Int J Earth Sci (Geol Rundsch) (2009) 98:1741–1766
DOI 10.1007/s00531-008-0322-3

ORIGINAL PAPER

Life in the sublittoral zone of long-lived Lake Pannon: paleontological analysis of the Upper Miocene Szák Formation, Hungary

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Received: 7 December 2007 / Accepted: 19 April 2008 / Published online: 9 May 2008

Abstract Life and depositional environments in the sublittoral zone of Lake Pannon, a large, brackish Paratethyan lake from the Late Miocene, were reconstructed from fossils and facies of the Szák Formation. This formation is exposed in several, roughly coeval (9.4–8.9 Ma) outcrops, located along strike of the paleo-shelf-break in northwestern Hungary. The silty argillaceous marl of the formation was deposited below storm wave base, at 20–30 to 80–90 m water depth. The abundance of benthic organisms indicates that the bottom water was usually well oxygenated. Interstitial dysoxia, however, may have occurred immediately below the sediment–water interface, as evidenced by occasional preservation of trace fossils such as *Diplocraterion*. The fauna comprised endemic mollusks, including brackish cockles of the subfamily Lymnocardiinae, dreissenid mussels (*Congeria*), and highly adapted, uniquely large-sized deep-water pulmonate snails (planorbids and lymnaeids). Ostracods were dominated by endemic species and, in some cases, endemic genera of candonids, leptocytherids, cyprids, and loxoconchids. Fish remnants include a sciaenid otolith and the oldest skeletal occurrence of *Perca* in Europe. The phytoplankton comprised exclusively endemic coccolithophorids, mostly endemic dinoflagellates (prevailingly *Spiniferites*), and cosmopolitan green algae. The Late Miocene fauna and flora of Lake Pannon were in many ways similar to the modern Caspian biota, and in particular cases can be regarded as its precursor.

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Keywords Lake Pannon · Caspian Sea · Long-lived lakes · Paleoecology · Depth tolerance

Introduction

Lake Pannon was a large, long-lived, brackish lake that occupied the Pannonian Basin System in the Late Miocene and earliest Pliocene. The lake hosted a highly endemic fauna and flora, of which the mollusks, ostracods, fishes, dinoflagellates, calcareous nannoplankton and some other algal groups are known as fossils (Papp et al. 1985; Stevanović et al. 1990). The biota of Lake Pannon originated partly from restricted marine, partly from freshwater taxa. The mollusks and ostracods provide outstanding examples of adaptive radiations in the lake, leading to a breathtaking species diversity in many groups (Müller et al. 1999; Geary et al. 2000).

The lake's biota displays close similarities to that of the modern—or, rather, of the pre-twentieth-century—Caspian Sea. This similarity is partly a consequence of the fact that both basins were once part of a larger brackish-water basin system, the Paratethys. Species that evolved in the isolated Lake Pannon during the Late Miocene could successfully migrate into, and survive through the Pliocene and Pleistocene within, the Black Sea and Caspian Basins. The other, perhaps more important, factor that caused ecological similarities between Lake Pannon and the Caspian Sea is the analogous physical development of the two waterbodies, which triggered sometimes very similar, sometimes more contrasting ecological and evolutionary response of the biota.

A paleoecological survey of mollusks in Lake Pannon indicated that the profundal environments (basin floor, slope) were inhabited by a low-diversity group of bivalves and a few gastropods, whereas the littoral and shallow water environments (shelf) hosted a rich and diverse fauna of brackish to freshwater clams and snails (Juhász and Magyar 1992; Magyar 1995). In between these two extremes, a specific, medium-diversity mollusk fauna lived on the muddy bottom of the sublittoral zone. This zone was rarely or never affected by sand deposition, but it still received some light to maintain a relatively ecologically diverse association of mollusks and other animals. The estimated water depth for this zone is of tens of metres; it included the upper part of the slope, and, during periods of high lake level, the "outer shelf" as well.

The sublittoral deposits of Lake Pannon are exposed in a long and narrow zone along the western margin of the Transdanubian Range in northwestern Hungary (Fig. 1), where they are called Szák Formation (Jámbor 1980). We collected fossils and carried out paleoecological observations in eight, roughly coeval outcrops of this zone with the objective of better understanding the sublittoral environment and its life in Lake Pannon and comparing them with those of the present-day Caspian.

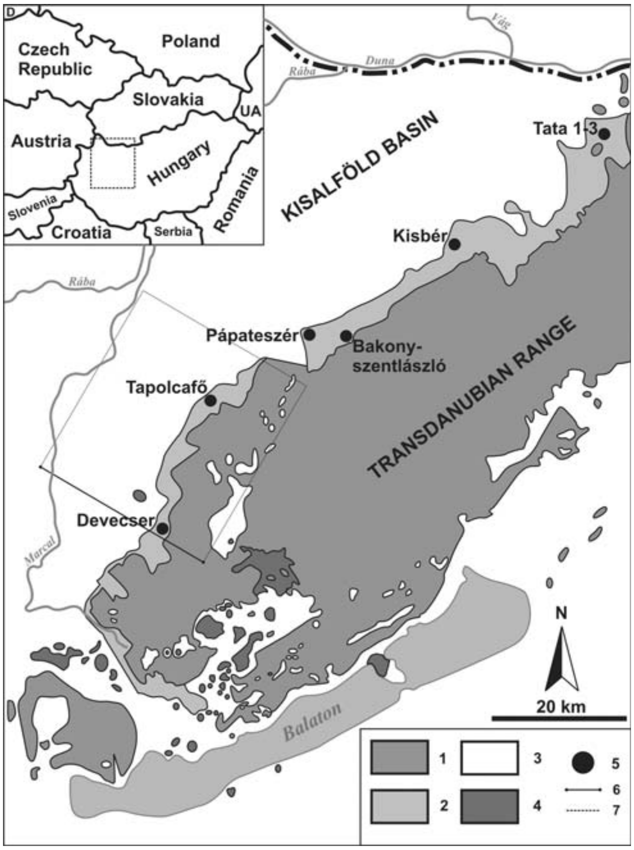


Fig. 1 Location and geological map of the study area in NW Hungary (without the Quaternary; based on Jámbor 1980). *1* pre-Late Miocene basement, *2* sublittoral deposits of Lake Pannon (Szák Formation), *3* littoral to deltaic deposits of Lake Pannon and overlying fluvial sediments (Dunántúl Group), *4* Upper Miocene-Pliocene volcanics (Tapolca Formation), *5* location of investigated outcrops, *6* location of seismic profile in Fig. 2, *7* location of block diagram in Fig. 2

Geological background

The Pannonian Basin System formed in the late Early Miocene and in the Middle Miocene as a result of extension and rifting governed by thrusting in the surrounding Carpathian orogene (Horváth et al. 2006). At about the Middle Miocene-Late Miocene boundary, the water body of the basin became isolated from the sea, and Lake Pannon formed. The lake reached its largest areal extent at ca. 9.5 million years ago, as basin subsidence continued due to cooling of the lithosphere. Many intrabasinal ridges and basement highs, including the Transdanubian Range (Fig. 1), were partly or completely inundated by this time (Magyar et al. 1999).

The lake's basin was gradually filled by sediments that rivers transported from the surrounding uplifted areas. Sediment influx and shoreline progradation from the NW was especially intense (Pogácsás et al. 1988; Vakarcs et al. 1994). The paleo-waterdepth of Lake Pannon can be reconstructed from basin morphology revealed by seismic surveys (Fig. 2). A generalized basin profile comprises a low-gradient morphological shelf, a slope clinoform with up to 5° gradient, and a flat basin floor. The heights of clinoforms indicate that the lake water depths (not taking into account the effect of subsequent compaction) were typically between 200 and 400 m in the lake, although considerably larger depths might have occurred in subbasins that were reached by shelf accretion only in the late phase of basin development. The basin floor and the slope were prevailingly muddy with intermittent turbidite deposition, whereas the shelf was characterized by sand-prone deltaic sedimentation (Juhász 1992).

The Kisalföld (or Danube) Basin (Fig. 1) received sediments from the north, northwest, and west (Magyar et al. 2007). The shelf-break (shelf/slope boundary) gradually shifted towards the SE (Fig. 2). The sediments deposited in Lake Pannon and in the adjacent fluvial systems draped the entire (or almost the entire) Transdanubian Range by the end of the Miocene (Jámbor 1980; Magyar et al. 1999).

Sometime in the Pliocene the Transdanubian Range was tectonically inverted; it started to uplift, whereas the Kisalföld Basin continued to subside (Horváth and Cloetingh 1996; Horváth and Tari 1999). This differential motion was so intense that the originally SE-dipping Lake Pannon clinoforms have been tilted backwards in the intermediate zone between the range and the basin (see the right side of the seismic profile in Fig. 2). Miocene sediments have been eroded from the top of the range, and Lake Pannon deposits became exposed in a few km wide and ca. 120-km-long zone along the northwestern edge of the range (Fig. 1). In map view, the offshore deposits occur immediately next to the basement rocks, whereas the deltaic sediments of the shelf outcrop in a parallel zone further to the west. Because the axis of the elongate Transdanubain Range paralleled the strike of the shelf-margin clinoforms, the sediments exposed along the foot of the range are roughly coeval.

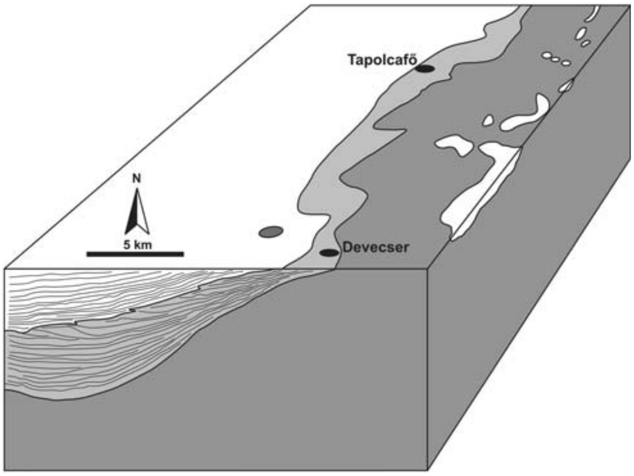


Fig. 2 Block diagram from the eastern margin of the Kisalföld Basin (for location and colour code see Fig. 1). The *line* drawing of a seismic profile in the front indicates shelf accretion from NW to SE, and post-depositional westward tilting. The strike of the Transdanubian Range (NE-SW) is perpendicular to progradation, suggesting that the outcrops along the northwestern foot of the range, including those at Devecser and Tapolcafő, are roughly coeval. Not to vertical scale. The total thickness between the top of the seismic profile and the bottom of Lake Pannon deposits along the SW vertical edge of the block is approximately 800 m

The generalized stratigraphy of Lake Pannon deposits in this area is as following. The basement consists of mostly Oligo-Miocene, partly Mesozoic rocks. The Late Miocene Lake Pannon sequence starts with the Kisbér Gravel Formation (Jámbor 1980); its maximum thickness is about 10 m, but it often occurs only as a thin transgressive lag. The overlying sublittoral deposits comprise the Szák Formation (Jámbor 1980). It is a homogenous, unstratified, grey or bluish-grey clayey silt and silty argillaceous marl that reaches a few tens of m thickness in the outcrops. Its upper, oxidized part is yellow in colour. The Szák Formation, where not directly exposed, is either conformably overlain by the littoral, silty or sandy layers of the Somló Formation (Jámbor 1980), or unconformably covered by thin Quaternary deposits.

Materials and methods

Outcrops

Eight outcrops have been investigated (Table 1). In general, they expose grey, unstratified, homogenous clayey fine silt and argillaceous marl with platy parting. The ratio of the silt component is often increasing upwards. The carbonate content of the sediment is typically between 25 and 35%. The mollusk shells are usually evenly distributed, suggesting autochtonous or almost autochtonous burial. The most common mollusk species is *Congeria czjzeki*, hence the popular name "czjzeki marl".

At the town of Tata, the Szák Formation is exposed in three outcrops along the eastern side of the Budapest–Vienna railway line (Cziczer and Magyar 2006). The southernmost outcrop (Tata 1) is the only location where we could study the transgressive lag at the bottom of the Szák Formation. This several-cm-thick stratum overlies a coarse-grained, grey Oligo-Miocene sandstone, and is composed of pebbly sand and silt, abunding in fossil bivalves. The shells are often abraded, reflecting intense wave

Table 1 The investigated outcrops of Szák Formation

Outcrop	Location	Exposed thickness (m)	Lithology	Sedimentary structure	Polarity measurement	Investigated fossils				
						Mollusks	Ostracods	Fish	Dinoflagellates	Nannoplankton
Tata 1	N 47° 38’ 52.36” E 18° 21’ 05.35”	19	Lowermost part pebbly silt, upper part silty claymarl	Lowermost part stratified, upper part homogenous		•			•	•
Tata 2	N 47° 39’ 12.07” E 18° 21’ 00.23”	26	Silty claymarl	Homogenous, with one coquina layer	•	•	•			•
Tata 3	N 47° 40’ 11.05” E 18° 19’ 49.93”	25	Silty claymarl	Homogenous		•		•		
Kisbér	N 47° 30’ 36.93” E 18° 01’ 29.02”	18	Silty claymarl	Homogenous, with trace fossils	•	•	•	•	•	•
Bakonyszentlászló	N 47° 24’ 14.11” E 17° 49’ 13.79”	15	Silty claymarl, silt	Locally stratified		•				•
Pápateszér	N 47° 22’ 25.05” E 17° 41’ 24.66”	10	Clayey silt	Homogenous		•				•
Tapolcafő	N 47° 17’ 15.73” E 17°30’ 27.88”	20	Lower part clayey silt, upper part silt, clay, marl	Lower part homogenous, upper part stratified, laminated	•	•				
Devecser	N 47° 05’ 48.44” E 17° 25’ 13.53”	18	Silty claymarl	Homogenous		•				•

action. The most common mollusk fossil in this layer is *Congeria partschi*, a species which is otherwise not common in the Szák Formation, and generally considered to have been a shallow water dweller. The middle outcrop (Tata 2) proved to be the richest in mollusks of all the outcrops we investigated during this study. A single coquina lense within the argillaceous marl contained some reworked littoral forms, such as *C. partschi* and *Melanopsis pygmaea*. The northernmost outcrop (Tata 3) was the least fossil-rich of the three Tata outcrops. In all the three outcrops, the Szák Formation is unconformably overlain by a few-m-thick Pleistocene cover.

The peculiarity of the Kisbér outcrop is that the trace fossils are relatively common. Mollusks and ostracods are also abundant. In Bakonyszentlászló, mollusks are common, but their preservation is usually worse than in Tata and Kisbér. The Pápateszér and Tapolcafő outcrops are poor in mollusk fossils; the upper third of the latter, with laminites and poorly preserved leaves, is entirely devoid of them. This part of the sequence probably belongs to the Somló Formation. Finally, the Devecser outcrop contains a lot of mollusk shells, but the overall diversity is lower than in Tata or Kisbér.

Sampling and laboratory procedures for magnetostratigraphy

Magnetostratigraphic investigations have been carried out in three outcrops (Table 1).

Dry and weathered materials were removed from the wall of the claypits, and the samples were cut from undisturbed, unaltered and wet sediments at ~50-cm stratigraphic intervals. Modifications due to weathering were observed in the upper part of the exposures and in several beds, but these oxidized sediments were not sampled. The cubical samples were cut from the unconsolidated sediments with a brass knife and placed in plastic boxes, which were then sealed and stored in a refrigerator to inhibit desiccation.

The samples were processed at the joint laboratory of the Geological Institute of Hungary and Eötvös Loránd Geophysical Institute. Laboratory measurements employed a two-axis CCL cryogenic magnetometer. Following measurement of the natural remanent magnetization, a series of pilot samples were selected for progressive alternating field (AF) demagnetization. These pilot samples were demagnetized in a one-component Schoenstedt demagnetizer up to 90 mT or until the intensity decreased below the noise level of the magnetometer. The relatively soft secondary magnetizations disappeared at 15–30 mT, and the majority of inclinations exhibited no hint of different polarities near the threshold level of stability. The remaining samples were demagnetized at two or three steps in the range of 15–50 mT. The stable directions were used to calculate the latitude of the virtual geomagnetic pole (VGP).

Methods of carbon and oxygen isotope measurements

Stable isotope investigations have been carried out on mollusk shells from outcrop Tata 2. Carbon and oxygen isotope compositions were determined using the conventional H_3PO_4 digestion method at 25°C (McCrea 1950) and a Finnigan MAT delta S mass spectrometer at the Institute for Geochemical Research, Hungarian Academy of Sciences, Budapest. The results are expressed in the δ-notation $[\delta = (R_1/R_2 - 1) \times 1{,}000]$, where R_1 is the $^{13}C/^{12}C$ or $^{18}O/^{16}O$ ratio in the sample and R_2 the corresponding ratio of the standard (V-PDB for C and V-SMOW for O), in ‰. Reproducibilities are better than ±0.1‰.

