

Dedicated to Prof. Dr F. F. STEININGER

Miocene “*Hungarocypris*” species of Lake Pannon (Central and South-Eastern Europe) transferred to *Herpetocyrella* DADAY, 1909 (Ostracoda, Cyprididae)

With 11 Text-figures and 2 Tables

DAN L. DANIELOPOL, ROBERT BUTTINGER, RADOVAN PIPÍK, MARTIN GROSS,
RADU OLTEANU & JOSEF KNOBLECHNER

Abstract

The genus *Hungarocypris* VÁVRA, 1906 is known in Europe by a unique species, *Hungarocypris madarászi* (ÖRLEY, 1886). Its morphological characteristics are briefly reviewed and compared with those of *Herpetocyrella mongolica* DADAY, 1909 from Lake Issyk-Kul, Kyrgyzstan. Two cypridoidean species, *Hungarocypris auriculata* (REUSS, 1850) and *Hungarocypris hieroglyphica* (MÉHES, 1907) from Upper Miocene deposits of Lake Pannon (Central and South-Eastern Europe), are compared to *H. madarászi*. Morphological traits of the fossil species point to close phylogenetical affinities with *H. mongolica*, and therefore transferred to *Herpetocyrella* DADAY, 1909. *H. auriculata* is described, based on material from the Vienna Basin, the Eisenstadt-Sopron Basin and from the Styria Basin (Austria). Further, this species is compared to *H. hieroglyphica* from Banat (Romania). The morphological variability of the former species is presented. Palaeobiogeographical and palaeoecological implications are briefly emphasized.

Key words: Ostracoda, comparative morphology, (palaeo)biogeography, *Hungarocypris*, *Herpetocyrella*, Lake Pannon

Introduction

The extant living non-marine ostracod fauna in Europe is dominated by representatives of the superfamily Cypridoidea BAIRD, 1845, respectively by two families, the Cyprididae BAIRD, 1845 and the Candonidae KAUFMANN, 1900 (LÖFFLER & DANIELOPOL 1978). The majority of species belonging to these two families have carapaces between 0.5 and 2.5 mm in length. There is only one exception, *Hungarocypris madarászi* (ÖRLEY, 1886), which has a giant size, respectively a carapace length of 3.5–5 mm (MEISCH 2000). This latter species lives commonly in shallow freshwater habitats with summer temperature above 20 °C (LÖFFLER 1961). It is morphologically related to two other living species, *Hungarocypris gavemül-*

leri VÁVRA, 1906 (the type species of the genus *Hungarocypris* VÁVRA, 1906) and *H. asymmetricus* VÍCTOR & FERNANDO, 1981, both known from freshwater habitats in South-Eastern Asia (VÍCTOR & FERNANDO 1981).

Lake Pannon is an ancient palaeolake, which originated in Central Europe during the Upper Miocene (at about 11.6 Ma BP) from the transformation of the large inland sea called “Central Paratethys” and existed until at about 5.8 Ma BP (KÁZMÉR 1990, MAGYAR et al. 1999, RÖGL 1999, HARZHAUSER & MANDIC 2008). During its existence, the lake experienced wide changes in its chemical composition and/or saline concentrations (HARZHAUSER et al. 2007). The ostracod fauna was dominated by representatives of the superfamily Cytheroidea BAIRD, 1850 (loxoconchids, hemicytherids, lep-

Prof. Dr Dan L. DANIELOPOL (Corresponding author <dan.danielopol@oeaw.ac.at>), Österreichische Akademie der Wissenschaften, Kommission für die paläontologische und stratigraphische Erforschung Österreichs, c/o Institut für Erdwissenschaften, Universität Graz, Heinrichstrasse 26, A-8010 Graz, Austria; Robert BUTTINGER, Universität Wien, Geozentrum, Department für Paläontologie, Althanstrasse 14, A-1090 Wien, Austria; Radovan PIPÍK, Slovenská Akadémia vied, Geologický ústav, Severná 5, SK-97401 Banská Bystrica, Slovakia; Dr Martin GROSS, Landesmuseum Joanneum, Abteilung Geologie und Paläontologie, Raubergasse 10, A-8010 Graz, Austria; Dr Radu OLTEANU, c/o Institutul National de Geologie Marină și Geoecologie – Geocomar, Str. Dimitrie Onciul 23-25, RO-70318 București, Romania; Josef KNOBLECHNER, Österreichische Akademie der Wissenschaften, Institut für Limnologie, Mondseestrasse 9, A-5310. Mondsee, Austria.

