
2. Neogene dreissenids in Central Europe: evolutionary shifts and diversity changes

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Abstract

Neogene dreissenid evolution in central and south-eastern Europe is a prime example for the impact of geodynamics on biotic radiations. Two former paleogeographic entities provided the habitat for a conspicuous development at ~30-5 my. One of these aquatic systems was the Oligocene to Miocene Paratethys Sea and its late Miocene to Pliocene descendent Lake Pannon. The second was the Oligocene to middle Miocene Dinaride lakes. Both of these partly coeval waterbodies harbored radiations of dreissenid bivalves with several cases of morphological parallel evolution. The dreissenid faunas of each biogeographic unit display phases of high morphological disparity with a time offset of at least 5 my.

The ecological niches settled by dreissenid bivalves and the life-strategies they developed during that time are unique for this group, which today is typically comprised of byssate filter-feeding epibionts. Like their modern relatives, the Miocene dreissenids conquered both freshwater and brackish habitats but always avoided normal marine environments. Beyond a large number of "ordinary" byssate epibionts, the Miocene and Pliocene dreissenids also developed lineages adapted to soft-bottom habitats. One group within *Mytilopsis* developed sediment-reclining strategies, whereby the dreissenomyid flock even managed to penetrate the sediment by active burrowing. Filter feeding was probably the prevailing feeding strategy for *Mytilopsis*, *Dreissena* and the dreissenomyids throughout the considered interval. *Congerina* probably utilized chemosymbiosis as an additional energy source. In total, we have distilled the stratigraphic and geographic data of about 200 Neogene dreissenid taxa (species and subspecies) from the highly complex literature to show evolutionary trends and important changes in diversity patterns.

Introduction

Eurasian Neogene dreissenids were studied early on (e.g. Partsch, 1836) due to their conspicuous morphologies and clear endemic evolution and radiation (e.g. Andrusov, 1897). Since then, an enormous mass of literature has dealt with systematic, biostratigraphic and phylogenetic aspects of the group (see Babak, 1983, Nuttall, 1990 and Schultz, 2005 for reviews and key references). Herein, we largely follow the systematic treatment in Nuttall (1990).

Within central and south-eastern Europe the dreissenids developed chiefly in three aquatic systems: the Paratethys Sea and its descendant Lake Pannon, as well as the Dinaride Lake system (Fig. 1). This chapter summarizes

the published dreissenid taxa of these areas and discusses general ecological and evolutionary trends derived from that data-set. These trends are strongly influenced by the geodynamic development and increasing continentalisation of Europe during the Neogene.

Paratethys Sea and Lake Pannon

The Paratethys Sea was a northern satellite sea of the Western Tethys (= Proto-Mediterranean) (Fig. 1A, C). It arose during the latest Eocene and early Oligocene due to the rising Alpine island chains, which acted as geographic barriers (Rögl, 1998). During its maximum extent, the Paratethys Sea spread from the Rhône Basin in France towards Inner Asia (Popov et al., 2004). Subsequently, the newly formed Paratethys was partitioned into two large

geotectonic units which underwent different environmental histories due to differently timed geotectonic developments and global sea-level fluctuations that controlled marine and non-marine phases (Popov et al., 2004). The smaller western part is termed the Western and Central Paratethys. Marine conditions of the Central Paratethys prevailed from the Oligocene to the transition from the middle to the late Miocene. A short-term interruption by a brackish to freshwater phase due to disrupted marine gateways occurred in the early Miocene Ottnangian age (~18 my). This episode is reflected by a first radiation event within the Paratethyan dreissenids. During the late middle Miocene Sarmatian age (~12.7 my), a second nearly total isolation of the Paratethys took place. Again, this coincided with a peak in dreissenid diversity, although hypersaline conditions apparently dominated the Sarmatian sea-water (Piller and Harzhauser, 2005).

Finally, at the beginning of the late Miocene, the Central Paratethys Sea was replaced by the brackish Lake Pannon

(Fig. 1D). Lake Pannon became restricted to the Pannonian Basin System (Magyar et al., 1999a), whereas the adjacent Dacian Basin became incorporated into the geotectonic frame of the Eastern Paratethys. The establishment of the long-lived Lake Pannon at 11.6 my was the foundation for the biggest peak in the history of dreissenid evolution.

The Dinaride Lakes:

Seemingly independently from the Paratethyan faunas, a second pool of dreissenid evolution formed in the Miocene Dinaride Lake System (DLS; Fig. 1B). This system formed during the late Oligocene and Miocene in today NW-SE trending intramountain basins parallel to the slowly rising Dinaride mountain chains (Pavelić, 2002). Extensional tectonics generated enhanced subsidence of elongated depressions during the early to late Miocene. The comparatively low terrigenous input supported the diversification of lacustrine environments, including both deep- and shallow-water habitats. This habitat

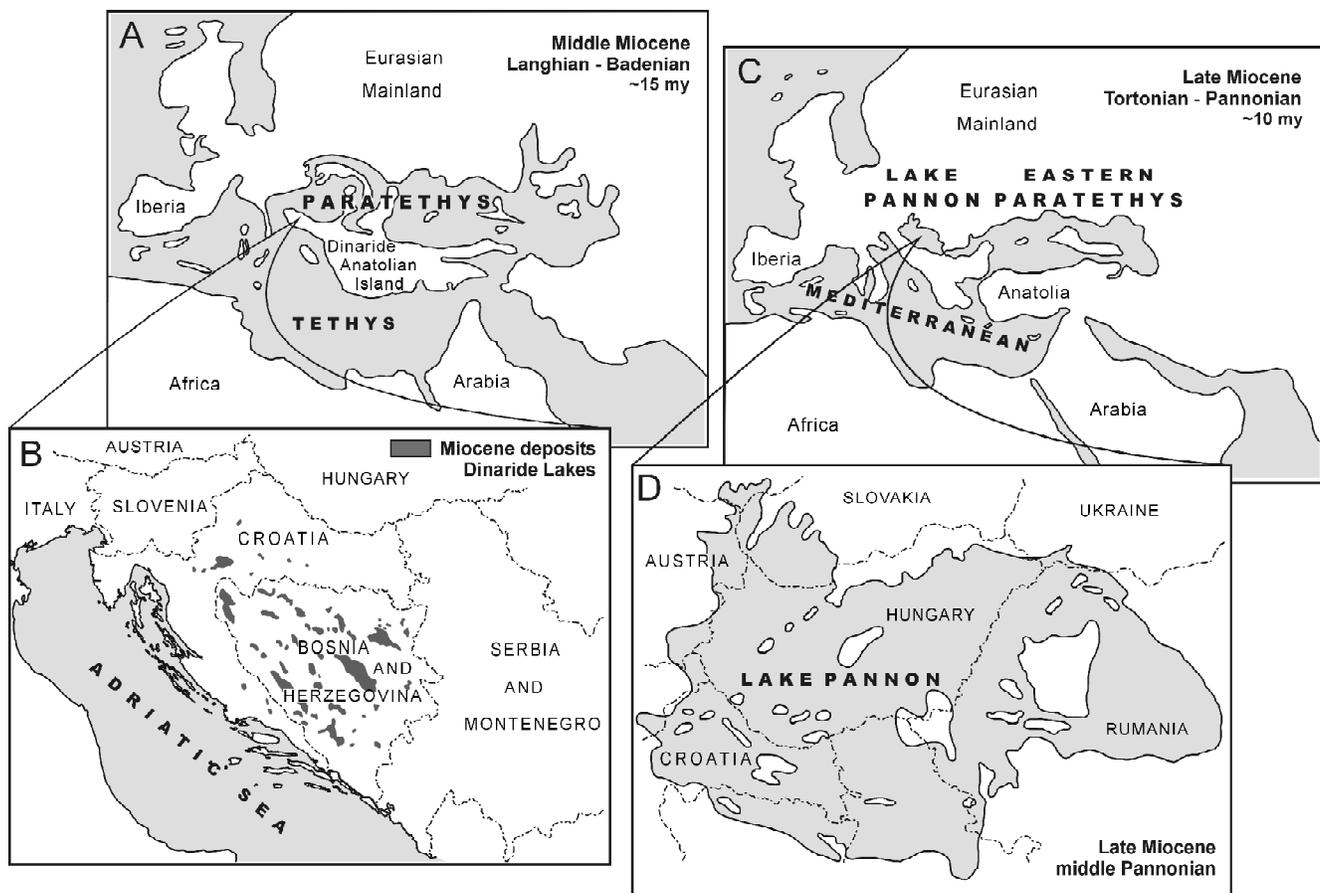


Figure 1. Eurasian paleogeography during the middle Miocene (A) and late Miocene (C) (modified after Rögl, 1998; Popov et al., 2004). Insert B shows the modern distribution of Miocene sedimentary remnants of the Dinaride Lake System (from Kochansky-Devidé and Slišković, 1978 and Pavelić, 2002). Insert D indicates the extension of Lake Pannon during the middle Pannonian (after Magyar et al., 1999a).

Table 1. Literature-based compilation of dreissenid taxa of the Dinaride Lake System (DLS), the European Paratethys Sea (PS), Lake Pannon (LP) and the Dacian Basin (DB). Occurrences in the Euxinic Basin (EB) are partly included. Some of the subspecies may turn out to represent only morphotypes. References are provided in the text.

