Phylogeny, palaeoecology, and invasion of non-marine waters by the late Miocene hemicytherid ostracod *Tyrrhenocythere* from Lake Pannon

RADOVAN PIPÍK

Pipík, R. 2007. Phylogeny, palaeoecology, and invasion of non-marine waters by the late Miocene hemicytherid ostracod *Tyrrhenocythere* from Lake Pannon. *Acta Palaeontologica Polonica* 52 (2): 351–368.

Species of the ostracod genus *Tyrrhenocythere* were found in sediments at the western margin of the Danube Basin, dated as Pannonian zone MN9/MN10 of the late Miocene, together with the euryhaline ostracods *Euxinocythere*, *Loxoconcha*, *Cyprideis*, *Hemicytheria*, *Amplocypris*, and Paratethyan Candoninae. Sandy and clayey deposits intercalated with lignite seams, as well as the ostracod assemblages, reflect oscillations of Lake Pannon water level and salinity, from freshwater to pliohaline. *Tyrrhenocythere* most probably evolved by phyletic transformation from *Hemicytheria*. The hinge and the central muscle scars of *Tyrrhenocythere* are plesiomorphic characters and the two genera differ in the arrangement of the marginal pore canals (MPC). The transformation of simple, straight and thin MPC in *Hemicytheria* to polyfurcate MPC in *Tyrrhenocythere* can be observed in sympatric and contemporaneous populations in Lake Pannon. On the basis of ornamentation, *T. pezinokensis* with heavily calcified valves bearing distinct ornamentation could be a descendent of ribbed and heavily calcified *Hemicytheria* and possibly represents an extinct lineage, while the lightly calcified *T. transitivum* sp. nov., *T. rastislavi* sp. nov., and *T*. sp. 1, and *T*. sp. 2 are possibly related to reticulated and punctate *Hemicytheria*. This model assumes that more than one *Hemicytheria* lineage transformed their arrangement of MPC, and suggests that *Tyrrhenocythere* is a polyphyletic genus. After the retreat of Lake Pannon, *Tyrrhenocythere* species immigrated, together with other ostracod and molluscan fauna, into the Dacian Basin and Eastern Paratethys. Later, in the uppermost Messinian, they colonised the western Mediterranean. Late Miocene and Pliocene *Tyrrhenocythere* are found in brackish or mixed brackish/freshwater taphocoenoses, but the Pleistocene examples also adapted to freshwater/oligohaline lacustrine environment (Griffiths et al. 2002: 252). While salinity ranges of *Tyrrhenocythere* have shifted, toward freshwater since the late Miocene, temperature preference did not change. The mean annual air temperature of the Pannonian (15.6–21.7°C) is close to the temperature preference of living *Tyrrhenocythere*, with mean annual temperature 12 to 16°C. Two new species, *T. rastislavi*, and *T. transitivum* are described.

Key words: Ostracoda, Hemicytherinae, *Tyrrhenocythere*, marginal pore canals, Miocene, Lake Pannon, phylogeny.

Radovan Pipík [pipik@savbb.sk], Geologický ústav, Slovenská akadémia vied, Severná 5, SK-974 01 Banská Bystrica, Slovakia.

Introduction

The ostracod genus *Tyrrhenocythere* appeared suddenly and diversified in the Pontian (Late Tortonian; Olteanu 1989a: 726; Griffiths et al. 2002: 253), supposedly forming a good stratigraphical marker because no species of the genus are found in older deposits (Olteanu and Vekua 1989: 73). Since the Pontian, this genus became widely distributed in the brackish and freshwater basins of the Paratethys and Mediterranean regions. Its wide geographical range (Tunoglu and Gökçen 1997: 364) and ecological plasticity have resulted in the description of numerous synonymous species (Krstić 1977: 396). After a rapid radiation mainly in the Pontian of the Eastern Paratethys (Krstić 1977: 399; Tunoglu and Gökçen 1997; Tunoglu 2001) its diversity declined. Extant *Tyrrhenocythere* is represented by the single species, *T. amnicola* (Sars, 1887), or by four distinct subspecies (Schornikov 1981), or regarded by some authors as the separate species *T. amnicola* and *T. donetziensis* (Dubowsky, 1926) with different ecological requirements and geographical pattern (Boomer et al. 1996: 79; Griffiths et al. 2002: 253). Olteanu and Vekua (1989: 71) suggested that the differences in geochemical composition of the Central Paratethys and Eastern Paratethys caused the transformation of *Hemicytheria* and their replacement during the Pontian by *Tyrrhenocythere*. A morphometric analysis revealed a similar phylogenetic pathway, with the branching of *Tyrrhenocythere* from *Hemicytheria* during the middle Miocene (Bachnou et al. 1999: 201) and the adaptation of *Tyrrhenocythere* to low salinity (Gramann 1971: 95).

The purpose of this article is to report five *Tyrrhenocythere* species from Pannonian (Tortonian) deposits exposed on the western margin of the Danube Basin (Fig. 1). It provides stratigraphical data based on mollusc, mammal, and ostracod zones used in the Central Paratethys area. The article compares differences in hinge structure between *Hemicytheria* and *Tyrrhenocythere* and examines the differentiation and reorganisa-

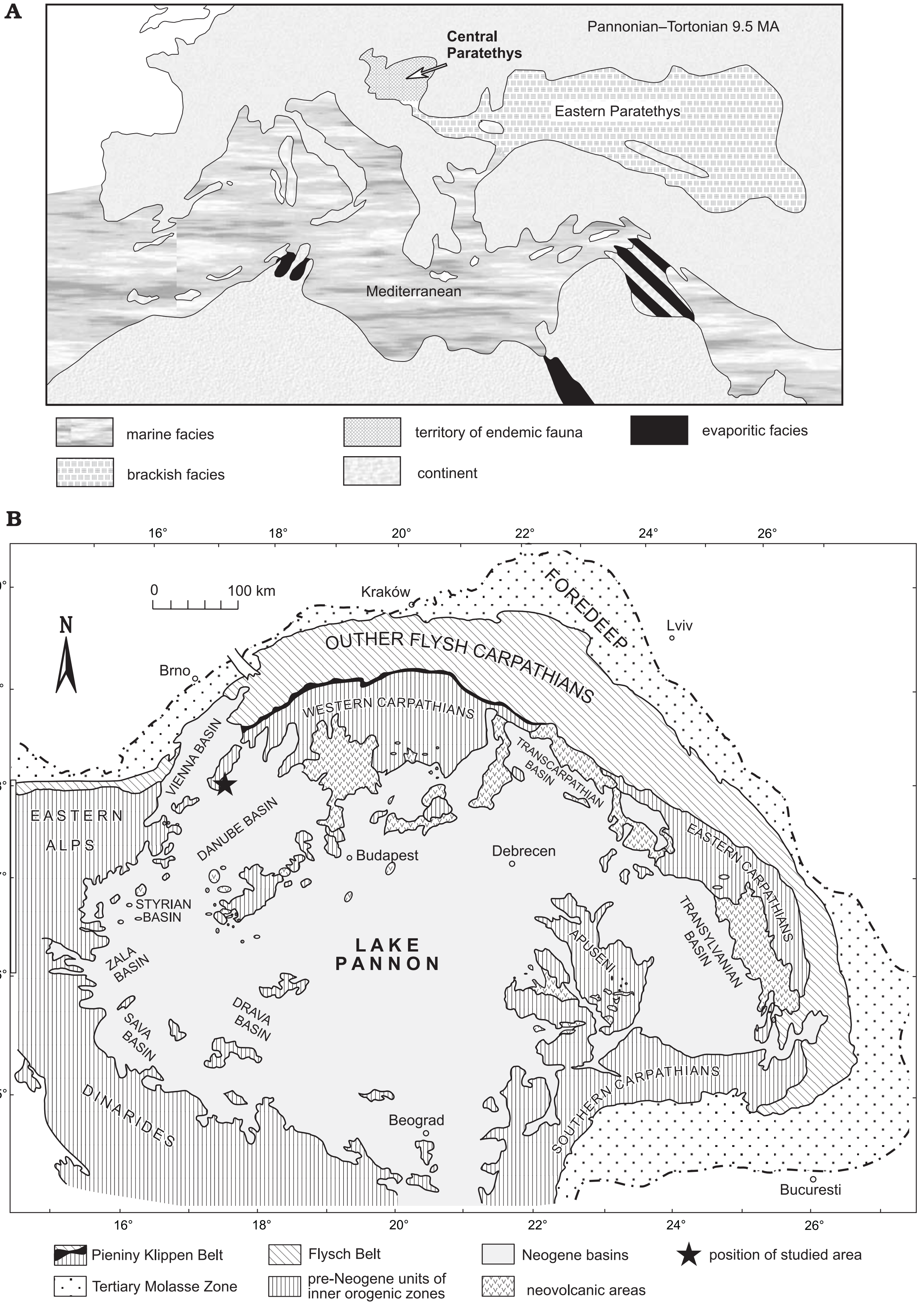

Fig. 1. **A**. Palaeogeographical map of Europe in the upper Miocene (9.5 Ma) (after Steininger and Rögl 1985). **B**. Lake Pannon in a time of maximum flooding surface in Pannonian zone E (*Spiniferites paradoxus* Biochron) (after Kováč 2000).

tion of marginal pore canals in *Hemicytheria* in Lake Pannon populations. It analyses the palaeoenvironment of early *Tyrrhenocythere* species and the shift in their salinity tolerance, and examines the origin and radiation of *Tyrrhenocythere* in the context of the palaeogeographical evolution of the Paratethys since the middle Miocene.

Institutional abbreviation.—SNM, Slovak National Museum in Bratislava, Slovakia.

Other abbreviations.—A, adult; ADM, antero-dorsal margin; AM, anterior margin; AVM, antero-ventral margin; DM, dorsal margin; h, height of the valve in mm; h/l, height / length ratio; MPC, marginal pore canals; l, length of the valve in mm; LV, left valve; N, number of measured specimens; PDM, postero-dorsal margin; PM, posterior margin; PVM, postero-ventral margin; RV, right valve; VM, ventral margin; φ, average; ♀, female valve; ♂, male valve.

Geological palaeoenvironmental setting

The clay pit at Pezinok is situated on western margin of the Danube Basin (Slovakia), east of the town of Pezinok (Fig. 2A; 48°16'720" N and 017°16'340" E). This locality is well known for its rich fossil record of molluscs, ostracods, mammals, pollen and macroflora (Sitár 1958; Holec et al. 1987; Fordinál 1997; Pipík 1996, 1998; Sabol et al. 2004).

Sandy and clayey deposits intercalated with lignite seam (Fig. 2B) to reflect significant oscillations of water level in Lake Pannon (Pipík 1998: 169). Six lacustrine cycles (starting with layer 45) are overlain by alluvial plain facies and belong to one 3rd-order sedimentary sequence (Baráth et al. 1999: 15).

The presence of the rodents *Anomalomys gaillardi*, *Graphiurops austriacus*, *Eomyops catalaunicus*, *Microtocricetus molassicus*, *Trogontherium minutum*, and the perissodactyl *Hippoterium primigenium* in layer 26, can be correlated with the lower part of MN10 (Sabol et al. 2004: 72).

Thirty gastropod and 17 bivalve species reported from the layers 26, 34, 36, and 42 contain taxa with long stratigraphical ranges, including entire Pannonian age (*Theodoxus intracarpaticus*, *Melanopsis bouei affinis*) or those limited to the Pannonian E (*sensu* Papp 1951) (*Congeria subglobosa*, *Monodacna viennensis*, *Didacna deserta*, *Melanopsis vindobonensis*, *M. sturii*; Fordinál 1997: 265).

The forty ostracod species recorded from layer 48 to 10 (in 22 layers in total) can be attributed to three palaeoecologically distinctive assemblages, which alternate irregularly in the sedimentary sequence (Pipík1998: 168). According to Jiříček (1985: 380) and Pipík (1998: 168) these assemblages contain species with a stratigraphical range from Pannonian zone A to Pannonian zone E (*Amplocypris abscissa* [Reuss, 1850], *A. recta* [Reuss, 1850], *Loxoconcha rhombovalis* Pokorný, 1952, and *Euxinocythere lacunosa* [Reuss, 1850]). The species occurring in the Pannonian E (*Cyprideis heterostigma* [Reuss, 1850], *C. alberti* Kollmann, 1958, *Hemicytheria reniformis* [Reuss, 1850], and *H. biornata* [Zalányi, 1944]) are known from layer 48 to 33. Four valves of *Cyprideis heterostigma* were found in layer 26.

Thus, the deposits from layer 48 to 33, and possibly 26, correspond with Pannonian zones E when the lake achieved its largest areal extent. This time period is correlated with *Spiniferites paradoxus* Biochron dated to 9.5 Ma (Kováč et al. 1998: 450; Magyar et al. 1999a: 159) and could be an equivalent of the upper part of mammalian zones MN9 and the lower part of MN10 of the Vallesian (compare with Rögl et al. 1993: 508). The deposits of alluvial plain facies above the layer 19 could be attributed to Pannonian zone F. This suggests that the lower part of this outcrop is Pannonian zone E and the upper part Pannonian zone F, correlatable with mammalian zones MN9/MN10 (Fig. 3).