rocytherids). There were generally few Cyprididae species with valves of medium to large size (1.5–2.0 mm length). Some of them were assigned (KRSTIĆ 1967) to the genus *Hungarocypris*. They occur mainly in the Lower Pannonian, e.g. frequently in marginal settings of Lake Pannon (POKORNÝ 1952, OLTEANU 1971, KRSTIĆ 1967, 1973/1974, SOKAČ 1972, JIŘIČEK, 1985, GROSS 2004).

Taking into account the geographic distribution of living and fossil *Hungarocypris* species, VICTOR & FERNANDO (1981) offered a scenario for the geographical distribution of this ostracod group. It was considered that *Hungarocypris* originated in Lake Pannon during a time of warm climate from where the genus spreads eastwards in the Palearctic (e.g. South-Eastern Asia, Celebes Island). This (palaeo)biogeographical evolutionary model takes into account that *Hungarocypris* species switched their mode of life from one adapted to brackish water to completely fresh limnic ones. Following this scenario, one would expect to find other *Hungarocypris* species similar to the Pannonian ones, more commonly nowadays in Europe, which is not the case (LÖFFLER & DANIELOPOL 1978, MEISCH 2000).

KRSTIĆ (2006) figured valves of the living species *Herpetocyrella mongolica* DADAY, 1909 from Lake Issyk-Kul, Kyrgyzstan. One of us (D.L.D.) recognised the astonishing similarity of this species with fossil *Hungarocypris* species from Lake Pannon. Therefore we proceeded to a comparative morphological study between the living species *H. madarászi* and two fossil species, *Hungarocypris auriculata* (REUSS, 1850) and *Hungarocypris hieroglyphica* (MÉHES, 1907) as well as with published information concerning *H. mongolica*. We document herein, that at least the fossil Miocene “*Hungarocypris*” species we investigated belong to *Herpetocyrella* DADAY, 1909. Subsequently, we describe the widely spread fossil species *H. auriculata* and compare it to *H. hieroglyphica*. These data allow to propose alternative views to the (palaeo)biogeographical model of VICTOR & FERNANDO (1981). It will offer us also the possibility to suggest a research programme in order to improve our knowledge on the palaeoecology and systematics of the Miocene “*Hungarocypris*” from Lake Pannon. A better knowledge of this group would enable us to use them for palaeoecological reconstructions and possibly for biostratigraphical correlations within the area of Lake Pannon.

Material and methods

Table 1 presents an overview of the investigated material. Additionally, we use information from published descriptions that was reanalysed using geometric morphometric techniques. For discussion we used published data too (OLTEANU 1971, GROSS 2004). Text-figure 1 shows the location of the areas from where we describe or discuss the ostracod material.

One adult female and one juvenile of *H. madarászi* were collected by the late H. LÖFFLER (University of Vienna) in 1961 in the

Dorflacke or “Dorfsee”, an astatic freshwater system, in Burgenland, eastern Austria.

H. auriculata from Sankt Margarethen, in Burgenland comes from the site “Altes Zollhaus” (Eisenstadt-Sopron Basin, Pannonian “D”, *Mytilopsis spathulata* Zone, layer 16 and 17; HARZHAUSER et al. 2002).

The material will be deposited in the collection of the Department of Geology & Palaeontology of the Landesmuseum Joanneum (Graz).

