. Therefore, the faunas of the various localities are united into three stratigraphic groups:

LP, Phase I: 11.6–10.0 Ma: 150 gastropod species of 34 genera are described from this early phase of Lake Pannon (species/genera ratio = 4.4) (Brusina; 1884a, 1896, 1897, 1902a; Lörenthey, 1894; Halaváts, 1903; Jekelius, 1944; Papp, 1951, 1953; 1985b, Sauerzopf, 1953).

The early gastropod fauna of Lake Pannon is dominated by Melanopsidae (38), Pyrgulidae (33) and Planorbidae (29). Neritidae (18), Stenothyridae (11), Valvatidae (9), Hydrobiidae (7), Lymnaeidae (3) and Bithyniidae (1) contribute to a lesser amount. The endemicity is high (86%), although some species appeared already in the Paratethyan Sarmatian lakes. The larger part of the fauna is small-sized, ranging from 2–8 mm; a size class between 10–30 mm is frequently represented within the lymnaeids, planorbids and melanopsids. Nevertheless, the early Lake Pannon witnesses also a tendency to gigantism by species of the *Melanopsis fossilis*-complex, which may attain a maximum size of 80 mm, and by *Tinnyea escheri vasarhelyii* (Hantken, 1887), which may exceed 100 mm in length.

LP, Phase II: 10.0–8.0 Ma: During the phase of the maximum extent of Lake Pannon, 254 species of 40 genera (species/genera ratio = 6.4) existed (Stoliczka, 1862; Fuchs, 1873; Brusina 1884a, 1892, 1897, 1902a; Handmann, 1882; Halaváts, 1887, 1892, 1903, 1910; Gorjanović-Kramberger, 1901; Lörenthey, 1902; Moos, 1944; Papp, 1951, 1985a,b; Sauerzopf, 1953; Bartha, 1956, 1953, 1959; Lupu, 1963; Lueger, 1979, 1980; Jiriček, 1985; Fordinál, 1997, 1999; Harzhauser et al., 2002).

The increase in species richness compared to LP I is largely due to the radiation of Melanopsidae (60), Pyrgulidae (58), Planorbidae (39), Hydrobiidae (25) and Valvatidae (20). A slight increase in numbers is also evident for the Neritidae (23), Stenothyridae (14) and Lymnaeidae (10); only the Bithyniidae (1) remain on a low level. The species-level endemicity (89%) is comparable to the early Lake Pannon fauna. Moreover, the size structures of the faunas are comparable.

LP, Phase III: 8.00–5.8 Ma: The late phase of Lake Pannon gave rise to a huge diversity of 284 gastropod species of 48 genera (species/genera ratio = 5.9) (Rolle, 1861; Fuchs, 1870a,b; 1873; Hoernes, 1875; Herbich and Neumayr, 1875; Lörenthey, 1893a,b,c, 1895; Brusina 1896, 1902a; Halaváts, 1887, 1897, 1892, 1904, 1915, 1923; Gorjanović-Kramberger, 1901; Soós, 1934; Moos, 1944; Strausz, 1951; Papp, 1951, 1985b; Sauerzopf, 1953; Bartha, 1954; Bartha and Soós, 1955; Gillet and Marinescu, 1971; Marinescu, 1973; Schlickum, 1978, 1953, 1979; Korpás-Hódi, 1983; Stevanović and Papp, 1985; Stevanović, 1941, 1978, 1985, 1990a,b,c; Basch, 1990; Müller and Szónoky, 1990; Fordinál, 1994, 1996, 1998; Szilaj et al., 1999; Harzhauser and Binder, 2004).

The maximum diversity of Lake Pannon III is contributed by Planorbidae (53), Pyrgulidae (48), Melanopsidae (41), Lymnaeidae (40) and Valvatidae (30). Hydrobiidae (24), Viviparidae (19), Neritidae (11), Stenothyridae (11) and Bithynidae (2) follow in decreasing numbers. Compared to LP I and LP II, an increase in species richness within the viviparids, planorbids and lymnaeids is evident, whilst the melanopsids and pyrgulids lose ground. The species-level endemicity remains high (83%). The bulk of the fauna is still represented by small-sized gastropods (2–8 mm), whereas the giant melanopsids have vanished. Large-sized taxa of up to 100 mm diameter are now represented by the limpet-like lymnaeid *Valenciennius* (Rousseau, 1842).