Taxon	Distribution	Egerian	Eggenburgian	Otrnangian	Karpatian	Badenian	Sarmatian	E Pannonian	M Pannonian	lower Late Pannonian	upper L. Pannon./Pontian	E Dacian	L Dacian	late Late Pannonian (LP)	Pontian (DB)	Meotian (DB)
Genus <i>Mytilopsis</i> Conrad, 1858																
<i>M. aletici</i> (Kochansky-Devidé & Sliškovic, 1978)	DLS					1	1									
<i>M. amygdaloides</i> (Dunker, 1848)	PS			1												
<i>M. cf. amygdaloides</i> (sensu Kochansky-D. & Sliškovic, 1978)	DLS			1	1	1										
<i>M. andrussowi</i> (Rzehak, 1893)	PS			1												
<i>M. antecroatica</i> (Katzer, 1921) [syn. <i>kucici</i> (Brusina)?]	DLS			1	1	1										
<i>M. balatonica balatonica</i> (Partsch, 1836)	LP							1	1	1	1			1		
<i>M. balatonica cavernosa</i> (Brusina, 1902)	LP										1			1		
<i>M. balatonica chilotrema</i> (Brusina, 1892)	LP										1			1		
<i>M. balatonica labiata</i> (Andrusov, 1897)	LP								1	1	1			1		
<i>M. balatonica praecisa</i> (Brusina, 1902)	LP										1			1		
<i>M. balatonica protracta</i> (Brusina, 1902)	LP								1	1	1			1		
<i>M. balatonica sharpei</i> (Brusina, 1902)	LP										1			1		
<i>M. baschi</i> (Vrsaljko & Sremac, 1999)	LP							1								
<i>M. basteroti</i> (Deshayes, 1836)	PS	1	1	1	1	1										
<i>M. bella</i> (Papaianopol, 1992)	DB												1			
<i>M. beregovi</i> (Kojumdžieva, 1968)	PS						1									
<i>M. boeckhi</i> (Wenz, 1931)	DLS			1	1											
<i>M. bosniaca</i> (Katzer, 1913)	DLS			1	1	1										
<i>M. budmani</i> (Andrusov, 1897)	LP										1			1		
<i>M. buria</i> (Papaianopol, 1992)	DB												1			
<i>M. buzoiensis</i> (Papaianopol, 1992)	DB												1			
<i>M. carasi</i> (Jekelius, 1944)	PS						1									
<i>M. caucasica</i> (Seninsky, 1905)	DB												1			
<i>M. clavaeformis</i> (Krauss, 1852)	PS			1												
<i>M. cor</i> (Kochansky-Devidé & Sliškovic, 1978)	DLS				1	1										
<i>M. cricovens</i> (Papaianopol, 1992)	DB												1			
<i>M. croatica</i> (Brusina, 1874)	LP										1			1		
<i>M. cumanica</i> (Papaianopol, 1992)	DB												1			
<i>M. cvitanovici</i> (Brusina, 1907)	DLS			1	1	1										
<i>M. czjzeki czjzeki</i> (Hörnnes, 1867)	LP							1	1							
<i>M. czjzeki alata</i> (Gillet & Marinescu, 1971)	LP										1			1		
<i>M. dacica</i> (Papaianopol, 1992)	DB												1			
<i>M. dactylus</i> (Brusina)	LP										1			1		
<i>M. dalmatica</i> (Brusina, 1874)	DLS			1	1	1										
<i>M. deserta</i> (Papaianopol, 1992)	DB											1				
<i>M. digitifera</i> (Andrusov, 1897)	LP, DB, EB								1	1	1			1	1	
<i>M. doderleini</i> (Brusina, 1892)	LP							1	1							
<i>M. dravarensis</i> (Toula, 1913)	DLS			1	1	1	1									
<i>M. dreissenopsis</i> (Papaianopol, 1992)	DB												1			
<i>M. drziewi</i> (Brusina, 1902)	LP								1							

Taxon	Distribution	Egerian	Eggenburgian	Otrtrngian	Karpatian	Badenian	Sarmatian	E Pannonian	M Pannonian	lower Late Pannonian	upper L. Pannon./Pontian	E Dacian	L Dacian	late Late Pannonian (LP)	Pontian (DB)	Meotian (DB)
<i>M. scaphula</i> (Andrusov, 1897)	DLS			1	1	1										
<i>M. schuetti</i> (Schlickum, 1964)	PS			1												
<i>M. scrobiculata scrobiculata</i> (Lorenthey, 1902)	LP							1	1							
<i>M. scrobiculata carinifera</i> (Lorenthey, 1902)	LP							1								
<i>M. similis</i> (Papaianopol, 1992)	DB												1			
<i>M. simulans simulans</i> (Brusina, 1893)	LP										1			1		
<i>M. simulans batuti</i> (Brusina, 1902)	LP										1			1		
<i>M. simulans emiliae</i> (Brusina, 1902)	LP										1			1		
<i>M. simulans mutabilis</i> (Brusina, 1902)	LP										1			1		
<i>M. simulans turgida</i> (Brusina, 1897)	LP										1			1		
<i>M. slavonica</i> (Andrusov, 1893)	LP							1								
<i>M. sliškovici</i> (Kochansky-Devidé & Sliškovic, 1978)	DLS			1	1	1	1									
<i>M. soceni</i> (Jekelius, 1944)	PS						1									
<i>M. socialis socialis</i> (Kochansky-Devidé & Sliškovic, 1978)	DLS			1	1											
<i>M. socialis pennata</i> (Kochansky-Devidé & Sliškovic, 1978)	DLS			1	1											
<i>M. soklici</i> (Kochansky-Devidé & Sliškovic, 1978)	DLS			1	1											
<i>M. spathulata spathulata</i> (Partsch, 1836)	LP								1							
<i>M. spathulata preabalatonica</i> (Sauerzopf, 1952)	LP								1							
<i>M. spathulata kosanini</i> (Pavlovic, 1927)	LP								1	1	1			1		
<i>M. subcarinata</i> (Deshayes, 1838)	DB, EB										1	1			1	
<i>M. subclaviformis</i> (Rzehak, 1893)	PS			1												
<i>M. subdigitifera</i> Stevanovic, 1978	LP								1							
<i>M. submirabilis</i> (Tselidze)	DB												1			
<i>M. stojcicae</i> (Kochansky-Devidé & Sliškovic, 1978)	DLS				1	1										
<i>M. taciturna</i> (Papaianopol, 1992)	DB												1			
<i>M. tinnyeana</i> (Lorenthey, 1902)	LP								1							
<i>M. triangularis</i> (Partsch, 1836)	LP										1			1		
<i>M. trnski</i> (Brusina, 1902)	LP									1	1			1		
<i>M. turgidopsis</i> (Andrusov, 1929)	DB												1			
<i>M. turislavica turislavica</i> (Jekelius, 1944)	LP							1								
<i>M. turislavica turislavica</i> (Sauerzopf, 1952)	LP							1	1							
<i>M. unguicaprae</i> (Münster in Goldfuss, 1837)	LP								1	1	1			1		
<i>M. valahica</i> (Papaianopol, 1992)	DB												1			
<i>M. venusta</i> (Kochansky-Devidé & Sliškovic, 1978)	DLS			1	1											
<i>M. voltica</i> (Papaianopol, 1992)	DB											1				
<i>M. volucris</i> (Kochansky-Devidé & Sliškovic, 1978)	DLS				1	1										
<i>M. vuki</i> (Brusina, 1897)	LP									1	1			1		
<i>M. zagradiensis</i> (Brusina, 1884)	LP, DB								1	1	1			1	1	
<i>M. zahalkai</i> (Spalek, 1937)	LP								1	1						
<i>M. zosi</i> (Andrusov, 1897)	DLS			1	1											
<i>M. zujovici</i> (Andrusov, 1897)	LP								1							
Genus <i>Congerina</i> Partsch, 1836																
<i>Congerina banatica</i> Hörnes, 1875	LP								1							
<i>Congerina brandenburgi</i> Brusina, 1902	LP									1	1			1		

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<i>Congerina brkici</i> Basch, 1992	LP										1			1		
<i>Congerina dalmatica</i> sensu Sauerzopf, 1952	LP							1								
<i>Congerina dubocaensis</i> Stevanovic, 1951	LP										1			1		
<i>Congerina ghergutai</i> Jekelius, 1944	LP								1							
<i>Congerina hemiptycha</i> Brusina, 1902	LP								1							
<i>Congerina markovici</i> (Brusina, 1884)	LP, DB										1			1	1	
<i>Congerina pancici</i> Pavlovic, 1927	LP								1							
<i>Congerina partschi partschi</i> Czjzek, 1849	LP							1	1							
<i>Congerina partschi carinacurvata</i> Papp, 1953	LP							1	1							
<i>Congerina partschi firmocarinata</i> Papp, 1953	LP								1							
<i>Congerina partschi globosatesta</i> Papp, 1953	LP								1							
<i>Congerina partschi leobersdorfensis</i> Papp, 1953	LP							1								
<i>Congerina partschi subpannonica</i> Sauerzopf, 1952	LP							1								
<i>Congerina praerhomboides</i> Stevanovic, 1951	LP									1						
<i>Congerina rhomboidea rhomboidea</i> Hörnes, 1870	LP, DB, EB										1			1	1	
<i>Congerina rhomboidea alata</i> Brusina, 1874	LP										1			1		
<i>Congerina rhomboidea dilatata</i> Stevanovic, 1961	LP										1			1		
<i>Congerina rhomboidea rumana</i> Stefanescu, 1896	LP, EB							1								
<i>Congerina subglobosa subglobosa</i> Partsch, 1836	LP								1							
<i>Congerina subglobosa gigantea</i> Pavlovic, 1927	LP								1							
<i>Congerina subglobosa sopronensis</i> Vitális, 1934	LP							1	1							
<i>Congerina subglobosa longitesta</i> Papp, 1953	LP								1							
<i>Congerina susedana</i> (Vrsaljko & Sremac, 1999)	LP								1							
<i>Congerina vugroveci</i> Sremac, 1981	LP								1							
<i>Congerina zsigmondyi</i> Halaváts, 1882	LP								1							
Genus Dreissena van Beneden, 1835																
<i>Dreissena accurtii</i> (Andrusov, 1893)	LP							1								
<i>Dreissena anisoconcha</i> (Andrusov, 1893)	LP, DB									1	1			1	1	
<i>Dreissena auricularis auricularis</i> (Fuchs, 1870)	LP, DB										1			1	1	
<i>Dreissena auricularis gibberula</i> (Andrusov, 1897)	LP									1	1			1		
<i>Dreissena auricularis simplex</i> (Fuchs, 1870)	LP										1			1		
<i>Dreissena baraganica</i> (Andrusov, 1897)	DB												1			
<i>Dreissena benedeni</i> (Andrusov, 1897)	DB												1			
<i>Dreissena berbestiensis</i> Fontannes, 1886	DB											1				
<i>Dreissena bipartita</i> (Andrusov, 1897)	LP										1			1		
<i>Dreissena cristellata</i> (Roth, 1881)	LP											1				
<i>Dreissena cuculata</i> Brusina, 1902	LP										1			1		
? <i>Dreissena cymbula</i> (Andrusov, 1893)	DLS						?	?								
<i>Dreissena dobrei</i> Brusina, 1902	LP										1			1		
<i>Dreissena elongata</i> Jekelius, 1932	LP											1				
<i>Dreissena exigua</i> Roth, 1881	LP											1				
<i>Dreissena matavulji</i> Brusina, 1902	LP										1			1		
<i>Dreissena muensteri</i> (Brusina, 1893)	LP											1				
<i>Dreissena obliqua</i> Seninski, 1905	DB												1			

