

Physical and biological properties of the late Miocene, long-lived Turiec Basin, Western Carpathians (Slovakia) and its paleobiotopes

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Abstract The Turiec Basin (TB) of Slovakia formed in the Miocene when the West Carpathians escaped from the Alpine region. The 1,250-m-thick sedimentary Neogene fill of the basin preserved fossil leaves as well as endemic bivalves, gastropods, and ostracodes. The paleolimnologic changes recorded in the TB infill were derived from the most abundant fossils, the ostracodes. Five contemporaneous ostracode assemblages within the Late Miocene lacustrine system were distinguished through statistical analysis. These assemblages have low species similarity, between 2.1 and 24.1%, and are recognized by shape differ-

ences among the Candoninae. The ostracode assemblages, mollusca fossils, and Sr-isotope ratios suggest a low-salinity environment at the beginning of the Late Miocene, during a brief connection with the Central Paratethys. When the connection ceased, the basin became an isolated freshwater lake, with five zones differentiated ecologically and bathymetrically using the ostracode assemblages. Taxonomic comparison of the faunas of the TB and the freshwater to brackish Neogene basins of Europe demonstrates the endemic character of the TB ostracode fauna. The biologic characteristics of the ostracode families, along with the geology of the lake basin, suggest that the longevity of the Late Miocene lake probably exceeded 1 Ma.

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Introduction

Geologic and tectonic setting

The Turiec Basin (TB) of Slovakia is one of the Western Carpathian intermontane basins (Fig. 1A) that formed during the Middle and early Late Miocene (Nemčok et al. 1998) as a result of the Alpine Orogeny and its relationship to the Carpathian Mountains. The Western Carpathian area is interpreted as an escaping tectonic block that moved eastward during the compression from Alpine thrusting. The Turiec Basin is situated within this collisional orogenic zone and continental volcanic arc, on this fault-bounded block inside the Central Slovak Fault System (Kováč and Hók 1993). The basin started to open during the Middle Miocene, perhaps as an extensional basin. Acceleration of subsidence occurred in the late Middle Miocene, along normal to strike-slip faults, to reach a maximum during the Late Miocene (Rakús et al. 2005).

Sedimentation in the TB was mainly controlled by faults at the basin's western margin (Fig. 1B) (Hók et al. 1998). The sedimentary Neogene fill of the TB reaches up to 1,250 m (Fig. 1B) and could have been episodically connected at that time with the back-arc Carpathian basins. The oldest deposits are represented by the Middle Miocene sedimentary, volcano-sedimentary and volcanic andesitic complex found at 908.7–1,387.0 m in core GHŠ-1 (Fig. 2). Voluminous volcanic activity south of the basin continued during the Middle/Late Miocene. A rhyolitic volcanic complex, drilled at a depth 550.0–551.5 m in core GHŠ-1 (Gašparík et al. 1974), is comparable to the rhyolitic formation of the Central Slovakia Volcanic Field, with a K–Ar radiometric age of 12.4 ± 2.2 – 10.7 ± 0.3 Ma (Konečný et al. 1983). During the Late Miocene, any TB connections with Lake Pannon, a back-arc lake basin, were cut by the uplifting mountains and rising stratovolcanoes. By that time, the TB was filled by coarse carbonate and siliciclastic deposits, with huge conglomerate fans during stages of rapid subsidence. The northern and central parts of the basin reveal lacustrine, marginal to offshore clay and silt facies

(Hók et al. 1998). During the Pliocene and Quaternary, subsidence of the TB ceased and sedimentation became fluvial in origin. Drainage switched to the north and there was erosion, as shown by river terraces (Nemčok and Lexa 1990).

Data on the fauna (Protozoa–Testacea, Mollusca, Ostracoda, fish otoliths) and flora (Diatomaceae, pollen, fossil leaves) and the entire lithologic sequence of core GHŠ-1, date sedimentation in the TB from the Middle Miocene to Pleistocene (Gašparík et al. 1974). Because the studied successions that contain ostracode assemblages (Fig. 3) are situated above the rhyolitic volcanic complex, the evolution of the TB fauna is dated to the Late Miocene. The objective of this study was to test whether the Late Miocene TB fill can be regarded as evidence for a long-lived paleolake (sensu Gorthner 1994).

Materials and methods

Data collection

Sampling for ostracodes was done in all recognized lithologies in the basin, namely in clay, sand, gravel, slightly lithified limestone, marl, and lignitic clay (ESM1). Details about geographic location, lithology, fossils, and distribution of the ostracode fauna in the cores and exposures are given in Pipík (2001).

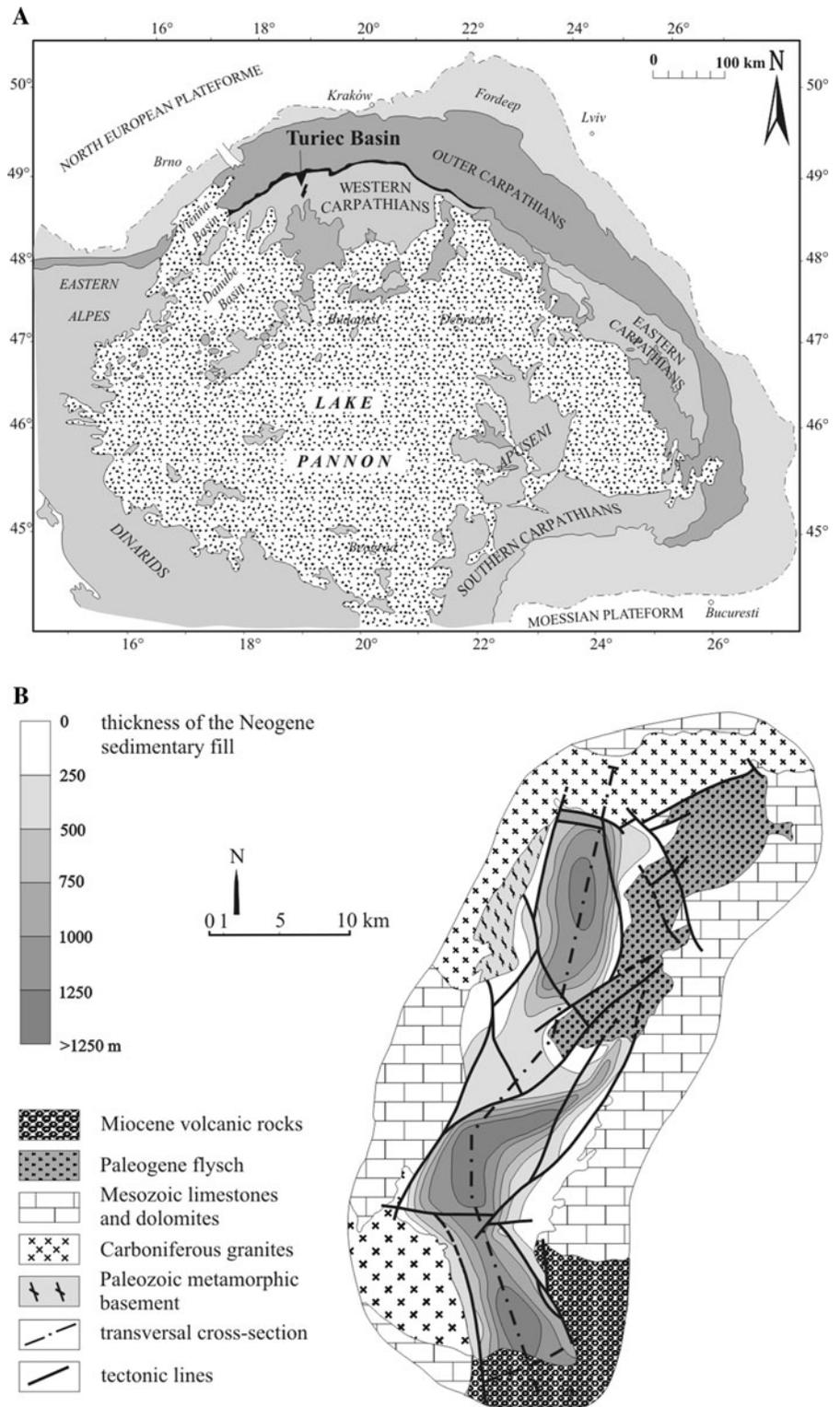
Material from previous geologic investigations is stored at Charles University, Prague, Czech Republic (collection of Prof. Pokorný) and at the State Geological Institute of Dionýz Štúr in Bratislava, Slovakia. The ostracode fauna designations were revised by Pipík (2001) mainly for taxonomic purposes. Three samples from Late Miocene deposits in the old clay pit at the Martin locality were also analyzed (see Fig. 2 for location).