Although Lake Pannon is often referred to as the centre of *Melanopsis* evolution (Bandel, 2000; Geary et al., 2002), its most conspicuous radiations are found within the Pyrgulidae, with several endemic genera such as *Goniochilus* (Sandberger, 1875), *Lisinskia* (Brusina, 1897), *Gyromelania* (Wenz, 1939), *Scalimelania* (Wenz, 1939) and *Beogradica* (Pavlovic, 1903). *Microbeliscus* (Sandberger, 1875), a questionable pyrgulid with heterostrophic protoconch, is another endemism. Among the Lymnaeidae, the evolution of deep-water, limpet-like morphologies (*Provalenciennesia* Gorjanović-Kramberger, 1923, *Velutinopsis* Brusina, 1884a and *Valenciennius*) is noteworthy. Another endemism is represented by the succinid *Papyrotheca* (Brusina, 1893), which documents the rare adaptation of a terrestrial gastropod to aquatic environments.

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4.1.7. Lake Dacia (LD, ~5–3 Ma)

This initially brackish aquatic system gave rise to at least 119 gastropod species of 21 genera (species/genera ratio = 5.7) (Wenz, 1942; Hanganu, 1972; Hanganu and Papaianopol, 1982; Lubenescu and Zazuleac, 1985; Motas and Papaianopol, 1984; Papaianopol, 1995). The most prominent group is represented by the quickly radiating Viviparidae (50). Other important groups are the Melanopsidae (16), Hydrobiidae (15) and Bithyniidae (11). All other families are subordinate: Neritidae (9), Valvatidae (8), Planorbidae (6), Pyrgulidae (3), Lymnaeidae (1). Endemism is moderate on the species-level (60.5%) and absent on the generic level. Most species are small-sized (<10 mm); only the viviparids develop giant sized species of up to 55 mm in height. [Several elements with Lake Pannon affinities settled the Dacian Basin during the Late Miocene; herein, however, only the Pliocene assemblages are considered.]

4.1.8. Lake Transylvania (LT, ~4.5–3 Ma)

The fauna is mainly known from the paper of Jekelius (1932), who described 63 species of 17 genera from Lake Transylvania (species/genera ratio = 3.7). The fauna is manifold and not dominated by a certain gastropod family. Stenothyridae (12), Pyrgulidae (10), Viviparidae (9) and Hydrobiidae (9) are most species rich, followed by Valvatidae (6), Planorbidae (6), Lymnaeidae (4), Melanopsidae (3), Bithyniidae (3) and Neritidae (1). Endemicity is high (73%) within species but absent for genera. The size structure of the fauna ranges from 4–17 mm and is rather uniform. Larger taxa are represented solely by *Viviparus* (Montfort, 1810) (<40 mm).

4.1.9. Lake Slavonia (LS, ~4–3 Ma)

The fauna of that lake was studied mainly during the 19th century. In total, 183 gastropod species of 29 genera are described (species/genera ratio = 6.3) (Brusina, 1874, 1884b, 1878, 1896, 1902a; Fontannes, 1886; Herbich and Neumayr, 1875; Neumayr, 1869, 1897, 1880; Neumayr and Paul, 1875).

The fauna is dominated by Melanopsidae (42), Viviparidae (35) and Hydrobiidae (28). Aside from the rare Stenothyridae (1) and Lymnaeidae (5), all other groups contribute in comparable numbers: Planorbidae (18), Neritidae (15), Valvatidae (16), Bithyniidae (12). The fauna is generally small-sized (<10 mm) except for the partly large-sized viviparids, whose size may exceed 50 mm. The faunistic relation of Lake Slavonia to Lake Pannon and Lake Transylvania is responsible for a moderately high endemicity of 63%.

4.1.10. Lake Kosovo (LK, ~3–2 Ma)

Lake Kosovo harboured a poorly diverse gastropod fauna of 35 species of 9 genera (species/genera ratio = 4; Atanacković, 1959; Atanacković and Stefanović, 1990). Viviparidae dominate with 15 species, followed by the Planorbidae (12), of which 8 species belong to the endemic sinistral genus *Kosovia.* Other species are represented by Melanopsidae (3), Neritidae (2), Hydrobiidae (2) and Stenothyridae (1). The endemicity is very high (92%). Most of the taxa range from 10–15 mm in size. Larger species of up to 25 mm are represented only by *Viviparus*.