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<i>Dreissena polymorpha</i> (Pallas, 1771)	LP, DB										1			1	1	
<i>Dreissena rossii</i> (Brusina, 1893)	LP										1			1		
<i>Dreissena sabbae</i> (Brusina, 1892)	LP										1			1		
<i>Dreissena semendriensis</i> (Stevanovic, 1951)	LP										1			1		
<i>Dreissena serbica serbica</i> Brusina, 1894	DB										1				1	
<i>Dreissena serbica oresacensis</i> (Stevanovic, 1951)	LP										1			1		
<i>Dreissena superfoetata</i> Brusina, 1884	LP									1	1			1		
<i>Dreissena tenuissima</i> Sinzov	LP, EB									1	1			1	1	
<i>Dreissena valahica</i> Papaianopol, 1992	DB												1			
<i>D. (Pontodreissena) rostriformis</i> (Deshayes, 1838)	LP, DB, EB									1	1			1	1	
<i>D. (Modiolodreissena) simplex</i> (Barbot, 1875)	LP, DB, EB									1	1			1	1	
<i>D. (Modiolodreissena) rimestiensis</i> Fontannes, 1886	LP, DB, EB										1	1		1	1	
<i>D. (Modiolodreissena) rumana</i> Sabba, 1896	DB, EB											1				
Genus <i>Dreissenomya</i> Fuchs, 1870																
<i>Dreissenomya croatica</i> (Brusina, 1884)	LP										1			1		
<i>Dreissenomya intermedia</i> (Fuchs, 1873)	LP								1	1	1			1		
<i>Dreissenomya nevenskae</i> Roška 1973	DB															1
<i>Dreissenomya papyracea</i> Stevanovic, 1978	DB										1				1	
<i>Dreissenomya rumana</i> (Wenz, 1942)	DB										1				1	1
<i>Dreissenomya schroeckingeri</i> (Fuchs, 1870)	LP										1			1		
<i>Dreissenomya subrotundata</i> (Pana, 1966)	DB															1
<i>Dreissenomya unionides</i> Fuchs, 1870	LP, DB										1			1		1
<i>Dreissenomya zujovici</i> Brusina, 1902	LP								1	1	1			1		
<i>Dreissenomya lithodomiformis</i> Pavlovic, 1927	LP								1							
Genus <i>Sinucongeria</i> Lörenthey, 1894																
<i>Sinucongeria arcuata</i> (Fuchs, 1870)	LP, DB									1	1			1	1	
<i>Sinucongeria aperta</i> (Deshayes, 1838)	LP, DB, EB										1	1	1	1	1	1
<i>Sinucongeria brandenburgi</i> (Drevermann, 1905)	LP										1			1		
<i>Sinucongeria dactyla</i> (Brusina, 1891)	LP										1			1		
<i>Sinucongeria lata</i> (Drevermann, 1905)	LP										1			1		
<i>Sinucongeria primiformis</i> (Papp, 1949)	LP								1							
<i>Sinucongeria semilunata</i> (Pana, 1966)	DB										1				1	1

diversification sparked the spectacular Miocene radiation of the benthic fauna. This evolutionary impulse began more than 10 my prior to the radiation in Lake Pannon (Magyar et al., 1999a; Müller et al., 1999). Geographically, the deposits of the DLS cover parts of Croatia, Bosnia, Herzegovina, Serbia and Montenegro. Thus, the fauna of the DLS formed a biogeographic barrier between the Tethyan realm in the south and the Paratethyan assemblages in the north. Some mollusc genera, such as the de-coiled elongated planorbid *Orygoceras*, first

appeared in the early Miocene of the Dinaride lakes and persisted into the late Miocene to re-appear in Lake Pannon (Harzhauser et al., 2002a). No such convincing lineages can be demonstrated within the dreissenids. Instead, evolution yielded morphologies highly reminiscent of the much younger Lake Pannon faunas. The same phenomenon is expressed within the gastropod genus *Melanopsis*, which tend to iterative development of morphologies even within Lake Pannon (Geary et al., 2002).

The final disintegration of the DLS occurred during the

late Miocene, apparently coinciding with the decline of Lake Pannon and the tectonic inversion of the Pannonian Basin System.

Material and database

This study presents a set of presence-data for the early Miocene to early Pliocene dreissenid taxa of the Dinaride Lake System, the European (Western and Central) Paratethys, and Lake Pannon and adjacent aquatic systems such as that of the Dacian Basin. These data are compiled from own observations and a broad range of literature: a. European Paratethys: Egerian from Harzhauser and Mandic (2001); Eggenburgian faunas from Steininger et al. (1971); Ottnangian faunas from Steininger (1973); Karpatian and Badenian faunas from Schultz (2005); Sarmatian faunas from Jekelius (1944), Kojumdgieva (1969), and Papp (1974); b. Lake Pannon and Dacian Basin: Pannonian faunas from Lörenthey (1902), Jekelius (1944), Papp (1985), and Schultz (2005); late Pannonian/Pontian faunas from Basch (1990), Basch and Žagar-Sakač (1992), Gillet and Marinescu (1971), Müller (1990), and Stevanović (1990); Dacian faunas from Jekelius (1932) and Papaianopol (1995). Additional data from Marinescu (1977) and Brusina (1902); c. Dinaride Lake System: early to late Miocene from Brusina (1902), Kochansky-Devidé (1978) and Kochansky-Devidé and Slišković (1978, 1980).

Complete taxonomic data-sets are provided in Table 1. Not all of these species-level taxa are revised, and over-splitting of morphologically variable species might have caused some “over-completeness”. New systematic studies will no doubt refine our dataset, but the general trends and patterns discussed herein appear to be fairly robust.

The calibration and correlation of the chronostratigraphic and geochronologic frame follows Gradstein et al. (2004) and Popov et al. (2004). In the late Miocene, four additional stratigraphic subunits are differentiated for Lake Pannon. The early Pannonian corresponds with the zones A-C of Papp et al. (1985), whereas the middle Pannonian correlates with the zones D-E. Their calibration to the standard scale follows Harzhauser et al. (2004). Two stratigraphic units of the late Pannonian correspond to Lake Pannon’s Lower and Upper Pontian sensu Stevanović et al. (1990). Their boundary coincided with the boundary of the *Congeria praerhomboides* - and *C. rhomboides* - Zones and is calibrated to the standard scale following Magyar et al. (1999b). Note that, according to its original definition, the Pontian is an Eastern Paratethys stage, where it superimposes the Meotian stage. The most recent calibrations in the Dacian Basin estimated the Meotian/Pontian boundary at 6.15 ± 0.11 my (Snel et al., 2005).

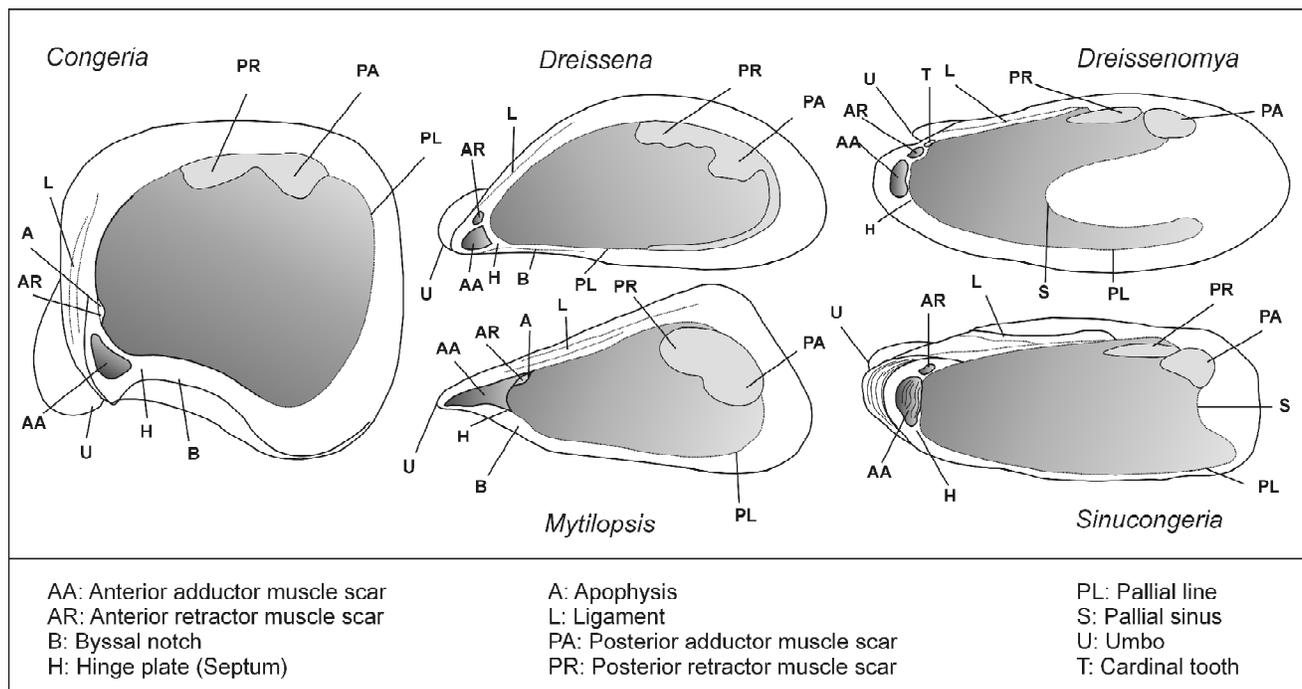


Figure 2. Basic shell morphology of *Congeria*, *Dreissena*, *Mytilopsis*, *Sinucongeria* and *Dreissenomya* (compiled and modified from Morton 1970, Marinescu 1977, Harzhauser and Mandic, 2004; Basch and Žagar-Sakač, 1992; Nuttall, 1990). Note the major reorganization of dreissenomyiid morphology due to the adaptation to an infaunal mode of life.