Despite the numerous fossiliferous layers in the described exposure, *Tyrrhenocythere* species appear suddenly in the sedimentary sequence, only in layer 35 and in the uppermost part of layer 36+37, marked as 36+37A. A detailed sedimentological analysis of this 1 m thick sequence reveals variable bed thicknesses (i.e., 36+37) and significant environmental fluctuations. A generalised section scheme is as follows (Fig. 2C):

- 34 grey, sandy clay with ostracods and with disarticulated valves of *Congeria subglobosa* at the base (150 mm),
- 35 grey, laminated, sandy clay with ostracods (350 mm),
- 36+37A molluscan detritus and sand with *Melanopsis* and ostracods (50 mm),
- 36+37B grey clay with small lenses of light sand; detritic layer (5 mm) in the upper most part (150 mm),
- 36+37C lignite (20 mm),
- 36+37D brown and rusty brown, sandy clay with molluscan detritus and tiny, light sandy lenses (70 mm),
- 36+37E dark brown, sandy clay (80 mm),
- 36+37F blue and grey clay (110 mm),
- 36+37G lignite (90 mm),
- 38 blue and grey clay with fossil roots.

Layer 36+37A is dominated by *Cyprideis seminulum* (Reuss, 1850), *C. alberti*, *C. heterostigma*, and *C. regularis* Jiříček, 1972, which represent 83% of all adult valves in the sample residue; these are the main taxa of the assemblage of *Cyprideis* species (Pipík 1998: 168). Less common species are *Amplocypris recta*, *Cypria abbreviata* (Reuss, 1850), *Xestoleberis* sp., *Loxoconcha rhombovalis*, *Euxinocythere* sp., and *Hemicytheria reniformis*. The most common mollusc is the gastropod *Melanopsis* (10 species and subspecies), with some contribution from *Pyrgula*, *Micromelania*, *Congeria*, and *Mytilopsis* (Fordinál 1997: 267).

The ostracod fauna of layer 35 is more diverse. It is composed of 19 species dominated by representatives of *Cyprideis* (the same species as in layer 36+37A which here represent here 65% of all adults in the residue), followed by *Cypria abbreviata*, *C. dorsoconcava* Krstić, 1975, *Hemicytheria reniformis*, *H. brunennsis* (Reuss, 1850), and *Amplocypris recta*.

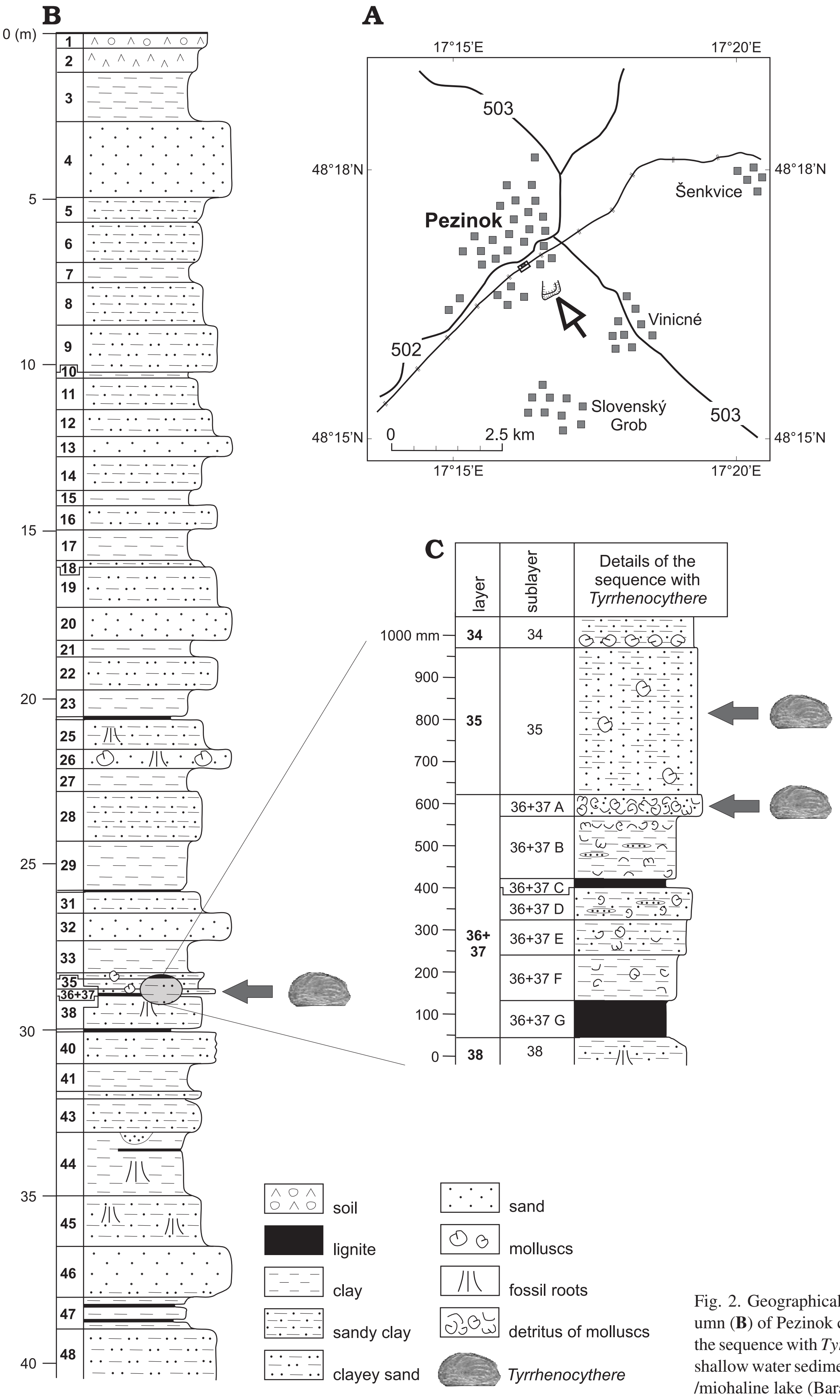

Fig. 2. Geographical sketch (**A**) and lithological column (**B**) of Pezinok clay pit (Pipík 1998). **C**. Detail of the sequence with *Tyrrhenocythere* mirror swamps and shallow water sedimentation on the bord of freshwater-/miohaline lake (Baráth et al. 1999).

Uncommon, and represented by one or two valves, are *Loxoconcha rhombovalis*, *Euxinocythere lacunosa*, *Pontoniella multipora* (Pokorný, 1952), and *Darwinula stevensoni* (Brady and Robertson, 1870). There are also juvenile specimens of *Euxinocythere* sp., *Amplocypris abscissa*, *Lineocypris* sp., and *Hemicytheria folliculosa* (Reuss, 1850).

In agreement with previous palaeontological observations (Krstić 1977: 395), early *Tyrrhenocythere* species are of minor importance in the taphocoenoses, representing up to 6% of all adult individuals in layer 36+37A, and only 1% in layer 35. Because of this low frequency, the material for systematic studies were obtained by picking from 500 g of washed residue.

Tyrrhenocythere did not occur in the overlaying grey, sandy clay with *Congeria subglobosa* (layer 34) or laminated clay (layer 33) with *Camptocypria praebalcanica* (Krstić, 1972) dominant in both layers, *Amplocypris abscissa*, *Cypria abbreviata*, *C. dorsoconcava*, *Cyprideis alberti*, *C. regularis*, and *Pontoniella multipora*. They were also not found in association with freshwater ostracods (*Darwinula stevensoni*, *Cyclocypris* cf. *laevis* [O.F. Müller, 1776], *Zonocypris* sp., *Ilyocypris* sp., three species of *Candona* sensu lato; Fig. 2B; Pipík 1998: 168).

The described sequence (Fig. 2C) is the second of six sedimentary cycles recorded in the clay pit. The sequence starts with an erosional (transgressive) surface and blue and grey, laminated sandy clays (layer 38), rich in roots, wood, and plant fragments and is barren of ostracods. This facies is interpreted as having originated in a back-barrier landward position, which transformed to freshwater/miohaline swamps and ponds during the initial transgression phase. The uppermost portion of the cycle is truncated by a fossil-rich lag layer with a sandy matrix (layer 36+37A), which is overlain abruptly by hummocky cross-bedded fine sands (layer 35) of lower shoreface origin, representing transgressive facies (Baráth et al. 1999: 15). The next, third cycle in the outcrop, starts above the erosional flooding surface with a lag comprising thin sandy clay (layer 34) rich in molluscs (Fordinál 1997: 265) and dominated by the *Camptocypria praebalcanica* assemblage. The transgression starting from the first cycle culminates in the fifth cycle with a thin layer of green clay (layer 27). The overlaying alluvial plain includes four different lithofacies composed of palaeosol horizons, levee accumulations and crevasse splay deposits with freshwater mollusc and ostracod associations (Baráth et al. 1999: 15).

Mammalian forest inhabitants (*Paraglirulus*, *Graphiurops*, *Eomyops*, and *Albanensia*) are more abundant than open woodland dwellers (*Kowalskia*, *Parapodemus*). A higher diversity of arboreal mammals is interpreted as being

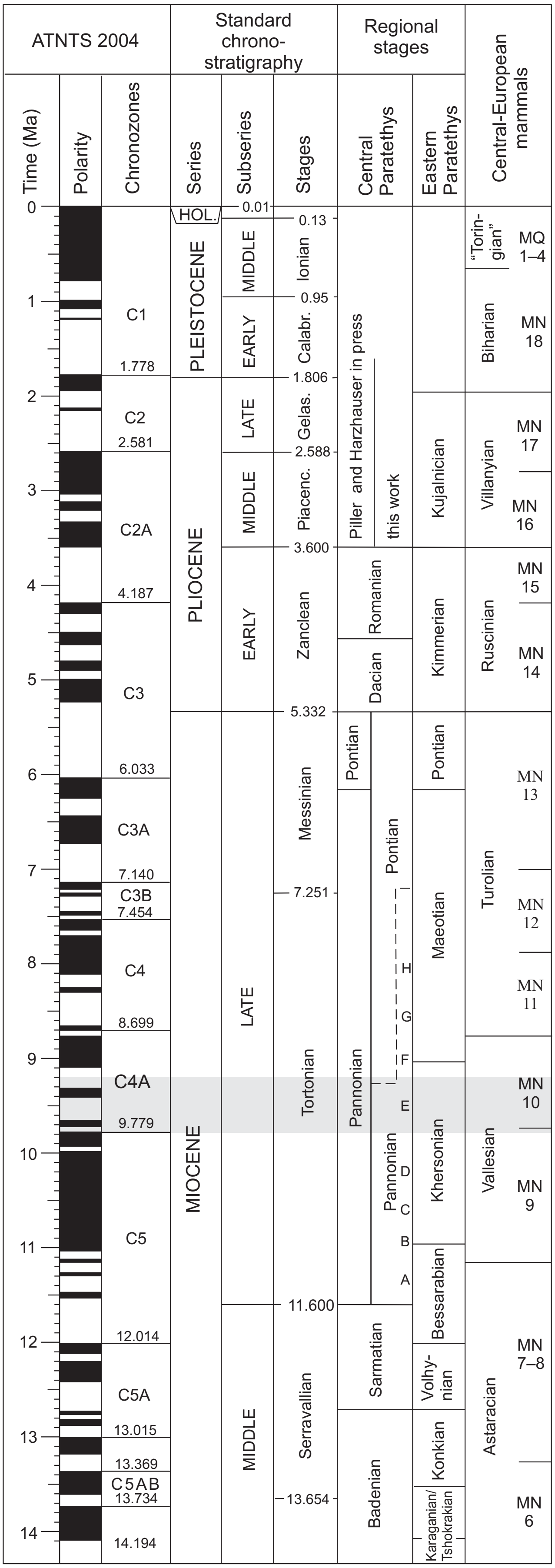

Fig. 3. Time scale and correlation chart of the Central Paratethys and Mediterranean stages (after Harzhauser and Piller in press; modified after Rögl et al. 1993; Magyar et al. 1999a, b). A grey shaded area indicates the age of the deposits with *Tyrrhenocythere*. Abbreviations: ATNTS 2004, Astronomically Tuned Neogene Time Scale (Lourens et al. 2004); HOL., Holocene; Calabr., Calabrian; Gelas., Gelasian; Piacenc., Piacencian.

related to the presence of large mixed coastal, flooded forests (*Anomalomys*—inhabitants of soft forest ground) near a lake or river (aquatic/semi-aquatic beavers *Trogontherium*; Joniak 2005). The forest covered by temperate plants (lower part of the outcrop) becomes richer in cooler climate floral elements in the upper part of the sequence (Sitár 1958: 90). Primary pollen data from the Pannonian sediments of the neighbouring Vienna Basin indicate a mean annual air temperature of 15.6–21.7°C (Kováč et al. 2005: 104).

As mentioned before, four fossil *Cyprideis* species dominate the *Tyrrhenocythere*-yielding association. *Cyprideis torosa* Jones, 1850, their widely distributed Recent counterpart 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: 463).

Hemicytheria are the exclusively fossil ostracods, apparently endemic to the Central Paratethys. Pannonian *H. folliculosa* and *H. reniformis* lived in the Vienna basin between salinity values of 3–8‰ (Pokorný 1952: 244) while Sarmatian *H. omphalodes* (Reuss, 1850) is also found associated with marine and brackish microfauna (Fordinál and Zlínska 1998: 145). *Amplocypris* are typical Lake Pannon fossil ostracods occurring in brackish associations (Krstić 1971: 394). *Xestoleberis* and *Loxoconcha* live in fully marine and brackish environments. *Euxinocythere* are known from brackish ostracod assemblages of the Paratethys and the Eastern Mediterranean, but they also became adapted to freshwater littoral to deep limnic conditions (Pipík and Bodergat 2004: 37). Recent *Cypria* are freshwater species tolerating mesohaline conditions (Meisch 2000), but fossil *Cypria abbreviata* and *C. dorsoconcava* are associated with *Cyprideis*, *Amplocypris*, *Hemicytheria*, and the Paratethyan Candoninae genera *Camptocypria*, *Pontoniella*, *Lineocypris*, *Bakunella*, and *Serbiella*.