4.1.11. Lake Šoštanj (LSO, 2.5 Ma)

This highly endemic Late Pliocene lake fauna (endemicity 87%) was included because of its “Miocene” fair. Only 8 species are reported by Rolle (1860, 1861) and Brezigar et al. (1985). Planorbidae and Hydrobiidae are represented by 3 and 2 species, whilst Bithyniidae, Melanopsidae and Valvatidae are documented only by 1 species each. The fauna is small-sized (2–10 mm). Only *Melanopsis* and valvatids grow to 16 mm.

4.1.12. Lake Petea (P, 0.1–0 Ma)

Only few papers deal with the Pleistocene to Holocene thermal-spring lake fauna of Lake Petea. Brusina (1902b), Kormos (1905) and Pauca (1937) described 23 species of 9 genera (species/genera ratio = 2.6). The composition is uniquely dominated by Melanopsidae, whose 12 species contribute more than 50% to the total fauna. Planorbidae (5) are the second important gastropod group in Lake Petea, whilst Neritidae (3), Lymnaeidae (2) and Valvatidae (1) are subordinate in species numbers. Aside from the fully endemic melanopsid fauna, which raises the endemicity of the fauna to 60.8%, most taxa are frequently found in Pleistocene and Holocene freshwater systems of Europe. The fauna is very small (<8 mm) aside from the melanopsids (height up to 20 mm).

5. Discussion

5.1. Gamma diversity: size does matter but heritage is fine as well

Species diversity in the studied lake systems ranges from low (<30; LSK, P, LSO) and moderate (30–50; RLS, SGL, LK) to high (51–100; PSL, LT) and very high (>100; DLS, LPI–III, LD). Among the classical extant long-lived lakes, only Lake Baikal (147 species) falls into the last grouping and even the high diversity class is represented only by few examples (Lake Tanganyika, 68; Lake Ohrid, 72) [see Brown (1994), Seddon (2000) and Sitnikova (1994, 2006) for data on extant lakes]. The high species number is correlated with high generic diversities (Fig. 5). This tight correlation ($r^2 = 0.9$) is in contrast to the “gut-feeling” that the enormous diversities of Lake Pannon or of Lake Slavonia are maintained by few genera such as *Melanopsis* or *Viviparus*. The origin of the diversity is less easily explained. A simple correlation of diversity with lake size is evident on a very rough scale ($r^2 = 0.6$). Thus, small systems such as Lake Skopje and Lake Petea yield low diversities compared to the huge Lake Pannon or Lake Slavonia. The relation, however, fails in intermediate systems. Presumably large systems such as the Rzehakia Lake System or the Paratethyan Sarmatian Lakes do not fit the pattern because they have fewer taxa than expected based on size. Moreover, the highest diversity is found in Lake Pannon III, which is smaller than Lake Pannon II. A problem of this approach may be the complex geometry and sometimes poorly known extent of the lakes, which may result in inadequate size estimates.

A second ad hoc explanation for differences in γ-diversities is the age of the communities. A clear hint for this age/diversity relation is the high species richness of Lake Pannon III, which

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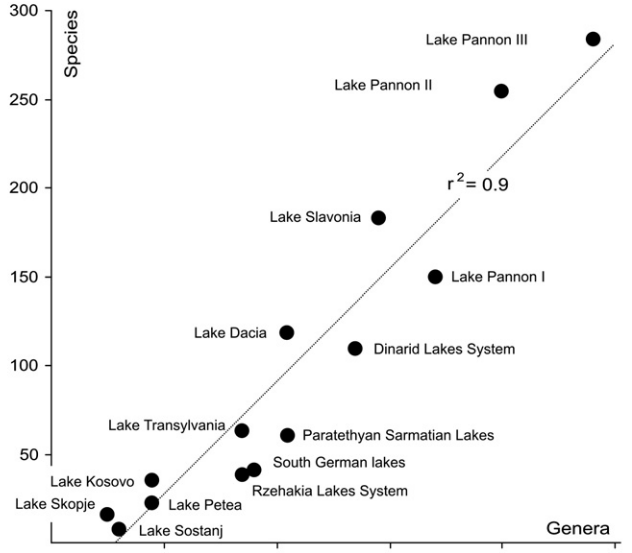