Systematics and Strategies

Family Dreissenidae Gray in Turton, 1840

Subfamily Dreisseninae Gray in Turton, 1840

Genus *Dreissena* van Beneden, 1835

Type species: *Mytilus polymorphus* Pallas, 1771

Like the primitive mytiliform *Mytilopsis*, *Dreissena* is a byssate epibiont and typical r-strategist that massively colonizes various primary and secondary hardgrounds. It developed from *Mytilopsis* by complete reduction of the apophysis, a protuberance of the septum that acted as a byssal/pedal retractor catchment (Nuttall, 1990; Fig. 2). In contrast to *Mytilopsis*, *Dreissena* is a typical inhabitant of freshwater riverine and lacustrine settings.

The late Pannonian and Pontian *Dreissena auricularis* (Fuchs, 1870) is the first uncontested representative, pointing to Lake Pannon as the centre of origin of *Dreissena*. The origination, however, may have taken place much earlier. Papp (1950) and Jekelius (1944) describe "*Dreissena*" *turislavica* (Jekelius, 1944) from the early Pannonian of Rumania (~11.5 my) and "*Dreissena*" *minima* (Lörenthey, 1911) from the middle Pannonian of Hungary (~11.0 my). As demonstrated by Papp (1950), both species developed by a step-wise reduction of the apophysis from typical *Mytilopsis*, with a broad range of intermediate stages. Hence, two lineages are documented, one leading from *Mytilopsis scrobiculata* *carinifera* (Lörenthey, 1902) to "*Dreissena*" *turislavica* and a second with *Mytilopsis*

gitneri (Brusina, 1892) as an ancestor of "*Dreissena*" *minima*. This clearly polyphyletic approach simply documents the problem of recognizing strongly reduced *Mytilopsis* from true *Dreissena*. The available material from Papp's study does not allow this problem to be solved. We therefore currently affiliate the two suspected species within *Mytilopsis*. About 30 species of that genus are described from the late Miocene and early Pliocene of Lake Pannon and the Dacian Basin. The largely unrevised subspecies – e.g. within *Dreissena auricularis* (Fuchs) – complicate an interpretation of the diversity.

Genus *Mytilopsis* Conrad, 1858

Type species: *Mytilus leucophaetus* Conrad, 1831

In both aquatic systems considered, *Mytilopsis* (Fig. 2) is by far the most diverse dreissenid genus; it is represented throughout the investigated time-slice. About 29 species and/or subspecies are documented from the Miocene of the Dinaride Lake System (Fig. 3). In the Paratethys and its descendant freshwater systems, 86 species and subspecies of *Mytilopsis* are recorded. The evolution peaked within Lake Pannon and the Dacian Basin. One of the best documented lineages in Lake Pannon is rooted in the Sarmatian *Mytilopsis praeornithopsis* (Papp, 1953). This species is the ancestor of the early Pannonian *Mytilopsis ornithopsis* (Brusina, 1892), which grades into the late early Pannonian *Mytilopsis hoernesii* (Brusina,

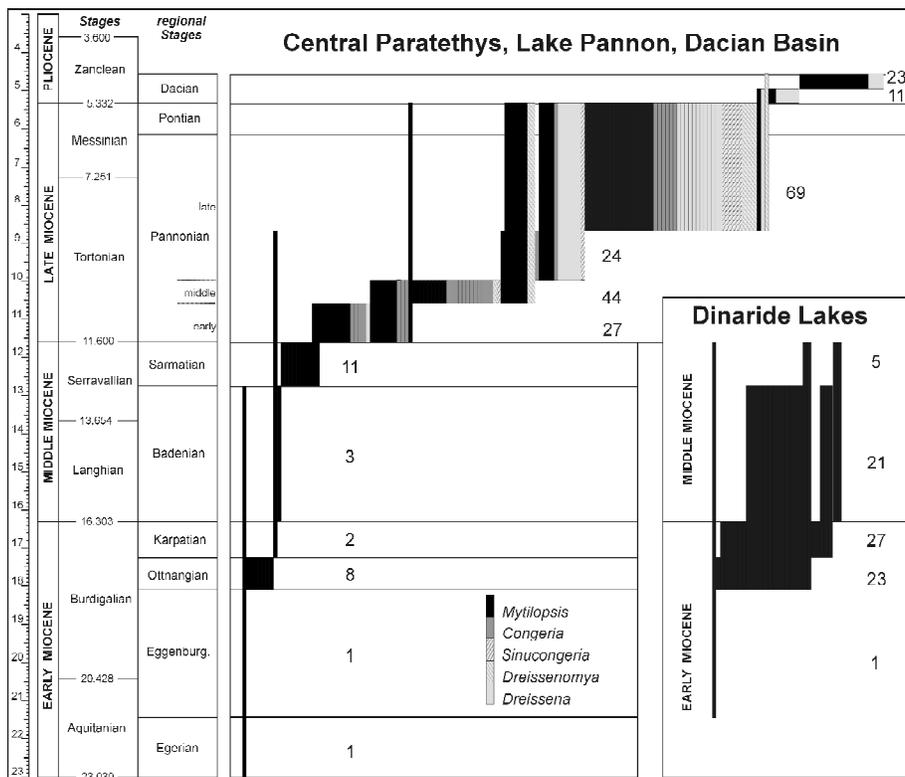


Figure 3. Miocene to Pliocene chronostratigraphy (after Gradstein et al., 2004 and Popov et al., 2004). Literature-based dreissenid taxa (see Table 1) are arranged according to their first occurrence; each bar corresponds to one species or sub-species; different signatures refer to genera. Note that the stratigraphic ranges for the Dinaride Lake taxa are uncritically adopted from Kochansky-Devidé and Slišković (1978).