Laboratory methods

Fossil analysis

About 500–1,000 g of each sediment sample collected for ostracode analysis was dried and mixed with a 10% solution of Na_2CO_3 . Sediment was then sieved using 1.00 and 0.08 mm sieves. The washed residue was placed in a solution of $\text{Na}_2\text{H}_2\text{P}_2\text{O}_7$ to remove small clay particles adhering to the ostracode valves. Species

Fig. 1 **A** Paleogeography of the Central Paratethys area (11–9 Ma) and the position of the Turiec Basin among the Late Miocene Basins (after Kováč 2000). **B** Modern adjacent geological units, thickness of the Neogene sedimentary fill, and principal Neogene tectonic lines of the Turiec Basin (Pipík and Bodergat 2008). For a transverse cross section line, see Fig. 3



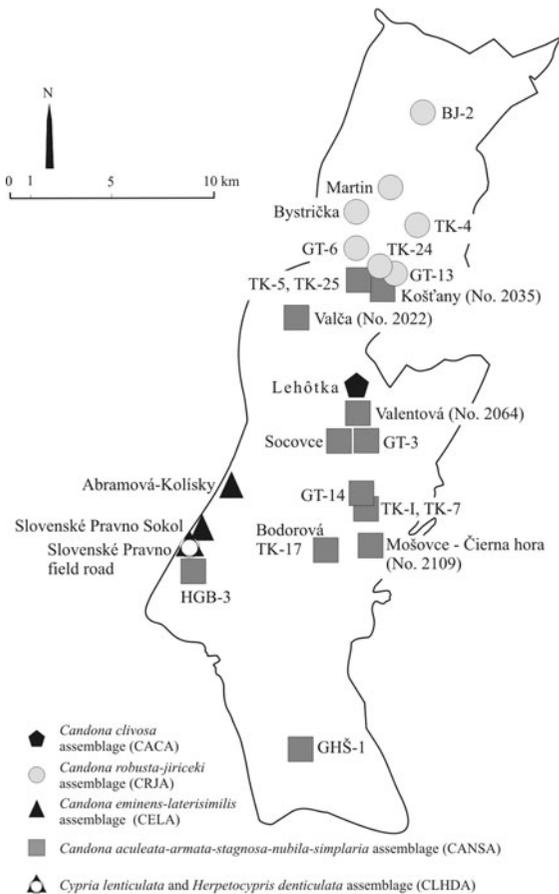


Fig. 2 Distribution of the ostracod assemblages on the present surface of the Turiec Basin

were identified by observing structural elements of the ostracode valves using optical and SEM methods. Optical observations documented the internal valve structures, as this method was more convenient for classification of the smooth taxa. Ornamentation was documented using SEM.

Statistical methods

A total of 187 ostracode samples from the entire area of the TB were analyzed statistically using Correspondence Analysis (CA) in SYSTAT to evaluate relations between observations (samples) and variables (species). The calculation matrix was composed of 81 variables and 187 observations using presence/absence data for species. Statistical analyses were not applied to the material from exposures, to cores with poorly preserved fauna (Vrútky, Dubná skala), to

samples from previous studies that lack exact stratigraphic and lithologic information (ESM2), or to cores documented in the literature (GT-3, GT-6, GT-13, GHŠ-1 and ZGT-3). Jaccard's similarity index was calculated to assess similarity between assemblages defined by CA. In addition, principal component analysis (PCA) was used to distinguish among the Candoninae species, especially through morphologic characteristics (ESM3) as well as geologic observations from exposures and cores (Pipík 2001). Two independent components, geographic area and ecology, were added to each extant species datum based on biologic observations (Meisch 2000). These analyses were then applied to paleoecologic interpretations, which also relied on macrofloristic, sedimentologic, and malacologic data.

Strontium isotopes

Sr isotopic composition ($^{87}\text{Sr}/^{86}\text{Sr}$) was measured on ostracode valves and mollusc shells and compared to shell data from the literature (Král' et al. 1995; Janz and Vennemann 2005) to evaluate a possible connection between the TB and the Central Paratethys. The TB shell fauna was analyzed using SEM to determine the extent of diagenetic shell alteration and identify the best fossils for Sr analyses. One to three ostracode valves, each valve weighing between 20 and 60 μg , were dissolved in 2 M HCl. Ion exchange chromatography (Pin and Bassin 1992) was applied to these solutions to extract Sr. This same method was used for extraction of Sr from small fragments of mollusc shells. Sr was loaded on Ta-activated W single filaments and $^{87}\text{Sr}/^{86}\text{Sr}$ data were measured on a fully automated Isomass VG54E mass spectrometer, using a SRM987 standard for reference. Three measurements gave a mean Sr isotopic value of 0.710244 ± 0.000018 (2σ error).

Results

Ostracode assemblages and their spatial distribution

The 85 identified species of ostracodes are listed in ESM2. Correspondence Analysis (CA) was applied to identify ostracode groups along gradients (ESM4). The CA plot was not detrended and shows a weak horseshoe

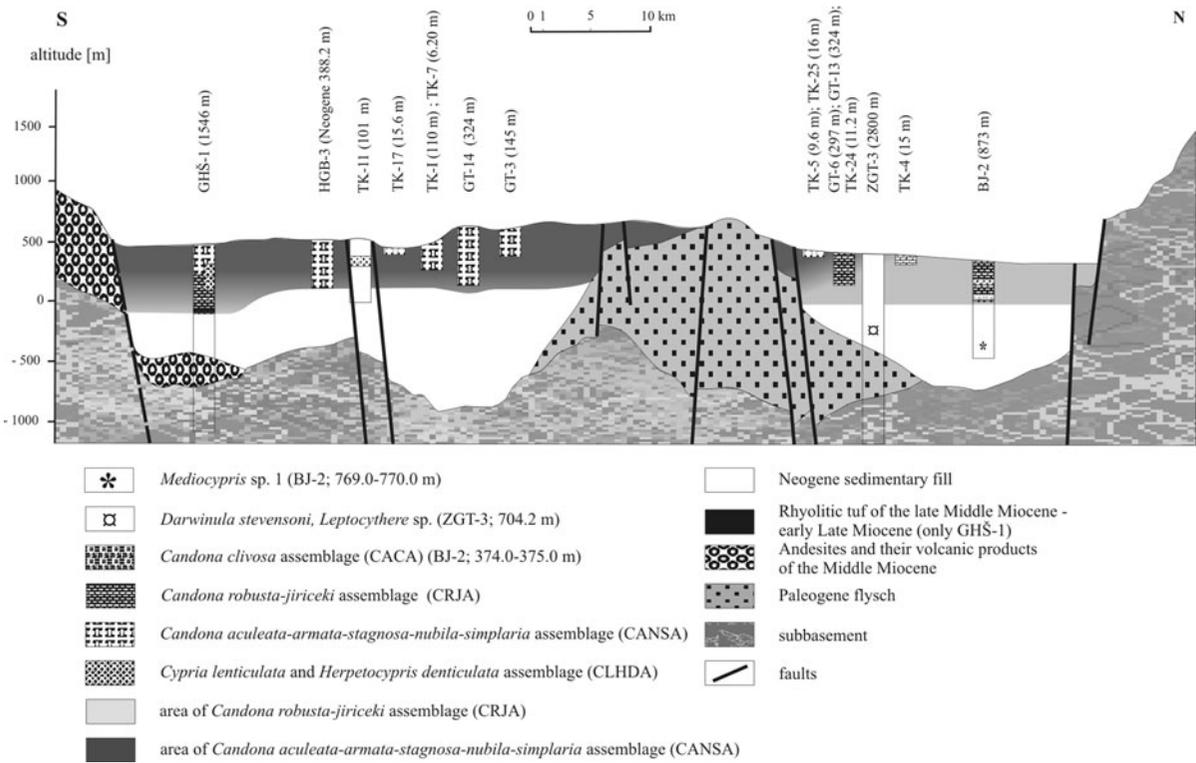


Fig. 3 North-south transverse cross-section of the Turiec Basin (see also Fig. 1) (Zbořil et al. 1985; Gašparík et al. 1995) and vertical distribution of the ostracod assemblages. The numbers