Phytoplankton studies

Although the primary focus of our study was benthic life in the sublittoral zone, we also investigated the phytoplankton in some pilot samples. Our objective was to better assess the biodiversity in this environment, and to provide data for biostratigraphic interpretation. Two palynological and six nannoplankton preparations have been investigated for dinoflagellates and coccoliths, respectively (Table 1). For the latter, standard smear slides were studied using a light microscope (1,000× magnification) at normal and crossed nicols.

Stratigraphic correlation and age

The depositional model of the Kisalföld Basin (Magyar et al. 2007) predicts that the investigated outcrops are roughly coeval, because the Transdanubian Range, and thus the zone of outcrops are more or less perpendicular to the direction of shoreline propagation (Fig. 2). This expectation is fully met on the level of biostratigraphic resolution; the investigated outcrops all belong to the upper part of the *C. czjzeki* Zone in terms of sublittoral mollusk biostratigraphy, and to the *Spiniferites paradoxus* dinoflagellate zone (Korpás-Hódi 1983; Sütő-Szentai 1991).

In order to establish a more precise correlation between the outcrops, magnetostratigraphic investigations were carried out in three locations: Tata 2, Kisbér, and Tapolcafő. The sampled 21 m thickness in Tata 2 almost covers the entire thickness of the Szák Formation at this location (26 m). In Kisbér and Tapolcafő, however, only the upper part of the profile was accessible for sampling; the lowermost 8–9 m of the clay was not exposed or was under water, respectively. The base of the Tata 2 section exhibits a short interval of normal polarity, followed by a reversed polarity zone, and the top of the section is normal again (Fig. 3). In Kisbér, the VGP plot shows predominantly normal polarity, and a narrow interval of reversed polarity at the base of the section (Fig. 3). The Tapolcafő section displays normal polarity (Fig. 3). A comparison of these records suggests that Tata has the most complete polarity record, and that the sampled intervals of the two other outcrops may correlate with the upper, normal polarity part of the Tata outcrop.

Magyar et al. (2007) conducted seismic correlations between four magnetostratigraphic test boreholes in the Kisalföld Basin. These correlations suggest that the seismic reflectors that emerge to the surface in the vicinity of Devecser within the sublittoral facies zone (Fig. 2) belong to polarity chron C4An, with an age of about 8.9–9.0 Ma in the time scale of Lourens et al. (2004). Somewhat to the north, near Tapolcafő, the reflectors are slightly older (9.1–9.3 Ma) and include the upper part of chron C4Ar. Therefore, the measured polarity profiles in Tapolcafő and Kisbér can be correlated with chron C4An, whereas in Tata with chron C4An and C4Ar, including C4Ar1n at the base of the sequence. The estimated age of the investigated outcrops is thus 9.4–8.9 Ma.

This age characterizes the Szák Formation outcrops in the northwestern foreland of the Transdanubian Range, where the formation was first described at the village of Szák (this outcrop is not accessible any more). If interpreted as a spatially contiguous but highly diachronous lithological unit across the Pannonian Basin, however, the Szák Formation can be older (e.g. Sopron, 10 Ma, Magyar et al. 2007) as well as considerably younger (e.g. Bátaszék, 7.5 Ma, Lennert et al. 1999) than the outcrops we investigated in this study.

Paleoclimate

Although paleoclimate is not the focus of our study, our objectives of reconstructing the environment and comparing the biota with that of the modern Caspian justify a brief overview here. Based on 34 palynological samples recovered from 5 boreholes that penetrated the Szák Formation at Naszály, Tata, and Pápa, Nagy (2005) quantitatively estimated the mean annual temperature as ranging between 12.2 and 13.4°C (average 12.6). The samples contained very few tropical elements, like *Podocarpus*, more subtropical forms, such as *Keteleeria, Liquidambar, Zelkova, Cedrus*, and *Ginkgo*, but they were dominated by temperate plants, such as Ericaceae, *Tilia, Ulmus, Carpinus, Castanea, Betula, Alnus, Corylus, Quercus, Fagus, Pterocarya, Carya*, and Coniferae, including *Pinus silvestris, Picea, Abies*, and *Tsuga*. Freshwater plants (Nymphaeaceae, *Myriophyllum, Sparganium, Typha*) and planktic green algae (*Botryococcus, Spirogyra, Cooksonella*) were also abundant (Nagy 2005). The inferred temperature fits into the general, slow cooling trend that followed the sudden temperature drop at the end of the Miocene Climatic Optimum (Böhme 2003; Jiménez-Moreno 2006).

A temporary increase in humidity around 10–9.5 million years ago within the Central Paratethys was recorded with independent methods. According to Lueger (1978), land mollusks indicate a temporary shift towards more humid, "Atlantic" climate in biozone F (ca. 9.8 Ma) of the Vienna

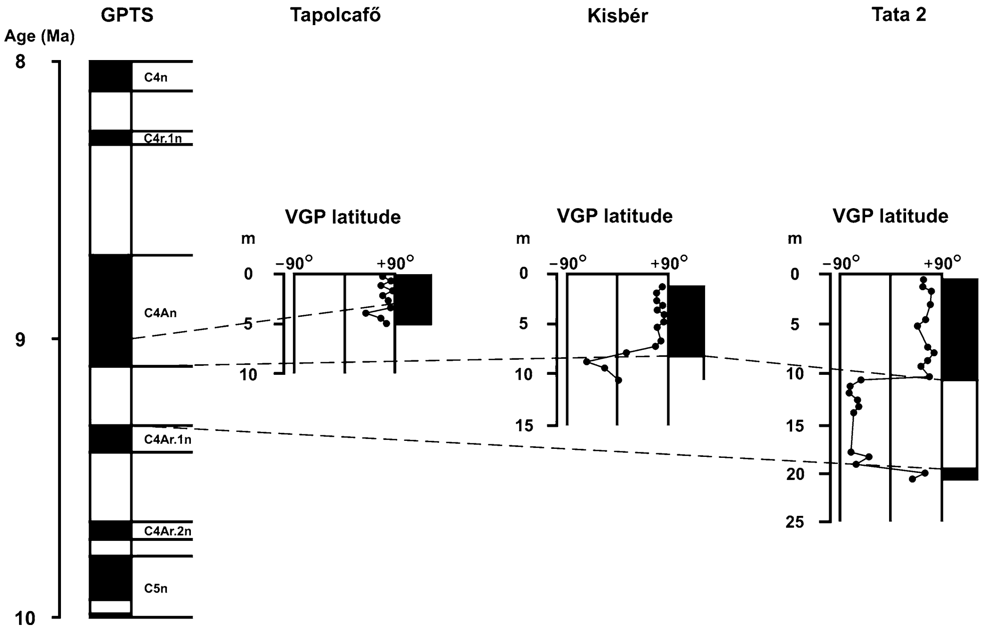


Fig. 3 *Plots* of latitudes of the virtual geomagnetic pole (VGP) for the outcrops at Tata 2, Kisbér and Tapolcafõ, and correlation of the polarity zones with the geomagnetic polarity time scale (GPTS) of Lourens et al. (2004). *Black* normal polarity; *white* reversed polarity

Table 2 Mollusks from the outcrops of Szák Formation

	Tata 1–3	Kisbér	Bakonyszentlászló	Pápateszér	Tapolcafő	Devecser
Lymnocardium majeri (M. Hörnes 1862)	•					•
Lymnocardium apertum (Münster 1839)	•					
Lymnocardium tegulatum (Halaváts 1886)	•		•	•		
Lymnocardium triangulatocostatum (Halaváts 1882)	•	•	•	•	•	•
Lymnocardium pseudosuessi (Halaváts 1882)	•	•	•			•
Lymnocardium aff. *brunnense* Andrusov 1903	•					
Lymnocardium aff. *secans* (Fuchs 1870)	•					
Lymnocardium aff. *rogenhoferi* (Brusina 1884)	•	•		•		
Lymnocardium aff. *zagrabiense* (Brusina 1874)				•		•
Lymnocardium sp.	•					
"Pontalmyra" otiophora (Brusina 1884)	•	•	•			•
Pontalmyra sp. 1	•					
Pontalmyra sp. 2	•					
Paradacna abichi (R. Hörnes 1874)		•	•	•		•
Paradacna sp. 1	•					
Paradacna sp. 2			•			•
Congeria czjzeki M. Hörnes 1870	•	•	•	•		•
Congeria maorti Barnabás & Strausz 1991		•				
Congeria cf. *zsigmondyi* Halaváts 1882						•
Congeria partschi Czjzek 1849	•					
Congeria ungulacaprae (Münster 1839)	•					
Pisidium krambergeri Brusina 1884					•	•
Valenciennius reussi Neumayr 1875	•	•	•	•	•	•
Radix kobelti (Brusina 1884)	•	•				•
Radix cf. *croatica* (Gorjanovic-Kramberger 1890)	•					
"*Gyraulus*" *tenuistriatus* (Gorjanovic-Kramberger 1900)		•				
"*Gyraulus*" sp.	•					
Valvata minima Fuchs 1877	•					
Micromelania fuchsiana Brusina 1874	•					
Melanopsis pygmaea Partsch 1856	•					

Basin. A stable isotope study of mollusk shells from various localities in western Hungary (Mátyás et al. 1996) showed that samples from the upper part of the sublittoral *C. czjzeki* zone, including those from Tata 2, represented a considerable excursion towards negative values in δ^{18}O. This pattern was interpreted to reflect increased humidity. Another isotope study by Harzhauser et al. (2007) confirmed the increasing humidity trend, but put the peak somewhat earlier (ca. 10 Ma). Fortelius et al. (2006) observed a minimum in mammal tooth crown height (hypsodonty) and inferred a precipitation maximum in the Pannonian Basin in MN9 and MN10 zones, i.e. 9–10 Ma. Quantitative estimates on the mean annual precipitation during the humidity peak are based on mammals (Bernor et al. 2003; van Dam 2006), herpetofauna (Böhme et al. 2006), and macroflora (Bernor et al. 2003; Bruch et al. 2006), and range between 1,000 and 1,350 mm. Variations in lake size may also reflect changes in humidity. Magyar et al. (1999) argued that Lake Pannon reached its largest extent during the *Spiniferites paradoxus* biochron, some 9.5 million years ago. Sacchi et al. (1999) interpreted the top of the *C. czjzeki* zone as a maximum flooding surface.

Various independent methods thus unanimously indicate a considerable humidity peak sometime between 10 and 9 Ma. The temporal (chronostratigraphic) correlation of the data requires further refinement, but it seems clear that the Szák Formation in the study area was deposited during or immediately after this "anomalously" humid period.

Animal life

Mollusks

Mollusks were found and collected in all the eight outcrops (Table 2, Figs. 4, 5, 6). The fossils were generally well

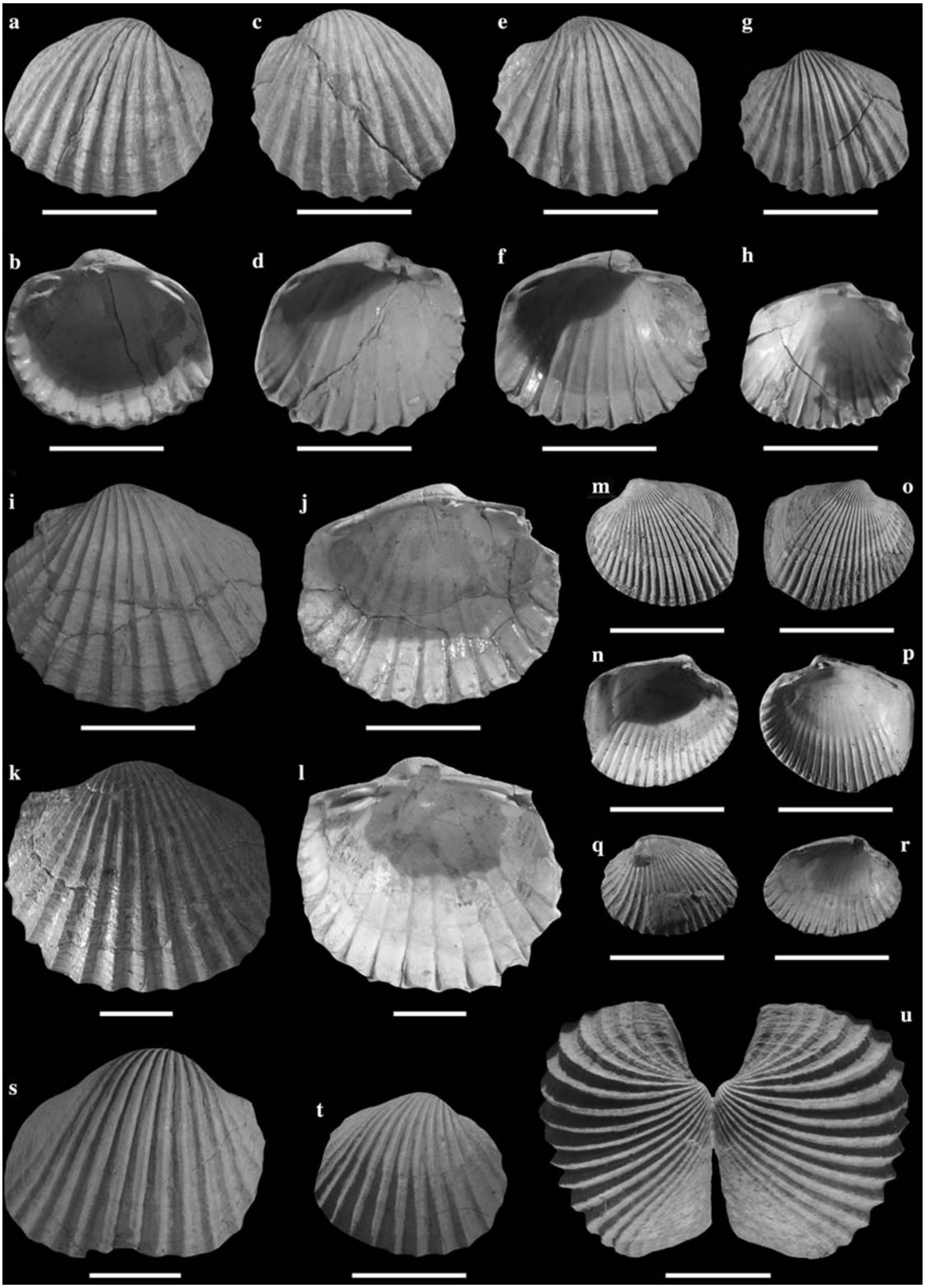


Fig. 4 Endemic brackish-water cockles (Lymnocardiinae) from the Szák Formation. **a–d** *Lymnocardium apertum* (Münster 1839), Tata 2. **e–h**, **t** *Lymnocardium* aff. *brunnense* Andrusov, Tata 2. **i–l** *Lymnocardium* aff. *rogenhoferi* (Brusina 1884), Tata 2: **i**, **j**, **l** Kisbér: k. **m–p** *Pontalmyra* sp. 1, Tata 2. **q**, **r** *Lymnocardium triangulatocostatum* (Halaváts 1882), Tata 2. **s**, **u** *Lymnocardium* aff. *secans* (Fuchs 1870), Tata 2. Scale bar, 1 cm