Late Miocene dreissenid settlement strategies

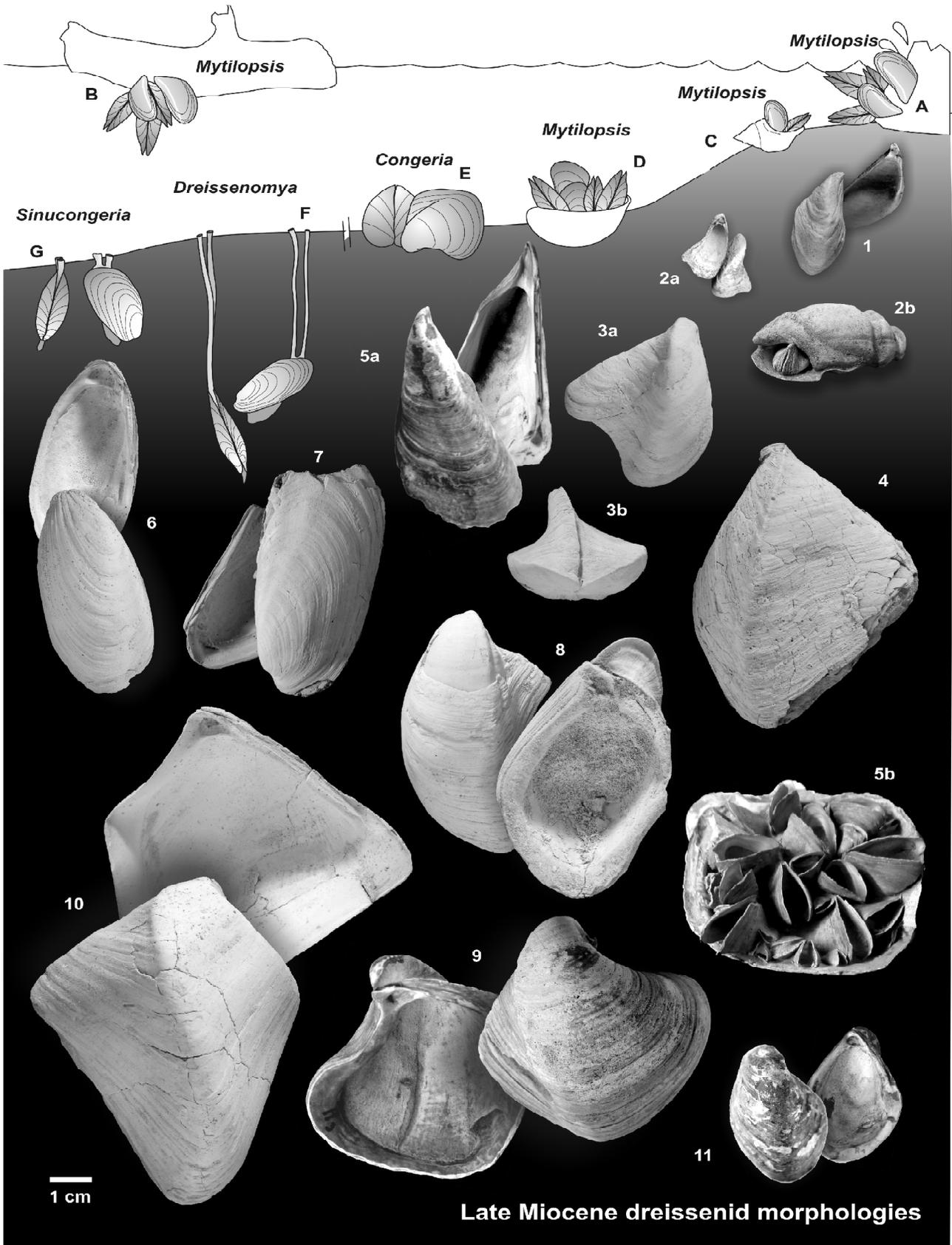


Figure 4. Modes of life of *Mytilopsis* (A-D), *Congeria*, *Sinucongeria* (E) and *Dreissenomya* (F) during the late Miocene (partly modified after Marinescu, 1977, Nuttall, 1990 and Harzhauser and Mandic, 2004; not to scale). Dreissenids conquered all aquatic habitats of Lake Pannon. The photos give an overview of characteristic morphologies and size relations: 1. *Mytilopsis neumayri* (Andrusov, 1897) [Götzendorf, Austria, late Pannonian] is an ubiquitous species which lived attached to pebbles and submerged plants. Morphologically, it represents the most primitive type within *Mytilopsis*, which is also developed in *Dreissena*. This shell morphology and the usually associated gregarious epifaunal mode of life is realized in the Paratethys and Lake Pannon as well as in the independent Dinaride Lakes. 2a. The irregular shape of *Mytilopsis doderleini* (Brusina, 1892) [Ollersdorf, Austria, middle Pannonian] reflects its crevice-dwelling mode of life as preserved in 2b, showing *Mytilopsis doderleini* in an aperture of *Melanopsis fossilis constricta* Handmann, 1887 [Siegendorf, Austria, middle Pannonian]. 3. *Mytilopsis ornithopsis* (Brusina, 1892) [3a. Vienna, Austria, 3b. Wrbitz, Czech Republic, both early Pannonian] a basal sediment-reclining form from Lake Pannon. 4. Via intermediate species the large-sized *Mytilopsis croatica* (Brusina, 1874) [Zagreb, Croatia, late Pannonian] evolved from the ornithopsis-stock. 5a. *Mytilopsis spathulata* (Partsch, 1836) [Vösendorf, Austria, middle Pannonian] is characteristic in sublittoral settings, where it frequently formed small nests in shells of *Congeria subglobosa* Partsch, 1836 (5b, same locality). 6. *Sinucongeria aperta* (Deshayes, 1838) [Kertsch Peninsula, Ukraine, Pontian] as a representative of the infaunal dreissenomyids. Morphologically, this genus was adapted only to shallow burrowing, whereas *Dreissenomya schroeckingeri* Fuchs, 1870 [7. Radmanest, Rumania, late Pannonian] lived deep in the sediment. 8. *Congeria pancici* Pavlovic, 1927 [Stegersbach, Austria, middle Pannonian] with sharp keel. 9. *Congeria subglobosa* Partsch, 1836 [Vösendorf, Austria, middle Pannonian]. 10. *Congeria rhomboidea* Hörnes, 1870 [Arpad, Hungary, upper Pannonian] is the largest representative but already displays a tendency to reduced shell thickness. 11. *Congeria zsigmondyi* Halavats, 1882 [Regelsbrunn, Austria, middle Pannonian] is a thick-shelled but atypically small *Congeria*. All specimens stored at the Natural History Museum Vienna.

1892). The latter gave rise to the middle to late Pannonian *Mytilopsis ungalacprae* (Münster in Goldfuss, 1837) and *Mytilopsis croatica* (Brusina, 1874).

Mytilopsis is an ubiquitous epibiont in all nearshore settings of Lake Pannon, often occurring in large populations. Occurrences of generalist species such as *Mytilopsis neumayri* (Andrusov) in fluvial settings associated with neritines (e.g. Harzhauser and Tempfer, 2004) or within lignitic plant debris (Harzhauser, 2004) suggests that some species might have lived attached to rocks and/or submerged plants, as does the morphologically similar extant *Dreissena polymorpha*. Others, such as the very elongated large-sized *Mytilopsis spathulata* (Partsch) and the smaller *Mytilopsis doderleini* (Brusina) utilized secondary hardgrounds, including empty shells of *Congeria subglobosa* Partsch (Fig. 4-5b) or apertures of melanopsid gastropods (Fig. 4-2b). These populations were limited only by available space within these micro-habitats. In the Dinaride Lake System, certain species such as *Mytilopsis dalmatica* (Brusina, 1874) became adapted to bottom-level conditions in deeper water.

Genus *Congeria* Partsch, 1836

Type species: *Congeria subglobosa* Partsch, 1836

According to Nuttall (1990) and Harzhauser and Mandic (2004), *Congeria* is an endemic Paratethys genus. With

Lake Pannon as its centre of origin, it comprises an independent species flock. All *Congeria*, but especially its type species, are characterised by an extremely thickened shell, being restricted to a semiepifaunal, byssate, sediment-reclining mode of life. *Congeria* is a surprisingly low-diversity genus with about 27 known species and subspecies-level taxa (Fig. 3). Several of the subspecies may represent simple morphotypes of the plastic *Congeria partschi*, *C. subglobosa* and *C. rhomboidea* clusters. Some evolutionary lineages, however, are quite clearly identified, e.g. *Congeria praerhomboidea* Stevanović > *C. rhomboidea* Hörnes > *C. alata* Brusina (Sanders et al., 2001; Gulyas, 2001) or *Congeria partschi* > *Congeria brandenburgi* Brusina. The status of the subspecies and the phylogenetic relationship between the *Congeria*-lineages remains to be clarified in detail. The first, comparatively small-sized *Congeria* (sensu Nuttall, 1990) originated in Lake Pannon during the early Pannonian (~11.5 my), represented by *Congeria partschi* Czjzek. After its middle Pannonian optimum, *Congeria* remained widespread during the late Pannonian (~10-6 my), but became extinct before the Pliocene.

In situ occurrences, such as those described by Harzhauser and Mandic (2004) for the middle Pannonian *Congeria subglobosa*, suggest *Congeria* to be a typical K-strategist that forms small, monospecific clusters of few specimens. This pattern is frequently taphonomically

obscured by within-habitat transport and accumulation of the heavy shells as shell lags or tempestites.

Congeria lived as a sediment recliner with the byssal/pedal gap pointing downward in oxygen-poor level-bottom environments. The monospecific patchy occurrence of *Congeria* in such environments was attributed by Harzhauser and Mandic (2004) to symbiosis with chemosynthetic bacteria, which provided the energy not only to survive the toxic conditions but also for the intensive shell mineralization.

Subfamily Dreissenomyinae Babak, 1983

The Dreissenomyinae are an endemic Paratethyan group which developed the maximum morphological deviation within the dreissenids due to their infaunal mode of life (Figs. 2, 4). They are a late Miocene offshoot of primitive Dreisseninae, apparently related with the modioliform group including *Mytilopsis amygdaloides* and *M. czjzeki* (Papp, 1951; Marinescu, 1977). The subfamily already became extinct during the Pliocene. The middle Pannonian *Sinucongeria primiformis* stock forms its earliest representatives. The Dreissenomyinae exhibited their maximum diversity in the Dacian Basin, while Lake Pannon was settled by only few species (Papaionopol et al., 1995). The subfamily comprises two genera only: *Sinucongeria* and *Dreissenomya*. *Carinatocongeria* Stevanović, 1990, with its type species *Congeria digitifera* Andrusov, 1897, is excluded (Vrsaljko and Sremac, 1999; Müller et al., 1999).

Genus *Sinucongeria* Lörenthey, 1894

Type species: *Congeria arcuata* Fuchs, 1870

A total of 7 species is described within this genus, which had its optimum in Lake Pannon and the Dacian Basin (Marinescu, 1977). The stratigraphically oldest record of the genus dates back to the middle Pannonian (~ 10.5 my), represented by *Sinucongeria primiformis* (Papp, 1949), which Papp (1951) interpreted as an offshoot of *Mytilopsis czjzeki* (Hörnes, 1870). The habitus as well as an integripalliate to slightly sinupalliate mantle scar of this earliest *Sinucongeria* still coincides with modioliform Dreisseninae. These early representatives were also epifaunal r-strategists, covering huge areas of lake Pannon with boom-and-bust populations (Harzhauser and Mandic, 2004). The first important morphological change in *Sinucongeria* took place during the late Pannonian with the rise of typical sinupalliate and infaunal forms. Accordingly, a shallow infaunal way of life – as is characteristic for more highly evolved *Sinucongeria* – did not develop before the late Pannonian (~9 my). These advanced *Sinucongeria*-species are comparatively scarce infaunal K-strategists (Harzhauser and Mandic, 2004).

The genus apparently disappeared during the Dacian,

although even Romanian occurrences are doubtfully discussed by Marinescu (1977).

Genus *Dreissenomya* Fuchs, 1870

Type species: *Congeria schroeckingeri* Fuchs, 1870

Dreissenomya is represented by at least 10 species within Lake Pannon and the Dacian Basin. The genus is characterised by a reduced septum in the form of a ledge spanning the anterior interior shell margins, serving for anterior adductor and pedal/byssal retractor attachment (Fig. 2). The shells of the earliest representatives are already deeply sinupalliate (Marinescu, 1977; Neveeskaya et al., 1993), pointing to a deep infaunal way of life. The genus is stronger laterally compressed, less dorsally pointed and more thin-shelled than *Sinucongeria*.

Dreissenomya is most probably an offshoot of a primitive *Sinucongeria*. The earliest representatives are *Dreissenomya zujovici* (Brusina, 1902) and *D. lithodomiformis* Pavlovic, 1927, which already appear in the middle and late Pannonian (Marinescu, 1977; Stevanović, 1990). In Lake Pannon, *Dreissenomya* became extinct before the Dacian and apparently vanished even earlier in the eastern regions (Marinescu, 1977).

Geodynamics and Dreissenid History in the Central Paratethys

1. Early Miocene – Tethyan swamps and the Paratethyan vanguard

Dreissenid diversity was generally low in the Paratethyan area from the Oligocene to middle Miocene (Figs. 3, 5). The Egerian to Eggenburgian mudflat faunas of the Central Paratethys yield mainly *Mytilopsis basteroti* (Deshayes). This thin-shelled, small to very small, mytiliform species develops compressed, strongly elongated shells with inflated central region. The investigated shells attain a maximum length of about 15 mm. Harzhauser and Mandic (2001) and Mandic et al. (2004) describe articulated, autochthonous populations of *Mytilopsis basteroti* in mudflat assemblages dominated by the bivalves *Polymesoda subarata*, *Crassostrea fimbriata*, and *Perna aquitanica* accompanied by the gastropod *Granulolabium plicatum*. These Paratethyan mudflat settings are interpreted as estuarine embayments with strongly reduced salinities fringed by mangroves (Barthelt, 1989; Mandic et al., 2004). In normal marine assemblages, *Mytilopsis basteroti* is always absent. Pure freshwater environments of the Egerian and Eggenburgian are well known and no dreissenid fauna was recorded.

The subsequent Ottnangian age (~18-17 my) was marked by geodynamic reorganisation of Paratethyan basins; an early Miocene global sea-level change (Haq et al., 1988) amplified the magnitude of that event. The

marine connections of the Paratethys with the early Mediterranean Sea and the Indo-Pacific were fully cut in the late Otnangian (~17.5 my), and brackish to freshwater sedimentary environments started to prevail (Kováč et al., 2004). This Otnangian crisis (Rögl, 1998) is reflected in nearshore settings by a peculiar evolutionary peak in bivalves. The result is a large number of endemic brackish genera such as *Limnopageta*, *Rzehakia*, *Lenticorbula*, and *Eoprosodacna*. This so-called "Rzehakia fauna" was also the pool for the first Miocene dreissenid radiation with at least 7 endemic species of *Mytilopsis* (Fig. 3; Steininger, 1973). These species already document a range of morphologies ranging from elongate [*Mytilopsis subclaviformis* (Rzehak, 1893)] to broad mytiliform [*M. clavaeformis* (Krauss, 1852)]. Amygdaloid outlines with convex margins are represented by *M. nucleolus* (Rzehak, 1883) and *M. amygdaloides* (Dunker, 1848). All species are of moderate size, ranging around 12-20 mm in length. The exception is *Mytilopsis andrussowi* (Rzehak, 1893), growing to a length of 30 mm.