Fig. 5. A tight correlation between species-level γ-diversity and the number of genera exists for the analysed faunas. A similar correlation of diversity and lake size is evident for the endpoints but is poor for the middlefield.

experienced more than 4 Ma of endemic evolution during the climatically challenging Late Miocene. This interpretation, however, is again too naive to be applied to all systems. Most of the investigated lakes with moderate to high diversities existed between 0.5 and <2.0 Ma. Despite the comparable ranges, the observed diversities differ strongly. This discrepancy is solved when calculating the numbers of species occurring in more than one lake. Early and Middle Miocene lakes have high endemisms and share less than 10 species. Several of the involved genera such as *Orygoceras* (Brusina, 1882) or *Ctyrokia* (Schlickum, 1965) have their first appearances in these lakes and lack any known geological history. Starting with the Paratethyan Sarmatian Lakes, this pattern changes and each system is "vaccinated" by its ancestor (Fig. 2). About 20 species persist from the PSL into the faunas of the early Lake Pannon, contributing to an initially high diversity. Lake Pannon II inherited 97 species from its early stage and 88 species ultimately persist into the latest phase of Lake Pannon, which therefore displays the highest diversity observed in this study. The comparably short-lived Pliocene Lake Slavonia bears 28 species which are rooted in Lake Pannon. Again, the high diversity is thus a matter of heritage rather than of autochthonous endemic evolution. The coeval Lake Dacia, after the take-over by freshwater settings, becomes invaded by a mixture of Lake Pannon species (14) and newly evolved species from Lake Slavonia (40). Similarly, Lake Transylvania seems to have profited from the evolutionary laboratory of Lake Slavonia, with which it shares 14 species. Thus, the first phases of radiations and the fastest evolutionary pulses can be postulated to have occurred in the Early Miocene lakes of the Balkanids (DLS, LSK) and in the Middle Miocene Sarmatian Paratethyan Lakes. The diversities of the Late Miocene and Pliocene lakes systems, however, were supported by gastropod lineages that developed in precursor-lakes. A similar mechanism was also documented for the extant gastropod fauna of Lake Tanganyika (Wilson et al., 2003).

5.2. Phylogenetic lineages and generic inter-lake relations

Numerous widespread non-endemic genera occur in most of the analysed lake faunas. Aside from the extinct thiarid *Tinnyea*, most of these genera are extant. Some extinct genera, however, display a striking fossil history indicating important faunal exchange between certain lake systems. Large stratigraphic gaps between the occurrences underline the highly incomplete record of the Neogene freshwater systems. The Dinarid Lake System was the presumed starting point for the evolution of the de-coiled planorbid *Orygoceras* (Brusina, 1882), the hydrobiid *Emmericia* (Brusina, 1870) and the melanopsid *Melanoptychia* (Neumayr, 1880). Thereafter, they are apparently absent from younger systems such as the South German Lakes and the Paratethyan Lakes but also from more or less coeval systems such as Lake Skopje and Lake Serbia. They, however, reappear 5 Ma later in the Late Miocene as constituents of the Lake Pannon fauna. The DLS element *Fossarulus* displays an even larger stratigraphic gap and reappears in the Pliocene in Lake Kosovo. Similarly, the sinistral planorbid *Kosovia* appears in the early Middle Miocene Lake Serbia and re-enters the scene c. 10 Ma later in Lake Kosovo. In respect to the very characteristic conchological features, convergent evolution is unlikely to be responsible for these chronologically disjunct occurrences. Other Dinarid Lake genera such as the hydrobiid *Prososthenia* and the pyrgulids *Marticia* and *Dianella* have a more continuous record and invade the coeval Lake Skopje. Afterwards, *Prososthenia* steps into the Paratethyan Sarmatian lakes, enters Lake Pannon and persists in Lake Transylvania, Lake Slavonia and Lake Dacia. *Emmericia*, the pyrgulid *Micromelania*, the bithyniid *Tylopoma* and the highly derived lymnaeid *Valenciennius*, too, manage to settle Pliocene descendants of Lake Pannon. Of these, only *Emmericia* persisted into the Holocene and is still found in Central Europe.