Extant thermoeuryplastic *Darwinula stevensoni* prefers ponds, lakes, and slow streams and occurs at depths of 0 to 12 m on muddy and sandy substrates. Although it is largely a freshwater species, it can tolerate an increase of salinity up to 15 ‰. *Cyclocypris* cf. *laevis* inhabits very variable freshwater milieu, tolerating low salinities down to 8‰ (Meisch 2000: 237). *Zonocypris* are known from freshwater, slightly alkaline, shallow continental environment of Africa tolerating relatively well the water turbidity (Babinot 2003: 7). Flowing waters could be documented also by a presence of *Ilyocypris* living in freshwater to oligohaline waters (Meisch 2000). *Paralimnocythere* sp., *Cypria* sp. and three species of *Candona* sensu lato live in freshwater environments and, in general, can occur in waters with slightly increased salinity.

Although extant *Tyrrhenocythere* species can live in freshwater with saline influence (Griffiths et al. 2002: 256), they are apparently absent in the freshwater/oligohaline ostracod assemblage from Pezinok. The stronger and heavier valves of Pannonian *Tyrrhenocythere* imply that they, similarly to their recent representatives (Schornikov 1969: 194), could tolerate moving water environment as well as or better than the above mentioned freshwater species of *Candona*, *Cyclocypris*, and *Cypria* which have smooth valves and the fragile *Paralimnocythere*. Based on this information, it is suggested that *Tyrrhenocythere* did not enter freshwater environments in the late Miocene and were physiologically adapted to only the brackish milieu.

Systematic palaeontology

Class Ostracoda Latreille, 1806

Order Podocopida Sars, 1866

Family Hemicytheridae Puri, 1953

Genus *Tyrrhenocythere* Ruggieri, 1955

Type species: *Cythere amnicola* (Sars, 1887); Recent, Syracuse, Italy.

Tyrrhenocythere pezinokensis (Jiříček, 1985)

Figs. 4A–F, 5G1, G2, J, 6F.

1985 *Hemicytheria pezinokensis* sp. nov.; Jiříček 1985: 405, pl. 56: 10–12.

1998 *Tyrrhenocythere pezinokensis* (Jiříček, 1985); Pipík 1998: pl. 2: 5, 6.

Remark.—The original description is incomplete, hence a description of the hinge, muscle scars and marginal zone is given based on the material collected in Pezinok clay pit, the layer 36+37A.

Material.—30 adult valves, 1 juvenile.

Description.—Muscle scars: a vertical row of six scars (the second and the third of the "standard" row of four each divided in two), with three additional anterior scars (Fig. 5G$_1$).

Hinge (amphidont): The hinge (Fig. 5G$_2$, J) of the LV is composed of a rhomboidal anterior socket; a square tooth that continues into a smooth bar; a posterior socket with an elongate opening toward the interior; a tiny tooth in the middle of the posterior socket. The hinge of the RV has a strong, elongated tooth divided into two lobes; a socket that passes into a

Fig. 4. Late Miocene hemicytherid ostracods from the layer 36+37A in Pezinok, Slovakia. **A**–**F**. *Tyrrhenocythere pezinokensis* (Jiříček, 1985). **A**. LV♀, SNM RP27-6, external lateral view. **B**. RV♀, SNM RP27-3, external lateral view. **C**. RV♂, SNM RP27-4, external lateral view. **D**. LV♂, SNM RP27-7, external lateral view. **E**. LV♀, SNM RP27-8, internal lateral view. **F**. RV♀, SNM RP27-5, internal lateral view. **G**–**M**. *Tyrrhenocythere rastislavi* sp. nov. **G**. LV♀, holotype, SNM RP27-9, external lateral view. **H**. RV♀, paratype, SNM RP27-13, external lateral view. **I**. LV♀, paratype, SNM RP27-10, external lateral view. **J**. RV♂, paratype, SNM RP27-14, external lateral view. **K**. LV♂, paratype, SNM RP27-11, external lateral view. **L**. LV♀, paratype, SNM RP27-12, internal lateral view. **M**. RV♀, paratype, SNM RP27-15, internal lateral view. **N**–**R**. *Tyrrhenocythere transitivum* sp. nov. **N**. LV♀, holotype, SNM RP27-16, external lateral view. **O**. RV♀, paratype, SNM RP27-20, external lateral view. **P**. LV♀, paratype, SNM RP27-17, external lateral view. **Q**. LV♀, paratype, SNM RP27-19, internal lateral view. **R**. RV♀, paratype, SNM RP27-22, internal lateral view.

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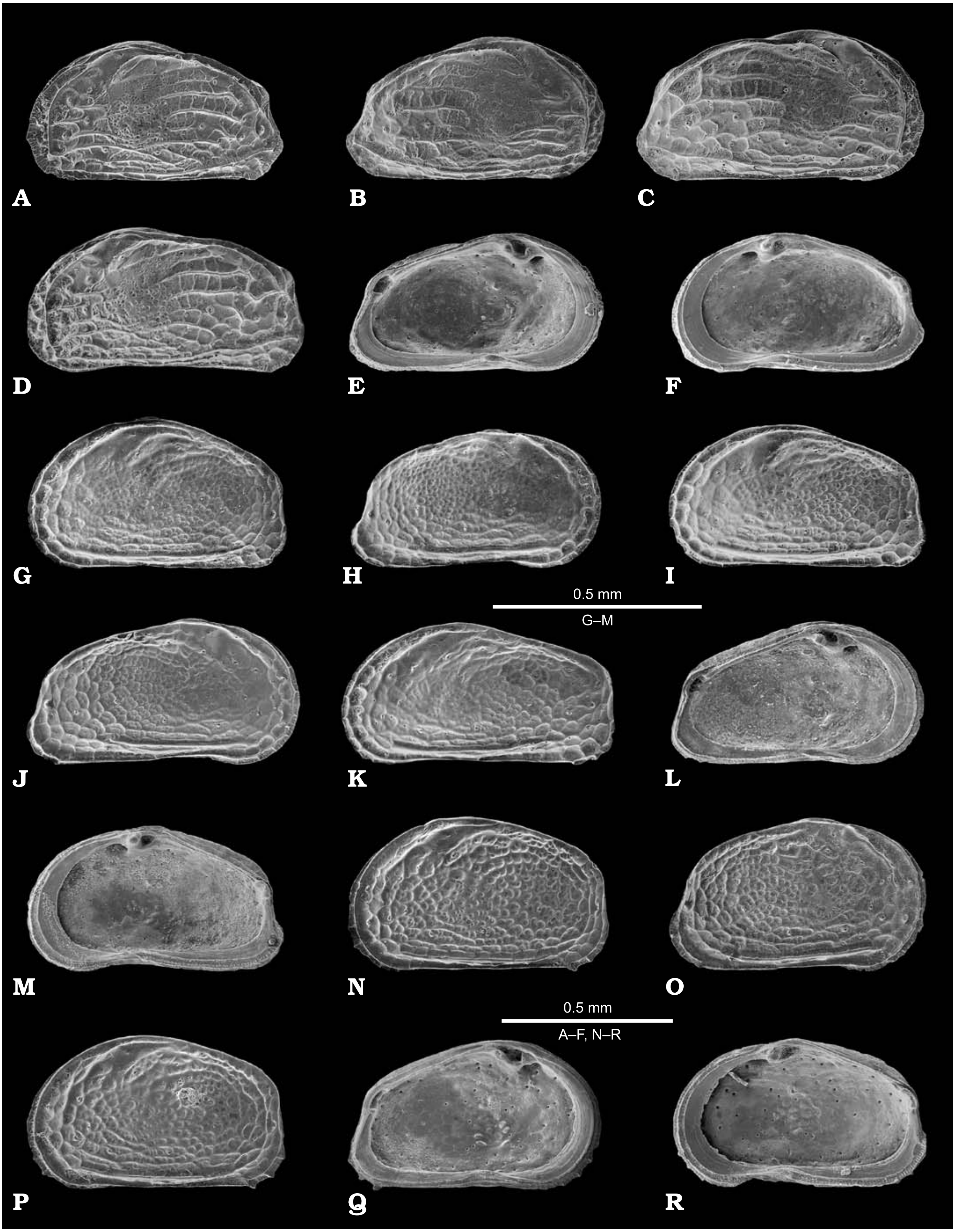
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Table 1. Dimensions in mm of *Tyrrhenocythere pezinokensis* (Jiříček, 1985), Pezinok, layer 36+37A. Abbreviations: h, height of the valve in mm; h/l, height/length ratio; l, length of the valve in mm; N, number of measured specimens; φ, average; ♀, female valve; ♂, male valve.

	N	l	φ	h	φ	h/l	φ
LV♀	14	0.758–0.803	0.777	0.409–0.439	0.429	0.538–0.564	0.552
RV♀	9	0.735–0.803	0.774	0.401–0.439	0.425	0.51–0.559	0.549
LV♂	5	0.848–0.879	0.865	0.432–0.447	0.438	0.491–0.513	0.506
RV♂	2	0.83–0.879	–	0.41–0.439	–	0.494–0.5	–
LV A-1	1	0.667	–	0.371	–	0.557	–

Table 2. Dimensions in mm of *Tyrrhenocythere rastislavi* sp. nov., Pezinok, layer 36+37A. Abbreviations: h, height of the valve in mm; h/l, height/length ratio; l, length of the valve in mm; N, number of measured specimens; φ, average; ♀, female valve; ♂, male valve.

	N	l	φ	h	φ	h/l	φ
LV♀	15	0.614–0.667	0.638	0.348–0.379	0.368	0.558–0.598	0.577
RV♀	15	0.614–0.651	0.632	0.341–0.371	0.358	0.549–0.593	0.567
LV♂	5	0.674–0.697	0.686	0.356–0.371	0.362	0.511–0.538	0.528
RV♂	4	0.682–0.697	–	0.348–0.379	–	0.511–0.543	–

slightly curved, smooth groove; a posterior elongated, kidney-shaped tooth composed of 3 tiny elements.

Marginal zone: inner lamella large, with a series of parallel striae; inner margin parallel with outer margin; 5 fully developed brush-like marginal pore canals (MPC); 6 to 8 MPC on ADM (Fig. 6F); AVM are separate or incompletely fused; simple MPC on VM; large zone of fusion; drop-like space between the "brushes" on AM; irregular, sinusoidal line of concrescence on AM.

Stratigraphical and geographical range.—The species, first described by Jiříček (1985: 405) from the Pannonian clay deposits in Pezinok, is still known only from its type locality.

Tyrrhenocythere rastislavi sp. nov.

Figs. 4G–M, 5E, H_1, H_2, K, 6G.

Derivation of the name: After Rastislav (846–870), prince and sovereign of Great Morava.

Type material: Holotype: SNM RP27-9, a complete LV♀ and 7 paratypes: SNM RP26-16-1, LV♂; SNM RP27-10, LV♀; SNM RP27-11, LV♂; SNM RP27-12, LV♀; SNM RP27-13, RV♀; SNM RP27-14, RV♂; SNM RP27-15, RV♀.

Type locality: Pezinok, clay pit, Danube Basin; coordinates—48°16'720'' N and 017°16'340'' E.

Type horizon: Pannonian, zone E, late Miocene, Neogene.

Material.—39 adult valves.

Diagnosis.—*Tyrrhenocythere rastislavi* sp. nov. differs from *T. transitivum* sp. nov. in having fully developed *Tyrrhenocythere* "brushes" on AM and PM, and by its low posterior. It differs from *T. incerta* Olteanu, 1989 (in Olteanu 1995: pl. 26: 2) in having posterior process on the PVM of the LV.

Description.—LV♀ (holotype): AM symmetrically curved; ADM curved without a visible anterior angle; DM right straight and sloping toward posterior; posterior angle clearly well visible, tapered; PM curved, slightly oblique and lower than AM; strongly rounded PVM with posterior processes; VM right, slightly concave before the middle; outline rectangular; maximum height at anterior, just behind the eye tubercle.

RV♀: AM symmetrically curved; DM long and largely curved; only the posterior has a marked angle; PM strongly curved; PVM rounded with distinctive posterior processes; VM curved in the anterior third then straight; outline sub-rectangular; maximum height before the lengthwise mid-point.

Sexual dimorphism: obvious; males longer with elongated rectangular valves and long DM.

Muscle scars: consisting of a vertical row of five scars (the second from top divided into two), with three additional anterior scars (Fig. 5H_1).

Normal pore canals: open.

Hinge (amphidont): the hinge (Fig. 5K, H_2) of the LV is composed of an elongated anterior socket; a square tooth that continues into a smooth bar that is thickened slightly posteriorly; an elongated posterior socket that is dorsally crenulated, opening toward the interior; a tiny tooth in the middle of posterior socket. The hinge of the RV has a strong, elongated tooth divided into two lobes; a square socket; straight, smooth groove; an elongated, kidney-shaped posterior tooth dorsally denticulated with five elements.