These taxa fall into two groups of species without geographic overlap. One center is situated in the Alpine

foreland basin and is represented by various localities in Bavaria (southern Germany). *Mytilopsis amygdaloides*, *M. clavaeformis*, *M. schuetti* and *M. rottensis* are known to originate in that area. The second group, comprising *M. nucleolus*, *M. subclaviformis* and *M. andrussowi*, is documented from Moravia in the Czech Republic. These coeval but biogeographically separate faunas point to two independent endemic centres within the late Otnangian Paratethys. Interestingly, the earlier-mentioned *Mytilopsis basteroti* is absent from the *Rzehakia* faunas but persists in the Paratethys area up to the younger Karpatian and Badenian. It is therefore interpreted as a typical mudflat element bound to the assemblages of estuarine *Polymesoda-Crassostrea-Granulolabium* facies, which are a heritage from the Oligocene Tethys.

2. Latest early to middle Miocene – dry spell and geodynamic fluke

Soon after, at about 16-15 my, marine conditions re-established in the Central Paratethys due to a major transgression through the Trans-Tethyan-Trench-corridor via Slovenia (Rögl, 1998). Simultaneously, dreissenid

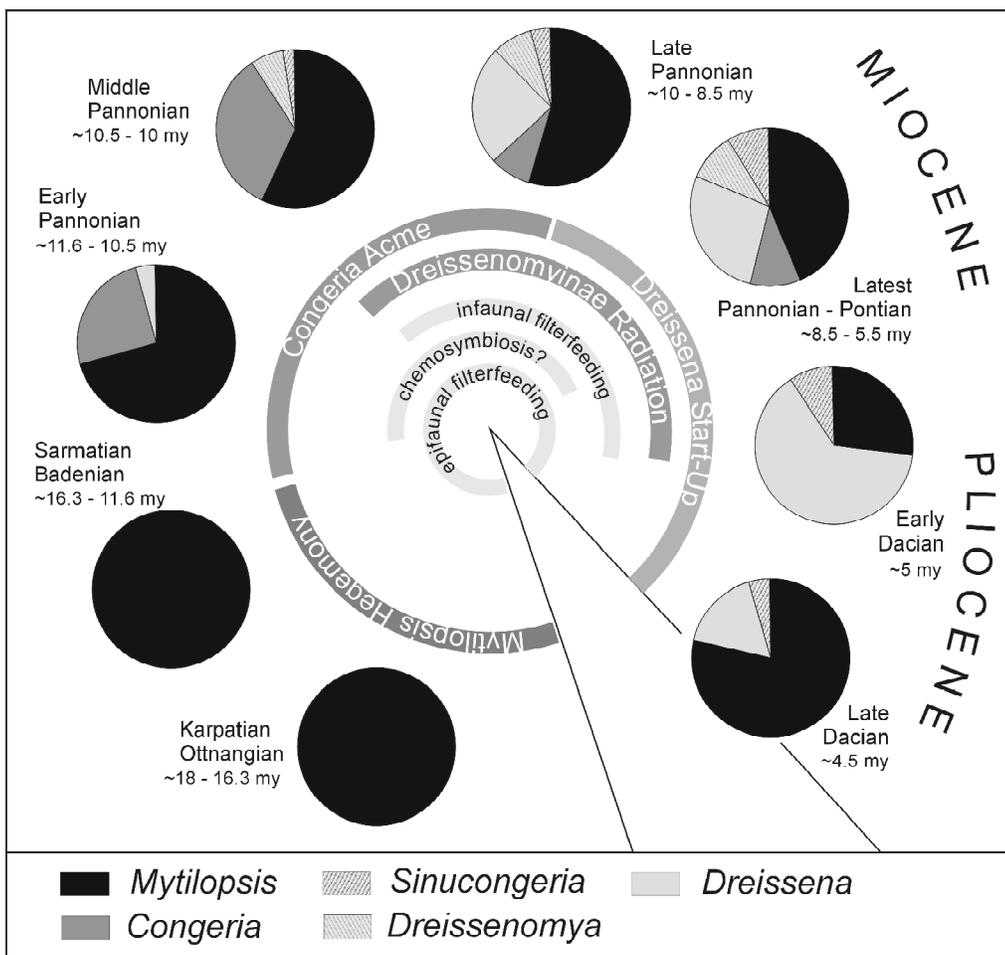


Figure 5. Generic radiation of the Neogene dreissenids from the middle Miocene to early Pliocene. The increased diversity coincides with an expansion of life habitats. The portions within the diagrams reflect the percentages of species of each genus. The *Congeria* acme during the Pannonian and its decline toward the end of the Miocene is well expressed; an interesting feature is the *Dreissena* take-over in the early Dacian, followed by a renewed *Mytilopsis* peak in the late Dacian.

diversity declined due to the loss of the late Ottnangian brackish-water settings (Fig. 3). Despite well-preserved late early Miocene (Karpatian) estuaries, such as in the Korneuburg Basin with its extended *Crassostrea* and *Perna* beds, and an extraordinary level of systematic investigations (Harzhauser et al., 2002a), only 2 Paratethyan dreissenid species are known from that interval. This low diversity continued into the middle Miocene Badenian (three species). At that time a major marine transgression related to global sea-level fluctuations (Haq et al., 1988) and the mid-Miocene climatic optimum (Shevenell et al., 2004) impacted the marine environments of the Paratethys Sea. Coral reefs, patch reefs and vast coralline shoals fringed the coasts of the Central Paratethys during the Badenian (16.3-12.7 my). This sea-level maximum, however, is also reflected by rarely developed (or preserved) brackish and freshwater settings and was thus unfavorable for dreissenid evolution.

The most common species during the Badenian is the small-sized, elongate, inflated *Mytilopsis sandbergeri* (Andrusov). Like *M. basteroti*, it is found in potamidid-mudflat assemblages, occurring for example in the lower Badenian Grund Formation in Lower Austria with *Terebralia bidentata*, *Tympanotonos cinctus* and *Melanopsis impressa* (Zuschin et al., 2004).

At the Badenian/Sarmatian boundary at about 12.7 my, an oceanographic crisis caused the complete collapse of marine ecosystems in the entire Paratethys Sea. All stenohaline organisms such as corals, echinoderms, pectinids, and sharks disappeared (Rögl, 1998). Among the gastropods, 588 species became extinct at that event (Harzhauser and Piller, subm.). The causes are still under debate; a salinity drop and/or eutrophication of surface waters and/or enhanced volcanism are among the potential triggers. The recovering aquatic pioneer assemblages are composed of few species which occur in enormous, sometimes rock-forming quantities (Harzhauser and Piller, 2004). The mollusc faunas are dominated by small to medium-sized bivalves such as *Venerupis gregarius*, *Ervillea podolica* and several dramatically radiating endemic cardiid lineages (Kojumdjieva, 1987). Shallow marine settings are often presented by tidal flats or estuaries settled by a rich but low-diverse mollusc fauna. Despite these favorable conditions and numerous vacant ecological niches in the Paratethyan Sea, dreissenid evolution was modest during the Sarmatian, represented solely by species of the genus *Mytilopsis*. Within *Mytilopsis*, however, the second Paratethyan radiation took place. At least 5 species are recorded by Jekelius (1944) from the Sarmatian of the Transylvanian Basin, and another 5 species are described by Kojumdjieva (1969) from the Bulgarian Sarmatian. The ecological range of these species

was quite similar to that of extant congeners. In the Sarmatian, all documented species occur exclusively in shallow sublittoral to littoral deposits. The usually disarticulated occurrence does not allow a clear decision about whether these shells are within-habitat (coastal marine) or were transported from nearby riverine settings. Co-occurring shells of the freshwater gastropod *Melanopsis impressa* indicate a fluvial influence. Morphologically, all species are small to medium-sized and more or less elongated triangular. *Mytilopsis soceni* (Jekelius, 1944) and *Mytilopsis politioanei* (Jekelius, 1944) range around 20-15 mm in length, whereas adult *Mytilopsis carasi* (Jekelius, 1944), *M. moesia* (Jekelius, 1944) and *M. ringeiseni* (Jekelius, 1944) range from 6-14 mm.

3. Late Miocene – the Pannonian “explosion(s)”

At about 11.6 my a glacioeustatic sea-level drop caused the final desintegration of the Paratethys Sea, and Lake Pannon arose in the inner-Carpathian basins (Magyar et al., 1999a; Harzhauser et al., 2004). The benthic ecosystem collapsed at that point and marine life completely vanished. This vast, probably brackish and slowly freshening long-lived lake was therefore settled by few survivors which inhabited an unbalanced, low-diversity ecosystem. Soon thereafter, the vacant niches were successfully conquered by cardiids, melanopsids and dreissenids (Müller et al., 1999). The following dramatic Pannonian radiation of the dreissenid lineage seems to be rooted at least partly in the Sarmatian Paratethyan fauna. Three species persisted from the Sarmatian into the early Pannonian: the small-sized *Mytilopsis praeornithopsis* (Papp), *M. moesia* (Jekelius) and *M. soceni* (Jekelius). All 3 survivors and Pannonian pioneers share several features. They are morphologically primitive and small-sized – meaning that no specialization can be inferred from the extremely simple morphologies – and they already vanish already in the middle Pannonian, probably due to replacement by more advanced species. During the early Pannonian the evolutionary radiation begins, reaching a first climax in the middle Pannonian; within *Congerina*, for example, the number of nominal taxa increases from 6 to 12.

A dramatic decrease in lake size to about the half of its maximum size occurred at the end of the middle Pannonian (Magyar et al., 1999a) at about 10-9.7 my. This was followed by a remarkable decrease in dreissenid diversity in the early late Pannonian. This bottle-neck event, however, was the starting point for a second major reorganization of the meta-community. The renewed stabilization of Lake Pannon during the late Pannonian (~10-6 my) resulted in the highest diversity peak ever recorded for any dreissenid flock.