behind core labels show the core length in meters. CELA is known only from the exposures. Vertically exaggerated

effect, a function of CA. Five ostracode assemblages were recognized by the CA and named for the most abundant ostracode species at the localities (ESM4, 5; Figs. 2, 3): CANSА—*Candona aculeata-armata-stagnosa-nubila-simplaria* assemblage; CRJA—*Candona robusta-jiriceki* assemblage; CACA—*Candona clivosa* assemblage; CLHDA—*Cypria lenticulata* and *Herpetocypris denticulata* assemblage; and CELA—*C. eminens-laterisimilis* assemblage. Their descriptions follow with localities shown in Fig. 2.

1. *Candona aculeata-armata-stagnosa-nubila-simplaria* assemblage (CANSА). This assemblage is composed of 28 taxa encountered at the Socovce exposure and in cores from the central and southern part of the TB. The revised ostracode fauna of cores GT-3 and GHŠ-1 also corresponds to this assemblage (Pipík 2001). In core GHŠ-1, three species of the CANSА assemblage (*Euxinocythere minuscula*, *Pseudocandona ex gr. centropunctata* and *P. pharia*) were found at depths from 7.0 to

281.0 m, above the rhyolitic volcanic complex. Candoninae with trapezoidal, triangular, and rectangular shapes, with pointed postero-ventral borders, dominate this assemblage.

2. *Candona robusta-jiriceki* assemblage (CRJA). The assemblage is composed of the genera *Candona*, *Euxinocythere*, *Ilyocypris*, and *Cypria*, with five extant (*Cavernocypris subterranea*, *Darwinula stevensoni*, *Fabaeformiscandona batatonica*, *Pseudocandona compressa*, and *Vestalenula pagliolii*) and two fossil (*Candona clivosa*, *Candonopsis arida*) species. Exposures and cores with this assemblage (Fig. 2) contained 21 species. A revision of the older ostracode collections (Pipík 2001) revealed that the ostracode fauna of cores GT-6 and GT-13, as well as that of GHŠ-1 from 7.0 to 360.0 m depth, also contained this assemblage. CRJA appeared mainly in the northern part of the TB, contemporaneous with CANSА or somewhat older, stratigraphically, in core GHŠ-1 (Fig. 3).

3. *Candona clivosa* assemblage (CACA). The Le-hôtka exposure on the eastern edge of the TB and the stratigraphic interval 374.0–375.0 m of core BJ-2 contained 15 species of which 10 were new, including those of the genera *Candona*, *Euxinocythere*, and *Cypria*. Three species are extant (*D. stevensoni*, *F. balatonica*, *Heterocypris salina*) and two are fossil (*C. arida*, *C. clivosa*). Candoninae were the most abundant species (10) and were represented by elliptical and rectangular valves with rounded postero-ventral borders (*Candona mocki*, *C. fatrica*, *C. arida*, *Fabaeformiscandona regia*).
4. *Cypria lenticulata* and *Herpetocypris denticulata* assemblage (CLHDA). The Slovenské Pravno exposure and core Veľký Čepčín TK-11 (99.5–101.0 m depth) from the southwestern edge of the TB contained 31 species, of which 19 species were new, three had been described previously (*C. arida*, *D. stevensoni* and *Candona neglecta*), and nine were left in open nomenclature. Eleven species were represented by only one to four valves. *Herpetocypris* sp. was observed in core GHŠ-1 in the interval 135.0–281.0 m. This assemblage was known from the old clay pit in Martin, near the Martin exposure (ESM1) (Pipík 2001), documenting a broader occurrence of this assemblage in the TB.
5. *Candona eminens-laterissimilis* assemblage (CELA). Several individuals of extant *Heterocypris salina* were recognized among 17 morphologically distinguishable species of this assemblage at only two exposures on the southwestern edge of the TB (Fig. 2). The valves of *Candona* are heavy and calcified, and have unusual characters for Candoninae valves, i.e. dorsum, protuberance, and spines.

Similarity among the assemblages

Eighteen (22%) of all the ostracode species were recorded in two distinct assemblages and only 2% (*C. arida*, *Cypria polyphema*) were found in three assemblages. Newly described *Euxinocythere aphroditae*, *E. delicata*, and cosmopolitan *Darwinula stevensoni* were present in four assemblages, representing 4% of the species. The other ostracode species (72%) were recorded in only one assemblage.

Jaccard's similarity index (Fig. 4) was low, varying between 2.1 and 24.1%, with the highest value observed between CRJA and CACA. Shared taxa included *C. clivosa*, *C. arida*, *Cypria polyphema*, *D. stevensoni*, *Euxinocythere aphroditae*, *E. delicata*, and *Eucypris* sp. 1. CLHDA was similar to CRJA and they had seven species in common: *Candona densa*, *C. arida*, *Cypria polyphema*, *D. stevensoni*, *E. aphroditae*, *E. lactea*, and *Herpetocypris pusilla*. A large difference in species composition was observed between CELA and other assemblages, except CANSAs. The similarity index varied between 2.1 and 6.7% and CELA shares only three species (*Pseudocandona vannieri*, *Heterocypris salina*, and *E. delicata*) with CLHDA, CRJA and CACA. On the other hand, relatively high similarity (18.4%) was observed between the CELA and CANSAs. They had seven common species (*Candona palustris*, *Cypria bodergatiae*, *C. isosceles*, *E. delicata*, *E. minuscula*, *Fabaeformiscandona* sp. 1, *P. pharia*.) that, apart from the two *Euxinocythere* species, did not appear in other assemblages.

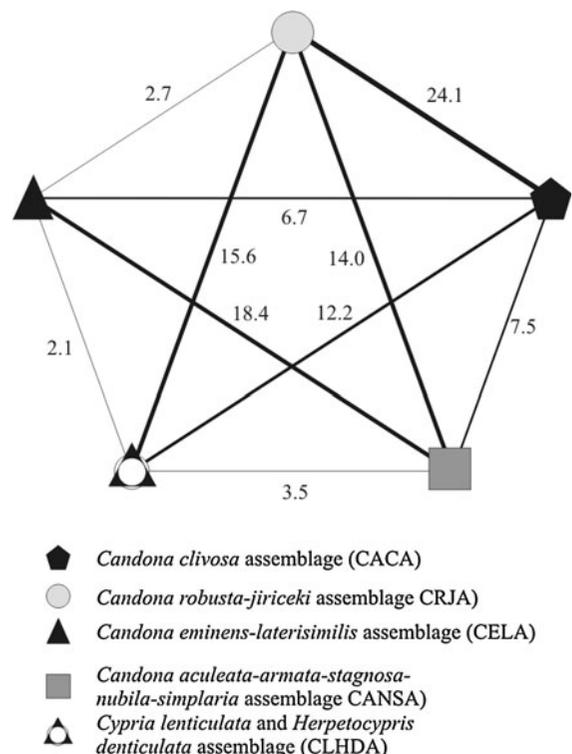


Fig. 4 Graphic showing the similarity between assemblages calculated by Jaccard's similarity index

The CANSA appeared more complex than the others. Indeed, on the CA plot (ESM4, 5), CANSA exhibited a linear distribution, with a continual change in species composition between the interval from 12.5 to 161.6 m in core HGB-3, 5.5–76.6 m in core GT-14, 174.5–300 m in core HGB-3, and 86.5–309.6 m in core GT-14 (Pipík and Bodergat 2007). These intervals had 12 species in common (*Candona expressa*, *C. lacustris*, *C. ossea*, *C. pacifica*, *C. palustris*, *C. robusta*, *Cyprina isosceles*, *E. minuscula*, *Fabaeformiscandona* sp. 1, *Pseudocandona carbonnelli*, *P. ex gr. centropunctata*, and *P. pharia*), with a similarity index as high as 42.9%.

