

Changes in Paratethyan marine molluscs at the Early/Middle Miocene transition - diversity, palaeogeography and palaeoclimate

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The transition from the Early Miocene to the Middle Miocene is a crucial point for the development of mollusc faunas (gastropods and bivalves) in the Central Paratethys. Here, we first discuss the confusing and partly contradictory stratigraphic concepts and correlations of Paratethyan and Mediterranean reference faunas. Then we show that the interplay of sea level fluctuations, climatic amelioration, immigrations, and blooms in autochthonous elements causes a complex pattern of faunal development. We focus on the so-called “Grund Fauna”, which flourished during the Early Badenian and is here treated as transitional between typical late Early Miocene and typical Middle Miocene faunas. This faunal type, originally defined in Austria, is represented within the entire Central Paratethys and is strictly stratigraphically determined. It developed during the early Middle Miocene and is interpreted by us to mirror a phase of optimal climatic conditions. This is most plausible in respect to the marginal position of the Central Paratethys. As a northern appendix of the early Mediterranean Sea, it spans a north-south gradient of about 4° latitude and is suggested to represent a type of “palaeo-thermometer”, which reflects slight expansions or restrictions of climatic belts. The Langhian climatic optimum, for example, seems to be reflected within Paratethyan mollusc faunas by the northward migration of Mediterranean thermophilic species during the Early Badenian.

Key words: Paratethys, molluscs, climatic optimum, Karpatian, Badenian, Helvetian.

INTRODUCTION

The early Middle Miocene is a time of an extensive marine transgression following a major drop of the sea level at the Burdigalian/Langhian transition (HAQ & al. 1988, HARDENBOL & al. 1998). The rising sea level and the associated climatic optimum must have strongly influenced the marine life on continental shelves around the globe. Molluscs as typical inhabitants of marine shelves are apparently the best fossil group to trace the changes in benthic life that occurred as a consequence of those processes. The Miocene Paratethys is a typical epicontinental sea characterized by an extraordinarily good and diversified mollusc record. It serves as an ideal fossil laboratory for such a survey.

The Paratethys Sea extended in the Oligocene and Miocene to the northern margin of the Mediterranean, from which it was separated by a land mass formed by the Alps, Dinardes, Hellenids and the Anatolian Massif. During the Early/Middle Miocene transition a broad connection with the Mediterranean enabled a free faunal exchange between those two regions (RÖGL 1998, STUDENCKA & al. 1998). The fossil molluscs at this transition are characterized by a generally good preservation and extraordinarily high species diversity at both sides of the barrier.

In our opinion, the Austrian faunas of Lower Austria and Styria best document the late Early Miocene (Karpatian) and early Middle Miocene (Early Badenian) mollusc assemblages of the western Central Paratethys

(Text-fig. 1). Known to science for more than 150 years, they were usually termed the “Grund Fauna” or “Fauna der Grunder Schichten” (e.g. HILBER 1879; TOULA 1884). These faunas have been frequently used as reference faunas for the comparison with other famed Paratethyan Early Badenian mollusc faunas from Poland (Korytnica) and (Lapugiu de Sus, Coștei), as well as with other classic Miocene sites of the Mediterranean and Atlantic regions (e.g., SACCO 1890-1904 for Italy, COSSMANN & PEYROT 1909-1934 for France, ERÜNAL-ERENTÖZ 1958 for Turkey, STRAUZ 1966 for Hungary, BAŁUK 1975, 1995, 1997, 2003 for Poland).

This paper therefore investigates changes in mollusc faunas at the Early/Middle Miocene transition, based on exceptional Central Paratethyan and especially Austrian fossil lagerstätten. The acmes in typical species as well as the development of species diversity are analyzed and interpreted in the context of palaeogeographic, palaeo-climatologic and evolutionary processes.

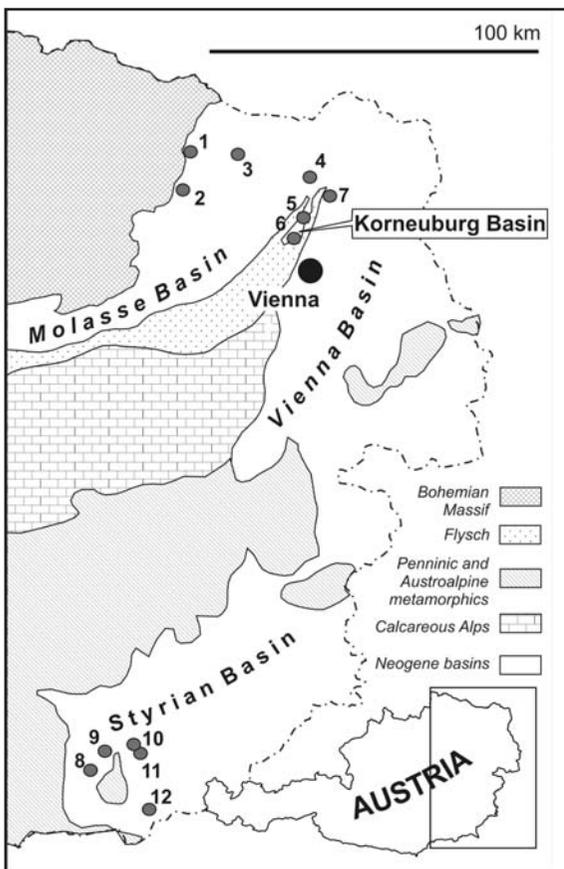


Fig. 1: Geographic location of some herein-mentioned Austrian localities yielding important Karpatian and Badenian mollusc faunas. 1. Eggenburgian sites, 2. Mühlbach, 3. Grund/Guntersdorf/Immendorf, 4. Niederleis, 5. Weinstein, 6. Korneuburg/Teiritzberg, 7. Niederkreuzstetten, 8. St. Florian, 9. Wetzelsdorf, 10. Pöls and Weindorf, 11. Wildon, 12. Gamlitz.

Tables with complete taxonomic datasets are provided as excel sheets at

<http://www.univie.ac.at/Palaeontologie/FWFP13745BIO>

EVOLVING STRATIGRAPHY - THE HISTORY OF CORRELATION

The recognition and separation of the Early Miocene and Middle Miocene Austrian faunas remained enigmatic throughout most of the 19th and 20th centuries due to a misleading original definition of the “Grunder Schichten”, followed by its erroneous correlations with corresponding successions abroad (e.g. GLAESSNER 1926; KAUTSKY 1928; SIEBER 1937). These historical misinterpretations continued to burden the international correlations for palaeogeographic and palaeobiological interpretations up until very recently (e.g. erroneous use of Tortonian in the Paratethys in VRIELYNCK & al. 1997). This handicap was the flash point for fierce controversies (e.g. FUCHS 1885 and BITTNER 1886). The following short overview of the historical development and the current state of knowledge serves to provide the basis for the stratigraphic correlations applied in the present study. Additionally, *Megacardita jouanneti*, a typical Badenian, large-sized carditid bivalve, will provide an example for the fatal manner in which poor taxonomy may impact biostratigraphic resolution.

“Grunder Schichten” and its relation to the “Helvetian” stage

The lithostratigraphic unit called “Grunder Schichten” by ROLLE (1859) was originally introduced for sediments which recently have been recognised as the Korneuburg Formation (Korneuburg Basin) and as the Grund Formation (Alpine Foredeep). Further problems concerning the correlation of the “Grunder Schichten” were due to merit of MAYER (1857; 1858; 1865; 1868) who assigned it to different Miocene stages: first to the Aquitanian (MAYER 1857), then to the Mayencian (Mayer 1865), and finally to the Lower Helvetian (MAYER 1868).

Its Helvetian position within later versions (MAYER 1874 a, b; MAYER-EYMAR 1881; 1884a, b; 1889) additionally resulted in the proposal for a substage termed “Grundin” (MAYER-EYMAR 1881). Whilst the initial Aquitanian and Mayencian correlations were abandoned, the Helvetian one established itself successfully and was applied until the initiation of the regional Central Paratethys stratigraphic divisions in the 60’ of the 20th century (cf. PAPP & al. 1978).