Finally, probably coinciding with the Messinian lago-mare event of the Mediterranean Sea, Lake Pannon vanished. This loss also reflects enhanced sediment infilling and the partial tectonic inversion of the Pannonian basin system (Magyar et al., 1999a). The superimposed, probably lower Pliocene deposits indicate that a freshwater lake system occupied the southeastern basin region. It was characterised by unionid bivalves and mass occurrences of the gastropod *Viviparus*. No diverse dreissenid fauna was present, with *Dreissena polymorpha* being the only representative. In contrast, the renewed transgression at the end of the Miocene apparently reached only the Dacian Basin, where brackish dreissenid-rich Pontian sediments overlay the evaporitic series (Stevanović et al., 1990b).

Discussion

Generic rise and decline

The generic diversity of the dreissenid family, based on the systematic treatment of Nuttall (1990), shifted distinctly during the Miocene to early Pliocene (Fig. 5). Over a time-span of at least 13 m years, from the late Oligocene to the middle Miocene, this bivalve family was represented by a single genus – a phase referred to as *Mytilopsis* hegemony (Fig. 5). A low generic diversity is

coupled with a generally low speciation and a narrow spectrum of ecological adaptations. This condition changed quickly with the formation of Lake Pannon at about 11.6 my, and *Congeria* and *Dreissena* appeared. The number of species represented by these genera is still low compared to that of *Mytilopsis*, which contains about 3/4 of all dreissenid species. The low species richness of *Congeria* changes towards the middle Pannonian, when the number of *Congeria* species peaks – referred to as *Congeria acme* (Fig. 5). The first representatives of the *Sinucongeria* and *Dreissenomya* flocks appear in Lake Pannon. During the late Pannonian, the percentage of species assigned to *Congeria* declines, a trend that continued up to the latest Pannonian and Pontian, culminating in the extinction of the genus at the end of the Miocene. This decline was buffered by a gradual increase of dreissenomyine diversity and the establishment of *Dreissena* from the late Pannonian to the Pontian. At that time, the dreissenids exhibited a maximum of ecological strategies – ranging from the “classical” epifaunal filter feeding via the atypical deep infaunal filter feeding to the proposed chemosymbiotic-living modes of certain *Congeria* (Harzhauser and Mandic, 2004). Dreissenomyine species diversity declines strongly during the Dacian. Instead, *Dreissena* becomes dominant

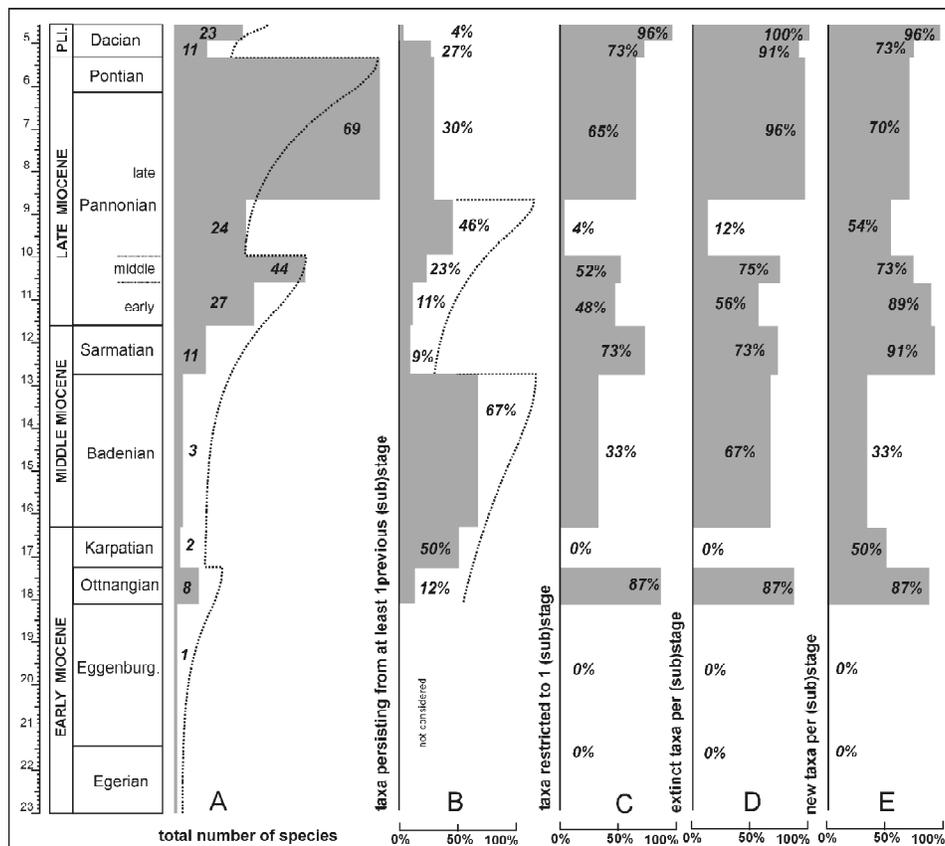


Figure 6.

A: Total number of dreissenid taxa recorded for each time-slice. Up to four diversification cycles are proposed.

B: Two distinct “aging”-cycles characterise the Neogene dreissenid evolution. The increase in percentages depends on the number of persisting taxa that already appear in a previous time-slice. Phases of high diversities are usually associated with low or moderate percentages of persisting taxa. This indicates that these diversities result from new radiations or immigrations rather than from accumulating old taxa.

C, D and E: Percentages of taxa restricted to one time-slice (C), extinction rates (D) and origin (E). Turnover rates are generally high; remarkable extinction-events occur in the Ottnangian due to the collapse of the endemic *Rzehakia* fauna and in the middle Pannonian.

and develops a first acme in the early Dacian. Finally, during the late Dacian, the generic diversity drops to two genera – *Mytilopsis* and *Dreissena*.

Patterns of extinction and renewal

Peak generic diversity roughly correlates with the phase of maximum species richness in the late Miocene (Figs. 3 and 6). This relation, however, is decoupled during the middle Pannonian, when *Congerina* and *Mytilopsis* account for high species numbers within a low generic diversity dreissenid fauna. A species-level analysis may therefore provide a more detailed insight into the evolutionary patterns. Changes in the total numbers of described species per stage and substage (Fig. 6A) suggests a pattern of 4 “increasing upward” cycles (each starting with a low number of species and culminating in a higher diversity). Of these, the first small but distinct cycle spans the Egerian to Eggenburgian and culminates in the moderately diverse Ottnangian “*Rzehakia*” fauna with 8 described species. The second cycle indicates a continuous increase in species numbers from the Karpatian through the middle Miocene up the middle Pannonian, with a first impressive peak involving about 44 species. The third cycle starts with the already fairly rich initial late Pannonian dreissenid fauna and grades into the absolute maximum of about 69 taxa in the late Pannonian to Pontian optimum. The fourth cycle spans the Dacian and documents a general decline in species richness compared to the late Miocene.

These diversity cycles do not coincide with faunal renewals. Only 2 “aging” cycles may be deduced from the dataset (Fig. 6B). The starting point for the first aging cycle is the strange Ottnangian “*Rzehakia*-fauna”, whose collapse is reflected as an extinction event (Fig. 6D). The percentage of persisting species increases during the late early and early middle Miocene from 12 to 67%. The late middle Miocene Sarmatian marks the turning point; only 9% of the new dreissenid fauna is composed of survivors from the Badenian. The gradual accumulation of persisting species levels off at about 46% during the early late Pannonian. The assemblages are slightly refreshed at the late Pannonian-Pontian, coinciding with the historical maximum dreissenid diversity.

The biostratigraphic significance of assemblages is well expressed by the percentage of species restricted to a single time-interval (Fig. 6C). Conversely, the rate of extinctions per time-slice is roughly correlated to that value (Fig. 6D). The fit of both trends is clear during the early Miocene, when long-lived species such as *Mytilopsis basteroti* in a generally very low-diversity dreissenid fauna are reflected in zero % extinction rates. The intervening Ottnangian endemism event is also expressed by coincident values of extinction and stratigraphic restriction. These

curves display a phase of misfit in the middle Pannonian due to a high extinction rate. At that time many species which persisted as early Pannonian relics disappeared, hinting at a major change in the biota at the middle to late Pannonian boundary. Thus, a generally low turn-over rate characterizes the early Miocene, except for the Ottnangian radiation peak. Beginning at the middle Miocene, the Paratethyan and Lake Pannon dreissenid assemblages exhibit a high turn-over rate; two maxima are evident, the first ranging from the Sarmatian to the middle Pannonian, the second from the late Pannonian to Pontian and Dacian.

Time and morphospace

A preliminary analysis of the morphologic variability of the Miocene and early Pliocene dreissenids of the Dinaride Lake System, the Paratethys Sea and Lake Pannon is presented in Fig. 7. For most species listed in Table 1, the maximum length and width were measured based on the type specimen and/or material published in the papers summarized in the chapter “Material and database”. This approach yields a single “ideal” value for each species. Despite this methodological caveat, our dataset reveals interesting patterns. Seven time-slices are chosen and data are plotted on a double-logarithmic scale; persisting species turn up on more than one slide.

A clear trend emerges within the Paratethyan/Lake Pannon lineages of *Mytilopsis*. Early to middle Miocene *Mytilopsis* occupy a very narrow area within the morphospace. Elongated and small morphologies are predominant. Increased size and broad morphologies with small length/width ratios explains the strong morphospace enlargement during the Pannonian – referred to as increasing disparity (Runnegar, 1987; Wills et al., 1994). This phase of high morphological disparity is long-lasting, i.e. about 6 m years, and is accompanied by a stepwise loss of small-sized *Mytilopsis* towards the late Pannonian, most conspicuously in the late Pannonian/Pontian and Dacian. Within the morphospace was apparently successively occupied by *Dreissena*, which established itself in the area where *Mytilopsis* had started in the early Miocene (Fig. 8). *Dreissena* might thus have occupied the niche of early representatives of *Mytilopsis*.