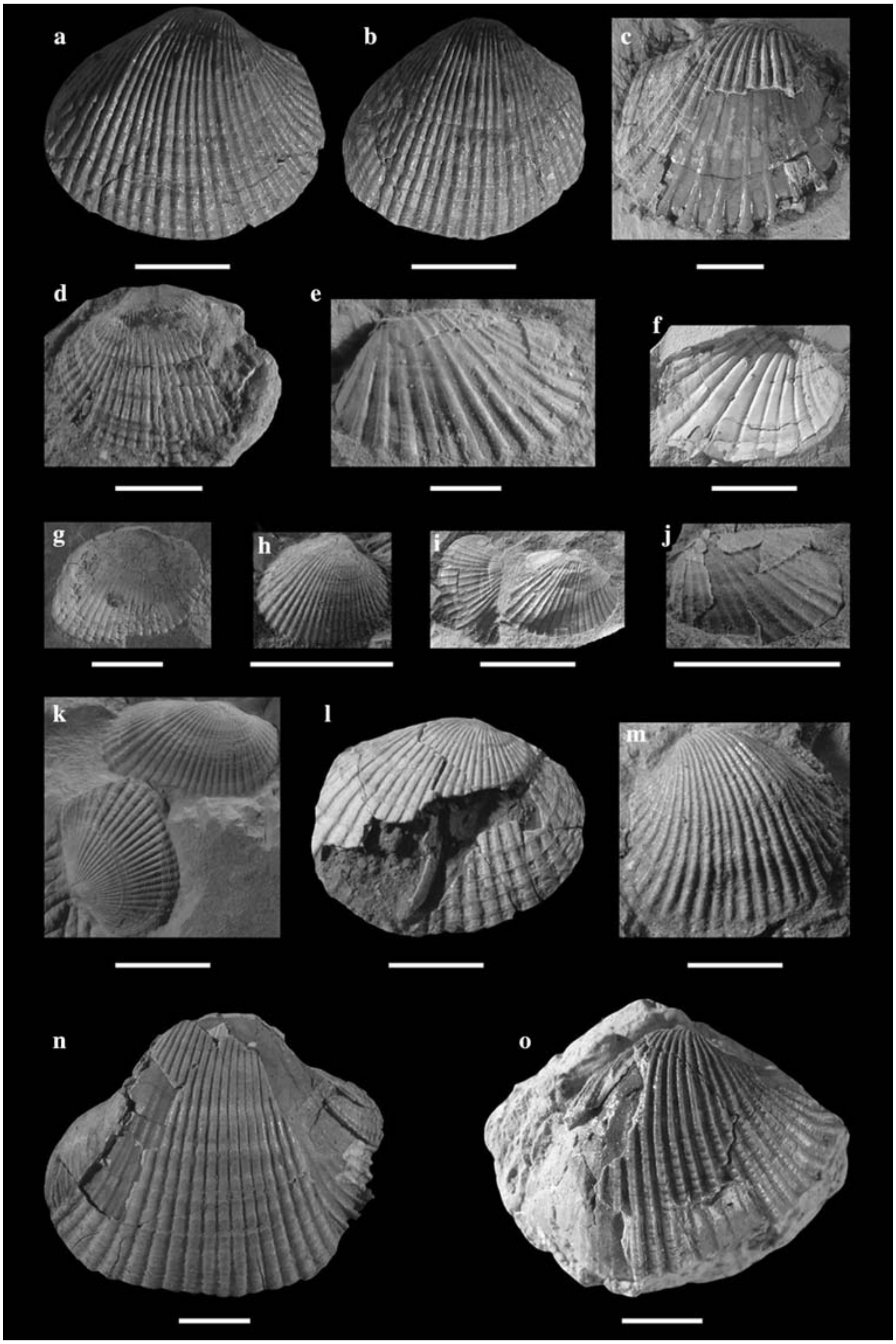


Fig. 5 Endemic brackish-water cockles (Lymnocardiinae) from the Szák Formation. **a**, **b** *Lymnocardium pseudosuessi* (Halaváts 1882), Kisbér. **c** *Lymnocardium* aff. *zagrabiense* (Brusina 1874), Devecser. **d** *Pontalmyra* sp. 2, Tata 1. **e** *Paradacna* sp.1, Tata 2. **f** *Paradacna abichi* (R. Hörnes 1874), Kisbér. **g**, **h** *"Pontalmyra" otiophora* (Brusina 1884), Bakonyszentlászló: g; Tata 2: h. **i** *Paradacna* sp. 2, Bakonyszentlászló. **j** *Paradacna* sp. 1(?), juvenile specimen, Tata 2. **k**, **l**: *Lymnocardium majeri* (M. Hörnes 1862), Tata 2. **m**, **o** *Lymnocardium tegulatum* (Halaváts 1886), Tata 1: m; Pápateszér: o. **n** *Lymnocardium* sp., Tata 2. Scale bar, 1 cm

preserved and evenly distributed in the argillaceous marl, reflecting autochtonous or almost autochtonous burial. Evidence of reworking was extremely rare.

All the 31 species we identified were endemic to the lake. However, some 3 million years later, during the Pontian age of the Eastern Paratethys, *Valenciennius* and

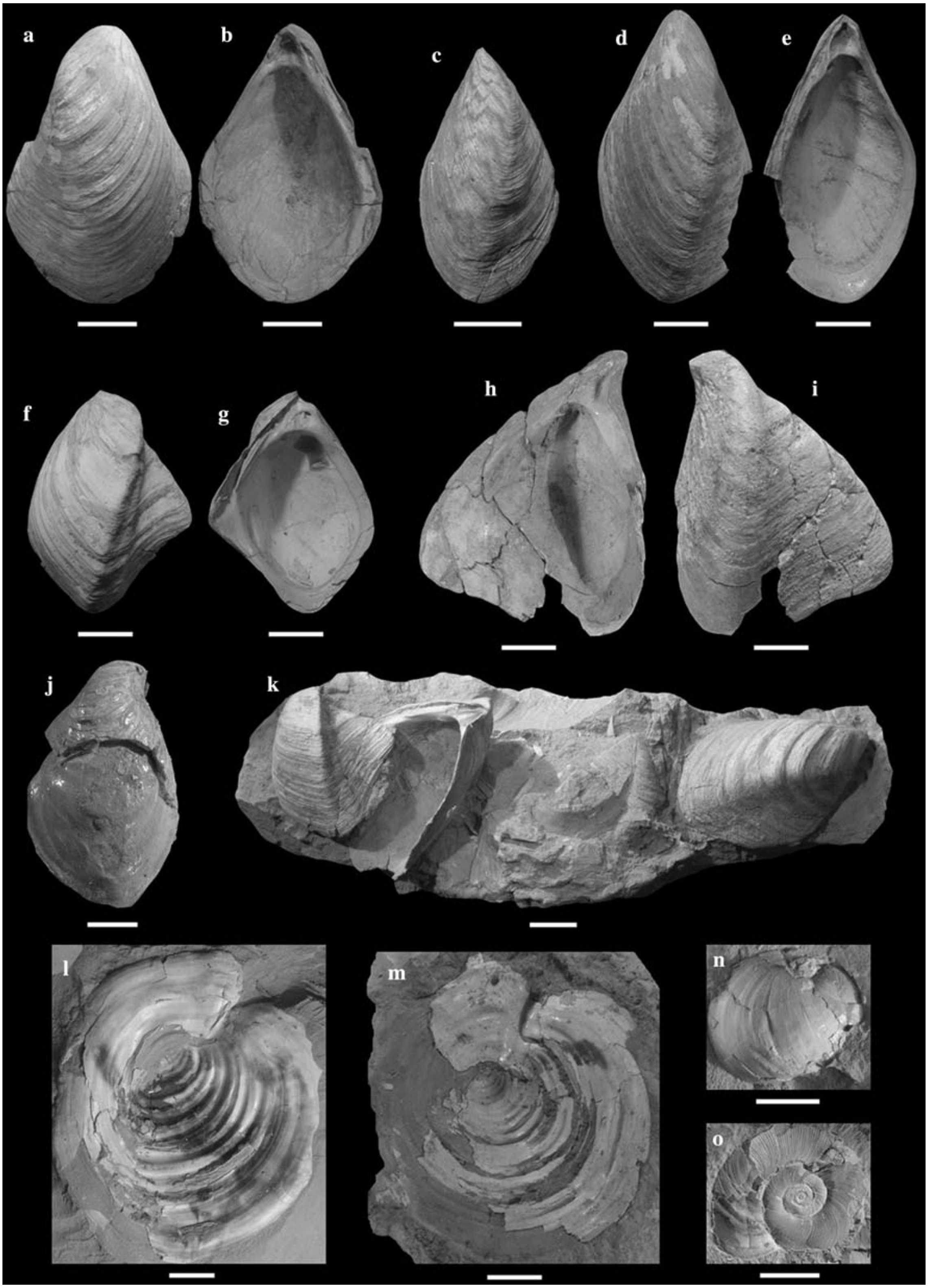


Fig. 6 Dreissenid mussels and pulmonate snails from the Szák Formation. **a–e** *Congeria czjzeki* M. Hörnes 1870, Tata 2. **f–g** *Congeria partschi* Czjzek 1849, Tata 2. **h–i** *Congeria ungulacaprae* (Münster 1839), Tata 2. **j** *Congeria* cf. *maorti* Barnabás & Strausz 1991, Kisbér. **k** a coquina from Tata 2, with (left to right) *C. partschi*, *C. ungulacaprae*, and *C. czjzeki*. **l–m** *Valenciennius reussi* Neumayr 1875, Tata 2: l; Tata 1: m. **n** *Radix kobelti* (Brusina 1884), Tata 2. **o** "*Gyraulus*" *tenuistriatus* (Gorjanovic-Kramberger 1900), Kisbér. Scale bar, 1 cm

Lymnocardium majeri spread into the Black Sea Basin (the latter as *L. peregrinum*), *“Pontalmyra” otiophora* and *Paradacna abichi* went to the Dacian Basin, to the Black Sea and Caspian Basins (Taktakishvili 1967, 1987), and even to the Mediterranean (Messinian “lagomare”; Esu 2007).

Brackish cockles (subfamily Lymnocardiinae) represent the most diverse group in the Szák Formation (Table 2, Figs. 4, 5). Recent Lymnocardiinae (if the stem genus *Cerastoderma* is not taken into account) are exclusively brackish water dwellers, living in the Paratethyan water bodies of the Black Sea and the Caspian and Aral Lakes. The modern genera of the subfamily (with the possible exception of *Didacna*), however, are usually considered to have been derived from Pliocene *Cerastoderma*; thus they cannot be directly linked to Lake Pannon endemics (Nevesskaja et al. 2001). Lymnocardiinae achieved a wide range of adaptations from shallow lagoons to profundal environments both in Lake Pannon and in the modern Caspian Sea.

The dreissenids are represented by genus *Congeria* in the sublittoral zone of Lake Pannon (Table 2, Fig. 6). Of the five species listed, only *C. czjzeki* is common. *C. partschi* was found in huge quantities in outcrop Tata 1, in the basal, pebbly transgressive lag. This species is not a typical sublittoral one; in fact, it is far more common in littoral, coarser-grained deposits. *Congeria* is completely missing from the present-day Paratethyan Basins (Black and Caspian Seas). Dreissenids are represented there by the genus *Dreissena*. Although the latter attained noteworthy adaptations in the Caspian Sea, including significant depth tolerance down to 500 m or more (Tarasov 1996; Tarasov and Chepalyga 1996), the morphological diversity of modern Caspian *Dreissena* cannot be compared to the spectacular bloom of forms in Lake Pannon *Congeria*.

Perhaps the most peculiar feature of the sublittoral mollusk community in Lake Pannon is the overwhelming dominance of pulmonates among snails (Table 2). The fossils of *Valenciennius reussi* and *“Gyraulus” tenuistriatus*, for instance, occur exclusively in deep-water (sublittoral and profundal) sediments (Fig. 6). In Lake Pannon pulmonates, the extreme ecological adaptations to deep water are not accompanied by spectacular morphological change. The only exception is the highly decoiled, limpet-like shell of the lymnaeid *Valenciennius* (Taktakishvili 1967). Although similar morphology occurs in other groups of Basommatophora, such as the freshwater *Ancylus* and *Acroloxus*, the large size and deep-water occurrence of *Valenciennius* led us to hypothesize that this animal had a very specific life strategy. This strategy could have involved floating or swimming in the water column, similarly to the taxonomically unrelated, but morphologically resembling marine *Carinaria*. In order to explore this issue, we measured the stable isotopic composition of some *Valenciennius* shells from the Tata 2 outcrop along with shells of cardiids and dreissenids that had been buried into the same layer. We supposed that if the water of Lake Pannon was stratified according to temperature or salinity, then the stable isotope values might reflect this difference between the benthic cardiids, dreissenids and lymnaeids (heavier values) and the—hypothetically—floating Valenciennius (lighter values).

In the δ^{18}O/δ^{13}C crossplot, *Valenciennius*, benthic cardiids and dreissenids, and the lymnaeid gastropod *Radix* cluster separately ($P = 91{,}67\%$; Fig. 7). The δ^{18}O values alone provide no opportunity for distinction between the various genera. The results conform to earlier measurements from this stratigraphic interval, showing generally rather negative values (Mátyás et al. 1996, Harzhauser et al. 2007). The δ^{13}C values, however, display a clear

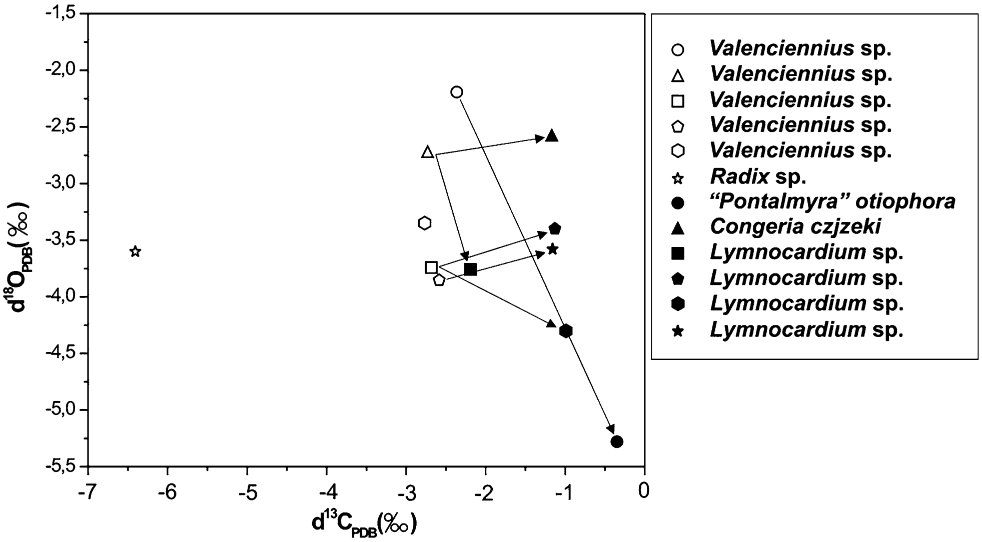


Fig. 7 Crossplot of δ^{18}O and δ^{13}C values from mollusk shells (outcrop Tata 2). Shells of *Valenciennius* display somewhat lower δ^{13}C than bivalves from the same thanatocoenoses (connected by *arrow*)

pattern in that *Valenciennius* shells contain less heavy isotopes than do bivalves from the same thanatocoenosis. This difference might be the result of various vital effects or diets of different species and thus does not provide evidence for any specific adaptation. The considerable difference in δ^{13}C values between the closely related genera of *Valenciennius* and *Radix* in the same outcrop, however, is noteworthy and deserving of further study.

Ostracods

Ostracods have been investigated in two outcrops. In Tata 2, 50 taxa have been identified from 26 samples (Fig. 8). In Kisbér 26 taxa were recovered from 13 samples, 19 of which are shared with Tata 2. Juvenile Candoninae have been recovered from five additional samples from Kisbér (Fig. 9). The ostracod valves are translucid, slightly yellow or white, seldom opaque. The associations are rich in juveniles of different ontogenic stages, particularly of Candoninae, indicating autochthonous burial of the microfossils (Ruiz et al. 2003). The rare freshwater taxa such as *Cryptocandona* and ?*Metacypris* could have been transported occasionally to the environment. Valves are frequently damaged and broken, especially in Tata, and particularly of the smooth, large, adult Candoninae. Small and ornamented valves, e.g. *Loxocorniculina djaffarovi*, are typically well preserved, with a considerably lower percentage of broken valves. The original species ratio was evidently changed during taphonomic processes and thus, species community structure was not calculated.