Ornamentation: the ornamentation changes from outer margin to the central area; polygonal fossae on outer margin without reticulation of second order become filled with circular to semicircular pits toward the centre; the polygonal fossae disappear toward the central area becoming pits; ornamentation absent along the anterior; strong ventral rib; an anterior rib starts in ADM and extends along the entire AM; it terminates on centro-ventral margin below the ventral rib; short, weak ribs are developed on the entire AM between the anterior rib and the ordinary polygonal fossae; the ribs represent the reinforced outer lamella in the position of the main canal joining distal MPC which are visible on surface as tiny riblets between anterior rib and external AM; similar ribs and riblets are developed on PVM; one to three short spines are present on the PVM; eye tubercle smooth; weak pore conuli

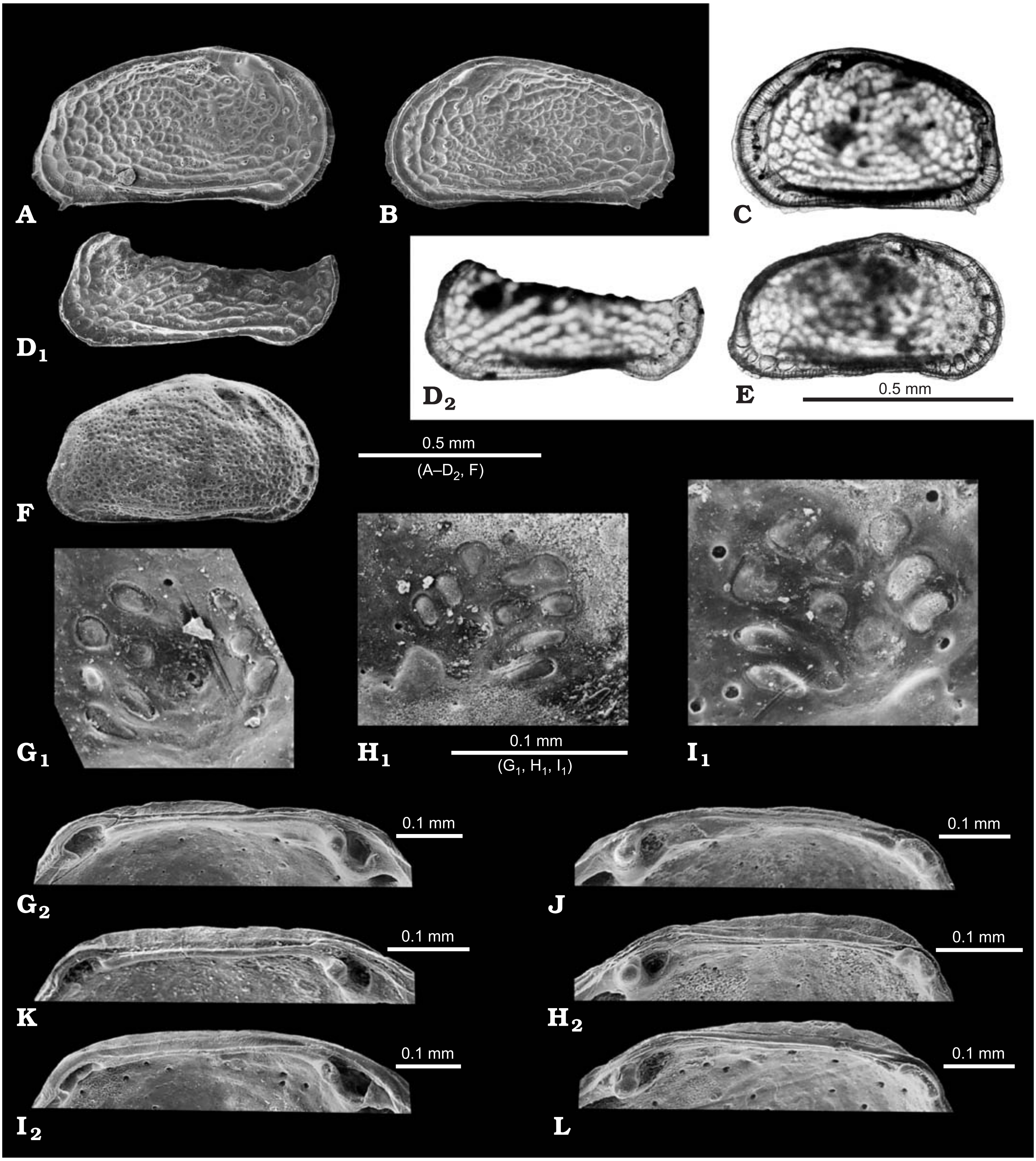

Fig. 5. Late Miocene hemicytherid ostracods from the layer 36+37A in Pezinok, Slovakia. **A**–**C**, **I**, **L**. *Tyrrhenocythere transitivum* sp. nov. **A**. RV♂, paratype, SNM RP27-21, external lateral view. **B**. LV♂, paratype, SNM RP27-18, external lateral view. **C**. LV♀, paratype, SNM RP26-4-4, external lateral view. **I**. LV♀, paratype, SNM RP27-19, internal lateral view; I_1, central muscle scars; I_2, detail of hinge. **L**. RV♀, paratype, SNM RP27-22, internal lateral view, detail of hinge. **D**. *Tyrrhenocythere* sp. 1, RV, SNM RP27-2, external lateral view; D_1, SEM photo; D_2, valve in transparent light. **F**. *Tyrrhenocythere* sp. 2, RV♀, SNM RP28-2, external lateral view. **G**, **J**. *Tyrrhenocythere pezinokensis* (Jiříček, 1985). **G**. LV♀, SNM RP27-8, internal lateral view, G_1, central muscle scars; G_2, detail of hinge. **J**. RV♀, paratype, SNM RP27-5, internal lateral view, detail of hinge. **E**, **H**, **K**. *Tyrrhenocythere rastislavi* sp. nov. **E**. RV♂, paratype, SNM RP26-16-1, external lateral view. **H**. RV♀, paratype, SNM RP27-15, internal lateral view; H_1, central muscle scars; H_2, detail of hinge. **K**. LV♀, paratype, SNM RP27-12, internal lateral view, detail of hinge.

occur more frequently on the anterior part of the valve than on the posterior.

Marginal zone: inner lamella large with a series of parallel striae; inner margin parallel with outer margin; 9 "brushes" on AM; each "brush" is composed of 7 to 10 canals, the last "brush" on ADM with 2–3 canals; "brushes" developed on AM and PM (Fig. 6G); MPC short and straight on centroventral margin; large zone of fusion, irregularly shaped between the "brushes"; irregular, sinusoidal line of concrescence.

Discussion.—*Tyrrhenocythere rastislavi* sp. nov. is smaller, and lower at the posterior, than *T. transitivum* sp. nov. (Fig. 7). The female LV of *T. incerta* from the Dacian of the Dacian Basin is more rectangular, elongated and without a posterior process on the PVM (Olteanu 1995: pl. 26: 2).

Stratigraphical and geographical range.—This species was found only in the Pannonian clay deposits in Pezinok

Tyrrhenocythere transitivum sp. nov.

Figs. 4N–R, 5A–C, I$_1$, I$_2$, L, 6E.

Derivation of the name: After intermediate arrangement of the anterior marginal pore canals between those of the genera *Hemicytheria* and *Tyrrhenocythere*.

Type material: Holotype: SNM RP27-16, a complete LV♀ and 7 paratypes: SNM RP26-4-4, LV♀; SNM RP27-17, LV♀; SNM RP27-19, LV♀; SNM RP27-18, LV♂; SNM RP27-20, RV♀; SNM RP27-21, RV♂; SNM RP27-22, RV♀.

Type locality: Pezinok, clay pit, Danube Basin; co-ordinates—48°16'720'' N and 17°16'340'' E.

Type horizon: Pannonian, zone E, late Miocene, Neogene.

Material.—42 adult valves, 52 juvenile valves.

Diagnosis.—*Tyrrhenocythere transitivum* sp. nov. differs of other *Tyrrhenocythere* in having incompletely developed "brushes" on AM. *T. transitivum* sp. nov. differs from *Hemicytheria folliculosa*, *H. marginata*, and *H. dubokensis* by having the MPC on AM divides into 2–4 canals, which subsequently bifurcate into 2–3 canals.

Description.—LV♀ (holotype): anterior curved; DM straight and sloping toward posterior, only the posterior angle is visible; PM straight to slightly curved; PVM strongly rounded with posterior process; VM straight; outline sub-rectangular; maximum height at anterior, behind the eye spot.

RV♀: AM symmetrically rounded; ADM slightly rounded to straight; DM straight and sloping toward posterior; anterior and dorsal angles rounded; PM straight to curved; PVM strongly rounded with distinctive posterior process; VM curved in the first third then straight; outline sub-rectangular; maximum height at anterior, behind the eye spot.

Sexual dimorphism: males longer with rectangular valves.

Muscle scars: consisting of a vertical row of 6–8 scars (the first and second from the top divided in two, the third can be thin and elongate or divided into two smaller elongate scars), with three additional scars anteriorly (Fig. 5I$_1$).

Normal pore canals: open, rare at the centre, more frequent toward outer margin.

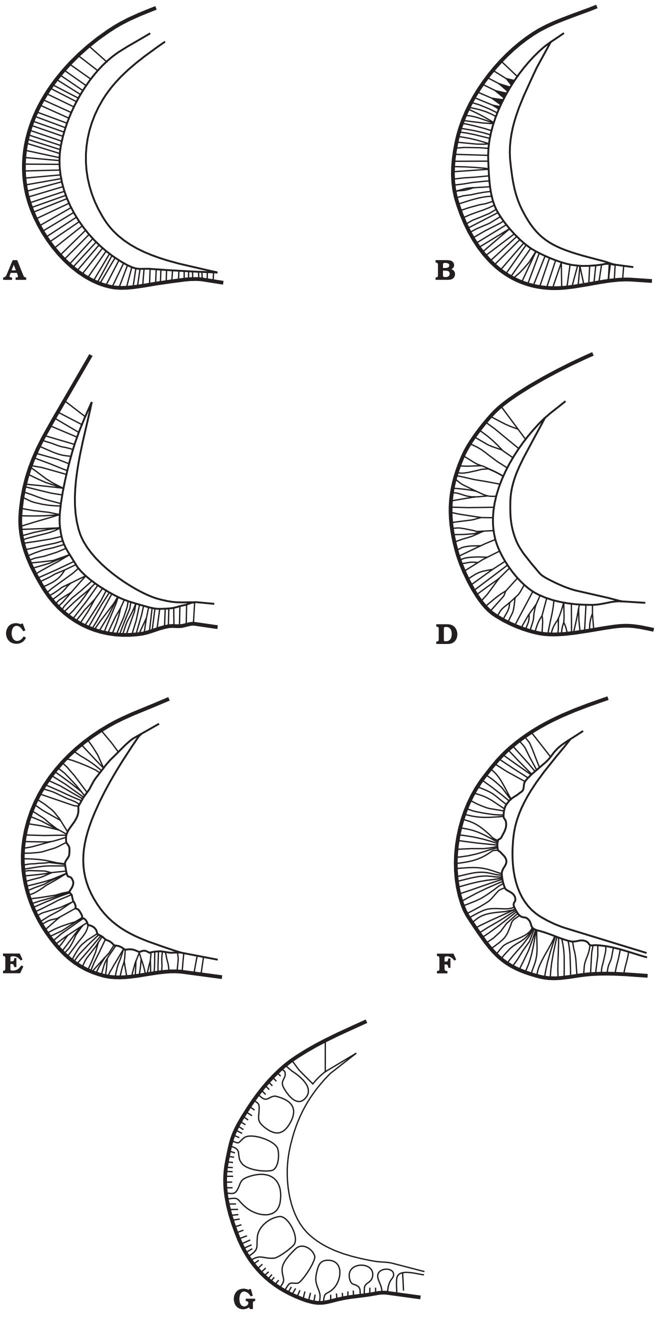

Fig. 6. Marginal pore canals on anterior margin and their transformation from straight *Hemicytheria* arrangement to brush-like *Tyrrhenocythere* one. **A**. *Hemicytheria reniformis* (Reuss, 1850), *Hemicytheria folliculosa* (Reuss, 1850), *Hemicytheria omphalodes* (Reuss, 1850), original by author. **B**. *Hemicytheria biornata* (Zalányi, 1944), original by author, *Hemicytheria maeotica* Olteanu 1989 after Olteanu and Vekua (1989). **C**. *Hemicytheria major* Sokač, 1972. **D**. *Hemicytheria marginata* Sokač, 1972 after Sokać (1972). **E**. *Tyrrhenocythere transitivum* sp. nov. **F**. *Tyrrhenocythere pezinokensis* (Jiříček, 1985). **G**. *Tyrrhenocythere rastislavi* sp. nov. original by author.

Hinge (amphidont): the hinge (Fig. 5I$_2$, J) of the LV is composed of a large, elongate and divided anterior socket; an elliptical tooth that continues into a thin, smooth bar; an elongated posterior socket with slight crenulations (3 elements) on the dorsal side that opens into the interior; a tiny tooth in mid-

Table 3. Dimensions in mm of *Tyrrhenocythere transitivum* sp. nov., Pezinok, layer 36+37A. Abbreviations: h, height of the valve in mm; h/l, height/length ratio; l, length of the valve in mm; N, number of measured specimens; φ, average; ♀, female valve; ♂, male valve.