The late Miocene “expansive phase”, expressed by peak morphological disparity of Lake Pannon *Mytilopsis*, is impressively paralleled by the much older species in the Dinaride Lake System. During the early and middle Miocene, they occupy a field within the morphospace which is very reminiscent of that of their Pannonian congeners. A time-offset of about 5 my between both disparity peaks indicates that these evolutionary pulses were completely independent, representing morphological parallel-evolution.

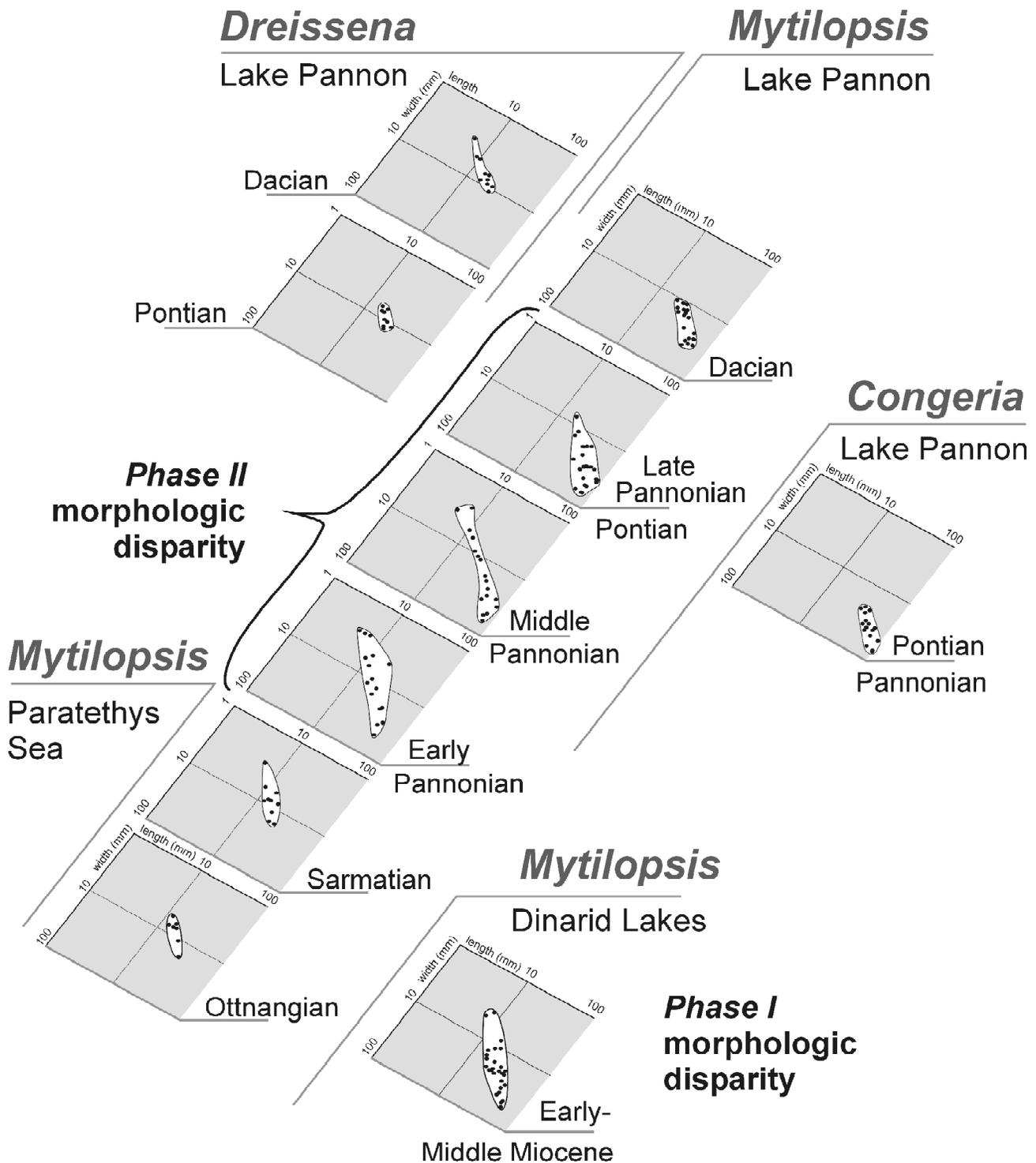


Figure 7. Morphospace occupied by dreissenids during the Neogene (each spot represents one taxon, listed in Table 1). The first phase of high morphological disparity in the early to middle Miocene Dinaride Lake System is comparable to the completely independent second phase in the Pannonian and Pontian of Lake Pannon. These phases have a time-offset of at least 5 my. *Congeria* occupies a very well-defined field which, however, displays an overlap with the late Pannonian and Pontian *Mytilopsis*-fields.

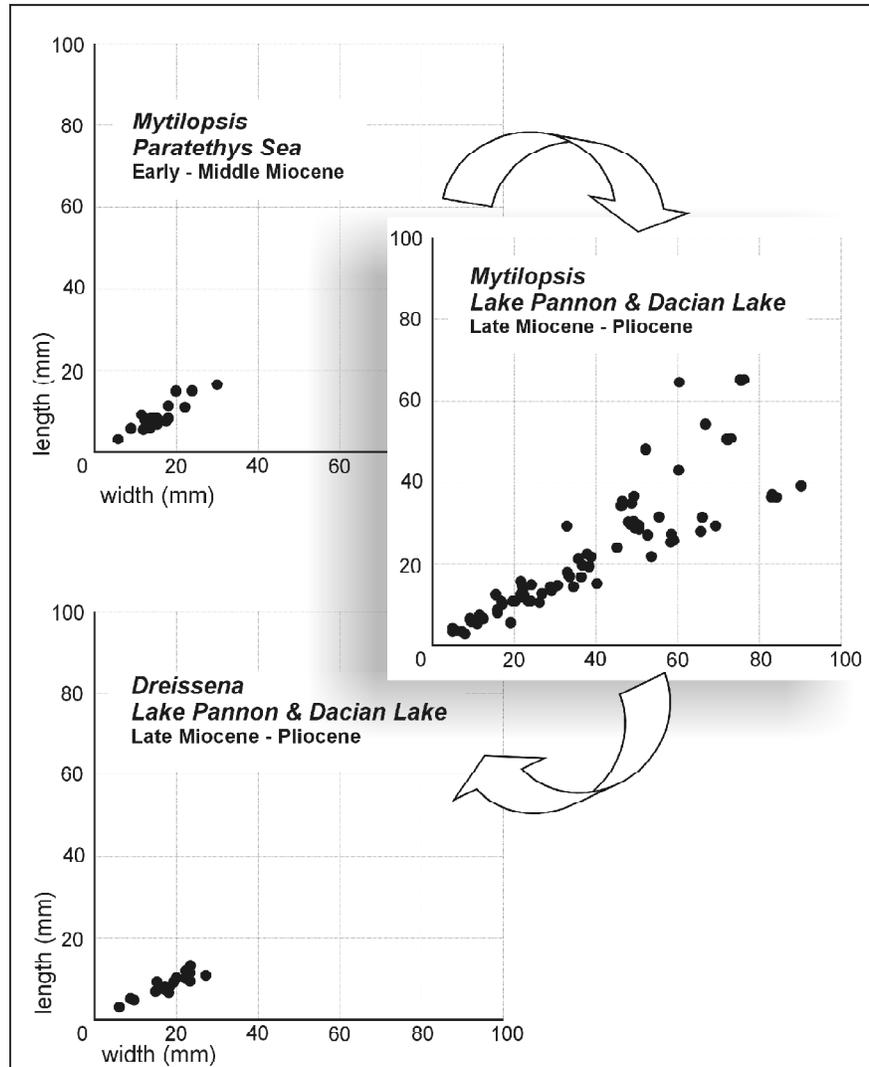


Figure 8. The morphospace occupied by *Mytilopsis* during the early and middle Miocene in the Paratethys is increasingly inherited by *Dreissena* in the late Miocene and Pliocene. This marks the beginning of spectacular radiation in *Mytilopsis*, which expanded its morphological limits, as reflected by the strongly scattered pattern of data-points.

Congeria, however, remains in a rather unique position; it occupies a very well-defined field in our plots (Fig. 7). The large and broad morphologies result in minimal overlap with large representatives of *Mytilopsis*. Moreover, the “small and elongate field” realized by *Mytilopsis* and *Dreissena* was never penetrated by *Congeria*.

Conclusions

The Neogene dreissenids of central and southeastern Europe are an outstanding model-group for the documentation of diversity and morphological evolution. Two seemingly independent biogeographic flocks developed. The older one flourished during the early to late Miocene in the Dinaride Lake System (DLS). The second developed in the Oligocene to mid-Miocene Paratethys Sea

and experienced an evolutionary burst during the late Miocene and early Pliocene. The faunistic relation between both biogeographic entities remains unresolved. Paleogeographic overlaps, as proven by the occurrence of the early to middle Miocene DLS dreissenid *Mytilopsis kucici* (Brusina, 1907) in the Karpatian of the Austrian Fohnsdorf Basin and the Vienna Basin (Papp, 1967; Schultz, 2005), are unknown during the late Miocene. Both biogeographic entities gave rise to phases of very high morphological disparity. A time-offset of about 5 my between the early to middle Miocene peak in the DLS and that of Lake Pannon points to independent parallel-evolution.

On the generic level, the maximum diversity was achieved during the late Pannonian in Lake Pannon, when the dreissenid family was represented by at least 5 genera,

including *Congeria*, *Dreissenomya* and *Sinucongeria*. *Congeria* is considered to be an endemic late Miocene offshoot of *Mytilopsis*. At the same time the range of ecological strategies peaked, comprising epifaunal (*Mytilopsis*, *Dreissena*) and infaunal (dreissenomyids) filter feeding and probably even chemosymbiosis (*Congeria*).

Low-diversity early to middle Miocene circum-Paratethyan faunas are contrasted by very species-rich endemic Lake Pannon assemblages. Two peaks with about 44 taxa (middle Pannonian) and 69 taxa (late Pannonian/Pontian) are documented.

Dreissena first occurred during the early late Miocene; it soon occupied the morphospace claimed by *Mytilopsis* during the early and middle Miocene. The latest Miocene and especially the Pliocene mark a distinct decline in generic diversity coinciding with a reduced morphological disparity. The loss of *Congeria* and of the Dreissenomyinae at the onset and during the Dacian limited feeding strategies to the ancestral nearshore epifaunal filter feeding that characterizes extant dreissenids.

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