Many taxa are left in open nomenclature due to an exclusive presence of the instars (*Lineocypris*) or

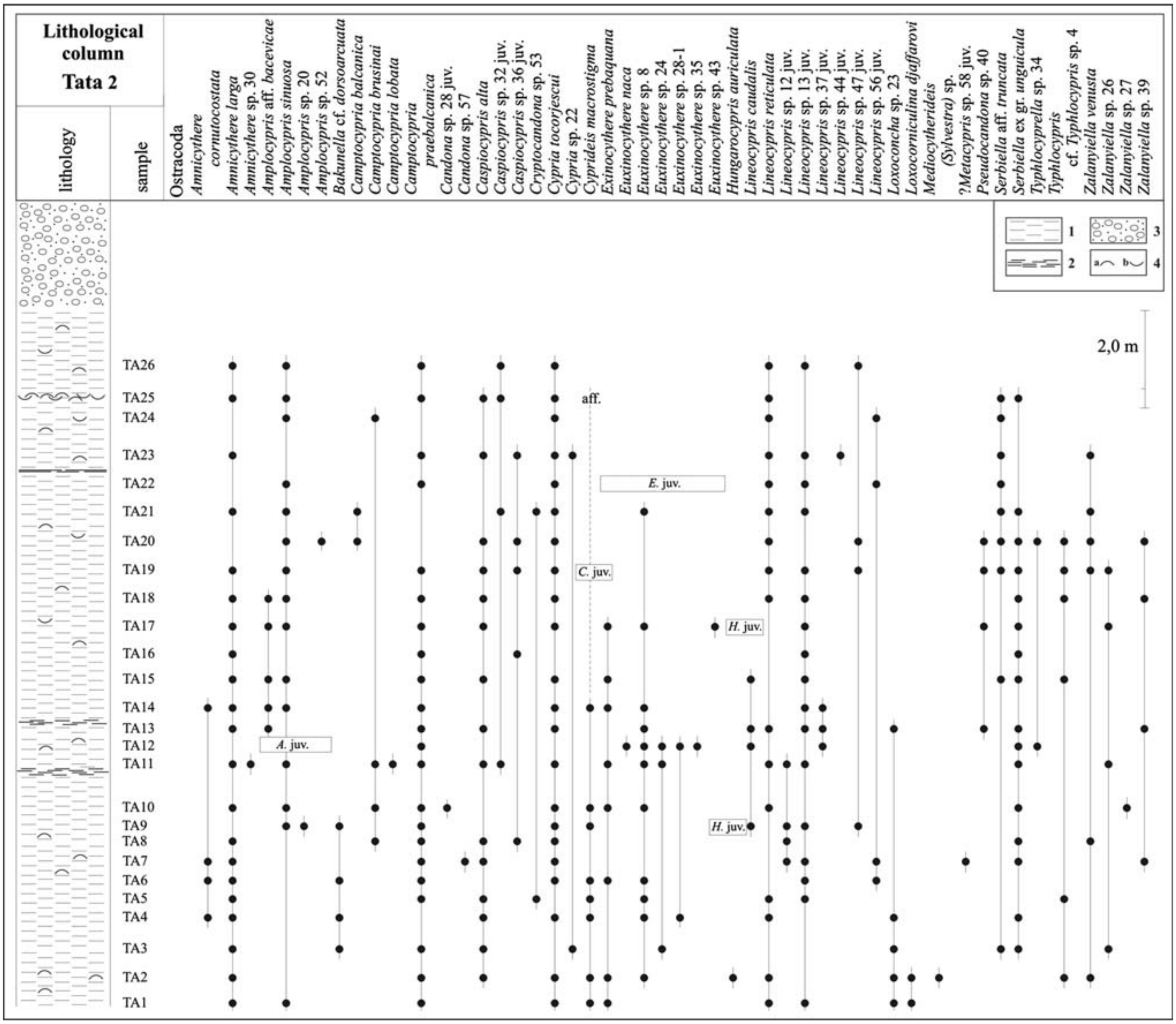


Fig. 8 Ostracods from outcrop Tata 2. *1* claymarl, *2* tectonised claymarl, *3* sandy gravel, *4* mollusk shells in (**a**) concave and (**b**) convexe position

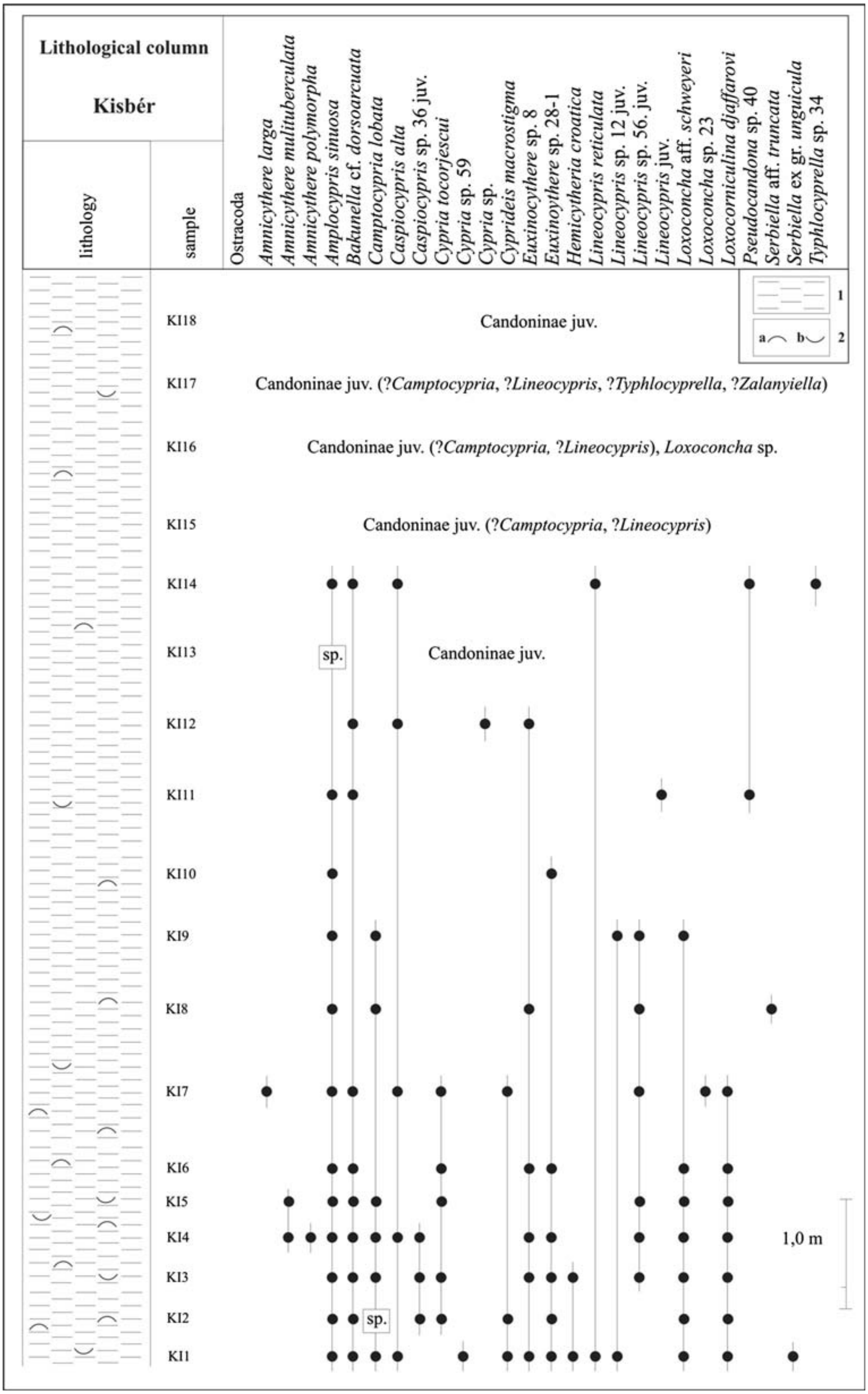


Fig. 9 Ostracods from the Kisbér outcrop. *1* claymarl, *2* mollusk shells in (**a**) concave and (**b**) convexe position

incomplete valves (*Zalanyiella*), which did not allow an exact determination of the species. *Euxinocythere* species in open nomenclature may represent new taxa.

The 26 taxa determined on the species level from the two outcrops were all endemic to Lake Pannon (Fig. 10). Half of them are not known to have ever left the intra-Carpathian area (*Amnicythere larga* Krstić 1973, *Amplocypris* aff. *bacevicae* Krstić 1973, *Amplocypris sinuosa* Zalanyi 1944, *Camptocypria brusinai* Sokać 1972, *Caspiocypris alta* (Zalanyi 1929), *Cyprideis macrostigma* Kollmann 1958, *Hemicytheria croatica* Sokać 1970, *Herpetocyprella auriculata* (Reuss 1850), *Lineocypris reticulata* (Méhes 1907), *Lineocypris caudalis* Krstić 1972, *Serbiella* ex gr. *unguicula* (Reuss 1850), *Typhlocypris* cf. *Typhlocypris* sp. 4 Krstić 1972, and *Camptocypria praebalcanica* Krstić 1972). Three species found their way to the Dacian Basin during Pontian time (*Cypria tocorjescui* Hanganu 1962, *Serbiella* aff. *truncata* Sokać 1972, and *Amnicythere polymorpha* Olteanu 1989; the latter is in fact found in Lake Pannon deposits for the first time). Six species migrated into the Euxinian (Black Sea) and Caspian Basins during the Pontian (*Amnicythere multituberculata* (Livental 1929), *Amnicythere cornutocostata* (Schweyer 1949), *Bakunella dorsoarcuata* (Zalanyi 1929), *Camptocypria balcanica* Zalanyi 1929, *Camptocypria lobata* Zalanyi 1929, and *Euxinocythere naca* (Méhes 1908) (Krstić and Stancheva 1990; Sokać 1990)). Two of these species, *A. multituberculata* and *B. dorsoarcuata* are still living in the Caspian Sea. Finally, during the Messinian "lagomare" event, *Euxinocythere prebaquana* (Livental 1929), *Loxoconcha* aff. *schweyeri* Suzin 1956, *Zalanyiella venusta* (Zalanyi 1929), and *Loxocorniculina djaffarovi* Schneider 1956 appeared in the Mediterranean, where they are used in paleontological studies as important biostratigraphic and paleoecological (brackish salinity) markers (Carbonnel 1978; Gliozzi and Grossi 2004).

With the exception of *Amplocypris* and *Hemicytheria*, which are Middle to Late Miocene Central Paratethyan and Lake Pannon endemics, respectively, these ostracod genera are all extant; thus their present-day ecology may serve as a tool to reconstruct the Lake Pannon environment.

Numerous *Amnicythere* species are living in the littoral and sublittoral zones of the Black and Caspian Seas at brackish salinity, but some species have been observed in freshwater bays and estuaries (Gofman 1966; Schornikov 1964, 1966). *Amnicythere multituberculata* (Livental 1929), an extant Lake Pannon species, lives today in the central and southern Caspian Basins at salinities of 11.5–13.5‰. It is missing in the northern Caspian Basin, however, where freshwater input from the Volga river effectively dilutes salinity (Gofman 1966).

Cyprideis torosa Jones, 1850, a widely distributed recent counterpart of the Upper Miocene *Cyprideis*, occurs in a wide range of salinities from almost freshwater to hypersaline conditions, but its greatest abundance is observed at salinities of 2–16.5‰ in coastal ponds, lakes, lagoons, estuaries, fjords, deltas, and salt marshes (Meisch 2000).

Recent *Cypria* are typically freshwater species that tolerate mesohaline conditions (ca. 5 to 18‰ according to Meisch, 2000).

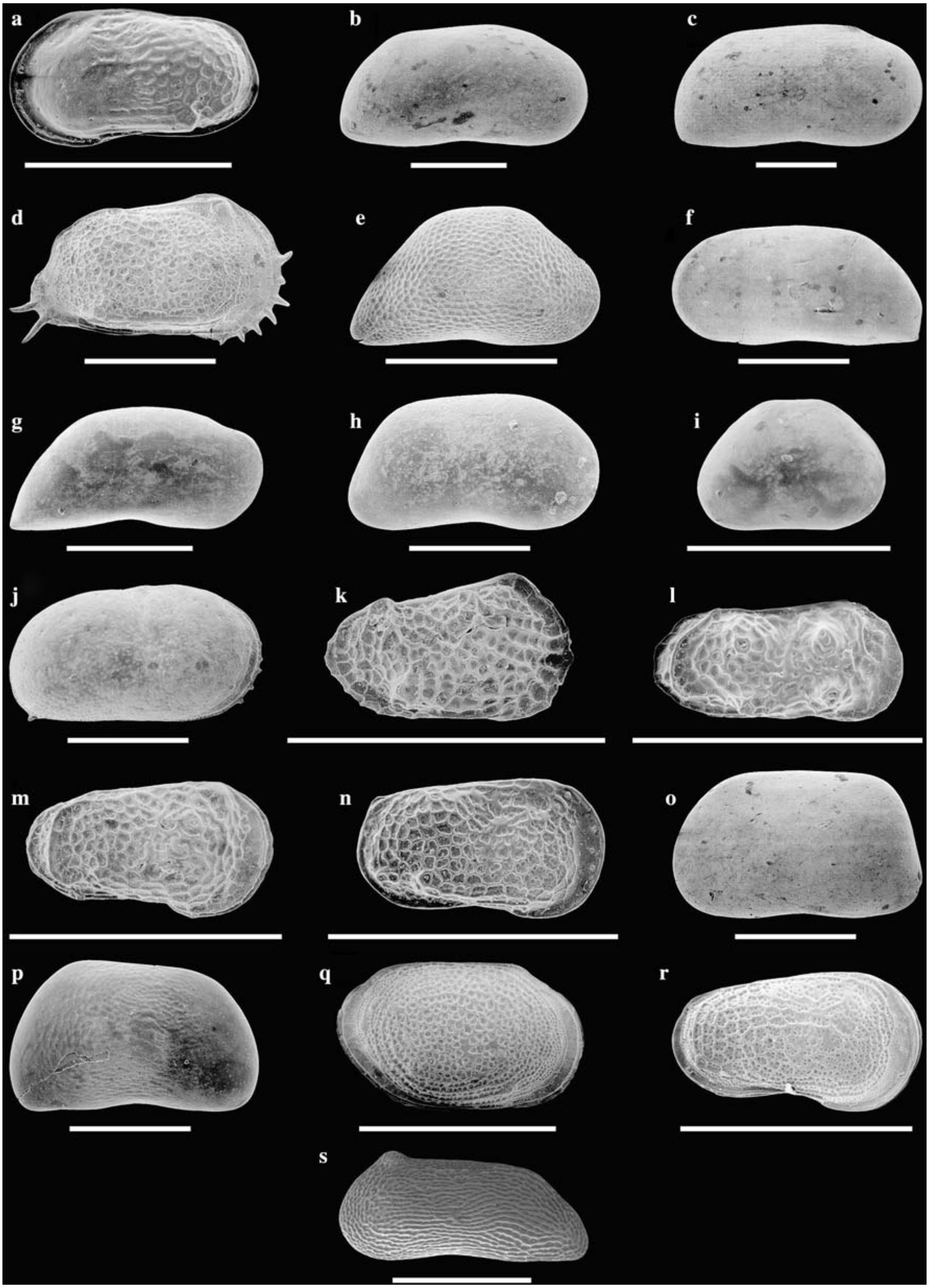
Fig. 10 Ostracods from the Szák Formation (Tata 2 and Kisbér). ▶ Abbreviations: *LV* left valve, *RV* right valve, ♀ female, *juv*.juvenile. **a** *Amnicythere cornutocostata* (Schweyer 1949); LV, Tata, sample TA14, No. RP29-1, external lateral view. **b** *Amplocypris* aff. *bacevicae* Krstić 1973; RV, Tata, sample TA14, No. RP29-2, external lateral view. **c** *Amplocypris sinuosa* Zalanyi 1944; RV, Tata, sample TA25, No. RP29-3, external lateral view. **d** *Hemicytheria croatica* Sokać 1970; RV, Kisbér, sample KI3, No. RP29-4, external lateral view. **e** *Bakunella* cf. *dorsoarcuata* (Zalanyi 1929); RV juv., Kisbér, sample KI14, No. RP29-5, external lateral view. **f** *Camptocypria brusinai* Sokać 1972; LV, Tata, sample TA8, No. RP29-6, external lateral view. **g** *Camptocypria praebalcanica* Krstić 1972; RV, Tata, sample TA8, No. RP29-7, external lateral view. **h** *Caspiocypris alta* (Zalanyi 1929); RV, Kisbér, sample KI1, No. RP29-8, external lateral view. **i** *Cypria tocorjescui* Hanganu 1962; RV, Tata, sample TA19, No. RP29-9, external lateral view. **j** *Cyprideis macrostigma* Kollmann 1958; RV♀, Tata, sample TA9, No. RP29-10, external lateral view. **k** *Loxocorniculina djaffarovi* Schneider 1956; RV, Tata, sample TA2, No. RP29-11, external lateral view. **l** *Euxinocythere prebaquana* (Livental 1929); RV♀, Tata, sample TA10, No. RP29-12, external lateral view. **m** *Euxinocythere* sp. 8; RV♀, Tata, sample TA12, No. RP29-13, external lateral view. **n** *Euxinocythere* sp. 28-1; RV♀, Tata, sample TA12, No. RP29-14, external lateral view. **o** *Lineocypris reticulata* (Méhes 1907); LV, Tata, sample TA25, No. RP29-15, external lateral view. **p** *Lineocypris* 13. ? juv.; RV, Tata, sample TA12, No. RP29-16, external lateral view. **q** *Loxoconcha* aff. *schweyeri* Suzin 1956; RV, Kisbér, sample KI5, No. RP29-17, external lateral view. **r** *Amnicythere polymorpha* Olteanu 1989; RV, Kisbér, sample KI4, No. RP29-18, external lateral view. **s** *Serbiella* aff. *truncata* Sokać 1972; RV, Tata, sample TA3, No. RP30-1, external lateral view. Scale bar, 0.5 mm. The figured individuals are deposited in the Slovak National Museum in Bratislava (Slovakia) under the numbers mentioned in the text (No. RPXX-YY)

At least three fossil species of *Herpetocyprella* can be recognized in Lake Pannon deposits. These were previously assigned to *Hungarocypris* (Danielopol et al. 2007). The single extant representative of *Herpetocyprella*, *H. mongolica* Daday 1909, is endemic to Lake Issyk-Kul, Kyrgyzstan, Central Asia. It lives together with other recent thalassic and athalassic forms, such as *Cyprideis torosa* and *Tyrrhenocythere amnicola* at a salinity of 6‰, in alkaline (pH about 8.6–8.9), highly oligotrophic and calcium-oversaturated waters with oxygen concentration of 6.8–9.6 mg O_2/l (Bronshtein 1947; Ricketts et al. 2001).