From the same region, at Drassburg, we studied several specimens of *H. auriculata* deposited in the ostracod collection of K. KOLLMANN at the Natural History Museum in Vienna (Geological-Palaeontological Department; samples *Eucypris? sieberi* 1990-0226 and 1990-0142).

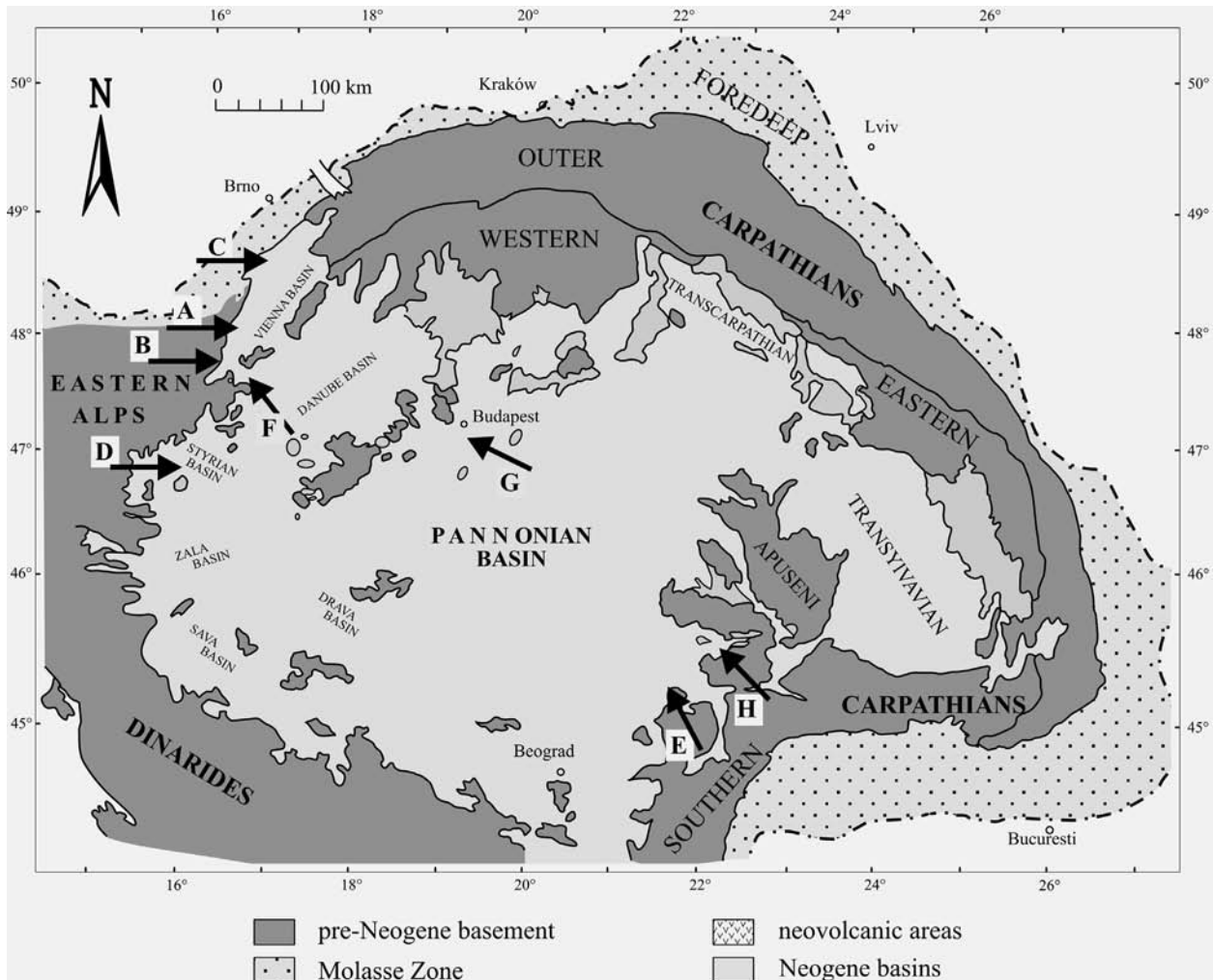
One specimen from the material belonging to the A. E. REUSS collection, labelled as sample 0112 in the REUSS ostracod collection at the Natural History Museum in Vienna originates probably from the type locality, which is given by this author (REUSS 1850: 52) as “Tegel zwischen Atzgersdorf und Altmannsdorf”. This site belongs to the 12th district of the city of Vienna today.