The Helvetian correlations of MAYER (1865; 1868; 1874 a, b; 1881, 1884a, b; 1889) also masked the stratigraphic position of the Helvetian stage, based originally (MAYER 1858) on the Miocene marine sediments in the region of Bern in Switzerland (compare RUTSCH 1958). Today it is termed the Belpberg Formation and dated as Early Burdigalian. PAPP & STEININGER (1973) showed that the fauna of the “Helvetian” of the Swiss marine Molasse is stratigraphically older than the fauna of the Grund and the Korneuburg Formations and correlated the succession with the Ottnangian stage of the Central Paratethys (Text-fig. 2).

“Burdigalian”, „Helvetian“ and “Tortonian” of the Paratethyan Miocene

The ultimate stumbling block of the Paratethyan Miocene stratigraphy arose with the inauspicious but most influential correlation of the Austrian and south European Miocene introduced by SCHAFFER (1927), who regarded the mollusc assemblage from the “Grunder Schichten” to be transitional between typical Early and typical Middle Miocene Austrian reference faunas. The mollusc fauna of the Eggenburg region in Lower Austria served as Early Miocene reference fauna. Originally,

Time (Ma)	Chronos	Polarity	Standard Stages	Central Paratethys Stages	Planktic Foraminifera	Calcareous Nannoplankton	Mammals	regional Foraminifera Zones	
15	C5An	Black	Serravallian	Sarmatian	M8	NN6	MN 8-7	<i>Porosonon. granosum</i>	
	C5Ar	Black						<i>Elphidium hauerinum</i>	
	C5AAn	Black		Langhian	Badenian	M7	NN5	<i>Elphidium reginum</i>	
	C5ABn	Black						Upper	<i>Bolivina/Bulimina</i>
	C5ABr	Black						Middle	<i>Spiroplectammina</i>
	C5ACn	Black	Upper Lagenidae Z.						
	C5ADn	Black	Early						M6
	C5ADr	Black							
	C5Bn	Black							
	C5Br	White			M5b		MN5	Lower Lagenidae Zone	
	20	C5Cn	Black	Burdigalian	Karpatian	M5a	NN4	MN4	
		C5Cr	Black			M4b			
		C5Dn	Black		Ottnangian	M4a			
		C5Dr	Black			M3			
		C5En	Black						
C5Er		White				Nn3	MN3		
C6n		Black	Eggenburg.		M2				
C6r		White					Nn2		

Fig. 2. Early to Middle Miocene geochronology and biostratigraphy modified after RÖGL & al. (2002), and references therein. The boundary between the Lower and the Middle Badenian correlates with the major sea level drop that occurred at about 14.8 Ma. due to the expansion of the East Antarctic ice sheet (FLOWER & KENNETT, 1993). Note that the upper part of the Upper Lagenidae Zone reaches into the Middle Badenian as documented by WEISSENBACK (1996). The Langhian/Serravallian boundary was recently re-calibrated by FORESI & al. (2002) to occur at 13.59 Ma. based on the LAD of *Sphenolithus heteromorphus*. This event marks the NN5/NN6 boundary and is proposed by HUDÁKOVÁ & al. (2000) to correspond to the Middle/Upper Badenian boundary. The light shaded area indicates the stratigraphic position of the Korneuburg Fm. (lower bar) and of the Grund Fm. (upper bar). The dark bar within the Grund Fm. corresponds to the position of the discussed mollusc fauna.

FUCHS (1873) assigned it to the “I Mediteranstufe”. Later, SCHAFFER (1927) correlated that fauna with the Burdigalian due to its similarity with the fauna from the stage’s type region in SW France. As the Early Miocene was therefore “occupied” by the Eggenburg fauna, SCHAFFER (1927) postulated a relationship of the obviously younger mollusc assemblage from the “Grunder Schichten” with the assemblage from the Turin Basin (NW Italy). Unfortunately the latter was erroneously attributed to the Helvetian (“Elveziano”) by SACCO (1890-1904). Thus, by accepting the Italian stratigraphic concept, SCHAFFER (1927) was in accordance with the erroneous results of MAYER (see text above) – a perfect vicious circle.

This division was doomed to failure mainly due to the misleading lithostratigraphic correlation by SACCO (1890-1904) in the Turin Mountains. He correlated two stratigraphically different pteropod marls as the same marker horizon, which he regarded as “Langhiano”. In fact the lower pteropod marl is of Early Burdigalian age, whilst the second formed during the Langhian (NOVARETTI & al. 1995; VAI 1996). According to SACCO (1890-1904) the “Langhiano” is overlain by the “Elveziano”, and therefore he considered the faunas of Baldissero, Termô-Fôra, Valle Cepi and others in the Turin Mountains, which are in fact positioned between these pteropod marls, as “miocene medio” or “Elveziano”. Actually, these sites are part of the Termô-Fôra Formation and are dated as Late Burdigalian in age (cf. FERRERO MORTARA & al. 1981).

As the “Tortoniano” followed the “Elveziano” in the stratigraphic concepts of SACCO (1890-1904), SCHAFFER (1927) completed the confusion by supposing that the “advanced” Austrian Middle Miocene fauna (including localities like Baden-Sooß or Gainfarn and formerly assigned by FUCHS 1873 to the “II. Mediteranstufe”) was an equivalent of the Tortonian.

Subsequently, the misleading use of the name Tortonian (Upper Miocene Mediterranean stage) for the Middle Miocene Paratethyan deposits became ubiquitous in the key-literature concerning the Paratethys province (e.g. KOJUMDIEVA 1960; STRAUZ 1966; BOHN-HAVAS 1969; BALUK 1975; ATANAKOVIC 1985).

Those misinterpretations formed the basis for almost 100 years of correlation mess (cf. PAPP & al., 1978). Text-fig. 2, however, indicates the current state of correlation of the Paratethyan and Mediterranean stages (compare also text below).

***Megacardita jouanneti* and the Trans-European “Helvetian” correlations**

RUTSCH (1971) emphasized the presence of *Megacardita jouanneti* (BASTEROT) in the Swiss marine

Molasse and the Helvetian historical stratotype. He pointed out that the earliest occurrences of this typical, large-sized bivalve throughout central and southern Europe coincide with the “Helvetian”. Thus, the bivalve seemed to allow a better handling of the “Helvetian”-problem.

Subsequent investigations, however, showed that the occurrences mentioned by RUTSCH (1971) are far from synchronous. As mentioned above, the Italian sections in the Turin Mountains are dated as Burdigalian. The French “Helvetian” successions of the Aquitanian Basin (e.g. Salles, the historical stratotype of the Sallomacian, and La Sime E Saucats), which commonly bear *Megacardita jouanneti*, are currently dated as Serravallian (cf. MARKS & VIGNEAUX 1971; MÜLLER & PUJOL 1979; BONGRAIN 1988; POIGNANT & al. 1997, LOZOUET 1998). The succession exposed at Salles is correlated with the N13-14 Zone of BLOW (1969) and NN7 Zone of MARTINI (1971) and is therefore distinctly younger than the Swiss “Helvetian” succession.

More absurdly, PFISTER & WEGMÜLLER (1998) showed that *Megacardita jouanneti* is absent from the Swiss Molasse but was confused by RUTSCH (1928; 1971) with another species which they described as *Megacardita guenterti* PFISTER & WEGMÜLLER. Thus, the favorite exemplar for correlation turned out to be entirely inappropriate.

BIOSTRATIGRAPHY AND PALAEOECOLOGY OF THE STUDIED FAUNAS

During recent years it became obvious that the so-called “Grund Fauna” consists of two stratigraphically quite different faunas (RÖGL & al. 2002). Ultimately, the late Early Miocene age of the Laa and Korneuburg Formations and the early Middle Miocene status of the fauna of the Grund and Gaiendorf Formations were accepted by most workers based on the increased biostratigraphic data:

Early Miocene

The Karpatian deposits of the Korneuburg Basin are dated as latest Early Miocene. The correlation of the mammal fauna with palaeomagnetic data allowed a dating as mammal zone MN 5, spanning a time of about 16.5-16.7 my (HARZHAUSER & al. 2002). The Karpatian molluscs derive from the Korneuburg Formation in the Korneuburg Basin and the Laa Formation in the Molasse Zone. The most important sections yielding Karpatian deposits, some of which were mentioned already by HÖRNES (1848; 1851-1856), ROLLE (1859) and MAYER (1857; 1858; 1865; 1868) are: Weinsteig,

Rückersdorf, Korneuburg/Teiritzberg, Niederkreuzstetten and Kleinebersdorf. The faunas consist exclusively of shallow-water, nearshore assemblages which lived under the changing conditions of an estuary (HARZHAUSER & al. 2002). Recently, the Karpatian mollusc faunas have been taxonomically revised by HARZHAUSER (2002), BINDER (2002) and CTYROKY (2002). In total, 230 taxa of gastropods, bivalves and scaphopods are documented.