Mediocytherideis (*Sylvestra*) is reported from marine environments of the Red Sea and brackish environments of the Mediterranean. Upper Miocene *Mediocytherideis* are associated with brackish taxa (Krstić and McKenzie 1991).

Euxinocythere and *Loxocorniculina* are known from brackish ostracode assemblages of the Paratethys and the Eastern Mediterranean, but *Euxinocythere* also tolerates freshwater littoral to deep limnic conditions (Pipík and Bodergat 2004).

Loxoconcha rhomboidea Fischer 1855, type species of the genus, is a phytal littoral and shallow littoral species living in fully marine environments, found rarely in outer estuaries. *Loxoconcha eliptica* Brady 1868 lives in brackish waters of estuaries, lagoons, and pools, and associates with algae and mud (Athersuch et al. 1989). Numerous



Loxoconcha are adapted to the brackish milieu of the Caspian Sea (Gofman 1966).

Candoninae are the most diversified group in Tata 2 and Kisbér. Beside *Candona* and *Cryptocandona*, other genera, such as *Bakunella*, *Lineocypris, Pseudocandona* (triangular Lake Pannon species are attributed into *Typhlocypris*), *Camptocypria, Caspiocypris, Serbiella, Typhlocyprella*, and *Zalanyiella* are typical for Lake Pannon. They have trapezoidal, elongated rectangular, or triangular shape. Such outlines are common in physically stable water environments (Carbonel et al. 1988). This hypothesis was successfully applied in a paleoecological model of the Turiec Basin (Pipík 2001), but we are far from concluding that this morphology reflects a stable environment in Lake Pannon as well. *Bakunella dorsoarcuata* is living in the central and southern Caspian Sea at salinities of maximum 13.5‰, in the sublittoral zone (Gofman 1966).

The distribution of families by species number in the entire fauna of Tata 2 and Kisbér is depicted in Fig. 11. The given ratios do not fully reflect the original composition of the biocenosis because they were strongly influenced by mechanical properties of the valves and other changes during taphonomic processes.

Ostracods of seven families have been found in these sublittoral deposits. In order to better reveal the high species diversity within Candonidae, this family is divided in the subfamilies Candoninae and Cyclocypridinae. Candoninae represents the most abundant taxon (29 species, 51%). It is composed of typical Paratethyan candonins—*Bakunella*, *Lineocypris, Serbiella, Camptocypria, Caspiocypris, Typhlocyprella*, and *Zalanyiella*. The second most diverse family is Leptocytheridae (13 species, 23%). The family Cyprididae is represented only by five species (9%) of endemic *Amplocypris* and *Herpetocyprella*. Cyclocypridinae and Loxoconchidae are rare, representing 7 and 5% of the total species, respectively. The “other families” in the diagram include Hemicytheridae and Cytherideidae (one species each), and a poorly preserved juvenile of ?*Metacypris* (Limnocytheridae). This latter genus is living in vegetated freshwater littoral water bodies (Meisch 2000).

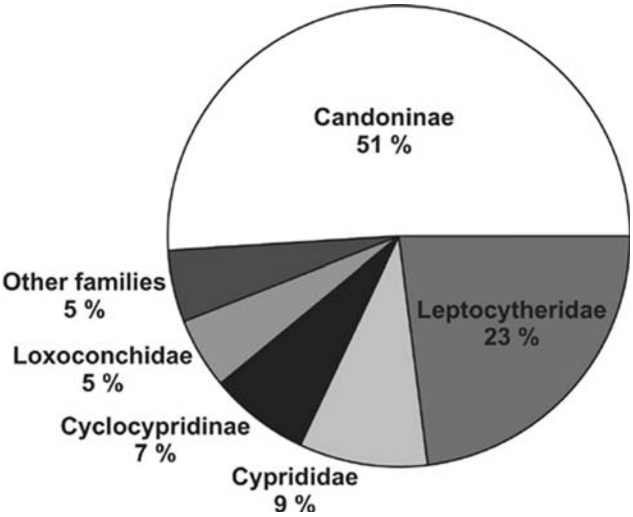


Fig. 11 Percentage of the ostracod species by families in sublittoral clay deposits of Szák Formation. Family Candonidae is divided to two subfamilies, Candoninae and Cyclocypridinae. “Other families” include Hemicytheridae, Limnocytheridae, and Cytherideidae

Fish

Fish skeletons are generally rare in Lake Pannon deposits. Otoliths, teeth, and scales are locally quite abundant, but they have been hardly documented and studied so far; therefore, little is known about the fish community of the lake (Brzobohatý and Pană 1985). From the Szák Formation we collected an otolith (Tata 3) and a skeleton (Kisbér).

The corroded otolith (Fig. 12) belongs to an adult individual of a member of the family Sciaenidae (croakers). The morphology is most similar to the recent species *Umbrina cirrosa* and will be referred to as *Umbrina* aff. *cirrosa* (Linnaeus 1758). Otoliths tentatively assigned to this species are known since the earliest Pannonian of the Central Paratethys (Brzobohaty in Schultz 2004).

Fig. 12 *Umbrina* aff. *cirrosa* (Linnaeus 1758). Otolith from the Szák Formation (Tata 3). Scale bar, 0,5 cm

The Kisbér fossil is a partially articulated skeleton of a percoid fish (Fig. 13). The fish is relatively poorly preserved and is missing the post-anal part of the body. The length from the tip of the snout to the beginning of the anal fin measured 75 mm, indicating a total length of about 130 mm. The systematic position within the Percoidae is supported by the following characters: (1) two separated dorsal fins; (2) origin of the first dorsal fin above the pectoral fin insertion, second dorsal fin opposite anal fin; (3) the first dorsal fin has 13 spines; (4) anal fin with two spines and few (? 5) segmented fin rays; (5) the first anal spine is strongly reduced; (6) the body and the posterior portion of the head are covered by small ctenoid scales (about three scales per vertebra); (7) 15 thoracic (pre-anal) vertebra; (8) operculum with one posterior orientated spine; (9) serration of the ventro-posterior border of the preoperculum not enlarged.

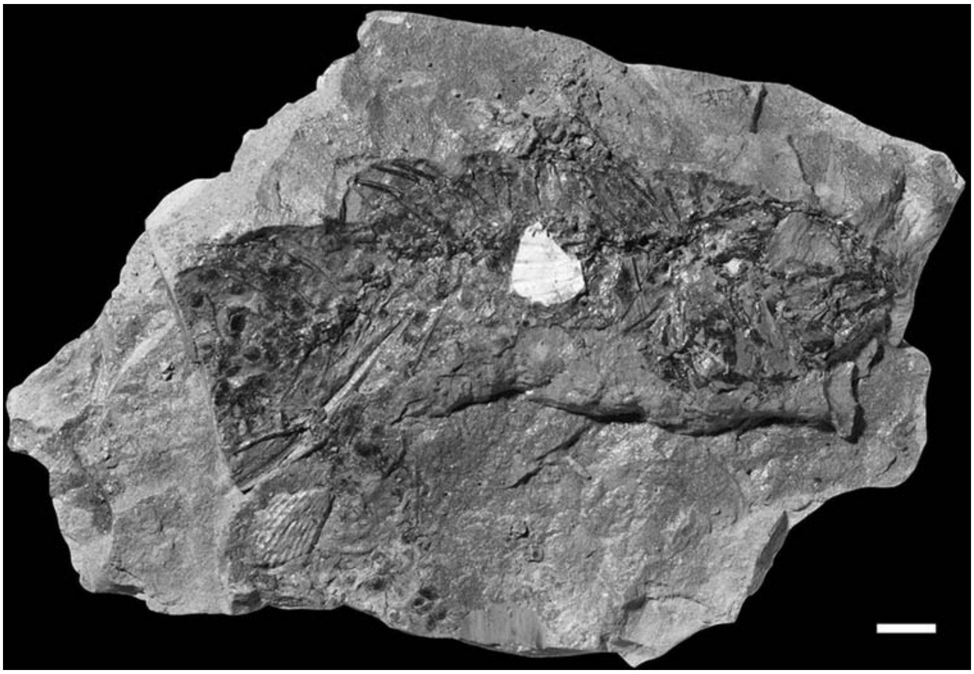


Fig. 13 *Perca* sp. (?*P. edlaueri*). Skeleton from the Szák Formation (Kisbér). Scale bar, 1 cm

Characters 2, 3, 4, and 8 support the affiliation of the fossil to the family Percidae (perches) and characters 1, 6 and 9 give indications of the genus *Perca* known today from three Holarctic distributed species. It differs from the extant species and from the fossil Pliocene species *P. fossilis* by characters 5 and 7, and the few segmented anal fin rays. In the latter respect, it more closely resembles the North American species *P. flavescens* (6–8 rays, Page and Burr 1991) than the Eurasian *P. fluviatilis* (8–9 rays, Bauch 1954; no data available for the Central Asian *P. schrenkii*) and the European *P. fossilis* (7–9 rays, Gaudant 1997). Of more or less similar age like the Kisbér clay are *Perca* otoliths from Öcs (southern part of the Transdanubian Range) and Eichkogel (Vienna Basin). The Öcs otoliths, described by Schubert (1912) as *Percidarum öcsensis* are, according to the author, closely related to *P. fluviatilis*. The Eichkogel material (MN11; Harzhauser et al. 2004) is described by Weinfurther (1950) as *Perca edlaueri*. This author concludes that his species more closely resembles the otoliths of *P. flavescens* than those of *P. fluviatilis*. It is not impossible that the otolith from Eichkogel and the skeleton from Kisbér belong to the same species; this is difficult to demonstrate, because the otoliths of the studied skeleton are too poorly preserved for dissection. Because of this limitation the Kisbér percid will be named here as *Perca* sp. (?*P. edlaueri*).

The described specimen represents the oldest European record of *Perca* which is based on skeletal material. Beside the above-mentioned records, otoliths described as *Perca* sp. and *P. praefluviatilis* are known from the Early Miocene Late-Cerithien- and Hydrobia-Beds (mammal “zones” MN2 and MN3) of the Mainz Basin (Reichenbacher 2000), but their generic status within the Percidae is not fully confirmed (B. Reichenbacher oral information 4/2006).

Perches of the genus *Perca* are relatively unspecialized regarding their habitats. They live today in lakes, ponds and rivers of different size and even enter brackish waters, such as the Baltic Sea and the Caspian and Aral Lakes. The feeding preference of small-sized individuals up to 150 mm (those comparable to the fossil specimen) is mostly zooplankton but contain rarely zoobenthos or small fishes (Gaschott 1928; Bauch 1954).

Similarly unspecialized are the members of the family Sciaenidae. Adults of the recent *Umbrina cirrosa* inhabit coastal marine waters in the East Atlantic, Mediterranean Sea, Black Sea, and Sea of Azov, and their juveniles enter the estuaries. In contrast to *Perca*, the feeding preferences are benthic invertebrates.

The presence of euryecious percids and sciaenids in the Szák Formation clearly indicates brackish water condition with a probable ecological niche partitioning between the zooplanctivorous *Perca* and the zoobenthivorous *Umbrina*.

Trace fossils

In general, Lake Pannon deposits contain several morphological types of ichnofossils (Jámbor 1987; Babinszki et al. 2003; Magyar et al. 2006). From the Szák Formation, Jámbor (1980) reported the mass occurrence of trace fossils in a 20–30 cm thick bed from well cores west of Tata. He described these fossils as “dumb-bell shaped structures in the surface, which reach down 20–30 cm perpendicular to bedding plane", and named them *Spirosiphonella pannonica* and *Minisiphonella transdanubica* (Jámbor 1980). He also mentioned the presence of crawling traces, especially in the lower part of the formation. We found trace fossils (trails) in the Kisbér outcrop. Based on the descriptions and photographs of Jámbor (1980) and our own observations, the following forms could be identified in the Szák Formation.

1. *Diplocraterion* Torell, 1870, *Diplocraterion* isp. (?*D. paralellum* Torell 1870). U-shaped, cylindrical burrows with a spreite (i.e. internal layering that fills the plane between the arms of the U), perpendicular to bedding plane. Diameter of tube, 5–6 mm. Distance between the two vertical parts of tube, 10–15 mm. Depth of tube, 20–30 cm. The host sediment and spreite has similar texture, a difference is only in colour: the burrow and spreite are darker. These are dwelling traces (*Domichnia*).
2. Trail. Single, straight, or Y-shaped branched, thin ridges parallel to bedding plane with unlined walls. Diameter of trails, 2–8 mm. Length of trails, 10–15 cm. Infillings are the same as the host sediment. These are crawling traces (*Repichnia*).

Diplocraterion was likely produced by suspension feeders or surface-detritus feeders (Fürsich 1974). Morton and Miller (1968) list several macroinvertebrate taxa (e.g. polychaetes, annelids, enteropneusts, echiurans) that create U-shaped structures in unconsolidated sediments along New Zealand's modern coasts. They observed that the echiurans produce 60 cm deep burrows. Similar, 30 cm deep, U-shaped burrows are constructed by echiurans in muddy marine environments along the North Sea coast, too (Hertweck 1970). In case of the Szák Formation traces (Jámbor 1980), the host sediment and the spreite show little difference in texture, suggesting that the host animal was a suspension feeder rather than a deposit-feeder.

The *Diplocraterion*-dominated ichnofacies is generally virtually monospecific with low species diversity and a high density of individuals; and the burrows are made by opportunistic animals. This kind of assemblage and the suspension feeding strategy are common in high-energy conditions, which occur mostly in shallow-water, marginal environments, where environmental survival parameters fluctuate rapidly (Mason and Christie 1986; Gaillard and Racheboeuf 2006). Therefore, in the literature, *Diplocraterion* previously has been reported from marine shallow-water, high-energy environments, in the Skolithos ichnofacies (e.g. Fürsich 1974, 1998), and in some cases related to storm events (post-event community) (e.g. Fürsich 1998; Pervesler and Uchman 2004). However, Frey and Goldring (1992) suggested that storm currents can transport the trace makers to deeper environment, and Olóriz and Rodríguez-Tovar (2000) stated that *Diplocraterion* points to a change from the Cruziana ichnofacies to a mixed Skolithos-Cruziana assemblage.

These interpretations cannot be readily applied to the Szák Formation, however, because it hardly contains storm deposits. Rhoads and Boyer (1982) claimed that sea-floor colonization exclusively by suspension-feeders is a common event at present-day poorly oxygenated bottoms. Similarly, Ekdale and Lewis (1991) suggested that *Diplocraterion* may indicate dysaerobic interstitial conditions, but oxygen still had to be sufficiently high to allow an opportunistic assemblage. Leszczynski et al. (1996), also described similar pioneer communities in oxygen-deficient bottom water. They stated that preservation of traces of suspension feeders is possible when deposit feeder activity decreases, for instance, owing to poor oxygenation.

Phytoplankton

Dinoflagellata

A palyonological sample from Tata 1 contained the following dinoflagellates (Fig. 14): *Spiniferites* cf. *bentorii* (Rossignol 1964) Wall & Dale 1970 (1 specimen), *Spiniferites membranaceus* (Rossignol 1964) Sarjeant 1970 (1), *Virgodinium asymmetricum* Sütő-Szentai (subm.) (8), *Chytroeisphaeridia cariacoensis* Wall 1967 (6), *Chytroeisphaeridia hungarica* Sütő-Szentai 1990 (18), *Impagidinium sphaericum* (Wall 1967) Lentin & Williams 1981 (1), *Millioudodinium detkensis* Sütő-Szentai 1990 (1), *Pontiadinium obesum* Sütő-Szentai 1982 (1), Dinoflagellata form 25 (?*Spiniferites paradoxus*, lateral view) (1), Dinoflagellata form 48 (1), Dinoflagellata form 67 (2), and Dinoflagellata form 72 (19). This association indicates the *Spiniferites bentorii coniunctus-Spiniferites paradoxus* zone (Sütő-Szentai 1988).