The most abundant sample of *H. auriculata* comes from the site Stavěšice (Czech Republic; Vienna Basin, in homogeneous, calcareous silt with lenses of bivalve *Mytilopsis* and gastropod *Melanopsis* dated as Pannonian B, *Mytilopsis ornithopsis* Zone, and labelled as the sample 9 (R.P.). The material will be housed in the collection of the Department of Geology & Palaeontology of the Landesmuseum Joanneum.

From the Styria Basin one of us (M.G.) collected material at Eisengraben near Feldbach (Pannonian “B”, *Mytilopsis ornithopsis* Zone; GROSS 2003) and at Unterbuchberg near Fürstenfeld (Pannonian “C”, *Mytilopsis hoernesii* Zone; KOLLMANN 1965). In both samples the number of juveniles dominated. Here are studied two adult valves from the former site and one from the latter. The material is stored in the collection

Tab. 1. Location of the investigated ostracod valves.

Taxa	Localities	Material (studied valves)
<i>Hungarocypris madarászi</i>	Dorflacke, Seewinkel N 47°43'36" / E 16°58'13"	1
<i>Herpetocyrella auriculata</i> (<i>H.a.</i>)	Sankt Margarethen N 47°45'48" / E 16°37'50"	14
<i>H.a.</i>	Drassburg N 47°44'41" / E 16°29'15"	8
<i>H.a.</i>	Atzgersdorf/Altmannsdorf (Vienna, 12th District)	1
<i>H.a.</i>	Eisengraben N 46°56'32" / E 15°51'54"	21
<i>H.a.</i>	Unterbuchberg N 47°03'34" / E 16°01'27"	22
<i>H.a.</i>	Stavěšice N 48°59'15" / E 17°02'11"	142
<i>Herpetocyrella hieroglyphica</i>	Soceni, Turislav Valley N 45°22'21" / E 21°57'07"	2



Text-fig. 1. Location map of studied ostracod material (after Kováč 2000): A–Vienna: Atzgersdorf-Altmanndorf; B–Burgenland: Sankt Margarethen, Drassburg; C–Stavšice; D–Styria Basin: Unterbuchberg, Eisengraben, Mataschen*; E–Banat: Soceni; F–Sopron*; G–Budapest*; H–Banat: Grosi* (data used only for discussion - *).

of the Department of Geology & Palaeontology of the Landesmuseum Joanneum.

In September 2006 we sampled outcrops in the Turislaw Valley at Soceni (Banat, Romania; Pannonian "D", M. HARTZHAUSER pers. comm.) from where E. JEKELIUS described his well-known mollusc fauna (JEKELIUS 1944). One has to note that only two specimens, one adult and one juvenile valve, were found here. These valves will be deposited in the collection of Department of Geology & Palaeontology of the Landesmuseum Joanneum.

H. mongolica from Lake Issyk-Kul, Kyrgyzstan, was studied from the photographs published by KRSTIĆ (2006: 357, Plate 62, Figs. 8, 9), which were digitised and further morphometrically analysed, like the specimens of REUSS and MÉHES. The valves belong to a Recent specimen collected by E. SCHORNIKOV. We analysed also the figures published by BRONSHTEIN (1947).