Additionally, data of the Karpatian from TEJKAL & al. (1967) are included and taxonomically revised. The sites expose various shallow-water sands to sandstones and deeper water marls; they are dated as latest Early Miocene (Karpatian) and belong to the Carpathian Molasse Zone (Slup, Dolni Netcice, Hevlin; sandstones, shallow-water sands and sandy marls), northern Vienna Basin (Dubovce, Radosovce), East-Slovakian Basin (Hlinne, Durkovec) and South-Slovakian/North-Hungarian Basin (Dolne Pribelce, Egyhazasgerge, Salgotarjan).

Middle Miocene

The early Middle Miocene Grund Formation belongs to the regional Early Badenian Lower Lagenidae Zone. The entire succession is dated as foraminifera “Zone with *Praeorbulina glomerata circularis*” and as nannoplankton zone NN5 by (RÖGL & al. 2002). This points to an absolute age of about 15.1 my for the mollusc faunas of the so-called “Grund horizon”. These data document a gap between the Karpatian mollusc fauna of the Korneuburg Basin and the Badenian section Grund of approximately 1.5 my. The Grund Formation includes the species-rich faunas from such historic localities as Grund, Immendorf, Windpassing, Braunsdorf and Guntersdorf. The molluscs are documented in detail by HÖRNES (1851-1856; 1859-1870), KAUTSKY (1928; 1936/37), SIEBER (1947; 1949), SCHULTZ (2002) and MANDIC (2003). The molluscs occur in highly diverse and densely packed tempestitic shell beds. The shells are typically abraded and were transported from agitated shallow-water habitats into a somewhat deeper pelitic, dysaerobic environment with monospecific *Thyasira* assemblages in life position (ZUSCHIN & al. 1999).

In the western continuation, the Gaindorf Formation - exposed at Gaindorf and Mühlbach - closely adjoins the Bohemian Massif and represents the proximal, coastal facies to the Grund Formation (ROETZEL & al. 1999). The biostratigraphic analysis precisely matched that of the Grund Formation (RÖGL & al. 2002, RÖGL & SPEZZAFERRI 2003). The integrated palaeoecological investigation at Mühlbach revealed a steep palaeocoast morphology initiated by a faulting zone at the north-western margin of the alpine Molasse Basin

(HARZHAUSER & al. 2003). A very good preservation and an apparently low grade of abrasion even for presumably allochthonous elements is explained by the very short transport and the moderately deep subtidal facies at the place of deposition (MANDIC & HARZHAUSER 2003).

In the eastern continuation to the Grund Formation, a synchronous development is exposed in the Niederleis Basin (MANDIC & al. 2002). This tectonic trough is positioned in the Waschberg Zone, which stabilized at the end of the Early Miocene and separates the Alpine Molasse Basin and the extending Vienna Basin. Rich mollusc assemblages are reported from the sites Niederleis and Nodendorf (cf. HÖRNES 1856; 1870; VETTERS 1910; 1914). At the important Nodendorf section a more than 1 meter thick coquina of giant *Crassostrea gryphoides* valves points to an estuarine environment, which developed on top of a fully marine sequence. The corresponding marine assemblages occur around Niederleis, where they document the close position of the palaeocoast in the north and the presence of a deeper subtidal, offshore facies in a southward direction (MANDIC & al. 2002).

The synchronous (Early Badenian) fauna of the Styrian Basin consists of collections from the localities Wetzelsdorf, Weitendorf, Pöls and St. Florian. The deposits have been termed “Floriner Schichten” by ROLLE (1856), and HILBER (1878) already postulated the synchronous position with the “Grunder Schichten” based on occurrences of taxa such as *Tympanotonus papaveraceus* (BASTEROT), *Turritella gradata* (MENKE) or *Ficus cingulata* (BRONN).

The important Lower to Middle Badenian localities of the Vienna Basin such as Baden-Sooß, Vöslau and Gainfarn are all younger than Grund, belonging to the Upper Lagenidae Zone. In contrast to the Grund Formation these localities already bear several species of the more advanced Middle Miocene faunas.

Additionally, we used taxonomically revised bivalve faunas from sections outside Austria (STUDENCKA & al. 1998). These are from Costei and Lapugiu de Sus (Romania) and Maloszew (Poland) belonging to the Lower Lagenidae Zone and from Mikulov (Slovakia), Varpalota (Hungary) and Tarnene and Yasen (Bulgaria) of the Upper Lagenidae Zone of the regional Central Paratethys foraminiferal ecozonation. The rich Early Badenian gastropod fauna from the Polish section Korytnica is described in detail by BALUK (1975; 1995; 1997; 2003) and belongs to the Lower Lagenidae Zone (RÖGL & BRANDSTÄTTER 1993). The distribution of studied taxa within Eggenburgian, Ottnangian and Late Badenian horizons is based on data published in STEININGER & SENES (1971), PAPP & al. (1973), STUDENCKA & al. (1998) and MANDIC & STEININGER (2003).

FAUNAL COMPOSITION AND TAXONOMIC DIVERSITY - ANALOGIES AND DISTINCTIONS

Gastropods

It is difficult to separate the Karpatian and the Early Badenian gastropod faunas in Lower Austria because of similarities in the taxonomic composition of the assemblages in the two time slices, which are due to coinciding facies. Additionally, there are only few genuine Karpatian

species. Only 9 species (about 7%) are currently documented solely from the Karpatian (HARZHAUSER 2002). These are *Agapilia pachii* (HÖRNES), *Turritella bellardi* MAYER, *Tornus kuemeli* HARZHAUSER, *Thais* nov. sp. *Clavatulula dorotheae* (HÖRNES & AUINGER) and *Clavatulula barbarae* (HÖRNES & AUINGER).

Further problems arise because several “old-fashioned” typical Early Miocene species such as *Melongena cornuta* (AGASSIZ), *Tudicla rusticula* (BASTEROT), *Euthriofusus burdigalensis* (BASTEROT) and *Ficus cingulata* (BRONN) display a unique acme in the Central Paratethys; this lasted from the Karpatian up to the Early Badenian (Early Langhian), before a Middle Badenian (Late Langhian) decline (Text-fig. 3).

In contrast, the Badenian assemblages are usually recognized easily by the much higher species richness, yielding many species unknown from Karpatian strata (Text-fig.4). Typical forms include *Cerithium procrenatum* SACCO, *Cerithium bronni* (HÖRNES), *Cassidaria cingulifera* (HÖRNES & AUINGER), *Cypraecassis cypraeiformis* (BORSON), *Bursa nodosa* (BORSON), *Charonia apenninica* (SASSI), *Charonia nodifera* (LAMARCK), *Murex (Tubicauda) spinicosta* (BRONN) and *Muricopsis cristatum* (BROCCHI). About 150 gastropod species of the Karpatian are contrasted by more than 500 species of the Early Badenian (cf. BALUK 1975, 1995, 1997, 2003). This “Badenian bloom” is traceable within most gastropod families but is most conspicuous within the cypraeids, turrids, cancellariids, nassariids or muricids. The Nassariidae, for example, are present with 8-13 species during the Eggenburgian to Karpatian, but in the Early Badenian they increase to 53 species within the Central Paratethys. Similarly, among the Rissoidae only 3 species of *Rissoa* and *Alvania* in the Karpatian of the Korneuburg Basin face 28 species of *Alvania* in the Badenian of the Central Paratethys (KOWALKE & HARZHAUSER submitted).