Another sample, taken from the grey, silty argillaceous marl of Kisbér, also contained a diverse assemblage (Fig. 14). Membranous *Spiniferites* were the most frequent forms, whereas the zone marker *Spiniferites bentorii coniunctus* Sütő-Szentai was rare. The common forms included proximate forms, such as *Impagidinium spongianum* Sütő-Szentai, *Impagidinium globosum* Sütő-Szentai, *Chytroeisphaeridia hungarica* Sütő-Szentai, *Chytroeisphaeridia tuberosa* Sütő-Szentai, *Virgodinium asymmetricum* Sütő-Szentai, *Millioudodinium foveolatum* Sütő-Szentai, *Millioudodinium pelagicum* Sütő-Szentai, *Millioudodinium transdanuvianum* Sütő-Szentai, *Millioudodinium baltesii* Sütő-Szentai, and a chorate form, *Spiniferites bentorii oblongus* Sütő-Szentai. This assemblage is typical of the *Sp. paradoxus-Sp. bentorii coniunctus* zone sensu Sütő-Szentai (1988, 1991), or of the *Spiniferites bentori coniunctus* subzone sensu Bakrač

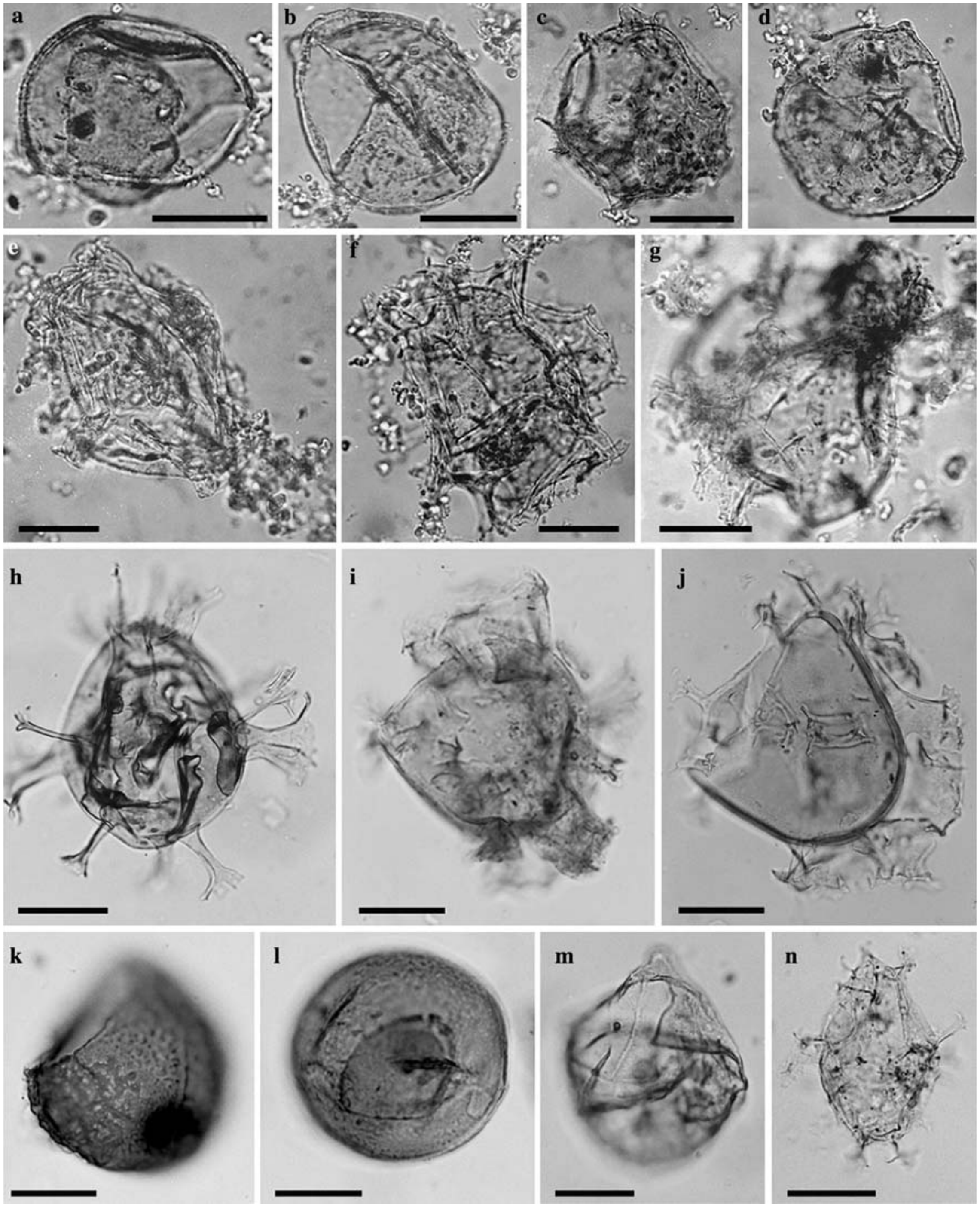


Fig. 14 Dinoflagellates from the Szák Formation. **a** *Chytroeisphaeridia hungarica* Sütő-Szentai 1990, Tata 1. **b**, **d** *Virgodinium asymmetricum* Sütő-Szentai (subm.), Tata 1. **c** *Impagidinium sphaericum* (Wall 1967), Tata 1. **e** Dinoflagellata form 25 (?*Spiniferites paradoxus*, lateral view), Tata 1. **f** *Spiniferites membranaceus* (Rossignol 1964), Tata 1. **g** Dinoflagellata form 48 (*Spiniferites* cf. *paradoxus*), Tata 1. **h** "*Spiniferites bentorii* subsp. *coniunctus*" Sütő-Szentai 1990, Kisbér. **i** *Spiniferites paradoxus* (Cookson & Eisenack 1968), Kisbér. **j** a transitional form between "*Spiniferites bentorii*" and "*Spiniferites paradoxus*", Kisbér. **k** *Impagidinium globosum* Sütő-Szentai 1985, Kisbér. **l** *Chytroeisphaeridia tuberosa* Sütő-Szentai 1982, Kisbér. **m** "*Millioudodinium foveolatum*" Sütő-Szentai 1982, Kisbér. **n**: *Spiniferites bentorii* subsp. *oblongus* Sütő-Szentai 1986, Kisbér. Scale bar, 25 μm

(2005). The processes of chorate forms were often broken, indicating some transport before burial in distal environments. The more robust proximate forms, however, remained intact. The same applies to some membranous forms, which are autochthonous in distal environments and probably could have a holoplanktic life cycle and stayed in the upper part of the water column like *Thalassiphora* (Pross 2001).

The high diversity and abundance of dinoflagellates in the samples suggest that sedimentation occurred in distal, quiet environment, in a time period corresponding to maximum flooding (TMF; Stover et al. 1996).

The dinoflagellate flora recovered from the Szák Formation is dominated by endemic forms. A recent study on the modern dinocysts of the Caspian Sea (Marret et al. 2004) also revealed significant endemism. Of the present-day Caspian dinocysts, *Lingulodinium machaerophorum, Pyxidinopsis psilata* and *Spiniferites cruciformis* also appear in Lake Pannon deposits. The first is in older, whereas the latter two are in deposits younger than the investigated outcrops. The Caspian endemic *Caspidinium rugosum* is very similar to the Lake Pannon endemic *Impagidinium globosum*, recovered, among others, from the Kisbér outcrop.

Chlorophyta

The green alga *Botryococcus braunii* Kützing 1848 was found in a sample from Tata 1, and it was also common in borehole samples from the Szák Formation (Nagy 2005). This organism can be found in both brackish and freshwater ecosystems worldwide. Occasionally it is found even in salt water. In the Caspian Sea it occurs in the almost fresh northern basin as well as in the brackish central and southern basins. Its Late Miocene mass occurrence is known from a eutrophic shallow estuarine environment adjacent to Lake Pannon in the Vienna Basin, where it is associated with the green alga *Pediastrum* (Pipík et al. 2004).

Coccolithophoridae

Pilot samples from six outcrops have been analysed. In each sample, rare, usually moderately preserved calcareous nannoplankton was observed. Assemblages are characterized by high percentage of reworked Paleogene-Lower/Middle Miocene and Cretaceous forms, such as *Coccolithus pelagicus* (Wallich, 1871) Schiller, 1930, *Cyclicargolithus floridanus* (Roth & Hay, 1967) Bukry, 1971, *Reticulofenestra umbilica* (Levin, 1965) Martini & Ritzkowksi 1968, *Reticulofenestra pseudoumbilica* (Gartner, 1967) Gartner, 1969, *Sphenolithus moriformis* (Brönnimann & Stradner, 1960) Bramlette & Wilcoxon, 1967, *Watznaueria barnesae* (Black, 1959) Perch-Nielsen, 1968, etc. The Pápateszér sample contained exclusively reworked forms, whereas a few species of in situ Lake Pannon nannofossils occurred in the other five samples (Table 3).

Reticulofenestra cf. *tegulata* Ćorić & Gross, 2004 was found only in one sample. *Lacunolithus menneri* Luljeva, 1989 is very rare in other Lake Pannon deposits. Luljeva (1989) used occurrences of endemic *L. menneri* and *Isolithus semenenko* Luljeva, 1989 for the subdivision of the Upper Miocene in the Eastern Paratethys in two zones: a lower with *L. menneri* and an upper with *I. semenenko*. In Tata 2, the two species were found together, in the same sample.

A monospecific occurrence of *I. semenenko* (Tata 1) as well as the occurrence of this species with *Isolithus pavelici* Ćorić & Vrsaljko (subm.) and *R.* cf. *tegulata* (Tata 2, Kisbér, Devecser; Fig. 15) are features that had been observed in the lower part of the carefully sampled and investigated Našice section, Croatia (Ćorić 2006). The biostratigraphic significance of this similarity, however, is not clear yet. The lower part of the Našice section represents the lowermost part of the Lake Pannon sequence with *Mecsekia ultima, Radix croatica,* etc., whereas our samples from the Szák Formation are much (about 2 million years) younger.

Typical for all investigated Szák Formation samples is the absence of genus *Noelaerhabdus*. Species of this genus, originally described from Pannonian sediments from Serbia (Jerković 1970, 1971), were used for the biostratigraphical subdivision of Lake Pannon deposits in the Romanian part of the Central Paratethys (Marunţeanu 1997). Sediments from the middle and upper part of Našice section are characterized by blooms of different *Noelaerhabdus* species. The lack of *Noelaerhabdus* in investigated materials from the Szák Formation is either a consequence of younger age or of different paleoecological conditions with

Table 3 Endemic nannoplankton from the outcrops of Szák Formation

	Tata 1	Tata 2	Kisbér	Bakonyszentlászló	Devecser
Isolithus semenenko Luljeva 1989	•	•	•		•
Isolithus pavelici Ćorić & Vrsaljko (subm.)		•	•		•
Lacunolithus menneri Luljeva 1989		•		•	
Reticulofenestra cf. *tegulata* Ćorić & Gross, 2004			•		

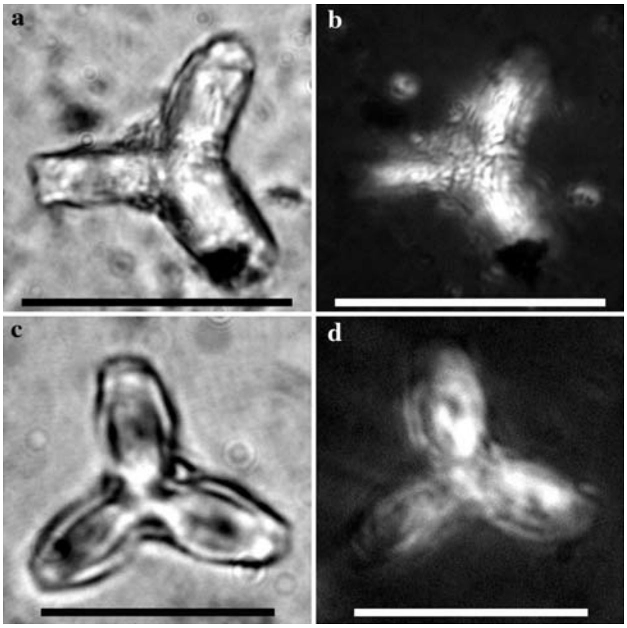


Fig. 15 *Isolithus semenenko* Luljeva (1989) from Tata 1 (**a**, **b**) and Kisbér (**c**, **d**); **a**, **c** with parallel, **b**, **d** with crossed nicols. Scale bar, 10 μm

respect to the southern (Croatian, Serbian, Romanian) localities.

No coccolithophorids have been described from the modern Caspian Sea.

Paleoecological discussion

Water depth and salinity

The first comprehensive paleoecological study of the Szák Formation fossils was carried out by Korpás-Hódi (1983). She studied Lake Pannon mollusk fauna from the northwestern foreland of the Transdanubian Range in boreholes (see that study for references to earlier geological and paleontological research in the area), and compared it to the present-day brackish-water associations of the Sea of Azov, Caspian Sea, and the lagoonal-deltaic environments of the Black Sea. This comparison is not a straightforward one; *Lymnocardium, Pontalmyra, Paradacna*, and *Valenciennius* all went extinct; the only Old World *Congeria* species is a highly specialized cave dweller; and the sublittoral to profundal pulmonate gastropods in Lake Pannon showed such unusual adaptations which, though not unparallelled, are very rare today. As a result of the comparative ecological study, Korpás-Hódi (1983) suggested that the fauna of the Szák Formation lived in the nutrient-rich aphytal part of the sublittoral zone, in a water depth of 15–80 m. She designated this fauna "*Congeria czjzeki-Paradacna abichi* paleocoenosis", and estimated its salinity tolerance as pliohaline (9–16‰).

The results of our study largely conform to the above conclusions. The platy parting of the argillaceous marl indicates non-agitated water and a distant, relatively deep water depositional environment. The general lack of coarse-grained intercalations and other sedimentological traces of agitated water in the outcrops suggests that the argillaceous marl was deposited well below the effective wave base. Along the western shore of the mid-Caspian Basin, where river deltas charge into the lake, clayey silt with 20–30% carbonate content, similar to that of the Szák Formation, becomes dominant over sandy sediments below 50 m water depth (Kosarev and Yablonskaya 1994). The coquina lense that we observed in Tata 2 outcrop contained some littoral shells, evidencing that rare storms could sweep the bottom of the basin. Therefore we think that the upper limit of the formation of the Szák argillaceous marl could have been at about the depth of the storm wave base. Again, in the Caspian Sea, 21–38 m average wave length was measured at Neftanyje Kamny, depending on wind direction (Kosarev and Yablonskaya 1994). The average wave length is usually correlated with the depth of the storm wave base, whereas the fair-weather wave base corresponds to half of the wave length. On this basis we speculate that the Szák Formation in the study area was deposited in at least 20–30 m water depth. The lower boundary of the sublittoral zone in the Caspian Sea is at about 80–100 m; below that depth both diversity and standing crop are sharply decreasing (Tarasov 1996, 1997). A sudden impoverishment of the mollusk fauna with depth is well-known in Lake Pannon deposits, too (Magyar 1995).

Although the entire fossil fauna and flora of the Szák Formation indicates a brackish environment in general, the paleosalinity can be quantitatively best estimated by ostracods. *Amnicythere multituberculata* and *Bakunella dorsoarcuata*, two extant species that probably evolved in Lake Pannon and were endemic to that lake until the latest Miocene, are living today in the central and southern Caspian Basins at salinities of 11.5–13.5‰ (Gofman 1966). *Bakunella dorsoarcuata* was found in sublittoral to profundal depths in the central and southern Caspian Basins (Boomer et al. 2005). These data corroborate the salinity estimation of Korpás-Hódi (1983) made on the basis of mollusk genera.

Vertical distribution patterns and adaptations

The sublittoral mollusk fauna of the Szák Formation is distinctly different from both the coeval littoral and profundal faunas. In terms of diversity, it is intermediate between the high-diversity shallow-water and the low-diversity deep-water faunas. In addition, the sublittoral fauna has some characteristic bivalve species which do not occur in the two other zones. These include *C. czjzeki* among dreissenids and a number of cardiids, of which *Lymnocardium majeri* and the *Lymnocardium rogenhoferi* group are the most common. The gastropods, however, seem to have followed a two-parted vertical distribution; in sharp contrast to the prosobranch-dominated littoral zone, the sublittoral and profundal environments of Lake Pannon were characterized by an overwhelming dominance of pulmonates. This pattern considerably differs from that of the modern Caspian, where even the profundal regions are dominated by prosobranch gastropods, such as Pyrgulidae (Tarasov 1996, 1997).