5.3. Convergent evolution

Aside from those partly enigmatic generic inter-lake relations, striking convergences help explain the numerous stratigraphic and biogeographic misinterpretations. Harzhauser and Mandic (2008) have pinpointed several examples within the dreissenid bivalves which developed unrelated morpho-pairs in the Dinarid Lake System and Lake Pannon. Even more astonishing is the convergent evolution of large-sized, limpet-like, deep-water-dwelling gastropods in these lakes. In the Dinarid Lake system, *Clivunella* and *Delminiella* represent this type. The origin of these taxa is unknown. The lymnaeid protoconch and earliest teleoconch of *Delminiella* point to an affiliation with the Lymnaeoidea. *Clivunella* lacks these conchological features and its ancylid early shell may point to a relation to the Planorboidea. These derived gastropods settled the deep lake habitats but were unable to spread into any other Early and Middle Miocene lakes. During the Late Miocene,

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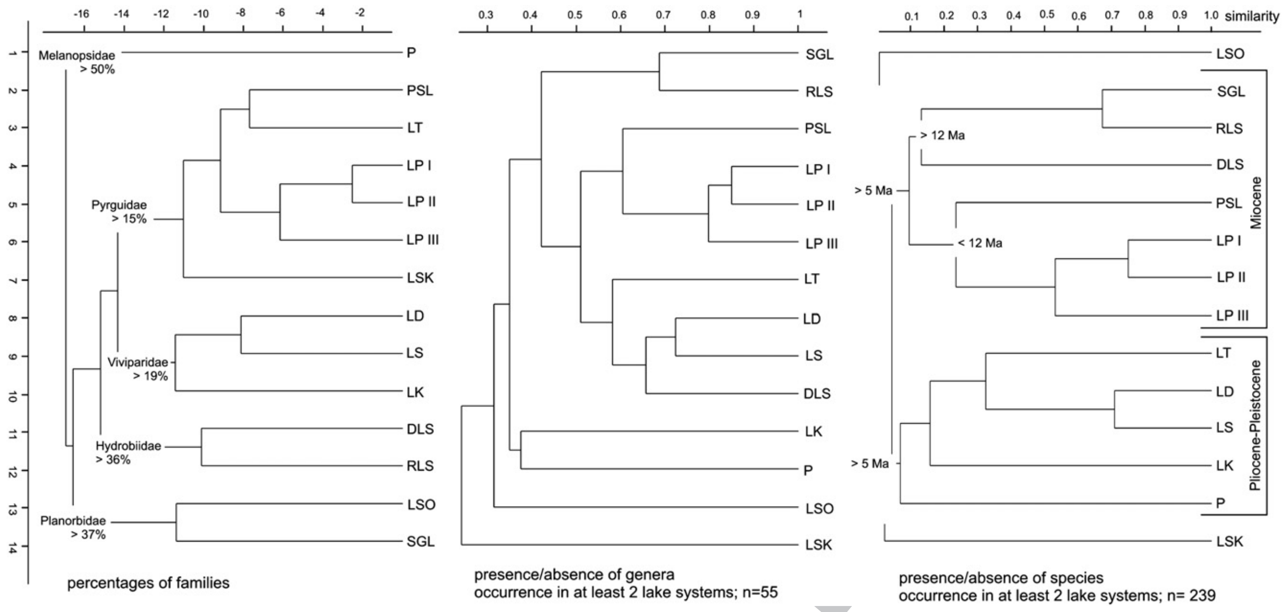

Fig. 6. Cluster analysis of the total gastropod faunas of each lake system for family-, genus- and species-level (see section 2 for methods). A biostratigraphic signal is evident on the species-level but becomes weak at higher hierarchies. The family-level analysis reveals rather a mixture of ecology and stratigraphy.

Lake Pannon saw a near-identical development, which led to the large-sized *Valenciennius*. In this case a good fossil record documents the evolution from inflated lymnaeids via various intermediate stages (e.g. *Provalenciennesia, Vetulinopsis*) to the depressed deep-water limpet *Valenciennius*. This gastropod managed to spread into coeval deposits of the Dacian Basin and survived until Pliocene times in Lake Slavonia.