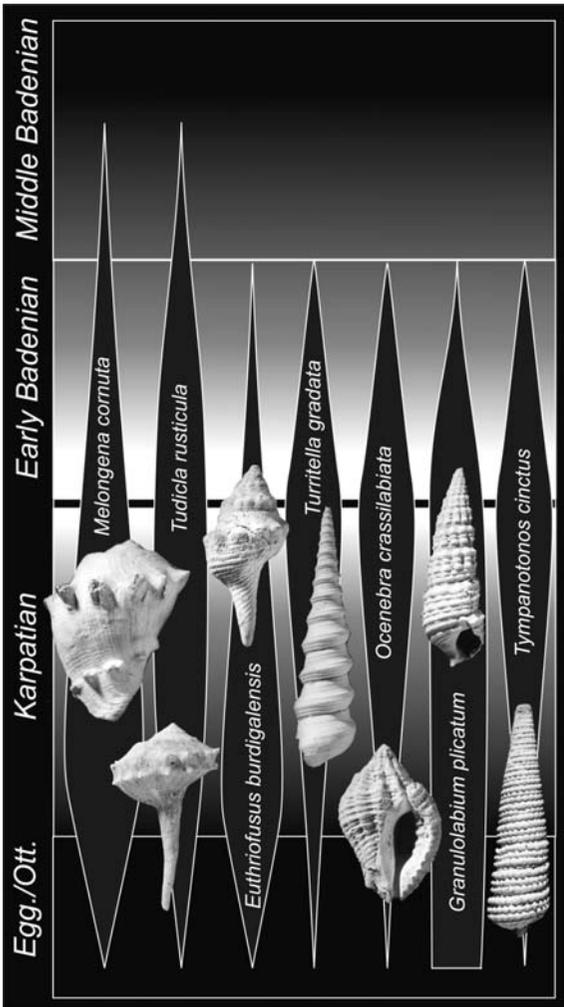


Fig. 3: Selected gastropod species which display their acme during the Karpatian stage and the Early Badenian Lower Lagenidae Zone but disappear or decline later on. Taxa such as *Granulolabium plicatum*, *Turritella gradata* or *Ocenebra crassilabiata* are typical constituents of Early Miocene assemblages and might be considered as the “last array” of the Early Miocene within the Middle Miocene “Grund Fauna”. Others such as *Melongena cornuta* and *Tudicla rusticula* persist into the Upper Lagenidae Zone but become subordinate and often small sized in the younger assemblages.

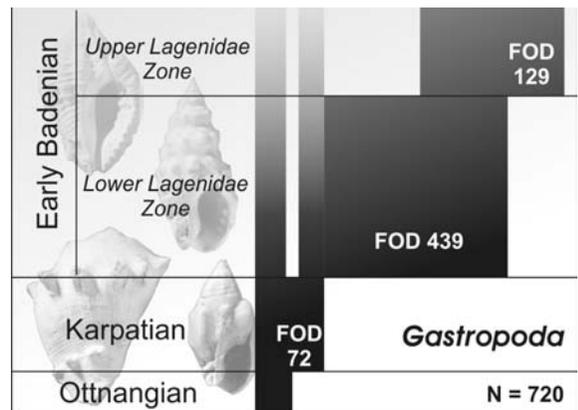


Fig. 4: First occurrences of gastropod species in the Central Paratethys during the Karpatian and Early Badenian, based on 720 species. The peak during the Lower Lagenidae Zone is evident.

Bivalves

For the purposes of the present analysis, the distribution of 382 species level taxa recorded in the Karpatian to Lower Badenian sediments of the Central Paratethys is traced within 3 time slices. These are Karpatian, Early Badenian Lower Lagenidae Zone and Early Badenian part of the Upper Lagenidae Zone (Text-figs. 2 and 5a-b). Additionally, the presence of herein recorded taxa in pre-Karpatian and post-Lower Badenian deposits of the Central Paratethys is considered to complete the dataset of their stratigraphical distribution.

A spectacular Middle Miocene bloom accentuates the shift between the Karpatian and the Badenian bivalve fauna. It began during the deposition of the Grund and the Gaindorf Formations and persisted throughout the Early Badenian. Hence, the Karpatian comprises 128 recorded species, whereas the Early Badenian yields about 350 species. With about 270 species, the “Grund horizon” alone (Lower Lagenidae Zone) comprises about twice as many species as are known for the whole Karpatian. Afterwards, the species

richness decreased slightly down to about 240 species in the Upper Lagenidae Zone. Apparently, within the Karpatian-Early Badenian period, the transitional Grund horizon marks the highest species richness during the studied interval (Textfig. 5a).

In addition to 128 taxa recorded in the Karpatian horizon of the Central Paratethys, there are some taxa that occur in the Badenian and are virtually absent in the Karpatian horizon but are recorded from horizons prior to it (e.g. Ottnangian and Eggenburgian). This may reflect taphonomic loss, but it is more likely that these taxa disappeared from the Central Paratethys during the regression in the Late Ottnangian/Kotsakhurian, where most of the region was occupied by a brackish, restricted sea dominated by the endemic bivalve *Rzehakia* (cf. PAPP & al. 1973).

The Karpatian is dominated by persisting species (57%) and only 10.2% of the fauna seems to be restricted to this Central Paratethys stage [e.g., *Modiolus excellens* CSEPREGHY-MEZNERICS, *Maetra* (*Barymaetra*) *nogradensis* CSEPREGHY-MEZNERICS]. About 18% of the fauna have their first occurrences [e.g., *Acanthocardia* (*A.*) *paucicostata* (SOWERBY), *Pelecypora* (*Cordiopsis*) *gigas* (LAMARCK)] whereas the remaining 14.8% are represented in the Central Paratethys by last occurrences [e.g. *Acanthocardia* (*A.*) *michelottiana* (MAYER), *Laternula fuchsi* (HOERNES)] (Text-fig. 5).

Among 271 taxa recorded in the Lower Lagenidae Zone, 45.4% are persisting, being significantly lesser than in the Karpatian. In contrast, 41.7% of the fauna experience their first occurrences in the Central Paratethys [e.g., *Aequipecten malvinae* (DU BOIS), *Plicatula* (*Plicatula*) *mytilina* PHILIPPI, *Lasaeina austriaca* (HÖRNES), *Crassatina* (*Crassatina*) *moravica* (HÖRNES)]. Consequently, less than 7% of the taxa have their last occurrences [e.g. *Rzehakia dubiosa* (HÖRNES)], coinciding with about 7% of taxa that area restricted to the Lower Lagenidae Zone [e.g., *Thyasira* (*Th.*) *michelottii* (R. HOERNES), *Arcopagia* (*A.*) *strohmayeri* (HÖRNES)] (Text-fig. 5). Finally, at least 15 species are absent from the Lower Lagenidae Zone but are present in the Karpatian and in Middle or Upper Badenian strata.

The faunal turnover from the Lower to the Upper Lagenidae Zone is moderate and the species richness drops only slightly (242 recorded taxa; Textfig. 5). As previously ascertained, only about 13% of the Lower Lagenidae Zone fauna (6.3% last occurrences along with 6.6% restricted taxa) disappear from the Central Paratethys in the Upper Lagenidae Zone, whereas 26% of the Upper Lagenidae Zone fauna (13.6% first occurrences along with 12.4% restricted taxa) are new for the Central Paratethys [e.g., *Solecurtus basteroti* (DESMOULINS), *Tellina* (*Laciolina*) *pretiosa* EICHWALD].

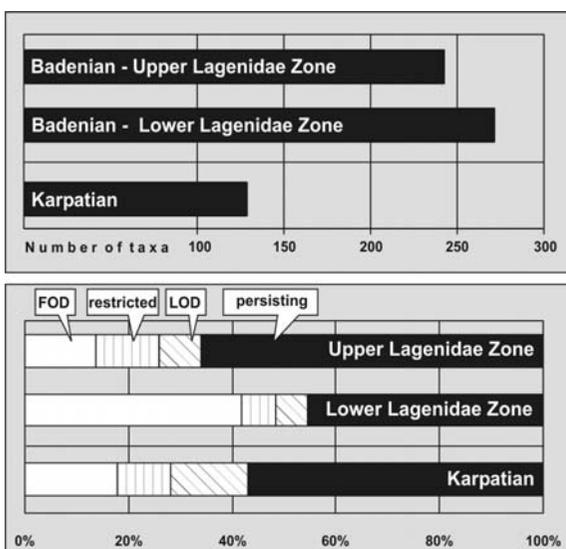


Fig. 5a: Development of species diversity within the bivalves during the Karpatian to Badenian transition. Note the diversity peak in the Badenian Lower Lagenidae Zone.