Aquatic pulmonates (lung snails) live in shallow freshwater and regularly come to the surface to breath air. In some long-lived lakes, however, pulmonats adapted to, and sometimes even radiated in, deep water environments (Boss 1978; Michel 1994). In Lake Baikal, one species of Acroloxidae and two species of *Choanomphalus* (Planorbidae) inhabit hard substrates in the profundal zone (Sitnikova 1994 and personal communication 2001). In the Caspian Sea, four species of *Andrusovia* (an endemic subgenus of *Anisus*) live in profundal depth, occasionally as deep as 870 m (Tarasov 1996). A common feature of all these modern profundal pulmonates is that they are very small (Davis 1982). The deep-water pulmonates of Lake Pannon, however, were large; they often attained larger size than their shallow-water relatives. The most unique feature of endemic Lake Pannon pulmonates was that they included lymnaeids. Although some lymnaeids are known to occur in surprisingly deep water in modern lakes (*Lymnaea peregra* down to 50 m in Lake Neuchatel (Piaget 1914) and down to 300 in Lake Geneva (Mouthon 1987)), these are cosmopolitan freshwater species and not highly derived endemics. Whereas planorbids, ancylids and acroloxids are known to show speciation in several modern long-lived lakes, little or no endemic radiation is observed among lymnaeids in those lakes (Boss 1978).

The sublittoral ostracod fauna of Lake Pannon also considerably differed from the littoral assemblages. In the outcrop of Bátaszék, for instance, 86% of specimens from a sublittoral layer belonged to the family Candonidae, 3% to Cyprididae, and 0% to Cytherideidae; a littoral fauna from a sandy intercalation in the same outcrop, however, yielded 24% Candonidae, 9% Cyprididae, and 38% Cytherideidae, the latter represented by *Cyprideis* (Lennert et al. 1999). In our study area no such direct comparison was possible, because the Szák Formation did not contain sandy intercalations with littoral fauna. Although the only *Cyprideis* species, *C. macrostigma* was abundant or even predominant in a few samples (KI1, KI2, TA1, TA2, TA4 and TA6, TA9, TA10, respectively), the overall poor diversity of family Cytherideidae and also of family Cyprididae is a diagnostic feature of the sublittoral fauna when compared to the littoral one. A somewhat older littoral fauna from Pezinok (Slovakia), for instance, was dominated by four *Cyprideis* species (*heterostigma, alberti, seminulum*, sp.) (Pipík 1998, 2007). The freshwater-influenced littoral deposits of Lake Pannon often yield *Heterocypris* and numerous freshwater taxa as well. In contrast, no typical actual holarctic or cosmopolitic genus (apart from accidental occurrences of *Cryptocandona* and ?*Metacypris*) appeared in the sublittoral fauna of the Szák Formation.

This sharp contrast between the littoral and the deep-water ostracod faunas is characteristic of the modern Caspian Sea as well. *Cyprideis torosa* is abundant or it has mass occurrence in littoral and coastal habitats, but it is entirely missing from sublittoral communities (Gofman 1966; Boomer et al. 2005).

Oxygen availability

Our observations on the sublittoral deposits and fossils of Lake Pannon do not offer an unanimous interpretation of oxygen levels at the bottom of the lake. The abundance of benthic mollusks and ostracods in the Szák Formation excludes a permanent anoxia in the lake. For instance, Candoninae, the most abundant ostracod subfamily in the investigated outcrops, are benthic dwellers without ability to swim and, as other crustaceans, they need oxygenated waters and avoid oxygen-deficient milieu. In this respect, Lake Pannon could be similar to the modern Caspian Sea. There are, however, important differences as well. While a strong N to S gradient in winter temperature between the northern and southern parts of the lake and freezing play an important role in the mixing mechanism of the Caspian (Kosarev and Yablonskaya 1994), the hydrological system of Lake Pannon must have worked differently. Paleobotanical data from the Szák Formation indicate a warm temperate climate without strong seasonality, thus freezing of the waters of Lake Pannon can be excluded even in the wide, freshwater-dominated northern shelf. Whatever the driving force of vertical mixing in Lake Pannon was, it seems to have worked efficiently. The continuous presence (and evolution) of a specific sublittoral and profundal fauna in Lake Pannon suggests that no basin-wide catastrophic deoxygenation events occurred.

On the other hand, some features of the Szák Formation seem to indicate restricted oxygen availability in the sublittoral zone of Lake Pannon. The abundance of the trace fossil *Diplocraterion* in a layer of the Szák Formation (Jámbor 1980) can be interpreted as colonization of a poorly oxygenated bottom by opportunistic suspension feeders. The preservation of trace fossils and a fish skeleton, however rare the latter was, did occur in the Kisbér outcrop, indicating restricted bioturbation. The widespread occurrence of the early diagenetic iron sulphide greigite in several horizons of the outcrops of the Szák Formation (Babinszki et al. 2007) also argues for an oxygen-deficient environment. The general understanding of the paleoenvironment, including a peak in humidity, anomalously high concentration of light oxygen isotopes in mollusk shells, lake level highstand, and even the occurrences of the trace fossil *Diplocraterion*, which is interpreted by Heinberg and Birkelund (1984) as characteristic of highstand systems tracts, favours an oxygen-depletion scenario. In the Caspian Sea, increased freshwater discharge and a consequent lake level highstand repeatedly caused catastrophic deep-water anoxia. This might be a reason of why no specific deepwater community developed in that lake (Dumont 1998).

These observations allow at least two ways of interpretation. According to the first one, dysoxic conditions may have developed in Lake Pannon and they could affect even the shelf areas (Harzhauser and Mandic 2004; Magyar et al. 2006; Starek and Pipík 2007), but these events must have been restricted both in space and time, and did not cause unrecoverable damage to the deep-water benthic communities. This scenario may account for the mass occurrence of *Diplocraterion* in a horizon of the Szák Formation. The second model is that of interstitial dysoxia, when the bottom waters are still sufficiently oxygenated, but interstitial waters in the substratum are not. This could explain the abundance of filter-feeding and grazing benthic organisms on the surface of the substratum on the one hand, and coeval formation of the early diagenetic greigite within the oxygen-depleted substratum on the other. The oxy/hypoxy transitional zone might have shifted occasionally up to the watercolumn, allowing the preservation of fish corpses.

Summary and conclusions

The Szák Formation, representing sublittoral deposits of the Paratethyan Lake Pannon, is exposed in several outcrops along the eastern margin of the Kisalföld Basin in NW Hungary. In terms of regional stratigraphy, it belongs to the *C. czjzeki* mollusk zone and to the *Spiniferites paradoxus* dinoflagellate zone, and its age is estimated 9.4–8.9 Ma from magnetostratigraphic and regional stratigraphic correlations. The dark, silty argillaceous marl was deposited during a lake-level highstand, under relatively humid, warm temperate climate (1,000–1,200 mm/year precipitation, 12–13°C mean annual temperature). The salinity of the water was probably between 10 and 15‰. Deposition took place at or below the storm wave base but still within the zone of photosynthesis, in the depth interval of 20–30 to 80–90 m. Oxygen availability was restricted in the substratum (and possibly sometimes in the bottom water as well), as indicated by early diagenetic greigite formation in the sediment and by the occasional preservation of trace fossils, such as *Diplocraterion*, a domichnia of a probably filter feeding organism (?echiuran worm).

Body fossils from eight outcrops of the Szák Formation represent mollusks, ostracods, fish, dinoflagellates, calcareous nannoplankton, and green algae. Endemic species dominate the biota in almost all groups. In mollusks, brackish cardiids (Lymnocardiinae), dreissenids (*Congeria*), and deep-water pulmonate snails (lymnaeids, planorbids) characterize the fauna, with some specific sublittoral or sublittoral-to-profundal species in each of the three taxa. The ostracod fauna is dominated by Candonidae, and it contains at least two extant species, *Amnicythere multituberculata* and *Bakunella dorsoarcuata*, that live in the sublittoral of the Caspian Sea at salinities of 11.5–13.5‰. The fish remnants represent euryecious percids and sciaenids, with a possible ecological niche partitioning between the zooplanctivorous *Perca* and the zoobenthivorous *Umbrina*. Trace fossils of soft-bodied animals occurred in one outcrop (Kisbér). Beside the cosmopolitan green alga *Botryococcus braunii*, the phytoplankton is represented by endemic species of coccolithophorids and prevailingly endemic forms of dinoflagellates.

The Late Miocene Lake Pannon fauna and flora are similar in many ways to the Paratethyan component of the modern Caspian biota. In some cases Lake Pannon was the very cradle of modern Caspian endemics. Despite the striking similarities, however, there are important differences between the faunas of the two lakes. One such particular feature is the evolution of large-sized lymnaeid gastropods, such as *Radix kobelti* and *V. reussi*, in the sublittoral and profundal zones of Lake Pannon.

Acknowledgments The stable isotope measurements of mollusk shells have been carried out by Attila Demény, Institute for Geochemical Research, Hungarian Academy of Sciences, Budapest. A part of this study was supported by the APVV agency (project APVT-51-045202) and by the VEGA agency (project No. 1/3053/06). I. Cziczer thanks Miklós Szónoky and Pál Sümegi for supporting his research through the Geological and Paleontological Department, University of Szeged. Several students, including Sándor Gulyás, Janina Horváth, Zsolt Veres and Áron Vavra assisted in the field work. The two reviewers, Frank Wesselingh (Leiden) and Mathias Harzhauser (Vienna) are thanked for their useful comments on the earlier version of the paper.

References

Athersuch J, Horne DJ, Whittaker JE (1989) Marine and brackish ostracods (Superfamilies Cypridacea and Cytheracea). E.J. Brill, Leiden, pp 1–343

Babinszki E, Sztanó O, Magyari Á (2003) Episodic deposition in the Kálla bay of Lake Pannon: sedimentology and trace fossils of Kálla Sand. Földtani Közlöny 133:363–382

Babinszki E, Márton E, Márton P, Kiss LF (2007) Widespread occurrence of greigite in the sediments of Lake Pannon: Implications for environment and magnetostratigraphy. Palaeogeogr Palaeoclimatol Palaeoecol 252:626–636

Bakrač K (2005) Palinološka karakterizacija naslaga srednjeg miocena jugozapadnog dijela Panonskog bazena (Palynology of the Middle and Upper Miocene deposits from the south-western parts of the Pannonian Basin). Ph.D. Thesis, University of Zagreb, Zagreb, pp 1–173

Bauch G (1954) Die einheimischen Süßwasserfische. Neumann Verlag, Berlin, pp 1–200

Bernor RL, Kordos L, Rook L, Agusti J, Andrews P, Armour-Chelu M, Begun DR, Cameron DW, Damuth J, Daxner-Höck G, de Bonis L, Fejfar O, Fessaha N, Fortelius M, Franzen J, Gasparik M, Gentry A, Heissig K, Hernyak G, Kaiser T, Koufos GD, Krolopp E, Jánossy D, Llenas M, Mészáros L, Müller P, Renne P, Roček Z, Sen S, Scott R, Szyndlar Z, Topál Gy, Ungar PS, Utescher T, van Dam J, Werdelin L, Ziegler R (2003) Recent advances on multidisciplinary research at Rudabánya, Late Miocene (MN9), Hungary: a compendium. Palaeontogr Ital 89:3–36

Boss KJ (1978) On the evolution of gastropods in ancient lakes. In: Fretter V, Peake J (eds) Pulmonates, vol 2A, Systematics, Evolution and Ecology. Academic Press, New York, pp 385–428

Böhme M (2003) Miocene climatic optimum: evidence from lower vertebrates of Central Europe. Palaeogeogr Palaeoclimatol Palaeoecol 195:389–401

Böhme M, Ilg A, Ossig A, Küchenhoff H (2006) New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene precipitation gradients in Europe. Geology 34:425–428

Boomer I, von Grafenstein U, Guichard F, Bieda S (2005) Modern and Holocene sublittoral ostracod assemblages (Crustacea) from the Caspian Sea: a unique brackish, deep-water environment. Palaeogeogr Palaeoclimatol Palaeoecol 225:173–186

Bronshtein ZS (1947) Fauna SSSR, Rakoobraznye, Tom II, Vyp. 1 Ostracoda Presnykh Vod. Academy of Sciences of the USSR Publishers, Moscow. (English translation 1988: Freshwater Ostracoda—Fauna of the USSR: Crustaceans, vol. II, No.1. AA Balkema, Rotterdam, pp 1–455)

Bruch A, Utescher T, Mosbrugger V, Gabrielyan I, Ivanov DA (2006) Late Miocene climate in the circum-Alpine realm—a quantitative analysis of terrestrial palaeofloras. Palaeogeogr Palaeoclimatol Palaeoecol 238:270–280

Brzobohatý R, Pană I (1985) Die Fischfauna des Pannonien. In: Papp A, Jámbor Á, Steininger FF (eds) Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys 7, Pannonien. Akadémiai Kiadó, Budapest, pp 426–439

Carbonel P, Colin JP, Danielopol DI, Löffler H, Neustrueva I (1988) Paleoecology of limnic ostracodes: a review of some major topics. Palaeogeogr Palaeoclimatol Palaeoecol Spec Issue Aspects Freshw Paleoecol Biogeogr 62:413–461

Carbonnel G (1978) La zone à *Loxoconcha djafarovi* Schneider (Ostracoda, Miocène supérieur) ou le Messinien de la vallée du Rhône. Revue de Micropaléontologie 21:106–118

Ćorić S (2006) Middle/Upper Miocene (Sarmatian/Pannonian) endemical calcareous nannoplankton from the Central Paratethys. 11th International Nannoplankton Association Conference, Lincoln, Nebraska, Program with abstracts, pp 32–34

Cziczer I, Magyar I (2006) Paleoecological and biostratigraphic study of Pannonian molluscs from Tata, NW Hungary. In: Hum L, Gulyás S, Sümegi P (eds) Environmental historical studies from the Late Tertiary and Quaternary of Hungary. Department of Geology and Paleontology, University of Szeged, Szeged, pp 45–55

Danielopol DL, Buttinger R, Pipík R, Olteanu R, Knoblechner J (2007) Miocene "*Hungarocypris*" species (Ostracoda Cyprididae) of Lake Pannon are not related to the Recent species *Hungarocypris madaraszi* (Örley). European Ostracodologisťs Meeting VI—Abstract Volume, Frankfurt am Main: 25

Davis GM (1982) Historical and ecological factors in the evolution, adaptive radiation, and biogeography of freshwater molluscs. Am Zool 22:375–395

Dumont HJ (1998) The Caspian Lake: History, biota, structure, and function. Limnol Oceanogr 43:44–52

Ekdale AA, Lewis DW (1991) Trace fossils and paleoenvironmental control of ichnofacies in a late Quaternary gravel and loess fan delta complex, New Zealand. Palaeogeogr Palaeoclimatol Palaeoecol 81:253–279

Esu D (2007) Latest Messinian "Lago-Mare" Lymnocardiinae from Italy: close relations with the Pontian fauna from the Dacic Basin. Geobios 40:291–302

Fortelius M, Eronen J, Liu L, Pushkina D, Tesakov A, Vislobokova I, Zhang Z (2006) Late Miocene and pliocene large land mammals and climatic changes in Eurasia. Palaeogeogr Palaeoclimatol Palaeoecol 238:219–227

Frey RW, Goldring R (1992) Marine event beds and recolonization surface as revealed by trace fossil analysis. Geol Mag 129:325–335

Fürsich FT (1974) On *Diplocraterion* Torrell 1870 and the significance of morphological features in vertical, spreite-bearing, U-shaped trace fossils. J Paleontol 48:952–962

Fürsich FT (1998) Environmental distribution of trace fossils in the Jurassic of Kachchh (western India). Facies 39:243–272

Gaillard C, Racheboeuf PR (2006) Trace fossils from nearshore to offshore environments: Lower Devonian of Bolivia. J Paleont 80:1205–1226

Gaschott O (1928) Einführung in die Systematik der Süßwasserfische Mitteleuropas.Die Stachelflosser. In: Handbuch der Binnenfischerei Mitteleuropas 3 (2). E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp 1–68

Gaudant J (1997) L'ichthyofaune pliocene de Willershausen am Harz (Basse Saxe, Allemagne)—un reexamen. Stuttgarter Beitr Naturkunde B 257:1–51

Geary DH, Magyar I, Müller P (2000) Ancient Lake Pannon and its Endemic Molluscan Fauna (Central Europe; Mio-Pliocene). In: Rossiter A, Kawanabe H (eds) Ancient lakes: biodiversity, ecology, and evolution. Adv Ecol Res 31:463–482, Academic Press, New York

Gliozzi E, Grossi F (2004) Ostracode assemblages and palaeoenvironmental evolution of the latest Messinian lago-mare event at Perticara (Montefeltro, northern Apennines, Italy). Revista Espanola de Micropaleontología 36:157–169