Most of the valves used for this study were photographed with a DS-5M Nikon digital camera fitted to a transmitted light microscope Nikon E-200. The microphotographs were further stored as tiff-files in an Eclipse data-bank using Eclipse-

net software version 1.20, developed by Laboratory Imaging s.r.o. Nikon Europe B.V. The valves examined at the Natural History Museum Vienna were photographed with a Zeiss stereo-microscope Stereo-discovery V 20 and stored on CD as tiff files. Further on the valves were processed for the digital outline production using the tps-dig software (ROHLF 2003), under a protocol described in the Morphomatica User-manual (BRAUNEIS et al. 2006). The geometric morphometric analysis of the outlines was performed using Linhart's B-spline algorithm computed with MORPHOMATICA software, version 1.6.0 (BRAUNEIS et al. 2006). This procedure allows one to evaluate the area deviation between two superimposed outlines for the amount of disparity of the total shape (NEUBAUER 2007). Outlines comparisons for shape were done in both "non-normalised" and "normalised" for total areas subroutines. A virtual mean outline (consensus shape) was computed from the data of individual outlines for various series of specimens, e.g. adults of Sankt Margarethen layer 16 or the Stavšice layer 9, series of adult and juvenile stages. For rapid recognition of the superimposed outlines, we use the vectors at the important control points, which inform on the relative morphological

differences between outline segments (cf. IEPURE et al. 2007). Additional information on the geometric morphometric approach of B-splines used for ostracod valves are published in BALTANÁS et al. (2003), MINATI et al. (2008), DANIELOPOL et al. (2008).

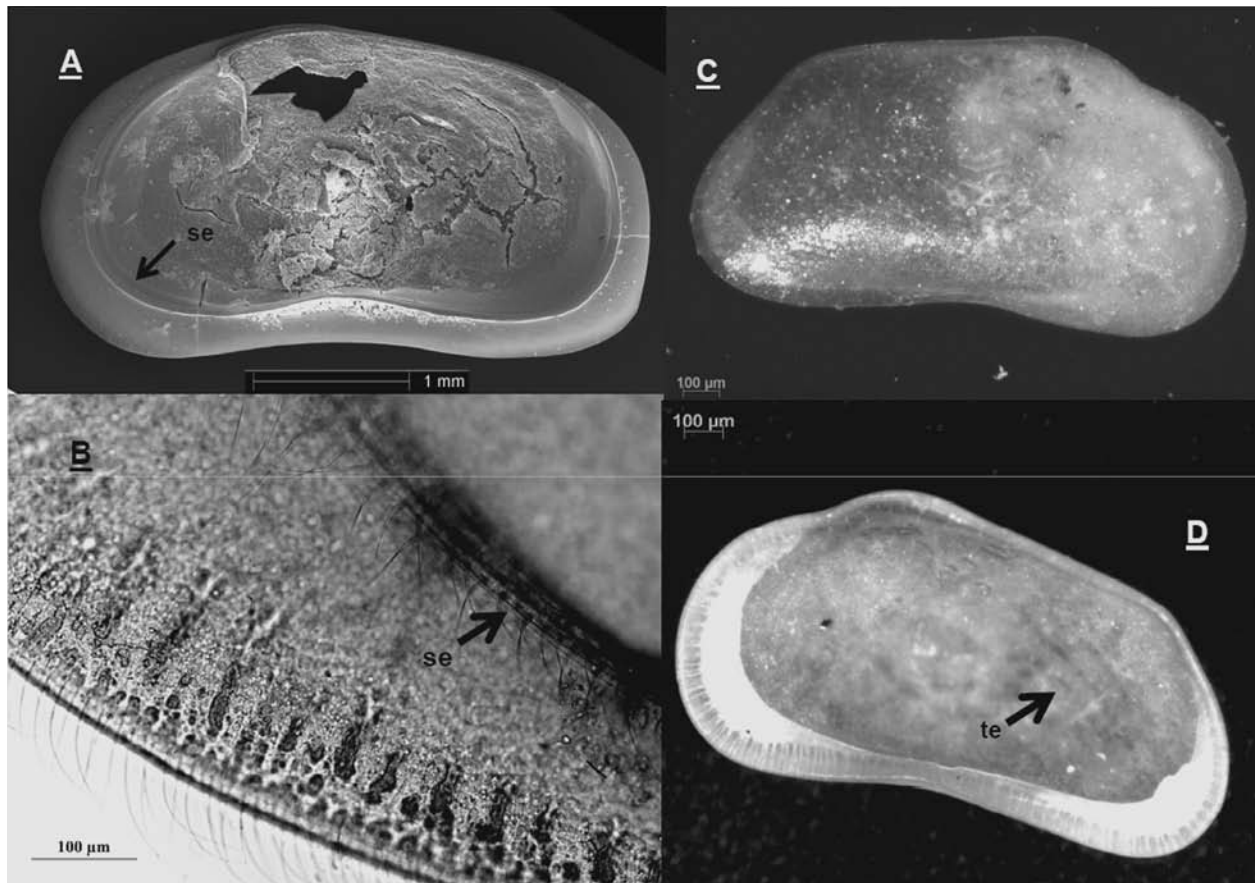
Beside basic statistics (arithmetic mean, standard deviation of the mean, coefficient of variation) calculated with the statistics program BIOMstat 3.3 (ROHLF 2002), we used multivariate analyses performed on pairwise dissimilarities matrix obtained in MORPHOMATICA (BRAUNEIS et al. 2006). Non-metric multidimensional scaling (N-MDS), and hierarchical clustering with group-average linking based on pairwise outline dissimilarities were performed with the PRIMER 6 package (CLARKE & GORLEY 2006).