The overall similarity between the CANSA and CRJA was 14%, but varied depending on the compared intervals in the cores. The similarity was very low (5.3%) between the CRJA and CANSA in the intervals 12.5–161.6 m (core HGB-3) and 5.5–76.6 m (core GT-14). It was higher (13.5%) within the intervals 174.5–300.0 m (core HGB-3) and 86.5–309.6 m (core GT-14) and highest (16.7%) within the interval 244.5–309.6 m (core GT-14). In this case, the assemblages shared *Candona simplaria*, *C. robusta*, *C. sp. 67*, and *E. aphroditae*. Despite the relatively high similarity index between CANSA and CELA, no similarity was observed between CELA and CANSA in the interval 244.5–309.6 m in core GT-14.

Geographic and paleoecologic origin of the Candoninae

Principal component analysis (PCA) was used to decipher the morphologic differences among the Candoninae, which represented 72% of all ostracode species in the TB. The majority of Candoninae have unknown ecologic requirements. The female left valves of 42 Candoninae were used in this factorial analysis (ESM2). Females were not known for all TB Candoninae and species shells collected for analysis had very similar right valves. Some species were represented only by instars or carapaces. Morphotypes with a slightly rounded dorsal, the right dorsal of *Candona palustris*, and *C. armata* shells with weak and heavy ornamentation were used.

Candoninae were divided into two morphologic groups in the TB fauna. The first two factors of PCA explained 28 and 13% of the total variance (ESM6). The most important variables of the first factor were width of the zone of fusion, shape of the postero-

ventral border, overlap extent, special features on the surface, and valve calcification. The second factor segregated species with a pointed dorsal border, maximal height at the center, and triangular shape. Points 22 (*C. palustris* with right dorsal and *C. lacustris*) and 31 (*C. sitari* and *C. ossea*) in ESM6 included morphologically identical species.

The Candoninae species on the left side of ESM6 are in CLHDA (2, 4, 6, 7, 10–13, 16–18, 39), CACA (1, 3–7, 9), and CRJA (1, 4, 8, 25, 35, 37). Extant Palearctic and Holarctic species 1, 2, and 8 are situated in this cloud (Fig. 5A) and they are characterized by a thin zone of fusion, rounded postero-ventral margin, weak overlap, and weak calcification. Fossil species 4 and 6 (*C. clivosa*), and the newly described TB species 3, 5, 6 (*C. densa*), 7, and 9–11 shared the same morphologic characters.

Candoninae with a broad zone of fusion, a trapezoidal shape, large overlap, and a pointed postero-ventral margin occupy the right side of the plot (ESM6). These characters were also found in the CANSA (14, 15, 19, 20, 22–26, 30–38) and CELA (14, 21, 22, 27–29, 41). Candoninae with such morphologic characteristics are common in the Late Miocene and Pliocene of the Paratethys (Fig. 5A). The presence of unusual characters (protuberances, tubercles, dorsum, and spines) differentiated the TB Candoninae from the Holarctic and Palearctic ones. Two taxa (40, 41) in the CANSA had a position orthogonal to other taxa, as a consequence of their triangular shape. This phenomenon is well known from middle and southeastern Europe (Meisch 2000; Pipík and Bodergat 2008) and from the Paratethys area (Krstić 1972; Freels 1980). Morphologic characters observed in the CELA and CANSA are also observed in Candoninae from long-lived Lake Baikal (eastern Siberia), and Lake Ohrid (Macedonia), as well as the Caribbean (Bronstein 1947; Broodbaker 1983; Mikulić 1961).

Candona incurva, *C. vahica*, *F. sp. 1*, *F. aff. lineata*, and *P. vannieri* exhibited ambiguous characters, which did not allow us to infer their geographic area from their valve morphology. *C. incurva* had a broad zone of fusion and a strong overlap, but also an elliptical form. *C. vahica* was subtrapezoidal, but with a rounded postero-ventral margin. *P. vannieri* had a broad zone of fusion and a rounded postero-ventral margin. *F. aff. lineata* and *F. sp. 1* had the morphologic characters of the species from the CLHDA, CRJA, and CACA, but they were associated with

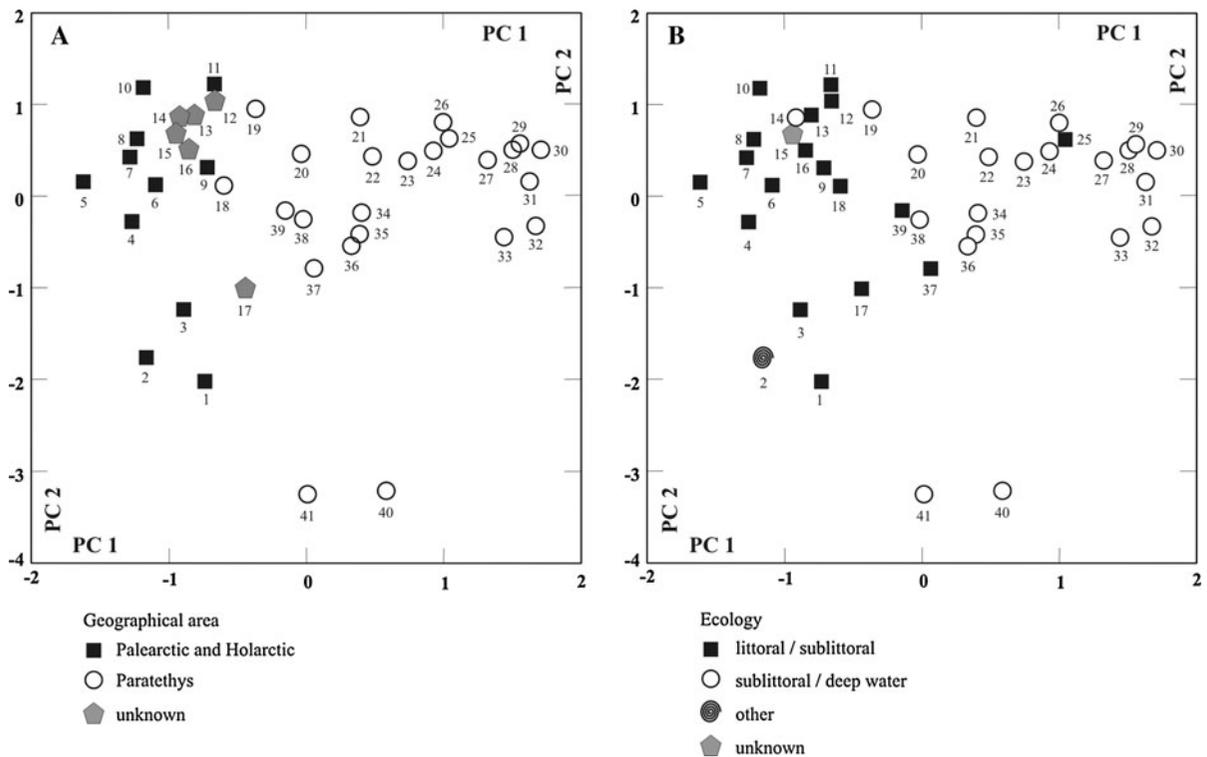


Fig. 5 Geographic area (A) versus environment (B) of the Turiec Basin Candoninae discriminated by valve shape (for label numbers see ESM6)

species from the CANSA and CELA. *F. aff. lineata* was a fossil species known from the Central Paratethys (Krstić 1972), but its paleoenvironment and associated species were not specified.