Fig. 5b: Percentile contribution of first occurrences (FOD), stratigraphically restricted species, persistent elements and last occurrences (LOD) within the bivalve faunas recorded in time slices of the Karpatian and Early Badenian (Lower Lagenidae & lower Upper Lagenidae Zones). Note the high contribution of first occurrences (FOD) to the assemblages of the Lower Lagenidae Zone. In the Upper Lagenidae Zone the first occurrences diminish and the transitional forms clearly predominate the assemblage.

Moreover, as only 7.9% of the species vanish in the Upper Lagenidae Zone as much as 66.1% of its fauna is represented by long-lived, persisting taxa.

Considering those families that contribute to the species richness of the Karpatian and the Lower Lagenidae Zone, a characteristic pattern appears (Text-fig. 6). The Karpatian assemblage is represented by 41 families. In contrast, the Lower Lagenidae Zone shows much higher diversity both on the species and family level. Of 58 families, 21 are unknown from the Karpatian horizon. The typical examples are Isognomonidae and Plicatulidae, both shallow-water thermophilic epibionts. Furthermore, the representatives of Galeommatoida such as Montacutidae, Leptonidae, Sporteliidae and Kelliellidae are all unknown from the Karpatian horizon. Galeommatoidae are a large but obscure, cosmopolitan group of generally small bivalves. They are free infaunal or byssate nestlers in crevices and rock undersides, commonly commensal with anemones, holothurians, echinoids, polychaetes and sipunculans, feeding on their food or excrements.

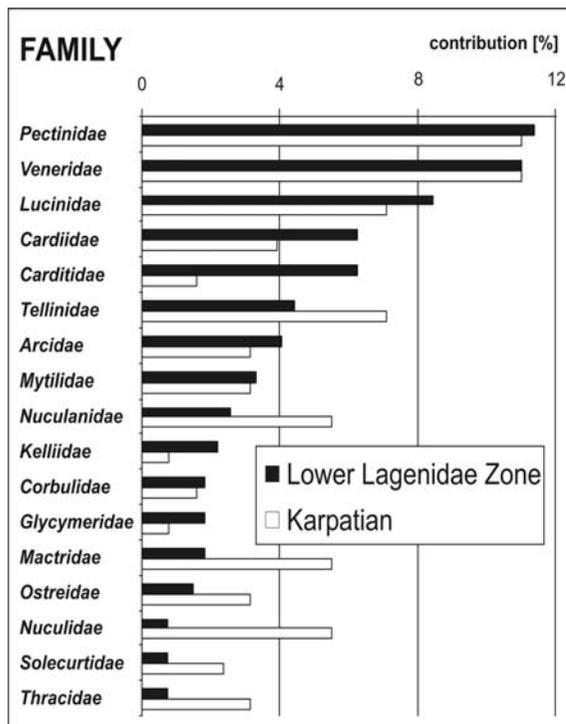


Fig. 6: Diagram showing the unequal impact of various bivalve families on overall species richness. Pectinidae, Veneridae and Lucinidae contribute to the faunas rather uniformly in the Early and Middle Miocene, being characterised by the highest species richness values. The Badenian transgression coincides with a considerable diversification of shallow-water cardiids and carditids. By contrast, indicators for deeper and colder water such as Nuculanidae, Nuculidae and Cuspidariidae are most conspicuous in Karpatian assemblages.

Pectinidae, Veneridae and Lucinidae are the most characteristic elements of Karpatian and of Lower Lagenidae Zone assemblages, comprising almost one third of all recorded species. Pectinids and venerids are the most diverse groups. The importance hierarchy for other families differs in the two studied horizons. Hence, in the Karpatian, Tellinidae, Nuculanidae, Mactridae and Nuculidae are all represented by 7 or more species. Those groups together with groups restricted to the Karpatian horizon include characteristic deep-water elements. Apparently the influence of the latter elements was considerably stronger within the Karpathian than within the Early Badenian assemblage. Hence, the diversification at the dawn of the Middle Miocene preferentially affected the shallow-water environment.

Whilst the deep-water assemblages were hardly affected due to rather stable conditions, the diversity of shallow-water habitats apparently increased. The herein-presumed climatic optimum during the early Middle Miocene is the most reasonable driving force behind such a habitat diversification.

In the Lower Lagenidae Zone, Pectinidae, Veneridae and Lucinidae are followed by Cardiidae, Carditidae, Tellinidae, Arcidae and Mytilidae - all represented by 9 or more taxa. Thereby, Cardiidae and Carditidae (with 17 taxa each show a conspicuous diversity peak. Especially the shallow-water, thermophilic Cardiidae, represented by only 2 taxa in the Karpatian, underwent a conspicuous radiation within the early Middle Miocene Central Paratethys.

DISCUSSION

Immigrants or natives?

Both the Karpatian and Early Badenian faunas are typical migrational faunas because they coincide with a marked transgressive event from the Mediterranean area into the Central Paratethys. These transgressions are divided by a massive regressive events coinciding with the Bur5/Lan1 sequence boundary of HARDENBOL & al. (1998). Subsequently, at the dawn of the Middle Miocene, the considered faunas, which derive mainly from littoral to shallow sublittoral environments, suffered a major incision and habitat constriction. These circumstances probably changed the composition of the faunas dramatically.

The character of the Early Badenian fauna, with its high number of new species, is not based on the evolution of new Paratethyan species but on massive immigrations from the adjacent Mediterranean basin. The

same scenario can be postulated for the Karpatian fauna, which was characterised by a high number of immigrations; this resulted for example in more than 70% of “Mediterranean” gastropod species within the Central Paratethyan Korneuburg Basin (HARZHAUSER 2002).

The same holds true for the bivalve records, where the autochthonous elements - species, unknown from the Mediterranean and NW Atlantic during the Early and Middle Miocene - do not exceed the 25% mark. Moreover, those values coincide almost exactly for both the Karpatian (23%) and the Lower Lagenidae Zone (24%) assemblages of the Central Paratethys. This is even more conspicuous because the assemblage of the

latter horizon comprises twice as many species (273) as the Karpatian one (142).

Early Badenian (Langhian) immigration instead of an “autochthonous evolutionary impulse” is obvious considering the stratigraphic ranges of the “new” taxa: they often first occurred in the Burdigalian of the Atlanto/Mediterranean area. Despite the documented open seaways and the fair possibilities for migration, several Early Miocene Mediterranean species did not enter the Central Paratethys before the Badenian (Text-figs. 7 and 8). Typical species include *Rimella (Dientomochilus) decussata* (DEFRANCE), *Peasiella reyti* (COSSMANN & PEYROT), *Fasciolaria (Pleuroploca) tarbelliana* (GRATELOUP) or *Morum (Oniscidia) cythara*