	N	l	φ	h	φ	h/l	φ
LV♀	20	0.742–0.803	0.778	0.447–0.485	0.467	0.577–0.626	0.601
RV♀	15	0.72–0.78	0.769	0.432–0.477	0.457	0.582–0.618	0.595
LV♂	4	0.818–0.848	–	0.447–0.47	–	0.545–0.553	–
RV♂	3	0.833–0.863	–	0.455–0.462	–	0.535–0.545	–
LV A-1	13	0.606–0.667	0.631	0.371–0.394	0.385	0.581–0.634	0.61
RV A-1	21	0.576–0.651	0.619	0.356–0.394	0.374	0.583–0.633	0.605
LV A-2	6	0.455–0.5	0.477	0.303–0.318	0.308	0.606–0.677	0.646
RV A-2	9	0.47–0.515	0.48	0.288–0.318	0.298	0.613–0.645	0.621
LV A-3	1	0.364	–	0.25	–	0.688	–

dle of posterior socket. The hinge of the RV has a tooth divided into two lobes; an elongated socket, a straight, smooth groove; a kidney-shaped elongated posterior tooth, dorsally delicately crenulated with 3 elements.

Ornamentation: prominent; central area with circular to semicircular pits; toward outer margin, the pits connect and form polygonal fossae with reticulation of second order; polygonal fossae on outer margin with smooth solum; a strong ventral rib along the PM terminating on PDM; an anterior rib starting in ADM and extending along the entire AM, terminating on centro-ventral margin below ventral rib; tiny riblets visible between anterior rib and external AM; similar ribblets developed on PVM; two-three parallel ribs on dorsal and one-two weak ventral ribs above ventral rib; three spines on PVM; five weak anterior spines; eye tubercle smooth; pore conuli on anterior and posterior.

Marginal zone: inner lamella large with a series of parallel striae; inner margin parallel with outer margin; large anterior MPC on AM divides into 2–4 canals which subsequently bifurcate into 2–3 canals (Fig. 6E); individuals with straight MPC are also observed; MPC on VM right, short and thin, some fused at the base; large zone of fusion; drop-like space between the anterior MPC; irregular, slightly sinusoidal line of concrescence on AM which become straight posteriorly.

Discussion.—A surface covered with circular to semicircular pits in combination with polygonal fossae is a very common feature in Pannonian *Hemicytheria*. *H. folliculosa* from the Pannonian of the Vienna Basin has a surface densely covered with circular pits and a slightly concave DM on the LV (Pokorný 1952: 289). Female LVs of *Hemicytheria dubokensis* and *H. marginata* each have a very high anterior and a low posterior connected by a long and straight DM (Sokać 1972: pl. 38: 3, pl. 36: 8; Krstić 1985: 139).

Stratigraphical and geographical range.—This species is known only from the Pannonian deposits in Pezinok.

Tyrrhenocythere sp. 1

Fig. 5D$_1$, D$_2$.

Material.—One incomplete RV, length 0.77 mm, with the dorsal part broken.

Description.—Ornamentation: polygonal fossae with smooth solum connected by ribs starting in the centre and extending toward the outer margin; ventral and anterior ribs highly visible; short, weak ribs developed on AM between anterior rib and ordinary polygonal fossae; the ribs represent reinforced outer lamellae where the main canal joins the distal MPC; similar ribs are developed on PVM.

Discussion.—The specimen differs from other hemicytherids from Pezinok with its brush-like *Tyrrhenocythere* arrangement of MPC; each with 7 to 10 short canals on AM and with 3–4 on PVM. A comparison of the outline with other species is problematic because1/3 of the valve is missing. The polygonal fossae may indicate that *Tyrrhenocythere* sp. 1 is related to the Lower Pannonian *Hemicytheria* sp. (*setosa*) from Serbia (*sensu* Krstić 1985: 141), Pontian and Pliocene *Tyrrhenocythere pontica* from the Eastern Paratethys (Krstić 1977: 401; Tunoglu 2001: 135), Dacian *T. filipescui*, *T. azerbaidjanica* (Livental, 1939) and *T*. sp. 1 of Olteanu, 1982 from Romania (Olteanu 1982: 8, 1995: 300). However, the fossae of *Tyrrhenocythere* sp. 1 are connected by ribs, in contrast to the aforementioned *Tyrrhenocythere*.

Stratigraphical and geographical range.—Pannonian clay deposits in Pezinok.

Tyrrhenocythere sp. 2

Fig. 5F.

Material.—One adult right valve.

Description.—RV: AM symmetrically rounded; DM tapered, rounded without a visible anterior angle; DM straight before mid-length and sloping slightly anteriorly, tapered above central muscle scars then straight and sloping toward the posterior; posterior angle tapered; PM curved, slightly oblique

Table 4. Dimensions in mm of *Tyrrhenocythere* sp. 2, Pezinok, layer 36+37A. Abbreviations: h, height of the valve in mm; h/l, height/length ratio; l, length of the valve in mm; N, number of measured specimens; ♀, female valve.

	N	l	h	h/l
RV♀	1	0.74	0.44	0.595

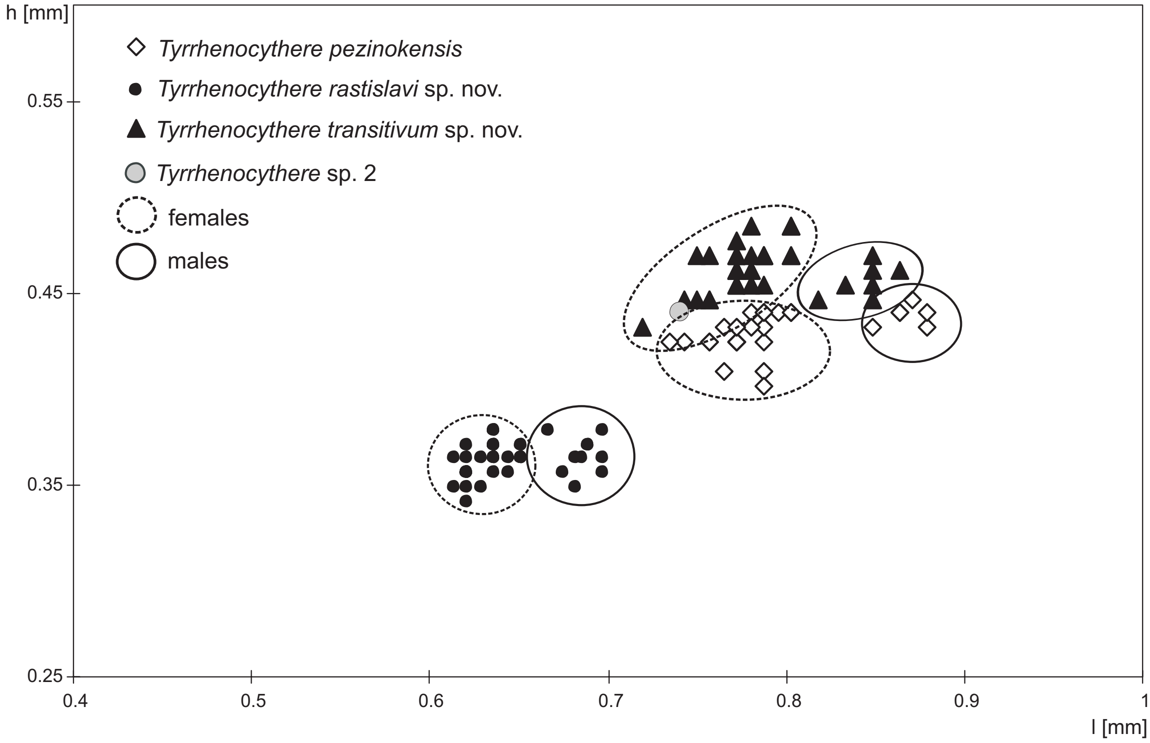

Fig. 7. Length (l) and height (h) ratio of early *Tyrrhenocythere* species from Pezinok (Danube Basin). The male valves are longer than the female ones.

and lower than AM; strongly rounded PVM with distinctive posterior process; VM right, slightly concave before the mid-length; outline subcircular; maximum height above central muscle scars.

Ornamentation: surface covered with small circular puncta; a weak ventral rib; anterior short ribs at the position of MPC, perpendicular with AM; weak and short ribs developed on the entire AM representing reinforced outer lamellae at the position of main canal joining distal MPC; eye tubercle smooth.

Marginal zone: inner lamella large with a series of parallel striae; inner margin parallel with outer margin; brush-like *Tyrrhenocythere* arrangement of MPC.

Discussion.—*Tyrrhenocythere* sp. 2 could be related to the group of semicircular forms with smooth, punctate to fossate species described by Krstić (1985: 399). The puncta of *Tyrrhenocythere* sp. 2 are deeper and regularly distributed throughout the surface without any sign of reticulation as it is visible in *T. donetziensis*, species with similar punctate surface (Boomer et al. 1996: 80, fig. 3A, B, D, E).

Stratigraphical and geographical range.—Pannonian clay deposits in Pezinok.

Hinge structures

The changes in hingement characterise the differences among Hemicytherinae genera . They are correlatable with changes in carapace morphology and allow for hypotheses on the phylogenetic relationships among the Hemicytherinae (Pokorný 1955: 29).

During the Pannonian, when the first *Tyrrhenocythere* species appear, only one genus of Hemicytherinae—*Hemicytheria*—was living in Lake Pannon.

The hinge of *H. folliculosa*, the type species of *Hemicytheria*, from Hennersdorf (Vienna Basin) is amphidont, consisting of the following elements from anterior to posterior in the LV: square socket–square tooth–smooth bar–dorsally denticulated socket. The complementary elements of the opposite RV appear as a strong tooth–square socket–smooth groove–strong, kidney-shaped tooth finely denticulated dorsally with 5 elements and opening toward the interior.

The hinge of *Tyrrhenocythere amnicola*, type species of *Tyrrhenocythere*, is also amphidont, consisting of the following elements in the LV: socket–strong knob-like tooth–smooth bar thickened anteriorly–posterior socket dorsally denticulated and opening toward the interior. The hinge of its RV has a knob-like anterior tooth–socket–straight grove–strong kidney-shaped tooth that is dorsally crenulated (Ruggieri 1955: 698). However, the posterior tooth can also be smooth (Schornikov 1969: 194). *T. pezinokensis* (Jiříček, 1985), *T. rastislavi* sp. nov., and *T. transitivum* sp. nov. have the same amphidont hinge (see the Systematic palaeontology chapter). The small variations in shape of the anterior tooth and socket and degree of fine denticules on posterior tooth are possibly species specific (Van Morkhoven 1962: 80).

Like *Tyrrhenocythere*, Miocene Hemicytherinae has smooth and denticulated hinge elements. *Aurila*, *Mutilus*, and *Elofsonella* have denticulated median bars and grooves, while *Hemicythere* (not *Hemicytheria*) has denticulated median elements and a denticulated posterior tooth. *Heterocythereis* has an elongated and clearly denticulated posterior tooth (Pokorný 1955; Van Morkhoven 1962).

It is evident that the hinge of *Tyrrhenocythere* is identical to the hinge of *Hemicytheria*. In this case the hinge itself did not change in phylomorphogenesis and it does not influence the shape of the dorsal margin as Pokorný (1955: 29) observed for Hemicytherinae. Similarly, no difference is observed in the central muscle scar pattern, which consists of three oval to circular frontal muscle scars and four elongate adductor scars, of which one or two are subdivided into two separate oval scars (see the Systematic palaeontology herein and Pokorný 1952: 291; Ruggieri 1955: 698). However, this pattern is a general characteristic of Hemicytherinae (Van Morkhoven 1962: 57). The hinge and the central muscle scars are plesiomorphic characters and the generic differences are based only on differences in the marginal zone and marginal pore canal arrangement.

Transformation of the marginal pore canals

The MPC of *Hemicytheria* are simple, straight, thin, and numerous while the MPC of *Tyrrhenocythere* are branching, brush-like and connected at the base. There are eight to nine "brushes" visible on the AM, each one comprising of four to nine canals. The "brushes" are observable on the PM too. *T. amnicola* has only three "brushes" on the posterior (Ruggieri 1955: 698). The majority of *T. pannonicum* Olteanu, 1986 specimens have six "brushes", each with three to six canals on the posterior (Olteanu 1986: 64). Various transitional forms from the upper Miocene of the Lake Pannon can be observed between these two extreme forms (Fig. 6).

Hemicytheria omphalodes, possibly the earliest representative of this genus, ranging from the late Badenian to the lower Pannonian (Gross 2006: 96), has 70 straight, thin, very dense MPC, each slightly enlarged at the base (Fig. 6A). This same arrangement is observed in *H. loerentheyi* (Méhes, 1908) (Pannonian zones A–C; Méhes 1908: pl. 8: 1), *H. folliculosa* (Pokorný 1952: 291), and *H. reniformis* (both from the Pannonian zone E; Pokorný 1944: 5).

The palaeopopulations of *H. biornata* from Pezinok (this study) show groups of 2–4 MPC connected at the base, most frequently at the AVM, but rarely in PM (Fig. 6B). Sokać (1972: 77, pl. 37: 10) observes the same but with more advanced organisation (more branches) in *H. major* Sokać, 1972 from the Upper Pannonian of Croatia (Fig. 6C).

H. marginata Sokać, 1972 from the Upper Pannonian and Lower Pontian again has the more advanced MPC arrangement (Fig. 6D). Some thin canals divide into two to four thin MPC at mid-length, while others are straight and autonomous. About 26 MPC are on the inner margin and 52 on the outer margin. A larger zone of fusion appears between the canals compared with type species of *Hemicytheria*. The width of the canal is the same along its whole length (Sokać 1972: 76, pl. 37: 1).