The shape of Candoninae shells was postulated to be related to the stability of the ostracode's environment (Danielopol 1980). For example, the shape of Palearctic Candoninae corresponds to the environment in which they lived. The rectangular, elongated or slightly triangular species lived in unstable environments, such as ponds or temporary basins. Candoninae that were triangular, trapezoidal, or had elongated shapes with pointed posteriors preferred stable conditions, i.e. environments with minimal fluctuations. We propose that the shapes of the TB Candoninae did not reflect a paleogeographic distribution, but corresponded to an evolutionary response to the specific paleoecologic conditions under which these Candoninae lived. Candoninae from the CLHDA, CRJA and CACA in Fig. 5B probably were adapted to fluctuating environments. They were associated mainly with Darwinulidae and Cyprididae, which inhabited

ecologically unstable littoral and sublittoral facies. The trapezoidal and pointed posterior taxa from the CANSA and CELA appear to have adapted to a physically stable paleoenvironment.

Isotopic evolution of the Turiec Basin

Both SEM and optical microscopy were used to identify shells with little or no alteration, to be used for Sr analyses. SEM photographs (ESM7 A-D) show the crossed-lamellar, prismatic, and foliated layers of the tests of TB gastropods that show no alteration. Fibers of the *Congerina* shell, however, appear connected, indicating some alteration (McArthur 1994).

All Sr isotope data from shells of the TB fauna listed in ESM8 were normalized to $^{87}\text{Sr}/^{86}\text{Sr} = 0.710250$, the value of reference sample SRM-987. The $^{87}\text{Sr}/^{86}\text{Sr}$ of all the samples from TB varied from 0.708011 ± 0.000015 to 0.708347 ± 0.000020 (ESM8). The values are significantly lower than seawater $^{87}\text{Sr}/^{86}\text{Sr}$ values during the Middle and Late Miocene, which rose from 0.70872 to 0.70902 (McArthur et al. 2001)

(Fig. 6A). They are also lower than the isotopic composition of late middle Miocene brackish molluscs from the Western Carpathians ($^{87}\text{Sr}/^{86}\text{Sr} = 0.708611 \pm 0.000010$, Král' et al. 1995). Brackish ostracodes from the Middle and Late Miocene deposits of the Central Paratethys (Janz and Vennemann 2005) had $^{87}\text{Sr}/^{86}\text{Sr}$ values ranging from 0.708715 ± 0.000010 to 0.708833 ± 0.000010 . Janz and Vennemann (2005) attributed the slightly lower isotopic ratios of these brackish ostracodes, compared to marine specimens, to the input of freshwater with an isotopic composition controlled by weathering of nearby Mesozoic carbonates, below 0.708.

Because the $^{87}\text{Sr}/^{86}\text{Sr}$ values of TB fauna shells are closer to Mesozoic values, their interpretation requires almost exclusive influence of freshwater, with no direct seawater input. As the Sr-isotopic composition of the TB fauna did not reveal a Paratethys influence in the basin, any connection between the TB and the Central Paratethys, as suggested by the presence of brackish genera *Congerina* (bivalve), *Melanopsis* (gastropod), and *Euxinocythere* (ostracode), was probably of very short duration. The isotopic signatures of TB faunal shells probably reflect the Sr composition of the

rock formations in the lake watershed (Semhi et al. 2000; Gierlowski-Kordesch et al. 2008).

The water evolution of the isolated lake in the TB basin can be derived from the Sr isotope data. The highest and most variable $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of TB shells, $\sim 0.708169 \pm 0.000009$ to 0.708320 ± 0.000016 (ESM8) were observed in the northern part of the basin. The rocks exposed in the north include Paleozoic metamorphic basement and Carboniferous granites, probably with high $^{87}\text{Sr}/^{86}\text{Sr}$, Mesozoic carbonates, and Paleogene flysch (Fig. 1A). This diversity of lithologies can explain the variability of isotope ratios in Late Miocene freshwaters. The exact contribution of each source, however, cannot be determined quantitatively because we do not have the needed variables to calculate mixing, mainly the Sr content of local Miocene rivers. We note that this part of the TB is dominated mainly by CRJA, which were adapted to fluctuating, unstable environments and had Sr isotope ratios reflecting that variability.

Shells from the southern part of the TB have low and more homogenous $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratios ($\sim 0.708011 \pm 0.000015$ – 0.708093 ± 0.000010). Here, influence of the Mesozoic carbonate

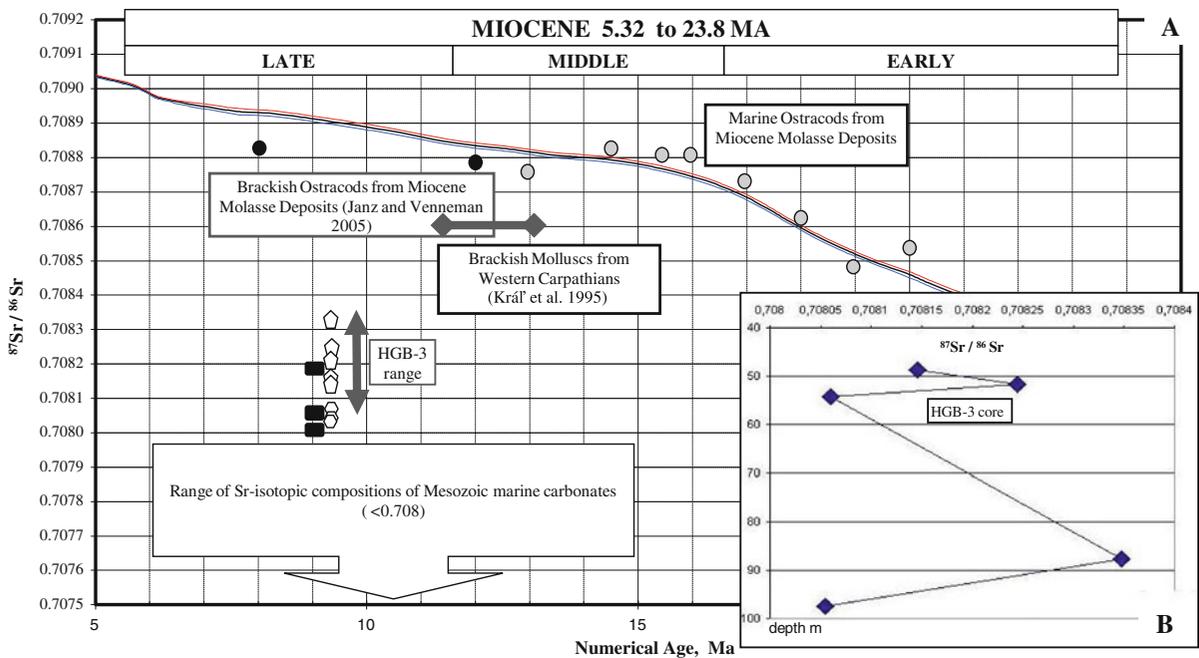


Fig. 6 Variations of $^{87}\text{Sr}/^{86}\text{Sr}$ during the Cenozoic (McArthur 1994) and isotopic compositions of the ostracod and mollusk valves from the Turiec Basin (A) and HGB-3 (B) black

rectangle ostracods; pentagon gastropods; hexagon bivalves. Position of late Miocene TB samples on the time scale is approximate

provenance, with $^{87}\text{Sr}/^{86}\text{Sr}$ lower than 0.708 (McArthur et al. 2001), and Miocene volcanic rocks in the southern area, could explain lower isotopic signatures of local lacustrine freshwater during the Late Miocene. The ostracodes in the southern part of the TB are dominated by the more stable CANSA assemblage, in agreement with more homogenous Sr isotope ratios.