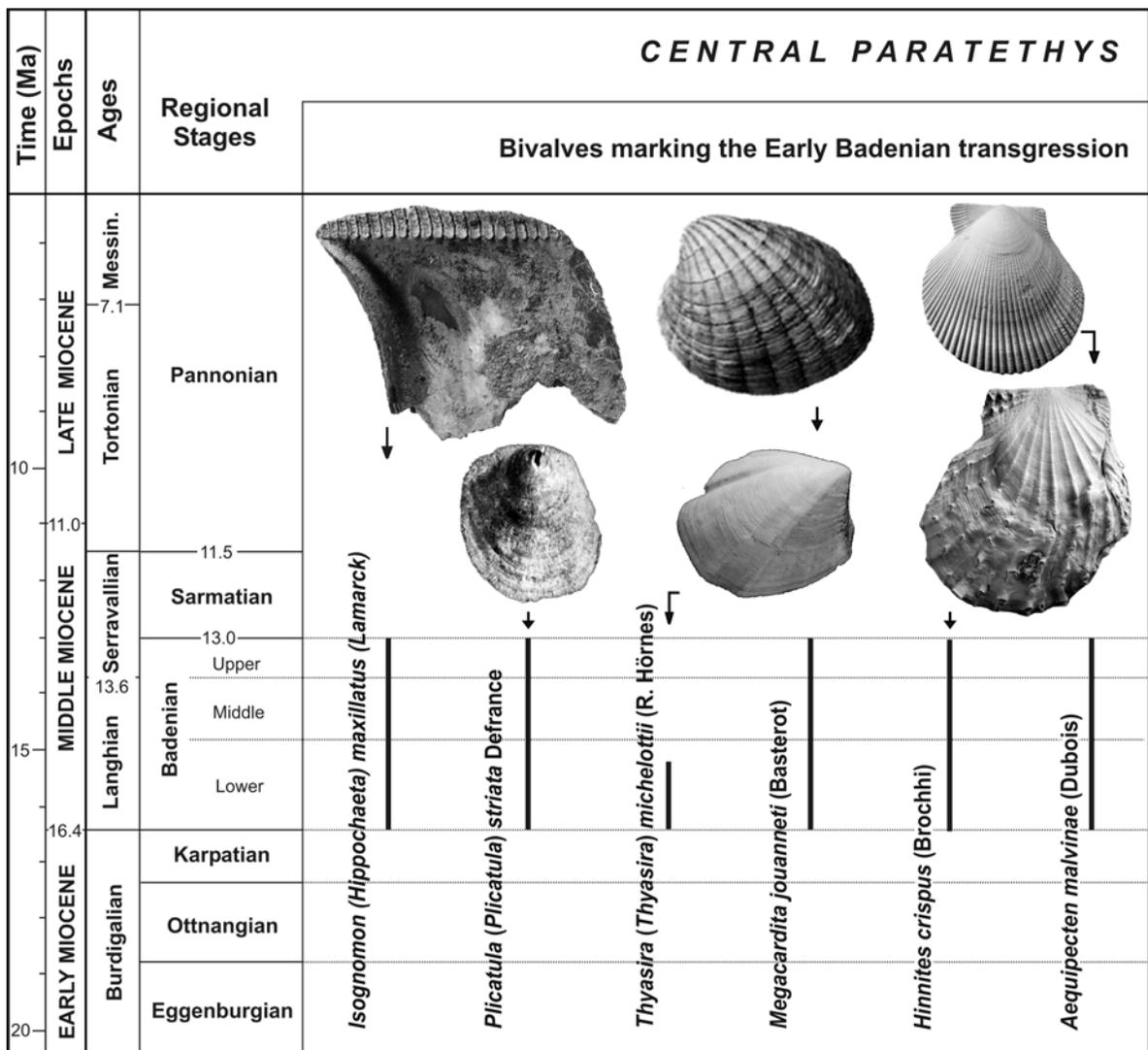


Fig. 7: Selected bivalve species, showing the first occurrence in the Paratethys with the beginning Badenian transgression. *Isognomon*, *Megacardita* and *Thyasira* are immigrants from the Mediterranean, where they are already established in the late Early Miocene. The first two taxa are suspected to indicate the early Middle Miocene warm spell in the Paratethys.

(BROCCHI). A Mediterranean origin is also likely for taxa such as *Malea (Cadium) denticulata* (DESHAYES) or *Pereiraea gervaisi* (VÉZIAN). The ecological conditions allowing the northward migration of these species were clearly not established before the Early Badenian. Similarly, the strombid *Tibia dentata* (GRATELOUP) is unknown from the Early Miocene of the Paratethys but forms extraordinary large populations in the East Mediterranean at that time (Mut Basin in Turkey, Qom Basin in Central Iran; own observation by the first author). Nevertheless, the same species appears in the Grund Formation during the Early Badenian and starts to form huge populations within the Styrian Basin, documenting a distinct extension of its optimum-zone into the southern Central Paratethys.

Among the bivalves, some of the Badenian immigrants with roots in the fauna of the Mediterranean Lower Miocene are *Isognomon (Hippochaeta) maxillatus* (LAMARCK), *Plicatula (Plicatula) mytilina* PHILIPPI, *Megacardita jouanneti* (BASTEROT) and *Thyasira (Thyasira) michelottii* (R. HÖRNES).

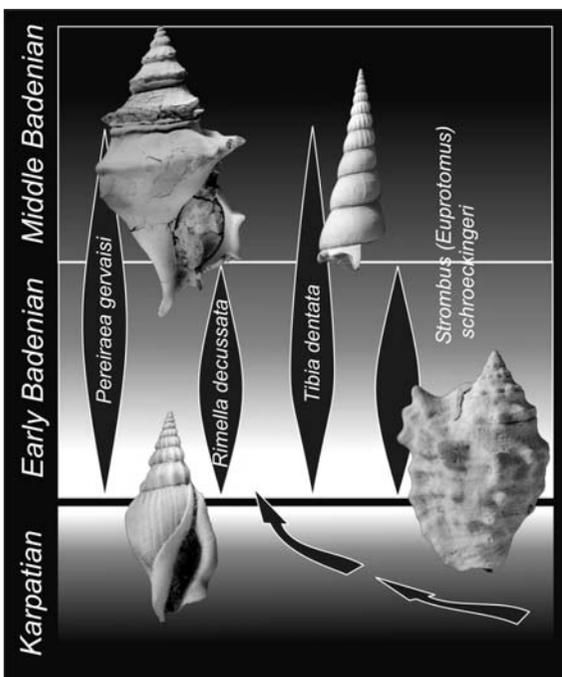


Fig. 8: Selected gastropod species documenting a wave of immigrations during the Early Badenian. Moreover, some of the presented species such as *Tibia dentata* and *Rimella decussata* are well established and frequent in the Burdigalian faunas of the East Mediterranean (own investigations of the first author) but did not enter the Paratethys at that time. This “pushing the frontiers” towards the north is interpreted by us to be stimulated by the Early Badenian (Langhian) climatic melioration.

Influence of palaeoclimate

This Early Badenian heyday of typical Early Miocene thermophilic taxa such as *Isognomon*, *Tibia*, *Rimella*, *Melongena* and *Tudicla* seems to be climatically triggered because it coincides with the climatic optimum spanning the Late Burdigalian and the Early Langhian (MC GOWRAN 1979; BEU & MAXWELL 1990; MILLER & al. 1991; RÖGL 1998; NISHIMURA & SUPARKA 1997; TSUCHI 1997). Another hint for this conspicuous warm spell is the evolution of the nassariid genus *Cyllenina* (Text-fig. 9). It is a rare constituent of Eggenburgian, Ottנגian and Late Badenian faunas because it con-

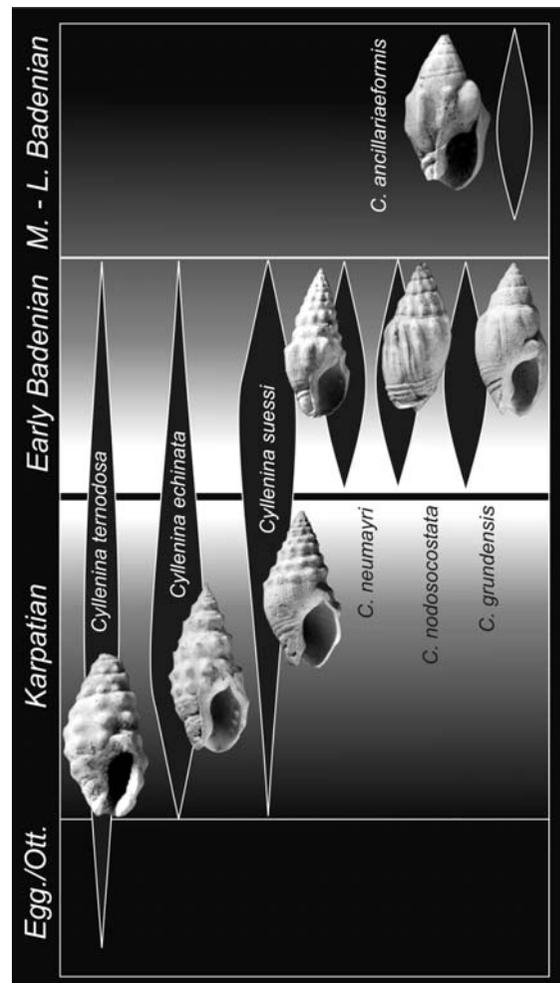


Fig. 9: Paratethyan representatives of the nassariid genus *Cyllenina* reflect an Early Miocene start up phase, which culminates in an Early Middle Miocene acme. This pattern might also be explained by a climatic warming starting during the Karpatian and peaking in the Early Badenian. Note the dramatic decrease in diversity of this genus in the Middle Badenian. The second acme of *Cyllenina* during the Early Pliocene in the Mediterranean Sea seems to confirm our interpretation of that genus as a thermophilic element.

tributes at maximum 1 species per assemblage. During the Karpatian, it is present with at least 3 syntopic species in the Korneuburg Basin. Soon after, during the Early Badenian, its diversity increases to 9 species - 6 of these occur in the Grund Formation. After this radiation, the number of species drops considerably down to 3 in the Late Badenian (HARZHAUSER & KOWALKE, submitted). The interpretation of this genus as a thermophilic element is strongly supported by the timing of its second major radiation, i.e. during the Early Pliocene warming in the Mediterranean Sea (cf. BELLARDI 1882).