5.4. Biostratigraphy versus ecology

An analysis of the individual lake faunas on various taxonomic levels (family, genus, species; Fig. 6) revealed quite deviating patterns. The species-level cluster analysis clearly traces the biostratigraphic signal. Aside from the outside branches (Lake Skopje, Lake Šoštanj), two main clusters separate the Miocene and the Pliocene–Pleistocene lake faunas. Moreover, the Miocene cluster falls apart into an Early to Middle Miocene cluster and a late Middle to Late Miocene cluster with a distinct Lake Pannon group. This biostratigraphic signal begins to become lost already in the genera-based analysis. Again, the Miocene cluster is evident and especially the (PSL(LPIII(LPII LPI)))-relation is strong due to the direct phylogenetic and geodynamic relationship of these systems. The Miocene DLS fauna, however, clusters within the Pliocene cluster due to the contribution of freshwater genera such as *Emmericia* and *Lithoglyphus.* On the family level, this biostratigraphic grouping becomes indistinct. Instead, five distinct clusters are evident. Lake Petea, with the unusually high amount of melanopsids, represents the outgroup. The remaining cluster separates into planorbid-dominated lakes such as the South German lakes and Lake Kosovo (>37% planorbids) and a second cluster which divided into 3 branches: hydrobiid-dominated lakes (DLS, RLS), pyrgulid-dominated lakes (PSL, LT, LP, LSK) and viviparid-dominated ones (LD, LS, LK). This stratigraphy-unrelated pattern reflects more ecological parameters. A simple salinity relation, however, is unlikely because the Pliocene freshwater systems Lake Transylvania and Lake Kosovo cluster together with the alkaline and saline systems such as Lake Pannon and the Paratethyan Sarmatian Lakes. Similarly, the hydrobiid-dominated branch unites the brackish Rzehakia Lake System with the freshwater Dinarid Lake System. Only the viviparid-dominated and the planorbid-dominated systems seem to correlate simply with freshwater settings. This is also indicated by the unionid-bivalve fauna of the viviparid lakes: Lake Slavonia and Lake Dacia. Despite the vanishing biostratigraphic signal a generalization is that the Early Miocene lake systems tend to be hydrobiid-dominated, the middle-Miocene and Late Miocene are pyrgulid-dominated and the Pliocene systems are usually viviparid-dominated.

5.5. Endemism of fossil and extant lake systems

Most extant faunas of ancient lakes display endemism rates between 40 and 80% at diversities between 24 and 147 species (Fig. 7). The observed endemisms of the herein-considered fossil lake faunas is generally comparable but tend to be even higher (60–98%). Neither the extant nor the fossil faunas show any correlation between species richness and endemism. Low-diversity faunas such as in Lake Skopje and Lake Kosovo display equally high endemism rates as the extremely diverse Lake Pannon and the Dinarid Lake System. The generally higher endemism in the fossil systems is probably related to an incomplete record of coeval lake faunas (e.g. Lake Skopje, Lake Kosovo). An exception seems to be Lake Pannon, whose extraordinary endemism might rather be related to adaptations

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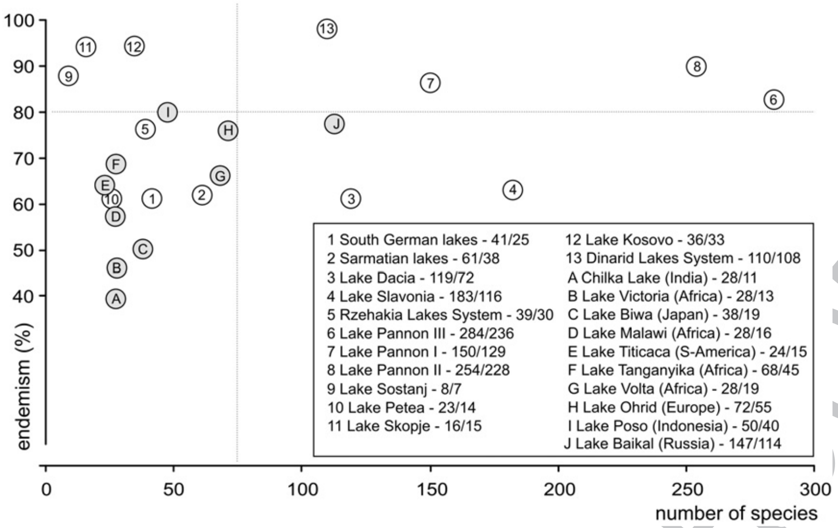