Tyrrhenocythere transitivum sp. nov. does not have a typical *Tyrrhenocythere* MPC arrangement but the MPC are more advanced along the *Hemicytheria–Tyrrhenocythere* continuum (Fig. 6E). The groups of MPC are large and show two branching levels—firstly, the base of group divides into 2–4 canals and successively these bifurcate into 2–3 canals; in total, 65–70 MPC are observed on the AM as in primitive *Hemicytheria*. A drop-shaped fused zone appears between the branches, typical of *Tyrrhenocythere*. However, some adult individuals have the *Hemicytheria* MPC arrangement, with rarely connected canals. In fact, a continuous series between the *Hemicytheria* and *Tyrrhenocythere* arrangements is observed in populations of *T. transitivum* sp. nov. The brush-like MPC are visible only in adults while the juveniles have short, straight, and simple MPC due to a short zone of fusion. The variable MPC arrangement was also observed in the Pliocene adults of *T. pontica* (Livental, 1939) in which two forms are present, either *Hemicytheria* type with reduced number of MPC or *Tyrrhenocythere* type, possibly ecologically induced (Olteanu and Vekua 1989: 67).

T. pezinokensis has five fully developed "brushes" with drop-like spaces between them but the MPC are much longer in comparison with typical *Tyrrhenocythere* (Fig. 6F). The six to eight MPC on ADM and AVM are autonomous or incompletely fused. A transformation to a full *Tyrrhenocythere* morphology culminates in a brush-like form of MPC visible in *T. rastislavi* sp. nov., *T.* sp. 1, and *T.* sp. 2 (Fig. 6G). All three species from Pezinok have an identical MPC arrangement to *T. amnicola* and Pontian and Pliocene *Tyrrhenocythere*.

This process of transformation can be observed in sympatric and contemporaneous Pannonian populations of Lake Pannon. *Hemicytheria* with straight and separate MPC and *Hemicytheria* with fused MPC are observed at the same stratigraphical level as the type species of *Tyrrhenocythere*. While the species diversity of *Hemicytheria* decreased during later Pontian time, *Tyrrhenocythere* began their radiation and its species spread quickly in the brackish and freshwater basins of Paratethys and Mediterranean regions.

Phylogenetic relationships

Tyrrhenocythere pezinokensis has a similar pattern of ornamentation of the outer lamella to *Hemicytheria omphalodes* and *H. loerentheyi*. The ribs, principal elements of ornamentation, start in the muscle scar area and extend both anteriorly and posteriorly, and are connected by short perpendicular and oblique ribs. All three species have a strong, long ventral rib extending from the anterior to the anterodorsal. Additionally, in *H. omphalodes* and *H. loerentheyi*, the ventral ribs are interrupted by anterior polygonal fossae. The outline in both species of *Hemicytheria* is more dorsally rounded and ven-

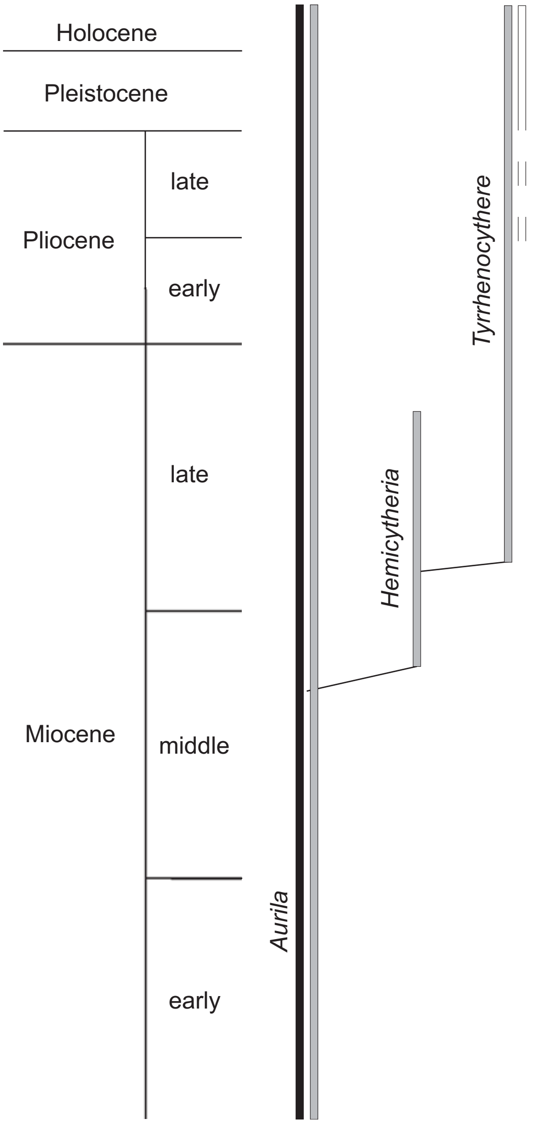

Fig. 8. Change of salinity tolerance in the course of phylogeny from fully marine/brackish *Aurila* through brackish *Hemicytheria* to brackish/freshwater *Tyrrhenocythere*; black, fully marine; grey, brackish; white, freshwater/oligohaline.

trally concave than in *T. pezinokensis*. As mentioned previously, *H. omphalodes* and *H. loerentheyi* have straight, thin and very dense MPC while *Tyrrhenocythere pezinokensis* has five fully developed "brushes" with drop-like spaces between them. It is likely that an ancestor of *T. pezinokensis* could be found among populations of *H. omphalodes* and *H. loerentheyi*. *H. tenuistriata* (Méhes, 1908), an index fossil of the Lower Pannonian in Serbia (Krstić 1985: 110) with heavy calcified valves and well-developed antero-posterior ribs, belongs to the same morphological group and could be the ancestor of *T. pezinokensis*.

In comparison with the lightly calcified carapaces of *T. transitivum* sp. nov., *T. rastislavi* sp. nov., *T.* sp. 1, and *T.* sp. 2, the heavily calcified valves and robust ornamentation of *T. pezinokensis* seem to be archaic. This species, *T. pezinokensis*, possibly represents an extinct lineage. No similar morphotype is found in younger deposits. As shown before, more than one *Hemicytheria* lineage transformed their arrangement of the MPC. On the basis of ornamentation, *T. transitivum* sp. nov., *T. rastislavi* sp. nov., and *T.* sp. 1. are possibly related to reticulated and punctate *Hemicytheria folliculosa*, *H. biornata* or *H. dubokensis* Krstić, 1963 living in the northern part of Lake Pannon during the Pannonian. The carapace of the semicircular *Tyrrhenocythere* sp. 2 is covered with small circular puncta. This type of ornamentation occurs in the rectangular *Hemicytheria hungarica* (Méhes, 1908) and the semicircular *H. ampullata* (Méhes, 1908) (see Méhes 1908: pl. 8: 7, pl. 9: 3), but no direct phyletic relation be shown between these species.

The documented morphological changes presume that more than one *Hemicytheria* species obtained *Tyrrhenocythere* characters and that thus *Tyrrhenocythere* is polyphyletic. In view of the plesiomorphic character of the hinge and central muscle scars, important systematic characters (see the Hinge structures chapter), a question rises of whether the brush-like MPC are a valid diagnostic character of the genus.

The brush-like MPC identical with type species are observed in three Pannonian species—*T. rastislavi* sp. nov., *T.* sp. 1, and *T.* sp. 2. The other species from the same stratigraphical level, *T. pezinokensis* and *T. transitivum* sp. nov. differ from this plan. They and the first variations in MPC of *Hemicytheria* appeared at a time when true *Tyrrhenocythere* existed but their arrangement of MPC was unstable, variable (*T. pontica* and *T. transitivum* sp. nov.) or resembling (*T. pezinokensis*) the true tyrrhenocytherid MPC. The above-mentioned three species would be false *Tyrrhenocythere*, phylogeneticaly related to *Hemicytheria*; however, the introduction of a new genus is inadvisable, because the species do not have an identical arrangement of MPC (see Fig. 6). It is possible that the brush-like MPC of *Tyrrhenocythere transitivum* sp. nov. only represents a phenotypical reaction to changing ecological conditions in the upper Miocene palaeolake, also proposed also by Olteanu and Vekua (1989: 71) and well documented in Pezinok (see the Palaeoenvironment of the early *Tyrrhenocythere* chapter). True *Tyrrhenocythere* would be a lineage, which appeared suddenly, without any transitional forms and a model of punctuated equilibrium would describe an origin of the genus, but the environmental factor(s) governing the evolution of not only *Tyrrhenocythere* but the entire Lake Pannon fauna and discussed below needs future investigation.

Palaeogeographical and palaeoecological steps in the evolution of *Tyrrhenocythere*

The isolation of the Central Paratethys from the Mediterranean led to a salinity decrease in the former during the Sarmatian (Fig. 3). The shallow epicontinental sea within a subtropical climate was connected only sporadically with the marine area. Since the mid-Sarmatian, *Hemicytheria omphalodes* occurred with *Aurila* in marine (*Pontocythere*, *Neocyprideis*) to brackish (*Cyprideis*) associations (Fordinál and Zlinská 1998: 145), and by the end of the middle Miocene, three species of *Hemicytheria* are known (Jiříček 1974: 447). Based on the carapace and hinge morphology and on ontological evolution, *Hemicytheria* are inferred to have evolved from *Aurila* (Cernajsek 1971: 574). During the late Miocene, the Central Paratethys become isolated from the Eastern Paratethys and the brackish/freshwater Lake Pannon arose within the Carpathian arc (Kázmér 1990). An extraordinary endemic fauna evolved (Müller et al. 1999) in this subtropical climate, changing gradually to the warm temperate climate with the introduction of seasonality (Kováč et al. 2005: 104).

This new, mainly deltaic environment, lasting during the early Pannonian zones A–C, was quickly colonised by ostracod and mollusc faunas that rapidly diversified in regard to morphology. The Hemicytherinae were represented by six species of *Hemicytheria*, of which the heavy ornamented *H. omphalodes* and *H. loerentheyi* are the most characteristic (Jiříček 1985: 381; Gross 2004). The overlying Pannonian zones D and E were transgressive where the deposition of the offshore basinal pelitic facies prevails. In the *Spiniferites paradoxus* Biochron (9.5 Ma, Pannonian E-zone), sea-level rise is inferred to have accelerated, the depth of sedimentation increased and the lake achieved its largest areal extent (maximum flooding surface; Kováč et al. 1998: 450; Magyar et al. 1999a: 159). The establishment of oxygen depleted muddy bottoms provoked a development of special morphological adaptation of molluscs (Harzhauser and Mandic 2004: 349). The species richness of *Hemicytheria* attained its maximum during that time (10 to 13 species; Jiříček 1985: 381; Sokać 1972: enclosure 2; Ljupko Rundić, personal communication 1997). Concurrently, *Hemicytheria* with modified MPC appeared (*H. biornata*, *H. major*, *H. marginata*) in Lake Pannon together with the five species of *Tyrrhenocythere* (this work), which show brush-like MPC. The reticulated *T. pannonicum* from the eastern margin of Lake Pannon (western Romania) is associated with typical Pannonian assemblage—*H. folliculosa*, *H. loerentheyi*, *Hungarocypris hieroglyphica* (Méhes, 1907), *Amplocypris recta*, *A. abscissa*, *Zalanyiella venusta* (Zalányi, 1929), *Caspiolla unguicula* (Reuss, 1850), and *Loxoconcha rhombovalis* (in recent literature, *T. pannonicum* is mentioned only from the Middle Pontian deposits of the Dacian Basin [Olteanu 1989a: 752]).

A sudden retreat of the Lake Pannon in the *Congeria praerhomboidea* Biochron (9.0 Ma, Pannonian zones F–H) led to the development of extensive lowlands with the deposition of alluvial and fluvial facies as well as the sedimentary environments of ephemeral lakes and swamps covered by vegetation (Magyar et al. 1999a: 160; Harzhauser and Tempfer 2004: 65), with local anoxic conditions (Magyar et al. 2006: 218).

Hemicytheria disappeared from the Vienna Basin and Hemicytherinae (Nagy-Bodor et al. 1989) became rare in the northern part of Lake Pannon. The lineage leading to the heavily calcified *T. pezinokensis* no longer appeared in ostracod associations. Only a few Pannonian ostracod species survived in the southern part of Lake Pannon until the early Pontian and were associated with typical Pontian species (Sokać 1989: 695). During the Pontian, the molluscan fauna of Lake Pannon migrated into the Eastern Paratethys due to palaeogeographical change (Müller et al. 1999: 53). Possibly, only *Hemicytheria maeotica* Olteanu, 1989 crossed the palaeogeographical border of Lake Pannon and lived in the Dacian Basin during the Meotian (Olteanu 1989b: 152). *Hemicytheria* have never reached the Eastern Paratethys. However "*Tyrrhenocythere*" with straight MPC were described from the late Pliocene of Georgia (Imnadze 1976: 34–39; Olteanu and Vekua 1989: pl. 2: 1–4). Southern Lake Pannon was settled during Pontian by *T. filipescui* (Hanganu, 1966), *T. triebeli* Krstić, 1963 (Sokać 1989; Krstić 1977: 402), but *Tyrrhenocythere* species were absent from the late Pliocene freshwater/saline lacustrine environments of the Paludinian Beds (the last stage of Lake Pannon; Krstić and Knežević 2003) deposited under a warm climate (Krstić et al. 2003). *T. filipescui*, *T. triebeli*, and another six *Tyrrhenocythere* species appeared suddenly and were greatly diversified during the Middle Pontian of the Dacian Basin, emigrating from surrounding basins (Krstić 1977: 402; Olteanu 1989a: 726) and favoured by a decrease in salinity (Olteanu and Vekua 1989: 71).