Another good candidate for tracing a climatic optimum are strombids (Text-fig. 10). Within this group, the rare *Strombus (Euprotomus) schroeckingeri* HÖRNES (in HÖRNES & AUINGER) is most promising due to its remarkable distribution. It is restricted to the southern basins of the Paratethys Sea and is documented from

Rumania, Bulgaria, Hungary, Bosnia and the Styrian Basin in Austria. In contrast, it is unknown from the Vienna Basin and the more northern Polish Foredeep. Aside from this geographic restriction, it is also stratigraphically confined to the Early Badenian and vanishes completely thereafter. The species is usually accompanied by a second strombid, *Tibia dentata* GRATELOUP. This species appears in the Chattian of the Atlantic, the Mediterranean and the Paratethys. It is usually a rather rare element but experiences an extraordinary bloom in the Early Badenian of the southern Central Paratethys, where its abundance is reflected in the informal term “*Rostellaria* Tegel” (= *Tibia* marls). In contrast to *Strombus (E.) schroeckingeri*, *Tibia dentata* reaches up to the northern Vienna Basin and the Polish Foredeep. Nevertheless, it becomes extremely rare in the Vienna Basin, where it is known from few fragments only,

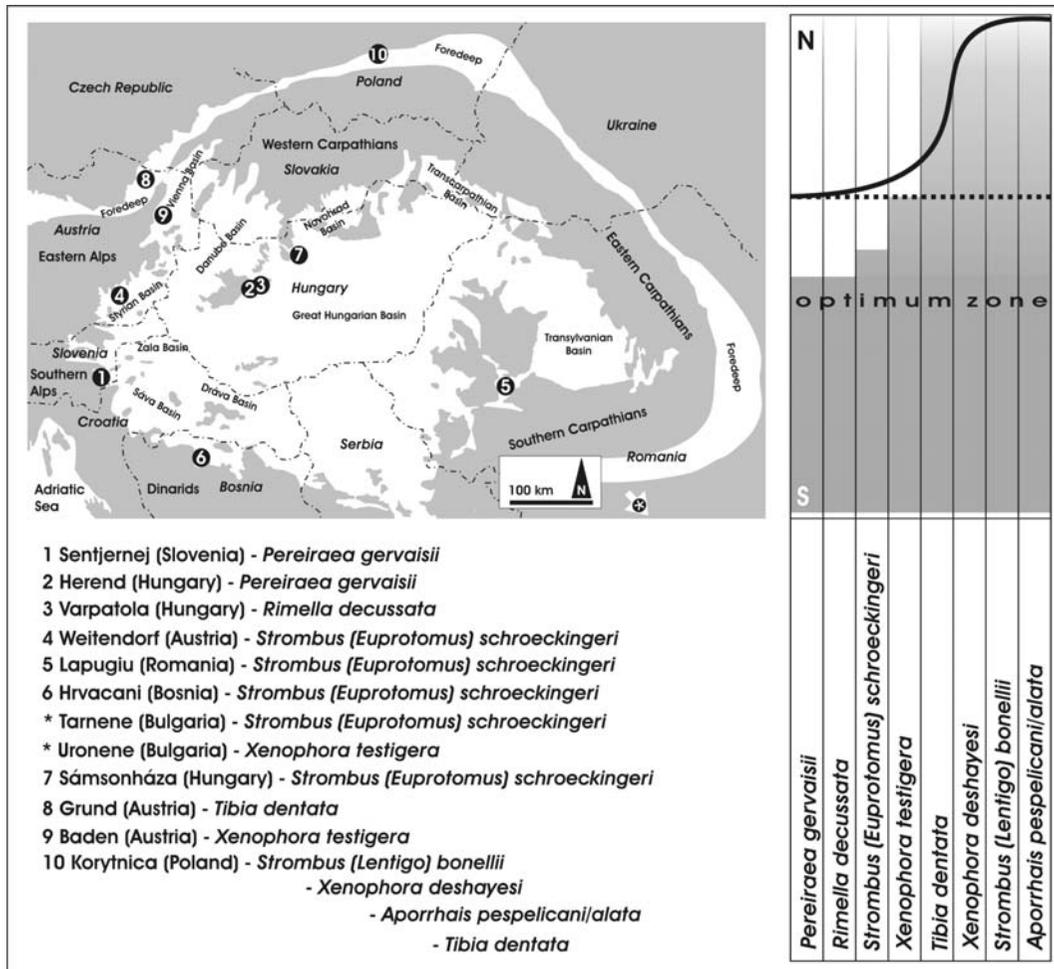


Fig. 10: Distribution of strombids and xenophorids in the Central Paratethys during the Early Badenian projected onto the Recent Carpathian-Pannonian Basin complex. The distribution pattern indicates a “piling” of species in the southern basins of the Paratethys. Moreover, the presumably most thermophilic taxa such as *Strombus (Euprotomus) schroeckingeri* and *Rimella decussata* are missing in the northernmost localities. This might reflect a – probably climatically controlled – north-south gradient within the Paratethys even during the Early Middle Miocene warming.

whilst it forms dense populations in the Styrian Basin.

The Styrian Basin is a region significantly impacted in the Early Badenian by the common presence of giant pectinids of the genus *Macrochlamis* [= *Gigantopecten*] (TEPPNER & DREGER 1918). These extinct, Neogene inhabitants of agitated, fully marine, shallow-water environments have large, heavy shells. They preferentially settled bioclastic carbonate platforms (BONGRAIN 1988) and coarse shallow-water siliciclastics (MANDIC & PILLER 2001). The extreme mineralization of the giant and heavy shells of *Macrochlamis*, correlating with high metabolic costs, imply favorable climate conditions (cf. GRECIAN & al. 2000). Moreover their frequent occurrence is apparently bounded to the presence of extended shelf regions typical for the eustatic sea level high-stand conditions and times of global warming (BONGRAIN 1988). The geographic and stratigraphic dis-

tribution of this extinct genus underlines its thermophily (Text-fig. 11). Geographically, it is restricted to the Mediterranean and Atlantic region, where its species never crossed the latitude of the Loire Basin. The large specimens with shells exceeding heights of 15 cm are indeed typical for transgressive and presumably warm periods during the Miocene (e.g. *Macrochlamis holgeri* - Late Eggenburgian of NE Austria, *Macrochlamis albina* - Early Badenian of SE Austria, Tortonian of SE France) and the Pliocene (e.g. *Macrochlamis latissima* - Piacenzian of N Italy). Its extinction at the end of Pliocene coincides with the initiation of the Late Pliocene to Pleistocene ice ages and the reduction of continental shelf regions. The holotype of *Macrochlamis dregeri* (a younger synonym of *Macrochlamis albina*) from the Early Badenian limestones of the Styrian Basin, with a shell height of 240 mm, is among the