Five ostracode samples were analyzed from core HGB-3 in the southern part of the basin. Their Sr isotopic ratios ranged from 0.708055 ± 0.000027 to 0.708347 ± 0.000020 (Fig. 6B, ESM8). Two samples have isotopic values that are similar to those from the northern part. This suggests some mixing of the Sr isotopic composition of lake waters with time, as registered in HGB-3. This may reflect input of northern drainage water into the southern part of the isolated basin or a change in freshwater input coming from the south. Ultimately, it could be related to a change in drainage from a tectonic event (Gierlowski-Kordesch et al. 2008) or extensive lake mixing during a flooding event.

Discussion

Comparison with European Neogene nonmarine basins

Late Miocene deposits of the TB contain 85 species, of which 50 are newly described (Pipík and Bodergat 2008). This large number of new species differs from those found in other studies of nonmarine Neogene ostracodes in Europe (ESM9). For example, in the Middle Miocene Steinheim Basin (Janz 1997), only four of the 44 freshwater species identified were also found in the TB. Only three species among 55 identified in the freshwater deposits of the Swiss Molasse Basin and Rhône Basin (Carbonnel 1969; Carbonnel et al. 1985) were present in the TB. Witt (2000) listed 29 nonmarine Early to Late Miocene species in the sub-alpine Molasse Basin of Bavaria and the freshwater basins from the western Czech Republic, of which only one species was also present in the TB.

The Paratethys area is known for its endemic and rich nonmarine fauna. Jiříček (1985) listed about 70 species from the Late Miocene brackish fauna of northern Lake Pannon (Pannonian Basin) (Fig. 1A). No species of that area were found in the nearby TB.

The Late Miocene freshwater fauna of the TB shares taxa only with Holarctic and cosmopolitan ostracode faunas (Pipík et al. 2004). Only five ostracode species from the southern Pannonian Basin were found in the TB. An example is *P. ex gr. centropunctata* in the Late Miocene and Pliocene of the eastern Paratethys (Mandelstam and Schneider 1963). Although the Late Miocene and Pliocene lacustrine deposits of Turkey and Greece were rich in freshwater ostracode species (70 taxa) (Freels 1980; Mostafawi 1994, 1996), they do not compare in diversity with the fauna of the TB. This short review shows that the ostracode fauna of the TB did not have an equivalent in diversity at the species level among the Neogene fresh and brackish water fauna of Europe.

Turic Basin and extant long-lived lakes

Longevity is the principal character defining long-lived lakes (Gorthner 1994). Martens (1994, 1997) and Martens et al. (1994) described the other features of long-lived lakes: (1) ecologic segregation of species, (2) intralacustrine evolution, (3) convergent faunal characters, (4) high faunal diversity, and (5) a tectonic basin origin. Endemism is a result of long-lived lakes, as shown in the East African lakes (Martens 1997).

The Miocene ostracode fauna of the TB can be characterized as endemic. Fifty-nine percent of the ostracode species were new (Table 1). This is supported by comparisons with other Miocene European basins. Furthermore, according to Gašparík et al. (1995), molluscs from the TB also show endemic characters.

Cyprididae were the richest family on the generic level (nine genera) in the TB Miocene, but the genera were represented by only one to three species, 12 species in total (Pipík and Bodergat 2008). Only three new cypridid taxa were encountered (Pipík and Bodergat 2004a), confirming their scarcity, and providing supporting evidence for a long-lived Miocene lake (Martens 1994) in the TB. The TB lake environment did not offer optimal conditions for Darwinulidae, and together with Ilyocyprididae, they had low species diversity (Pipík and Bodergat 2003a). The smallest adult specimens were in the Darwinulidae (*Vestalenula*), while the largest ones were in the Cyprididae (*Psychrodromus*) (Pipík and Bodergat 2003a, 2004a). Both genera, however, were not connected directly to the limnic environment. See

Table 1 Biological and physical features of the long-lived lakes (Martens 1994, 1997; Martens et al. 1994) and of the Turiec Basin

	Extant long-lived lakes	Turiec Basin
Darwinulidae	–	Rare
Candonidae	+	+
Cytheroidea	+	+
Cyprididae	Peripheric	Peripheric, littoral/ sublittoral
Sexual reproduction	+	+
Size	Small \leq 1 mm	0.455–1.394
Convergent characters	+	+
Intralacustrine evolution	+	+
Endemism	43–90%	59% new species
Other endemic groups	Fishes, molluscs, crustaceans, sponges	Molluscs
Ecological segregation of the species	+	+
Surface (km ²)	348–384 400	~ 320*
Age	>2 MA	?

+ present, – missing, * present area of the Miocene deposits (Gašparík et al. 1995)

the discussion on the marginal, littoral and sublittoral communities below.

The Cyprididae, Ilyocyprididae and parthenogenetic Darwinulidae, were encountered only in the northern and marginal deposits of the TB, in accordance with a limited presence in a long-lived lake (Martens 1994). In contrast, Cytheroidea and Candonidae were distributed throughout the TB and underwent intralacustrine evolution (Pipík and Bodergat 2004b, 2006, 2007). Sixty-one species of Candonidae were recognized in the TB, among which 40 are new species. A majority of Candonidae species (55) came from the subfamily Candoninae. This subfamily exhibited some intralacustrine evolution in other long-lived lakes and constituted almost two-thirds of the endemics (Martens 1994).

Sexual dimorphism was recognized in 45 species (52%) of the TB, predominantly from Candoninae and *Euxinocythere*. Sexes are not recognized in 19 species (22%) and 16 species (19%) had only females preserved. It seems that sexual reproduction and a benthic life were related to ecologic differentiation of the TB and permitted intralacustrine evolution of the Candoninae (Pipík and Bodergat 2007), whereby valves evolved to shapes like those of the Candoninae of Miocene Lake Pannon and the extant fauna of long-lived lakes.

Long-lived lakes normally exist within a tectonic basin because of a protracted history of subsidence, a conspicuous character of such water bodies (Gorthner

1994; Martens 1997). The TB formed during the Miocene on a tectonic escape block associated with the compressive interaction of the European Platform and Western Carpathians. This tectonic activity culminated at the end of the Middle and beginning of the Late Miocene (Kováč 2000). Fluvial, then lacustrine sedimentation in the TB, began in the Middle Miocene and there was intensive subsidence due to a dextral transtensional to extensional tectonic regime during the late Middle and Late Miocene. The area of the Neogene limnic deposits of the TB is 320 km², which is within the lower limit for areas of long-lived lakes (Martens 1997).

Paleoecologic model of the long-lived Turiec Basin

Salinity and possible water connection with Miocene Lake Pannon

The oldest TB deposits, at ~700 m below surface (Fig. 3), correspond to slightly haline environments. This inference is supported by the presence of oligo-miohaline *Mediocypris* in core BJ-2 and *D. stevensoni* and *Leptocythere* sp. in core ZGT-3 (Kheil 1968; Pipík 2001). Unfortunately, these lacustrine deposits do not contain other fossils that might indicate ecologic conditions at this stratigraphic level.

A range of salinity tolerances characterize the Miocene TB ostracodes: (1) freshwater forms that

tolerate low salinity, such as *C. neglecta*, and *Cypria*, oligohaline (*Ilyocypris*, *Eucypris*), (2) mesohalophilic forms (*H. salina*, *Herpetocypris*), and (3) oligo-pliohaline forms (*P. ex gr. centropunctata*) (ESM10). *Cypria* tolerate variations in salinity and *Euxinocythere* is known from brackish ostracode assemblages of the Paratethys and the eastern Mediterranean, whereas the species found in the TB are interpreted as members of freshwater assemblages (Pipík and Bodergat 2004b).