At this time, the genus *Tyrrhenocythere* emerged also in the Eastern Paratethys (Naidina 1989: 820). Due to the high intraspecific variation, numerous synonyms have been erected (Krstić 1977: 396). Reticulate species, (e.g., *T. pontica*) some of them with very strong ornamentation (*T. turcica* Tunoglu, 2001) prevail over smooth species (*T. dacicum* Olteanu, 1982; Olteanu 1989a: 752; Tunoglu 2001: 139). In the Sinop area (Turkey) they occur in oligohaline and lacustrine assemblages (Tunoglu and Gökçen 1997: 364).

Tyrrhenocythere species are not found in the Late Serravalian and/or early Tortonian deposits of the Eastern Mediterranean (Greece) within limnic and shallow marine ostracod assemblages (Mostafawi 1989). They migrated into the Mediterranean area with other Paratethyan faunas after the Messinian crisis when shallow brackish basins became widespread (Carbonnel 1980: 22; Cippolari et al. 1999: 162). Six *Tyrrhenocythere* species (*T. triebeli, T. filipescui, T. pannonicum, T. pignattii* Ruggieri, 1955, *T.* sp. 1, and *T.* sp. 3) in the Upper Pontian of the Eastern Mediterranean (Mostafawi 1996: 161; Galoukas and Danielopol 2004: 195) and two (*T. pontica, T. ruggieri* Devoto, 1964) from the top of N17-bottom of N18 (the uppermost Messinian) planktic foraminiferal zones in the western Mediterranean are recognised, together with brackish Pontian Paratethys ostracod genera (*Amnicythere, Cyprideis*, and *Loxoconcha*; Carbonel 1978: 116; Krstić and Stancheva 1989: 761; Cippolari et al. 1999: 159; Gliozzi 1999: 193), in shallow brackish littoral conditions with freshwater influences (Galoukas and Danielopol 2004: 188).

After the restoration of normal marine conditions during the Plio-Pleistocene time, *Tyrrhenocythere* species were still present in the Mediterranean. The extant fine punctuated *T. amnicola* appeared during this time interval in the Caspian Basin (Schornikov 1981: 109) and eastern Mediterranean (Mostafawi 1994: 101; Guernet et al. 2003: 85) with the reticulate *T. danatsasi* Fernández-González, 1994 and *T. helenica* Guernet, 1994 (Fernández-González et al. 1994: 93). The first evidence of *Tyrrhenocythere* from a freshwater/ oligohaline lacustrine environment cames from the Pleistocene of Italy and Greece (Devoto 1965: 311; Griffiths et al. 2002: 252). Older occurrences of *Tyrrhenocythere*, including those from the Paratethys, are from brackish or mixed taphocoenoses that are composed mainly of brackish ostracods, endemic Paratethys Candoninae and partially freshwater species (Fig. 8). Living populations of *Tyrrhenocythere* display a high intraspecific variation in shape and ornamentation. They inhabit brackish and fresh-water lakes, lagoons, deltas, estuaries, and rivers in the Ponto-Caspian region (*T. donetziensis*; Yassini and Ghahreman 1976: 177; Schornikov 1969: 194, 1974: 193) and the rivers of Mediterranean region (*T. amnicola*; Griffiths et al. 2002: 253). The easternmost population comes from Lake Issyk-Kul (Kyrgyzstan; Bronshtein 1947: 377). *Tyrrhenocythere* became extinct in the Aral Sea due to an increase in salt concentration (35‰). The original brackish biotope was colonised by the anomohaline *Cyprideis*, euryhaline *Loxoconcha*, *Leptocythere*, *Tyrrhenocythere*, and 8 minor freshwater taxa (Boomer et al. 1996). *Tyrrhenocythere* lived at a depth of about 30 m (possibly to 50 m) and in a salinity range of 0–14‰, preferring shell debris and diverse substrates (gypsum clay, clayey sand) covered by aquatic plants (Bronshtein 1947: 377; Schornikov 1974: 193; Krstić 1977: 399; Yassini and Ghahreman 1976: 183). The genus is an indicator of warm climatic conditions (Griffiths et al. 2002: 257) with a mean annual temperature of 12–16° C (Yassini and Ghahreman 1976: 184).

Conclusions

As was supposed by Krstić (1977: 399) and Bachnou et al. (1999: 201), the genus *Tyrrhenocythere* originated before the Pontian. Five *Tyrrhenocythere* species are described from the shallow lacustrine Pannonian deposits of the zone MN9/ MN10. They are minor taxa in this taphocoenosis and are associated with the euryhaline *Euxinocythere*, *Loxoconcha*, *Cyprideis*, *Hemicytheria*, *Amplocypris*, and Paratethyan Candoninae. *Tyrrhenocythere rastislavi* sp. nov., *T.* sp. 1, and *T.* sp. 2 have a MPC arrangement identical to the type species of the genus and Pontian and Pliocene *Tyrrhenocythere*. Specimens of *Tyrrhenocythere transitivum* sp. nov. show a continuous series in MPC arrangement from *Hemicytheria* to *Tyrrhenocythere*, while *T. pezinokensis* has long MPC connected at the base and with drop-like spaces between MPC. Based on valve ornamentation the latter species is related to *H. omphalodes* and *H. loerentheyi* while the former could be a descendant of reticulated and punctuated *Hemicytheria* of the Lake Pannon. This implies a polyphyletic origin for *Tyrrhenocythere* but it is possible that brush-like MPC of *T. pezinokensis* and *T. transitivum* are only a phenotypical reaction to changing ecological conditions in the upper Miocene palaeolake which appeared simultaneously with true *Tyrrhenocythere*.

Acknowledgements

This work was supported by the APVV agency (project APVT-51-045202) and VEGA agency (Project No. 1/3053/06). Many thanks to Mathias Harzhauser (NHM Wien, Austria) and Michal Kováč (Comenius University, Slovakia) who provided their stratigraphical and palaeogeographical knowledge on the Paratethys and Mediterranean realm. Thanks are also extended to Dan L. Danielopol (Institute of Limnology, Austria) and Irene Zorn (Geologische Bundesanstalt, Austria) for providing literature, to Jean-Paul Colin (Cestas, France) and Klement Fordinál (Geological Survey of Slovak Republic, Slovakia) for helpful remarks. Lee Hsiang Liow (University of Chicago, USA), Mervin Kontrovitz (University of Louisiana, USA) and Robin C. Whatley (Aberystwyth, United Kingdom) improved the language of this paper and provided useful comments. Thanks are also to the reviewers David J. Horne (University of London, United Kingdom) and Toshiaki Irizuki (Shimane University, Japan) for their constructive comments.

References

Babinot, J.-F. 2003. *Zonocypris digitalis* (Ostracoda, Crustacea), nouvelle espèce du Fuvélien (Campanien continental) de Provence (sud-est France). *Revue de Micropaléontologie* 46: 3–9.

Bachnou, A., Carbonnel, G., and Bouab, B. 1999. Morphométrie des Hemicytherinae (Ostracods) par modélisation mathématique du profil latéral externe. Application systématique et phylogénétique. *Compte Rendu de l'Académie des Sciences de Paris, Paléontologie* 328: 197–202.

Baráth, I., Fordinál, K., and Pipík, R. 1999. Lacustrine to alluvial sedimentary cyclicity (Pannonian, zone E, Danube basin). *Geologica Carpathica* 50: 14–16.

Boomer, I., Whatley, R., and Aladin, N.V. 1996. Aral sea Ostracoda as environmental indicators. *Lethaia* 29: 77–85.

Bronshtein, Z.S. [Bronštein, Z.S.] 1947. *Fauna SSSR, Rakoobraznye, Tom II, Vypusk 1 Ostracoda Presnyh Vod*. 370 pp. Academy of Sciences of the USSR Publishers, Moscow. (English translation 1988: *Freshwater Ostracoda—Fauna of the USSR: Crustaceans, Vol. II, No. 1*. 455 pp. AA Balkema, Rotterdam).

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.

Carbonnel, G. 1980. L'ostracofaune du Messinien: une preuve de la vidange de la Paratéthys. *Géologie Mèditerranéenne* 7: 19–24.

Cernajsek, T. 1971. Die Entwicklung und Abgrenzung der Gattung *Aurila* POKORNY (1955) im Neogen Österreichs (Vorbericht). *Verhandlungen der Geologischen Bundesanstalt* 3: 571–575

Cipollari, P., Cosentino, D., Esu, D., Girotti, O., Gliozzi, E., and Praturlon A. 1999. Thrust-top lacustrine-lagoonal basin development in accretionary wedges: late Messinian (Lago-Mare) episode in the central Apennines (Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* 151: 149–166.

Devoto, G. 1965. Lacustrine Pleistocene in the Lower Liri Valley. *Geologica Romana* 4: 291–365.

Dubowsky, N.V. 1926. Bemerkungen über einige Ostracoden der Schweny-Donets-Bassins. *Zoologischer Anzeiger* 65: 263–280.

Fernández-González, M., Frydas, D., Guernet, C., and Mathieu, R. 1994. Foraminifères et Ostacodes du Pliopleistocène de la region de Patras

(Grèce). Intérêt stratigraphique et paléogéographique. *Revista Española de Micropaleontología* 26: 89–108.

Fordinál, K. 1997. Molluscs (Gastropoda, Bivalvia) from the Pannonian deposits of the western part of Danube Basin (Pezinok-clay pit). *Slovak Geological Magazine* 3: 263–283.

Fordinál, K. and Zlinská, A. 1998. Fauna of the upper part of Holíč Formation (Sarmatian) in Skalica (Vienna Basin) [in Slovak with English abstract]. *Mineralia Slovaca* 30: 137–146.

Galoukas, S. and Danielopol, D.L. 2004. Taxonomic diversity of Late Cenozoic Cytheroidea (Ostracoda) from Cyprus Island. *Bolletiono della Società Paleontologica Italiana* 43: 181–199.

Gliozzi, E. 1999. A late Messinian brackish water ostracod fauna of Paratethyan aspect from Le Vicenne Basin (Abruzzi, central Apennines, Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* 151: 191–208.

Gramann, F. 1971. Brackish or hyperhaline? Notes on paleoecology based on Ostracoda. *In*: H.J. Oertli (ed.), Paléoécologie des Ostracodes. *Bulletin du Centre de Recherches* 5: 93–99.

Griffiths, S.J., Griffiths, H.I., Altinsaçli, S., and Tzedakis, Ch. 2002. Interpreting the *Tyrrhenocythere* (Ostracoda) signal from Palaeolake Kopais, central Greece. *Boreas* 31: 250–259.

Gross, M. 2004. Zur Ostracodenfauna (Crustacea), Paläoökologie und Stratigrafie der Tongrube Mataschen (Unter-Pannonium, Steirisches Becken, Österreich). *Joannea – Geologie und Paläontologie* 5: 49–129.

Gross, M. 2006. *Mittelmiozäne Ostracoden aus dem Wiener Becken (Badenium/Sarmatium, Österreich)*. 224 pp. Verlag der Österreichischen Akademie der Wissenschaften, Wien.

Guernet, C., Lemeille, F., Sorel, D., Bourdillon, C., Berge-Thierry, C., and Manakou, M. 2003. Les ostracodes et le Quaternaire d'Aigion (Golfe de Corinthe, Grèce). *Revue de Micropaléontologie* 46: 73–93.

Harzhauser, M. and Mandic, O. 2004. The muddy bottom of Lake Pannon—a challenge for dreissenid (Late Miocene; Bivalvia). *Palaeogeography, Palaeoclimatology, Palaeoecology* 204: 331–352.

Harzhauser, M. and Piller, W.E. (in press). Benchmark data of a changing sea—Palaeogeography, Palaeobiogeography and Events in the Central Paratethys during the Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology*.

Harzhauser, M. and Tempfer, P.M. 2004. Late Pannonian Wetland Ecology of the Vienna Basin based on Molluscs and Lower Vertebrate Assemblages (Late Miocene, MN 9, Austria). *Courier Forschungsinstitut Senckenberg* 246: 55–68.

Holec, P., Papšíková, M., Kraus, I., and Fordinál, K. 1987. Rekonstruktion der Lebensbedingungen an der wende Pannon-Pont auf der Lokalität Pezinok – Lehmgrube der Ziegelei (SO-rand der Kleinen Karpaten). *Acta Geologica et Geographica Universitatis Comenianae, Geologica* 43: 181–191.

Imnadze, Z.A. 1976. Representants of the subfamily Hemicytherinae in Pliocene deposits of western Georgia [in Russian]. *Trudy VNIGRI* 205: 32–41.

Jiříček, R. 1974. Biostratigraphische Bedeutung der Ostracoden des Sarmats s. str. *In*: E. Brestenská (ed.), *Chronostratigraphie und Neostratotypen, M_5, Sarmatien*, 434–457. VEDA, Bratislava.

Jiříček, R. 1985. Die ostracoden des Pannonien. *In*: A. Papp (ed.), *Chronostratigraphie und Neostratotypen, Miozän der Zentral Paratethys, Bd. VII, M_6 Pannonien (Slavonien und Serbien)*, 378–425. Akadémiai Kiadó, Budapest.