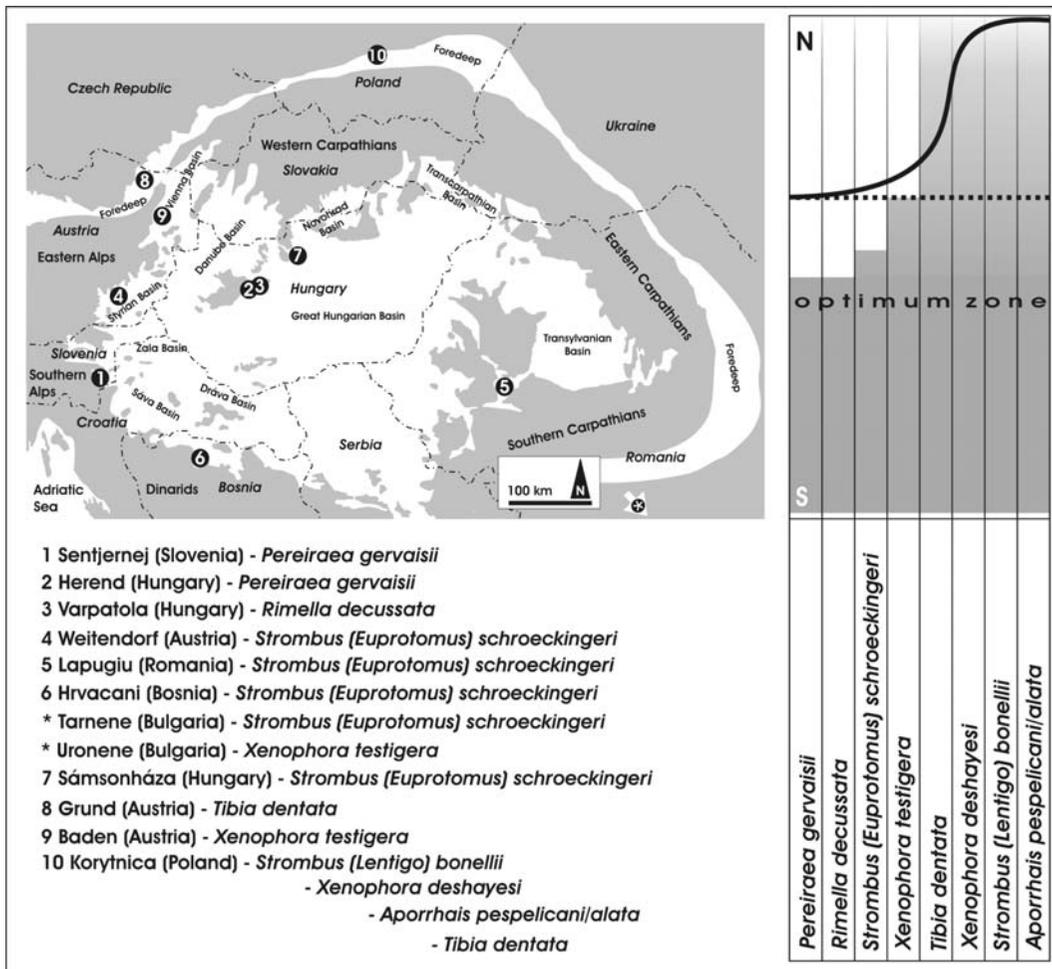


Fig. 11: The illustration shows the tentative evolution of the bivalve genus *Macrochlamis* subjected to chronostratigraphy, eustacy and isotopic events. Arrows mark the horizons with the occurrence of large-sized species (shell height > 15cm) in the Paratethys, correlating with global warming phases. The phylogenetic relationships are partly adopted from BONGRAIN (1992), the stratigraphic and palaeogeographic ranges are inferred from ongoing investigations by one of the authors (O.M.).

largest pectinids that ever lived in the Paratethys. The *Macrochlamis albina* group is apparently absent from the Badenian of the Alpine-Carpathian Foredeep and the northern Central Paratethys.

In addition to the diversification of the shallow-water bivalve assemblages, the climatic optimum is also indicated by re-immigration of representatives of the Isognomonidae; this common element in the Oligocene to Early Miocene of the Central Paratethys disappeared prior to the Karpatian. Additionally, the first occurrence of the Plicatulidae in the Central Paratethys Miocene within the Lower Lagenidae Zone is noteworthy. *Isognomon* and *Plicatula* are typical tropical representatives that are absent from the Modern Mediterranean Region.

Another example pointing to the influence of the palaeoclimate on the bivalve assemblage of the Lower Lagenidae Zone are the carditids. This family is today restricted to the tropical and subtropical regions and does not exceed the latitude of the Mediterranean Sea. These shallow-water representatives, which attach by byssus on roots of algae or on sides of rock crevices, are represented by only 2 species in the Karpatian horizon. The diversification to 17 species within the Lower Lagenidae Zone, including the introduction of taxa already present in the Mediterranean Late Burdigalian such as *Megacardita jouanneti*, is another indication for a warm spell reaching the Central Paratethys at the beginning of the Middle Miocene.

CONCLUSIONS

The late Early Miocene and the early Middle Miocene is documented in eastern Austria by two faunas: the Karpatian fauna of the Korneuburg Formation and the Laa Formation, and the Early Badenian fauna of the Grund Formation and the Gaindorf Formation. The latter faunas have equivalents in the Vienna Basin (Niederleis, Nodendorf) and in the Styrian Basin (e.g. Wetzelsdorf, Weitendorf, Pöls). Although formerly intermingled, the Karpatian and Badenian assemblages are separated by a stratigraphic gap of approximately 1.5 my.

Within the Paratethys the Early Badenian gastropod fauna is a valuable biostratigraphic indicator. Several species, such as *Trigonostoma crenatum* (HÖRNES), *Rimella (Dientomochilus) decussata* (DEFRANCE), *Pereiraea gervaisi* (VÉZIAN), *Strombus (Euprotomus) schroeckingeri* HÖRNES, *Malea (Cadium) denticulata* (DESHAYES) and *Cassidaria cingulifera* HOERNES & AUINGER, seem to be restricted to this rather short time slice. The same holds true for the bivalves. Hence, *Thyasira (Th.) michelottii* (R. HOERNES), *Saturnia pusio* (PHILIPPI), *Carditamera (Lazariella) hippoea*

(BASTEROT), *Clausinella bulgarica* (KOJUMDIEVA) and *Arcopagia (A.) strohmayeri* (HÖRNES), seem to be restricted to the Early Badenian.

A bloom of many Early Miocene (Karpatian, Burdigalian) relics characterizes the fauna of the early Middle Miocene in the Central Paratethys. Thus, the area acted as an Early Badenian sanctuary for several Early Miocene species, which are otherwise highly characteristic for the Karpatian or even Eggenburgian assemblages of the Paratethys. These “old fashioned” survivors such as *Tympanotonus papaveraceus* (BASTEROT), *Turritella gradata* MENKE, *Protoma cathedralis* (BASTEROT), *Euthriofusus burdigalensis* (DEFRANCE), *Ocenebra crassilabiata* (HILBER) and *Perrona louisae* (HOERNES & AUINGER) have a last but strong acme in the “Grund Fauna”, yet fade abruptly without reaching the Middle Badenian. Some of these relics are not “Kümmerforms” indicating a near extinction, but rather display a peak in both numbers of individuals and size. These species account for the transitional character of the fauna – linking the Early Miocene with the advanced Middle Miocene faunas.

Even within persistent species such as *Melongena cornuta* (AGASSIZ), *Genota ramosa elisae* HOERNES & AUINGER, *Tibia dentata* (GRATELOUP), *Gyrineum (Aspa) marginatum* (MARTINI), *Mitra scrobiculata* (BROCCHI), *Tudicla rusticula* (BASTEROT) and the *Nassarius dujardini-edlaueri-schoenni* group, an optimum during the Early Badenian is obvious. The resulting strange “Burdigalian” aspect of the Early Badenian mollusc assemblages is suggested to be related with the Langhian climatic optimum, which triggered the conspicuous bloom of the “last array” of Early Miocene species. A climatic zonation in the Middle Miocene Central Paratethys can be postulated from the presented gastropod data. A “drop-zone” is indicated by the restricted distribution of *Strombus (Euprotomus) schroeckingeri* and *Pereiraea gervaisii*. The giant pectinids of the *Macrochlamis albina* group confirm that this pattern is likely restricted to the southern border of the Central Paratethys.

The climatic optimum is well indicated by the high diversification of the mollusc fauna as shown for the bivalves in Text-fig. 6. Clearly, the diversification is most conspicuous within inhabitants of shallow-water environments. Additionally, typical shallow-water thermophilic taxa, such like *Isognomon*, which retreated from the Paratethys during the Ottnangian, re-entered the Central Paratethys with the Middle Miocene transgression. Others, such as *Plicatula*, which is restricted to the modern tropic oceans, entered the Paratethys for the first time. This is supported by the spectacular diversification event within the carditiid bivalves from 2 Karpatian up to 17 Lower Badenian species.

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