Other fossils can provide information on “salinity” of the TB lake as well. Freshwater diatoms in TB basin fill indicate salinity as low as 0.5‰ (Gašparík et al. 1974). The gastropods *Theodoxus*, *Melanopsis*, and *Hydrobia*, as well as the bivalve *Congeria*, are common in the brackish Miocene Paratethys facies, however their living representatives can tolerate freshwater conditions. The limnic gastropods are represented by freshwater *Ancylus*, *Gyraulus*, and *Lymnea*. Spongilidae (sponges) live only in freshwater environments (Pokorný 1954). Gobiidae tolerate fresh and brackish waters. Percidae and Cyprinidae (fish families) live in freshwater and seldom occur in brackish environments (R. Brzobohatý in litt.). A freshwater environment is also indicated by the aquatic macrophyte *Potamogeton*.

The presence of brackish molluscs and ostracodes suggests a connection between the TB and Pannonian Basin via its sub-basin, the Danube Basin (Fig. 1A). If the TB was connected with the Danube Basin, then this connection could not have occurred later than the time of the maximal extent of Lake Pannon, between 11.0 and 9.8 Ma. This agrees with K–Ar dating of the rhyolitic volcanic complex in core GHŠ-1 (Gašparík et al. 1974) and with the fact that all the studied ostracod assemblages are situated above this volcanic complex. At that time or earlier, the oligo-miohaline waters of Lake Pannon could have penetrated into the TB for a short time, sufficient for brackish taxa to invade the lake. As the connection ceased, the TB changed to an isolated, freshwater lake, as indicated by the large number of endemic species, the ostracode assemblages, the shapes of Candoninae, and $^{87}\text{Sr}/^{86}\text{Sr}$ values.

Marginal, littoral, and sublittoral communities

The terrestrial Late Miocene environment within the TB is interpreted as a fluvial system (*V. pagliolii*) (ESM10) with oxbow lakes containing *Nelumbium*

and *Scottia browniana*, and a marsh/wetland setting (*Myrica*). A coastal forest (*Glyptostrobus*, *Platanus*, *Alnus*, *Populus*,) with moist habitats (terrestrial gastropods *Helix*, *Carychium*, *Succinea*, *Strobilops*, *Vertigo*) transitioned to a low mountainous area covered by forest (*Fagus*, *Carpinus*, *Carya*, *Pterocarya*) (Pokorný 1954; Sitár 1969). Western and eastern margins were covered by huge alluvial fans composed mainly of Mesozoic carbonates (Fig. 7) (Hók et al. 1998). Temporary ponds and small lakes (*C. neglecta*, *Cyclocypris laevis*, *P. compressa*, *F. balatonica*) (ESM10) formed along the lake margin connected to the surrounding forest area. In these ponds and small lakes, salt content probably increased by evaporation during warm periods, as *Cypria*, *Ilyocypris*, and *Eucypris* were encountered in the sediments.

Psychrophilic *C. subterranea* and *Psychrodromus* are usually associated with groundwater. They colonize caves and springs, where cold water *P. aff. eremita* and *F. ex gr. breuili* occur. According to the requirements of *C. subterranea*, the temperature of the oxygen-rich springs was between 6 and 12°C. The spring ponds are sometimes inhabited by *F. balatonica*, *C. laevis*, and oligothermophilic *C. neglecta*. These Late Miocene springs could have been mineral-bearing, and were inhabited by *H. salina* (Meisch 2000). According to Buday (1962), the mineral sources were a consequence of tectonic activity and karstic Mesozoic carbonate bedrock, which contributed to the creation of the Late Miocene limestone on the edge of the lake.

Polycyclic coal sedimentation with rhizoliths and fossil trees in situ documents a shallow and dynamically changing environment (Pipík 2004). This marginal environment implies unstable ecologic conditions, mainly with respect to temperature (thermoeryplastic *Darwinula stevensoni*). Mesothermophils *F. balatonica*, *P. compressa* and *C. subterranea* may indicate lower water temperature.

The lake floor was divided into a littoral zone developed in the north and a deep profundal zone in the center and southern portion of the TB (Fig. 7). Paleoecologic data (Pipík 2004, 2005) show that the littoral zone in the north was occupied by CRJA (Fig. 7) and was composed of supralittoral and infralittoral zones. The supralittoral zone was indicated by *F. balatonica*, which commonly live in very shallow areas that dry out during summer. The infralittoral zone contained a macrophyte belt of

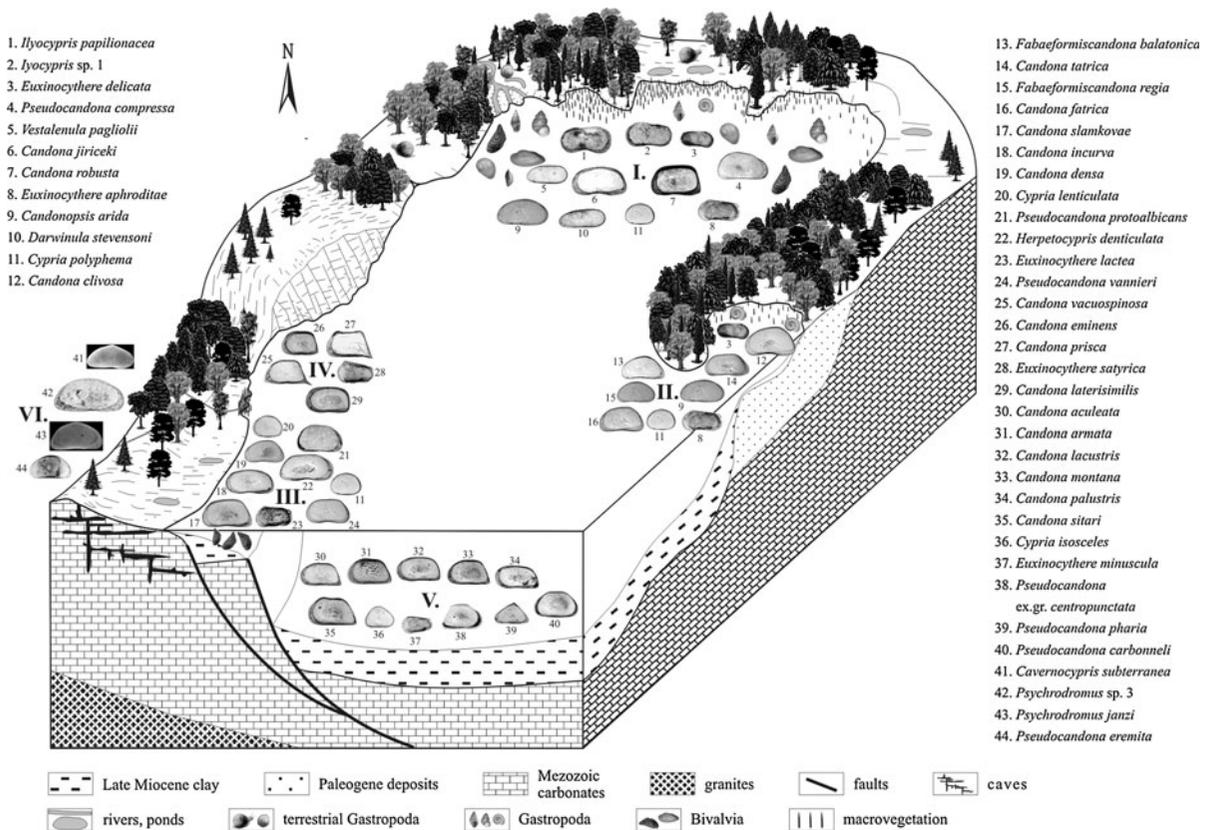


Fig. 7 Paleoecological model showing the paleobiotope of the Turiec Basin in late Miocene time and the characteristic species. Tectonic interpretation is modified from Hók et al. (1998). *I* Marshy littoral to sublittoral zone in the northern part, with slowly flowing water covered by water plants and inhabited by gastropods, bivalves and *Candona robusta-jiriceki* assemblage; coastal humid forest with oxbows and ephemeral environments occasionally with low salinity. *II* Swampy stagnant bay occupied by *Candona clivosa* assemblage; humid forest on the