Joniak, P. 2005. *New rodent assemblages from the Upper Miocene deposits of the Vienna Basin and Danube Basin*. Unpublished PhD thesis. 134 pp. Comenius University, Bratislava.

Kázmér, M. 1990. Birth, life and death of the Pannonian lake. *Palaeogeography, Palaeoclimatology, Palaeoecology* 79: 171–188.

Kováč, M. 2000. *Miocene Geodynamic, Paleogeographic and Tectonic Evolution of the Carpatho-Pannonian Region: New Inside to Neogene Basins of Slovakia* [in Slovak]. 204 pp. VEDA, Slovenská akadémia vied, Bratislava.

Kováč, M., Baráth, I., Kováčová-Slamková, M., Pipík, R., Hlavatý, I., and Hudáčková, N. 1998. Late miocene paleoenvironments and sequence stratigraphy: northern Vienna Basin. *Geologica Carpathica* 49: 445–458.

Kováč, M., Fordinál, K., Halásová, E., Hudáčková, N., Joniak, P., Pipík, R., Sabol, M., Kováčová-Slamková, M., and Sliva, Ľ. 2005. Western Carpathian fossil ecosystems and their relation to Neogene evolution of Euro-Asian continent [in Slovak]. *Geologické práce, Správy* 111: 61–121.

Krstić, N. 1971. Ostracodes biofacies in the Pannone. *In*: H.J. Oertli (ed.), Paléoécologie des Ostracodes. *Bulletin du Centre de Recherches* 5: 391–397.

Krstić, N. 1977. The ostracod genus *Tyrrhenocythere*. *In*: H. Löffler and D. Danielopol (eds.), *Aspects of Ecology and Zoogeography of Recent and Fossil Ostracoda*, 395–405. W. Junk Publishers, The Hague.

Krstić, N. 1985. Ostracoden im Pannonien der Umgebung von Belgrad. *In*: A. Papp (ed.), *Chronostratigraphie und Neostratotypen, Miozän der Zentral Paratethys, Bd. VII, M_6 Pannonien (Slavonien und Serbien)*, 103–143. Akadémiai Kiadó, Budapest.

Krstić, N. and Knežević, S. 2003. Succession of the Fauna of the Paludinian Beds. *In*: I. Papaianopol, F. Marinescu, N. Krstić, and R. Macalet (eds.), *Chronostratigraphie und Neostratotypen, Neogene der Zentrale Paratethys, Pliozän Pl_2, Bd. 10 – Romanien*, 83–92. Rumänische Akademie, Bucuresti.

Krstić, N., Pantić, N., and Radošević, B. 2003. Environment of Paludinian Beds. *In*: I. Papaianopol, F. Marinescu, N. Krstić, and R. Macalet (eds.), *Chronostratigraphie und Neostratotypen, Neogene der Zentrale Paratethys, Pliozän Pl_2, Bd. 10 – Romanien*, 94–101. Rumänische Akademie, Bucuresti.

Krstić, N. and Stancheva, N. 1989. Ostracods of Eastern Serbia and Northern Bulgaria with notice on a Northern Turkey assemblage. *In*: M. Malez and P. Stevanović (eds.), *Chronostratigraphie und Neostratotypen, Bd. VIII, Pontien Pl_1*, 753–819. JAZU and SANU, Zagreb.

Latreille, P.A. 1806. *Genera Crustaceorum et Insectorum secundum ordinum naturalem in familias disposita, iconibus exemplisque plurimus explicata. Tomus primus*. 302 pp. Amand Koenig, Parisiis.

Lourens, L.J., Hilgen, F.J., Laskar, J., Shackleton, N.J., and Wilson, D. 2004. The Neogene Period. *In*: F. Gradstein, J. Ogg, and A. Smith (eds.), *Geological Time Scale*, 409-440. Cambridge University Press, Cambridge.

Magyar, I., Geary, D.H., and Müller, P. 1999a. Paleogeographic evolution of the Late Miocene Lake Pannon in Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 147: 151–167.

Magyar, I., Geary, D.H., Lantos, M., Müller, P., and Sütö-Szentai, M. 1999b. Integrated biostratigraphic, magnetostratigraphic and chronostratigraphic correlations of the Late Miocene Lake Pannon deposits. *Acta Geologica Hungarica* 42: 5–31.

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

Méhes, G. 1908. Beiträge zur kenntnis der Pliozänen Ostrakoden Ungarns, II. Die *Darwinulidaeen* und *Cytheridaeen* der unterpannonischen Stufe. *Földtani Közlöny* 38: 601–635.

Meisch, C. 2000. *Freshwater Ostracoda of Western and Central Europe*. 522 pp. Spektrum Akademischer Verlag, Heidelberg.

Morkhoven, F.P.C.M. van 1962–1963. *Post-paleozoic Ostracoda, their Morphology, Taxonomy, and Economic Use, I* (1962), 204 pp.; *II* (1963), 478 pp. Elsevier Publishing Company, Amsterdam.

Mostafawi, N. 1989. Neogene Ostracoden von Chersonisos und Vrysses (Kreta, Griechenland). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 178: 183–201.

Mostafawi, N. 1994. Ostracoden aus dem Ober-Pliozän und dem Ober-Pleistozän des N-Peloponnes, Griecheland. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 194: 95–114.

Mostafawi, N. 1996. Neogene Ostracodenfaunen im Gebiet südlich von Thessaloniki (Nordgriechenland). *Senckenbergiana lethaea* 76: 159–173.

Müller, P., Geary, D.H., and Magyar, I. 1999. The endemic mollusks of the Late Miocene Lake Pannon: their origin, evolution, and family-level taxonomy. *Lethaia* 32: 47–60.

Nagy-Bodor, E. and Szuromi-Korecz, A. 1989. An evaluation of sporomorphs and ostracods of the Fehérpart exposure at Tihany, Lake Balaton. *Magyar Állami Földtani Intézet Évi Jelentése az 1988, Évröl* 2: 203–224.

Naidina, N.N. 1989. Pontian ostracodes of Eastern Paratethys. *In*: M. Malez and P. Stevanovič (eds.), *Chronostratigraphie und Neostratotypen, Pliozän Pl_1, Pontien*, 820. JAZU and SANU, Zagreb.

Olteanu, R. 1982. Genus *Tyrrhenocythere* Ruggieri, in the Dacic Basin. *Dari de Seama ale Sedintelor Institutul de Geologie si Geofizica, 3. Paleontologie* 69: 47–58.

Olteanu, R. 1986. New ostracods from the Pannonian deposits. *Dari de Seama ale Sedintelor Institutul de Geologie si Geofizica, 3. Paleontologie* 70–71: 55–72.

Olteanu, R. 1989a. La faune d'ostracodes pontiens du Bassin Dacique. *In*: M. Malez and P. Stevanovič (eds.), *Chronostratigraphie und Neostratotypen, Pliozän Pl_1, Pontien*, 722–752. JAZU and SANU, Zagreb.

Olteanu, R. 1989b. New ostracodes in Upper Neogene from Romania. *Memoriile Institutului de Geologie si Geofizica* 34: 123–182.

Olteanu, R. 1995. Dacian ostracodes. *In*: F. Marinescu and I. Papaianopol (eds.), *Chronostratigraphie und Neostratotypen – Neogene der Zentrale Paratethys, Bd. IX, Dacien Pl_1*, 268–386. Rumänische Akademie, Bucarest.

Olteanu, R. and Vekua, M. 1989. Quelques considérations sur les genres *Tyrrhenocythere* (Ruggieri, 1955) et *Hemicytheria* (Pokorný, 1955) (Ostracoda, Crustacea) du Néogène supérieur de la Paratéthys. *Geobios* 22: 65–79.

Papp, A. 1951. Das Pannon des Wiener Beckens. *Mitteilungen der Geologischen Gesellschaft in Wien* 1946: 39–41 and 1948: 99–193.

Pipík, R. 1996. *Paleoecology of the ostracod assemblages from Borský Sv. Jur and Pezinok* [in Slovak]. Unpublished M.Sc. thesis. 75 pp. Department of Geology and Paleontology, Comenius University, Bratislava.

Pipík, R. 1998. Salinity changes recorded by ostracoda assemblages found in Pannonian sediments in the western margin of the Danube Basin. *Bulletin des centres de recherches exploration-production Elf-Aquitaine* 20: 167–177.

Pipík, R. and Bodergat, A.M. 2004. *Euxinocythere* (Ostracoda, Cytheridae, Leptocytherinae) du Miocène supérieur du Bassin de Turiec (Slovaquie): taxonomie et paléoécologie. *Revue de Micropaléontologie* 47: 36–52.

Pokorný, V. 1944. La microstratigraphie du Pannonien entre Hodonín et Mikulčice (Moravie méridionale, Tchécoslovaquie). *Bulletin international de l'Académie tchèque des Sciences, Rozpravy II. třídy České akademie* 54: 1–25.

Pokorný, V. 1952. The Ostracods of the So-Called Basal-Horizon of the Sub-globosa beds at Hodonín (Pliocene, Inner Alpine Basin, Czechoslovakia) [in Czech with Russian and English abstracts]. *Sborník Ústředního ústavu geologického* 19: 229–396.

Pokorný, V. 1955. Contribution to the morphology and taxonomy of the subfamily Hemicytherinae Puri 1953 (Crust., Ostracoda). *Acta Universitatis Carolinae, Geologica* 3: 3–35.

Puri, H.S. 1953. The ostraocd Genus *Hemicythere* and its allies. *Journal of the Washington Academy of Sciences* 43: 169–179.

Rögl, F., Zapfe, H., Bernor, R.L., Brzobohatý, R.L., Daxner-Höck, G., Draxler, I., Fejfar, O., Gaudant, J., Herrmann, P., Rabeder, G., Schultz, O., and Zetter, R. 1993. Die Primatenfundstelle Götzendorf an der Leitha (Obermiozän des Wiener Beckens, Niederösterreich). *Jahrbuch der Geologischen Bundesanstalt* 136: 503–526.

Ruggieri, G. 1955. *Tyrrhenocythere*, a new ostracode genus from the Mediterranean. *Journal of Paleontology* 29: 698–699.

Sabol, M., Joniak, P., and Holec, P. 2004. Succesion(-s) of mammalian assemblages during the Neogene—a case study from the Slovak part of the Western Carpathians. *Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Geology* 31–32 (for 2001–2002): 65–84.

Sars, G.O. 1866. Oversigt of Norges marine Ostracoder. *Forhandlinger i Videnskab-Selskabet i Christiana* 1865: 1–130.

Sars, G.O. 1887. Nye bidrag til kundskaben om Middelhavets invertebratfauna. IV. Ostracoda mediterranea (sydeuropaeiske ostracoder). *Archiv foer Matematik og Naturvidenskab* 12: 305–312.

Schornikov, E.I. [Šornikov, E.I.] 1969. Subclass Ostracoda, shelled Crustacea, -Ostracoda Latreille, 1816 [in Russian]. *In*: *Opredelitel' fauny Černogo i Aral'skogo morei, tom II*, 163–217. Naukova dumka, Kiev.

Schornikov, E.I. [Šornikov, E.I.] 1974. Subclass Ostracoda, shelled Crustacea [in Russian]. *In*: F.D. Morduhaj-Boltovskoj, N.N. Kondakova, E.L. Markova, N.N. Romanova, and E.A. Âblonskaâ (eds.), *Atlas bespozvonočnyh Aral'skogo morâ*, 180–198. Piščevaya promyšlennost', Moskva.

Schornikov, E.I. [Šornikov, E.I.] 1981. *Tyrrhenocythere amnicola* (Crustacea)—politypic ostrakod species from Cainozoic of the south USSR [in Russian]. *In*: L.F. Bragina (ed.), *Biostratigrafiâ antropogena i neogena ûgo-zapada SSSR*, 107–122. ŠTIINCA, Kišinev.

Sitár, V. 1958. Pannonian flora from the Pezinok vicinity based on pollen analysis [in Slovak with Russian and German abstracts]. *Acta geologica et geographica Universitatis Comenianae, Geologica* 1: 89–93.

Sokać, A. 1972. Pannonian and Pontian ostracode fauna of Mt. Medvednica. *Palaeontologica Jugoslavica* 11: 9–140.

Sokać, A. 1989. Pontian ostracod fauna in the Pannonian Basin. *In*: M. Malez and P. Stevanović (eds.), *Chronostratigraphie und Neostratotypen, Bd. VIII, Pontien Pl_1*, 672–721. JAZU and SANU, Zagreb.

Steininger, E.F. and Rögl, F. 1985. Die Paläogeographie der Zentralen Paratethys im Pannonien. *In*: A. Papp (ed.), *Chronostratigraphie und Neostratotypen, Miozän der Zentral Paratethys, Bd. VII, M_6 Pannonien (Slavonien und Serbien)*, 46–56. Akadémiai Kiadó, Budapest.

Tunoglu, C. 2001. New Pontian *Tyrrhenocythere* (Ostracoda) species from Arakli (Trabzon), Eastern Black Sea Region of Turkey. *Yerbilimleri* 23: 129–143.

Tunoglu, C. and Gökçen, N. 1997. Pontian Ostracoda of the Sinop Area, Black Sea Coast of Turkey. *Revue de Micropaléontologie* 40: 347–366.

Yassini, I. and Ghahreman, A. 1976. Récapitulation de la distribution des ostracodes et des foraminifères du lagon de Pahlavi, province de Gilan, Iran du nord. *Revue de Micropaléntologie* 19: 172–190.