Comparative morphology of *Hungarocypris madarászi* (ÖRLEY, 1886), *Herpetocyprilla mongolica* DADAY, 1909 and the “*Hungarocypris*” species of Lake Pannon

The genus *Hungarocypris*, as commonly defined by neontologists, is a remarkable cypridid group having on the furca (uropodal ramus) two posterior setae, whereas most of non-marine

cypridids have one seta. Based on this peculiarity VÁVRA (1906) proposed this genus. Later on this morphological trait was used for elevating the taxon to the subfamily level *Hungarocypridinae* BRONSHTEIN, 1947 (cf. MEISCH 2000). Likewise DADAY (1909) based the genus *Herpetocyprilla* on a remarkable trait of the second antenna, respectively the lack of the distal natatory setae of the first endopodial segment. This is unique within the family Cyprididae. Hence, this genus was elevated to the subfamily rank, *Herpetocyprillinae* BRONSHTEIN, 1947 subsequently (HARTMANN & PURI 1974). For palaeontologists these morphological criteria are useless and therefore we have to see why and how the large cypridoid species occurring in the Lake Pannon were assigned to the genus *Hungarocypris* (e.g. KRSTIĆ 1967, 1973/1974, OLTEANU 1971, SOKAČ 1972, JIŘIČEK 1985; GROSS 2004). There is only one exception to this opinion, that of MANDELSHTAM & SHNEIDER (1963), who attributed the Pannonian ostracod *H. auriculata* to the genus *Herpetocyprilla*.

KRSTIĆ (1967) pointed out that the large cypridids with asymmetric valves and generally subrectangular valves occurring in Lake Pannon resemble the living species *H. madarászi*. In a subsequent publication, KRSTIĆ (1973/1974) compared the marginal structure of the inner side of the valves of two Pannonian species (*Eucypris auriculata* (REUSS, 1850), *Amplocypris pannonica* ZALÁNY, 1959), with those of *H. madarászi*



Text-fig. 2. A–B: *Hungarocypris madarászi*, Dorfacke, Seewinkel; A–right valve A-1 juvenile, inner view; B–adult female, anteroventral detail, inner view; C–D: *Herpetocyprilla auriculata*, right valve; C–Atzgersdorf-Altmanndorf, coll. A. Reuss, slide 0112, NHM-W; outer view; D–Drassburg, coll. K. Kollmann, slide 0226, NHM-W, inner view, male (arrows point to: se–selvage, te–traces of spermatic tubes; NHMW–Naturhistorisches Museum Wien, Department of Geology & Palaeontology).

and the eucypridid *Prionocypris zenkeri* (CHYZER & TOTH, 1858). The more or less digitiform structure of the anteroventral side of the inner lamella and the marginal branched canals visible in the case of *A. pannonica* were in KRSTIĆ’s opinion (op. cit.) similar to those of *H. madarászi* and different from those of *P. zenkeri*. From this reason, KRSTIĆ decided that the large Pannonian species fit best the genus *Hungarocypris*.