coast. *III* Littoral to sublittoral zone rich in bivalve shells and species of *Cyprina lenticulata* and *Herpetocypris denticulata* assemblage represent the shell zone. *IV* Sublittoral to deep zone with *Candona eminens-laterisimilis* assemblage, wetland on coast and forest with thermophile elements and mountain vegetation inland. *V* Sublittoral to deep zone in the central and south part of the basin, with *Candona aculeata-armata-stagnosa-nubila-simplaria* assemblage. *VI* Ostracods of cold springs and caves, found in assemblages 1, 3 and 4

Typha growing in water up to 1 m deep, giving way to a zone of submerged and floating-leaved vegetation (*Potamogeton*, *Nelumbium*). A deeper, infralittoral zone was covered by Charophyta, which also grew in shallow water. *C. laevis*, *Dolerocypris*, *Eucypris*, *P. compressa*, *D. stevensoni*, and *F. balatonica* characterized the macrophyte belt (Meisch 2000).

The northern part of the TB was inhabited by gastropods (*Viviparus*, *Theodoxus*, *Melanopsis*, *Planorbis*), bivalves (*Congeria*, *Unio*, *Anodonta*) (Gašparík et al. 1995) and fish (?*Cyprinidarum* sp., ?*Percoideorum* sp., R. Brzobohatý in litt.). Large shell accumulations of both gastropods and bivalves were

preserved in the sublittoral sediments (Pipík 2004, 2005). In modern Lake Ohrid, gastropod abundance is highest in the zone extending from 0 to 20 m and shell remains can be transported by water currents to a sublittoral shell zone (Stanković 1960; Shapkarev 1980).

The rheotolerant *Ilyocypris* and *D. stevensoni* provided data about slow-flowing waters associated with springs or seeps in the northern part of the TB, where the bedrock is dominated by Mesozoic carbonates. Limestones containing microbial textures, such as oolitic structure, occur in this area of the TB. In addition, the degree of fine preservation of the

macroflora (Sitár 1969) indicates early cementation. Cold springs and seeps enter modern Lake Ohrid in the karstic landscape (Stanković 1960), creating a good modern analog for the TB Miocene lake.

On the eastern border of the TB, the CACA, plant leaves, fish otoliths, and gastropod shells were preserved in marl (Fig. 7). Sitár (1969) inferred a swampy stagnant coast covered by *Typha* and *Poa-cites*, with *C. clivosa* indicating stagnant shallow water (Fuhrmann 1991) (ESM10). With the occurrence of lacustrine *C. arida* and evidence for stagnant waters, Sitár (1969) postulated a warm climate during sedimentation. These stagnant waters led to local anoxia, with deposition of pyrite-rich black clays at the northern margin of the basin along a shallow coastline (Pipík 2001). Shapes of Candoninae valves imply a physically unstable environment.

On the deeper western border of the TB, the CLHDA (Fig. 7) was composed of the trapezoidal Candoninae, rectangular Candoninae with rounded posterior, the shallow-water rheotolerant *D. stevensoni*, phytal *Cypridopsis*, the cave and cold spring *F. ex gr. breuili*, *P. aff. eremita* and *Psychrodromus*, and warm-climate *C. arida*. This assemblage was associated with abundant and mostly broken shells of the bivalve *Congerina ex gr. ornithopsis*. This suggests transport of fossil material from marginal, shallow-water environments into the sublittoral zone parallel to the lake edge (Shapkarev 1980).

Deep-water community

Profundal areas of the central and southern part of the TB lake were identified from ostracode assemblages. According to Danielopol (1980), the shapes of Candoninae from these profundal areas (Fig. 7) corresponded to a stable environment, without significant ecologic variations. It is obvious that the littoral and sublittoral zones undergoing daily and annual temperature fluctuations did not offer stable conditions. Rather, it was the profundal zone, 40 m below the water table, that may have been stable and cold. For example, the temperature at 100 m in Lake Ohrid varies only between 6.22 and 5.91°C (Stanković 1960). In contrast to the littoral zone, molluscs and fish otoliths were rarely found in the presumed profundal deposits of the TB (Pipík 2001). Where present, the TB mollusc shells are preserved in a distribution pattern similar to that in Lake Ohrid

(Stanković 1960). Like Lake Ohrid, the TB Miocene lake may have been thermally stratified.

Trapezoidal, heavily calcified Candoninae with specific ornamental features in the CELA (Fig. 7) contrast with the macrofloristic and sedimentologic data observed at the southwestern margin of the TB. A light grey to white calcareous sandy clay preserved a humid marsh and wetland plant community, with tropical and subtropical *Daphnogene polymorpha*, *Ficus cf. lanceolata*, *Sequoia langsdorfii*, *Celastrus cassinefolius*, and *Castanea atavia*. Occurrence of *Psychrodromus* at the Abramová—Kolíský exposure (ESM1) could indicate the influence of cold seeps in this environment. The subaerial and subaquatic, poorly bedded coarse-grained deposits, with both normal and reverse graded beds situated below and above the fossiliferous clay with ostracods, are interpreted as alluvial fans (Hók et al. 1998).

The origin of bathymetric differentiation can be related to the tectonic evolution of this area in the Middle and Late Miocene. The basin subsided along the active listric faults on the west margin and antithetic faults near the eastern margin, which originated from an extensional E-W regime (Hók et al. 1998). At the beginning of the subsidence, this environment was occupied by species known from the littoral community, *C. simplaria*, *C. robusta*, *C. sp. 67*, and *E. aphroditae*. As bathymetric differentiation continued, the Candoninae evolved and changed shape (Pipík and Bodergat 2007). Fine-grained sedimentation was then influenced by input of water from the north, as deduced from the isotopic evolution of the Turiec Basin, and occasionally perturbed by gravel and coarse-grained sands coming from the uplifted mountains along a steep gradient (Pipík 2001).

Conclusions

Longevity is the principal character that defines long-lived lakes (Gorthner 1994). Martens (1994, 1997) and Martens et al. (1994) described other features of long-lived lakes, i.e. ecologic segregation of species, intralacustrine evolution, convergent characters, faunal diversity, and geotectonic position.

Sedimentation in the Turiec Basin started during the Middle Miocene, but the Late Miocene was the main period of faunal evolution in the TB. This Late Miocene TB fauna (Table 1) is characterized by:

1. fifty new species, which represent 59% of all the TB species. Only 16 cosmopolitan, Holarctic, Palearctic and Paratethys species were recognized in the littoral deposits,
2. bathymetric differentiation of the lacustrine environment and ecologic and bathymetric segregation of species,
3. presence of Cyprididae and Darwinulidae in littoral and marginal biotopes and of Candoninae and Cytheroidae, represented here by *Euxinocythere*, over the whole basin,
4. abundance of Candoninae that underwent intralacustrine evolution and acquired characteristics homeomorphic with those of the Central Paratethys and Candoninae of extant long-lived lakes,
5. sexual reproduction recognized in 52% of the TB ostracod species,
6. $^{87}\text{Sr}/^{86}\text{Sr}$ reflecting the evolution of an isolated basin, and
7. geologic setting of the basin inside a collision orogene zone and an active volcanic arc.
8. These properties allow the TB to be categorized as a fossil long-lived lake.

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