Fig. 7. Endemism versus γ-diversity for fossil and extant ancient lakes [data for modern faunas from Brown (1994), Seddon (2000) and Sitnikova (1994, 2006)]. The endemism and species-richness of Lake Pannon, Lake Slavonia and the Dinarid Lake System are outstanding. The generally higher endemism in the fossil systems at comparable species numbers might hint at a still incomplete record of Neogene freshwater systems.

of the fauna to an aberrant water chemistry coupled with a geological longevity.

6. Conclusions

Many papers dealing with extant mollusc faunas of Eurasian aquatic systems refer to Lake Pannon when explaining extant biogeographic distributions and phylogenetic relations (e.g. Grigorovich et al., 2003; Bunje and Lindberg, 2007). Our dataset, however, points to a much more complex history of the faunas reaching back at least to the Early Miocene. High endemisms and low inter-lake relations of the Early and early Middle Miocene lake systems suggest that these experienced the first autochthonous evolutionary pulses. Many genera display their FADs in these systems (e.g. *Marticia, Kosovia, Orygoceras, Pyrgula, Dianella, Emmericia*). This pattern changed at the Middle/Late Miocene boundary when Lake Pannon inherited numerous species which evolved prior in the Sarmatian Paratethyan lakes. On the generic level, parts of the Lake Pannon fauna can be traced back even to the Early Miocene faunas of the Dinarid Lake System. The combined effect of heritage and new radiations in a geochemically unique aquatic system allowed Lake Pannon to accumulate an enormous diversity of 497 gastropod species. Lake Pannon itself acted as a stepping stone for species and genera which settled the descendant freshwater systems such as Lake Slavonia, Lake Dacia and Lake Transylvania. Generic endemism thus decreased during the Pliocene.

Generally, the lake faunas may be divided into pyrgulid-, hydrobiid-, viviparid- and planorbid-dominated lakes. The reason for this predominance of certain taxa is not fully understood. A simple relation to water chemistry is unlikely in respect to the similarities between the faunas of the slightly brackish and alkaline Lake Pannon (Harzhauser et al., 2007) and those of the freshwater fauna of the Dinarid Lake System.

A weak stratigraphic signal indicates that Early Miocene freshwater systems are hydrobiid dominated; Middle and Late Miocene systems tend to be pyrgulid dominated, whilst Pliocene ones are often viviparid dominated. A climatic control is not the main force behind the pattern because the temperate RLS faunas are hydrobiid dominated as are the DLS faunas which developed during the beginning Middle Miocene climatic optimum. At least the switch from pyrgulid- to viviparid-dominated lakes in the Pliocene seems to be mainly explained by the pure freshwater settings that replaced the slightly brackish and alkaline Lake Pannon environments.

The Neogene lake systems represent a unique laboratory of evolution. Examples of parallel evolution and the phenomenon of iterative morphologies make the analysis of ancient lake faunas a tantalizing endeavour. Repetitive morphologies of related lineages have been documented to occur in Lake Pannon melanopsids (Geary et al., 2002). Even more interesting are such iterative developments of unrelated taxa as shown for DLS and LP dreissenids (Harzhauser and Mandic, 2008). The most striking examples of such “morpho-pairs” is the DLS taxa *Delminiella* and *Clivunella* and the *Valenciennius*-lineage in Lake Pannon. The planorbid *Clivunella* and the lymnaeid *Delminiella* are two endemic limpet-like shells which, deriving from nearshore ancestors, adapted synchronously and independently to deep-water settings of the Dinarid Lake System. About 5 Ma later, the lymnaeids of Lake Pannon started to explore the deep-water habitats of that lake, resulting in the limpet-like *Valenciennius.* Such morpho-pairs have been the reason for frequent stratigraphic and biogeographic misinterpretations in the literature. Despite the huge dataset, comprising about 1184 gastropod taxa from 119 localities, the Neogene freshwater record is still poor. This fragmentary fossil record is underlined by disjunct stratigraphic occurrences of highly derived genera such as *Orygoceras* or *Kosovia* with gaps of 5–10 Ma.

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