Gofman EA (1966) Ekologia sovremennykh i novokaspiiskikh ostrakod Kaspiiskogo moria (Ecology of the living and new caspian ostracodes of the Caspian Sea). Nauka, Moscow, pp 1–183

Harzhauser M, Daxner-Höck G, Piller WE (2004) An integrated stratigraphy of the Pannonian (Late Miocene) in the Vienna Basin. Aust J Earth Sci 95–96:6–19

Harzhauser M, Mandic O (2004) The muddy bottom of Lake Pannon—a challenge for dreissenid settlement (Late Miocene; Bivalvia). Palaeogeogr Palaeoclimatol Palaeoecol 204:331–352

Harzhauser M, Latal C, Piller WE (2007) The stable isotope archive of Lake Pannon as a mirror of Late Miocene climate change. Palaeogeogr Palaeocimatol Palaeoecol 249:335–350

Heinberg C, Birkelund T (1984) Trace-fossil assemblages and basin evolution of the Vardekloft Formation (Middle Jurassic, Central East Greenland). J Paleontol 58:362–397

Hertweck G (1970) The animal community of a muddy environment and the development of biofacies as effected by the life cycle of the characteristic species. In: Crimes TP, Harper JC (eds) Trace fossils. Seel House Press, Liverpool, pp 235–242

Horváth F, Cloetingh S (1996) Stress-induced late-stage subsidence anomalies in the Pannonian Basin. Tectonophysics 266:287–300

Horváth F, Tari G (1999) IBS Pannonian Basin project: a review of the main results and their bearings on hydrocarbon exploration. In: Durand B, Jolivet L, Horváth F, Séranne M (eds) The Mediterranean Basins: Tertiary Extension within the Alpine Orogen. Geol Soc Lond Spec Publ 156:195–213

Horváth F, Bada G, Szafián P, Tari G, Ádám A, Cloetingh S (2006) Formation and deformation of the Pannonian Basin: constraints from observational data. In: Gee DG, Stephenson RA (eds) European lithosphere dynamics. Geol Soc Memoir 32:191–206

Jámbor Á (1980) Pannonian in the Transdanubian Central Mountains. Ann Hung Geol Inst 52:1–259

Jámbor Á (1987) Die Lebensspurenfauna der pannonischen (s.l.) Bildungen in Ungarn. Ann Hung Geol Inst 69:423–433

Jerković L (1970) *Noelaerhabdus* nov. gen type d'une nouvelle familia de Coccolithophorides fossils: Noelaerhabdaceae du miocéne de Yugoslavie. Micropal C r Acad Sc Paris, Ser D 270:468–470

Jerković L (1971) *Noelaerhabdus* bekei nov. sp. des coccolithophorides du pannonien de Belgrade. Bull Sci Sect A Yugosl 0758

Jiménez-Moreno G (2006) Progressive substitution of a subtropical forest for a temperate one during the middle Miocene climate cooling in Central Europe according to palynological data from cores Tengelic-2 and Hidas-53 (Pannonian Basin, Hungary). Rev Palaeobot Palynol 142:1–14

Juhász Gy (1992) Pannonian (s.l.) lithostratigraphic units in the Great Hungarian Plain: distribution, facies and sedimentary environment. Földtani Közlöny 122:133–165

Juhász Gy, Magyar I (1992) Review and correlation of the Late Neogene (Pannonian s.l.) lithofacies and mollusc biofacies in the Great Plain, eastern Hungary. Földtani Közlöny 122:167–194

Korpás-Hódi M (1983) Palaeoecology and biostratigraphy of the Pannonian Mollusca fauna in the northern foreland of the Transdanubian Central Range. Ann Hung Geol Inst 66:1–163

Kosarev AN, Yablonskaya EA (1994) The Caspian Sea. SPB Academic Publishing, The Hague, pp 1–259

Krstić N, McKenzie KG (1991) *Mediocytherideis* Mandelstam, 1956: diagnosis and relationships. Ann Géol Péninsule Balkanique 55:175–205

Krstić N, Stancheva N (1990) Ostracods of Eastern Serbia and Northern Bulgaria with notice on a Northern Turkey assemblage. In: Stevanović PM, Nevesskaya LA, Marinescu F, Sokać A, Jámbor Á (eds) Chronostratigraphie und Neostratotypen, Neogen der Westlichen ("Zentrale") Paratethys 8, Pontien. Jazu and Sanu, Zagreb Beograd, pp 753–819

Lennert J, Szónoky M, Gulyás S, Szuromi-Korecz A, Shatilova II, Sütő-Szentai M., Geary DH, Magyar I (1999) The Lake Pannon fossils of the Bátaszék brickyard. Acta Geol Hung 42:67–88

Leszczynski S, Uchman A, Bromley RG (1996) Trace fossils indicating bottom aeration changes: Folusz Limestone, Oligocene, Outer Carpathians, Poland. Palaeogeogr Palaeoclimatol Palaeoecol 121:79–87

Lourens LJ, Hilgen FJ, Shackleton NJ, Laskar J, Wilson D (2004) The Neogene Period. In: Gradstein F, Ogg J, Smith AG (eds) A geologic time scale 2004. Cambridge University Press, Cambridge , pp 469–471

Lueger JP (1978) Klimaentwicklung im Pannon und Pont des Wiener Beckens aufgrund von Landschneckenfaunen. Anzeiger der math-naturw Klasse der Österreichischen Akademie derWissenschaften 6:137–149

Luljeva SA (Люльева CA) (1989) ННовые Миоценовые и ППлиоценовые известковые наннофоссилии юга Украины. Доклады Академии наук Украинскои CCP, B 1:10–14

Magyar I (1995) Late Miocene mollusc biostratigraphy in the eastern part of the Pannonian Basin (Tiszántúl, Hungary). Geol Carpathica 46:29–36

Magyar I, Geary DH, Müller P (1999) Paleogeographic evolution of the Late Miocene Lake Pannon in Central Europe. Palaeogeogr Palaeoclimatol Palaeoecol 147:151–167

Magyar I, Müller PM, Sztanó O, Babinszki E, Lantos M (2006) Oxygen-related facies in Lake Pannon deposits (Upper Miocene) at Budapest-Kőbánya. Facies 52:209–220

Magyar I, Lantos M, Ujszászi K, Kordos L (2007) Magnetostratigraphic, seismic and biostratigraphic correlations of the Upper Miocene sediments in the northwestern Pannonian Basin System. Geol Carpathica 58:277–290

Marret F, Leroy S, Chalié F, Gasse F (2004) New organic-walled dinoflagellate cysts from recent sediments of Central Asian seas. Rev Palaebotany Palynol 129:1–20

Maruntֽeanu M (1997) Pannonian nannoplankton zonation. International Symposium Geology in the Danube Gorges, pp 263–265

Mason TR, Christie ADM (1986) Palaeoenvironmental significance of ichnogenus *Diplocraterion* Torell from the Permian Vryheid Formation of the Karoo supergruop, South Africa. Palaeogeogr Palaeoclimatol Palaeoecol 52:249–265

Mátyás J, Burns SJ, Müller P, Magyar I (1996) What can stable isotopes say about salinity? An example from the Late Miocene Pannonian Lake. Palaios 11:31–39

McCrea JM (1950) On the isotopic chemistry of carbonates and a paleotemperature scale. J Chem Phys 18:849–857

Meisch C (2000) Freshwater Ostracoda of Western and Central Europe. Spektrum Akademischer Verlag, Heidelberg, pp 1–522

Michel E (1994) Why snails radiate: a review of gastropod evolution in long-lived lakes, both recent and fossil. In: Martens K, Goddeeris B, Coulter G (eds) Speciation in ancient lakes. Arch Hydrobiol Beih Ergebn Limnol 44:285–317

Morton J, Miller M (1968) The New Zealand sea shore. Collins, London, pp 1–638

Mouthon J (1987) Contribution a la connaissance des Mollusques du lac Léman. Intérêt de l'étude des malacocénoses pour apprécier la qualité biologique des sédiments de ce plan d'eau. Rev Suisse Zool 94:729–740

Müller P, Geary DH, Magyar I (1999) The endemic molluscs of the Late Miocene Lake Pannon: their origin, evolution, and family-level taxonomy. Lethaia 32:47–60

Nagy E (2005) Palynological evidence for Neogene climatic change in Hungary. Occas Pap Geol Inst Hung 205:1–120

Nevesskaja LA, Paramonova NP, Popov SV (2001) History of Lymnocardiinae (Bivalvia, Cardiidae). Paleontol J 35(Suppl 3):S147–S217

Olóriz F, Rodríguez-Tovar FJ (2000) *Diplocraterion*: a useful marker for sequence stratigraphy and correlation in the Kimmeridgian, Jurrasic (Prebetic zone, Betic Cordillera, southern Spain). Palaios 15:546–552

Page LM, Burr BM (1991) A field guide of the freshwater fishes of North America and North Mexico. The Peterson Field Guide Series, Houghton Mifflin Company, Boston, pp 1–432

Papp A, Jámbor Á, Steininger FF (eds) (1985) Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys 7, Pannonien. Akadémiai Kiadó, Budapest, pp 1–636

Pervesler P, Uchman A (2004) Ichnofossils from the type area of the Grund Formation (Miocene, lower Badenian) in northern lower Austria (Molasse Basin). Geol Carpathica 55:103–110

Piaget J (1914) Premieres recherches sur les Mollusques profonds du Lac de Neuchatel. Bull Soc Neuchatel Sci Nat 40:148–170

Pipík R (1998) Salinity changes recorded by ostracoda assemblages found in Pannonian sediments in the western margin of the Danube Basin. Bull Centres Rech Exploration-production Elf-Aquitaine 20:167–177

Pipík R (2001) Les Ostracodes d'un lac ancien et ses paléobiotopes au Miocène supérieur: le Bassin de Turiec (Slovaquie). Thèse, Université Claude-Bernard, Lyon I, pp 1–337

Pipík R (2007) Phylogeny, palaeoecology, and invasion of non-marine waters by the late Miocene hemicytherid ostracod *Tyrrhenocythere* from Lake Pannon. Acta Palaeontol Pol 52:351–368

Pipík R, Bodergat AM (2004) *Euxinocythere* (Ostracoda, Cytheridae, Leptocytherinae) du Miocène supérieur du Bassin de Turiec (Slovaquie): taxonomie et paléoécologie. Rev Micropaléontol 47:36–52

Pipík R, Fordinál K, Slamková M, Starek D, Chalupová B (2004) Annotated checklist of the Pannonian microflora, evertebrate and vertebrate community from Studienka, Vienna Basin. Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Geology 31–32:47–54

Pogácsás Gy, Lakatos L, Révész I, Ujszászi K, Vakarcs G, Várkonyi L, Várnai P (1988) Seismic facies, electro facies and Neogene sequence chronology of the Pannonian Basin. Acta Geol Hung 31:175–207

Pross J (2001) Paleo-oxygenation in Tertiary epeiric seas: evidence from dinoflagellate cysts. Palaeogeogr Palaeoclimatol Palaeoecol 166:369–381

Reichenbacher B (2000) Das brackisch-lakustrine Oligozän und Unter-Miozän im Mainzer Becken und Haunauer Becken: Fischfaunen, Paläoökologie, Biostratigraphie, Paläogeographie. Courier Forschungsinstitut Senckenberg 222:1–143

Rhoads DC, Boyer LF (1982) The effects of marine benthos on physical properties of sediments: a successional perspective. In: McCall PL, Tevesz MJS (eds) Animal–sediment relations. The biogenic alteration of sediments. Topics Geobiol 2:3–52

Ricketts RD, Johnson ThC, Brown ET, Rasmussen KA, Romanovsky VV (2001) The Holocene paleolimnology of Lake Issyk-Kul, Kyrgyzstan: trace element and stable isotope composition of ostracodes. Palaeogeogr Palaeoclimatol Palaeoecol 176:207–227

Ruiz F, González-Regaldo ML, Muńoz JM, Pendón JG, Rodríguez-Ramírez A, Cáceres L, Rodríguez Vidal J (2003) Population age structure techniques and ostracods: applications in coastal hydrodynamics and paleoenvironment analysis. Palaeogeogr Palaeoclimatol Palaeoecol 199:51–69

Sacchi M, Horváth F, Magyari O (1999) Role of unconformity-bounded units in the stratigraphy of the continental record: a case study from the Late Miocene of the western Pannonian Basin, Hungary. In: Durand B, Jolivet L, Horváth F, Séranne M (eds) The Mediterranean Basins: Tertiary Extension within the Alpine Orogen. Geol Soc Lond Spec Publ 156:357–389

Schornikov EI (1964) An experiment on the distinction of the Caspian elements of the Ostracod fauna in the Azov - Black Sea Basin. Zoologitcheskii Zhournal 43:1276–1293

Schornikov EI (1966) *Leptocythere* (Crustacea, Ostracoda) in the Azov-Black Sea Basin. Zoologitcheskii Zhournal 45:32–49

Schubert RJ (1912) Die Fischotolithen der ungarischen Tertiärablagerungen. Jahrbuch der königlichen ungarischen geologischen Reichsanstalt 20:115–139

Schultz O (2004) Fish remains from the Lower Pannonian (Upper Miocene) of Mataschen, Styria (Austria). J Geol Paläontol 5:231–256

Sitnikova TYa (1994) Recent views on the history and diversity of the Baikalian malacofauna. In: Martens K, Goddeeris B, Coulter G (eds) Speciation in ancient lakes. Arch Hydrobiol Beih Ergebn Limnol 44:319–326

Sokać A (1990) Pontian ostracod fauna in the Pannonian Basin. In: Stevanović PM, Nevesskaya LA, Marinescu F, Sokać A, Jámbor Á (eds) Chronostratigraphie und Neostratotypen, Neogen der Westlichen ("Zentrale") Paratethys 8, Pontien. Jazu and Sanu, Zagreb Beograd, pp 672–721

Starek D, Pipík R (2007) Oxic and anoxic deposits of the Pannonian E (Late Miocene) from the Vienna Basin (sedimentological and micropaleontological description of sediments with *Congeria subglobosa* horizon. Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Geology 36:25–30

Stevanović PM, Nevesskaya LA, Marinescu F, Sokać A, Jámbor Á (eds) (1990) Chronostratigraphie und Neostratotypen, Neogen der Westlichen ("Zentrale") Paratethys 8, Pontien. Jazu and Sanu, Zagreb Beograd, pp 1–952

Stover LE, Brinkhuis H, Damassa SP, de Verteuil L, Helby RJ, Monteil E, Partridge AD, Powell AJ, Riding JB, Smelror M, Williams GL (1996) Mesozoic-Tertiary dinoflagellates, acritarchs and prasinophytes. In: Jansonius J, McGregor DC (eds) Principles and applications 2. Am Assoc Stratigraphic Palynol Found, College Station, pp 641–750

Sütő-Szentai M. (1991) Szervezvázú mikroplankton zónák Magyarország pannóniai rétegösszletében. Újabb adatok a zónációról és a dinoflagellaták evolúciójáról (Organic-walled microplancton zones of the Pannonian in Hungary. New data on the zonation and dinoflagellate evolution). Őslénytani Viták Discussiones Palaeontologicae 36–37:157–200

Sütő-Szentai M (1988) Microplankton zones of organic sceleton in the Pannonian s. l. stratum complex and in the upper part of the Sarmatian strata. Acta Botanica Hung 34:339–356

Taktakishvili IG (1967) Istoricheskoje razvitije semejstva Valencienniid. Mecniereba, Tbilisi, pp 1–194

Taktakishvili IG (1987) Sistematika i filogenija pliotsenovikh kardiid Paratetisa. Mecniereba, Tbilisi, pp 1–248

Tarasov AG (1996) Deep-water Caspian benthic fauna 1. Genesis and vertical zonation Zoologichesky Zhurnal 75:1763–1775

Tarasov AG (1997) Deep-water Caspian benthic fauna 2. Biological diversity. Zoologichesky Zhurnal 76:5–15

Tarasov AG, Chepalyga AL (1996) New data on the vertical distribution of Bivalvia in Caspian deep-water basins. Ruthenica 5:147–154

Vakarcs G, Vail PR, Tari G, Pogácsás Gy, Mattick RE, Szabó A (1994) Third-order Middle Miocene-Early Pliocene depositonal sequences in the prograding delta complex of the Pannonian Basin. Tectonophysics 240:81–106

Van Dam JA (2006) Geographic and temporal patterns in the late Neogene (12-3 Ma) aridification of Europe: the use of small mammals as paleoprecipitation proxies. Palaeogeogr Palaeoclimatol Palaeoecol 238:190–218

Weinfurter E (1950) Die oberpannonische Fischfauna vom Eichkogel bei Mödling. Sitzungsberichte der Österreichischen Akademie der Wissenschaften, mathem naturw Kl Abt I, 159:37–50