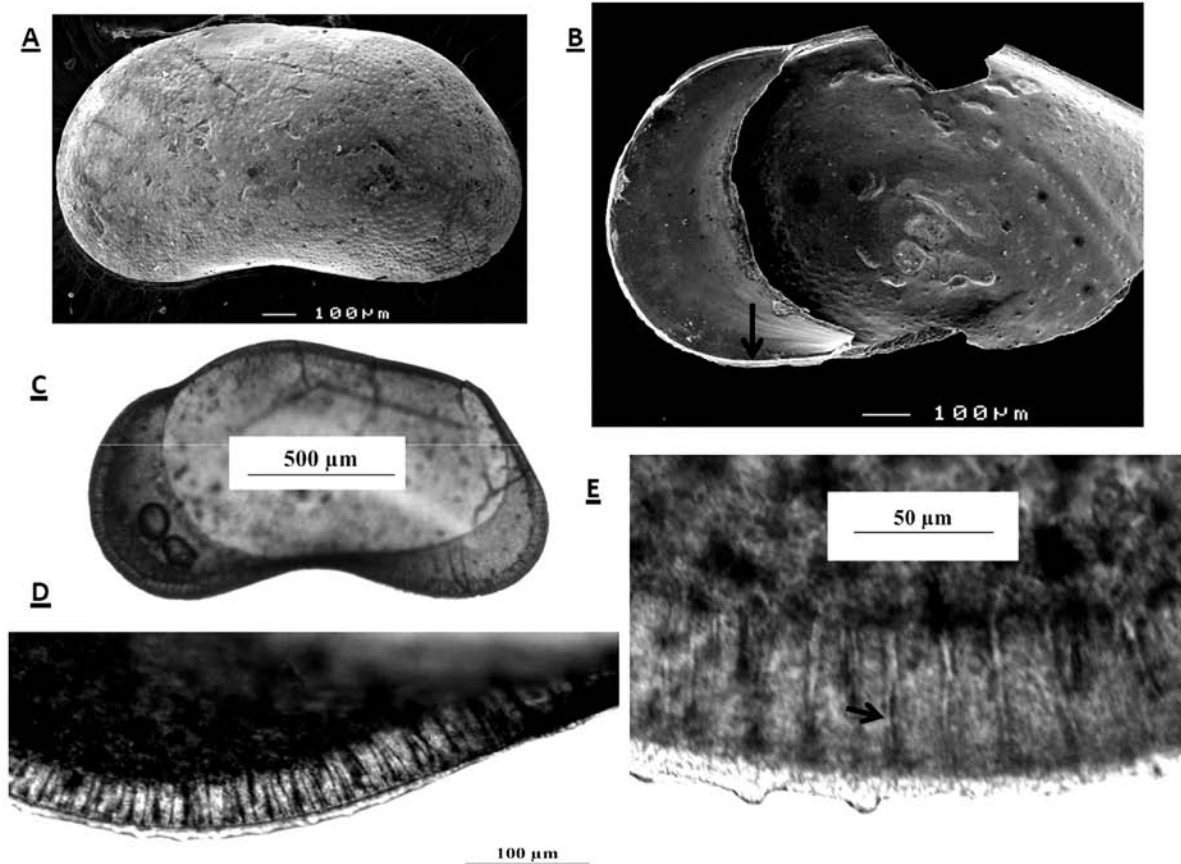
Examination of the inner valve details of the largest European species *H. madarászi* documents that KRSTIĆ overlooked important details of this species. The selvage is very peculiar (Text-fig. 2A), very prominent, being a continuous structure from the upper anterior side of the valve to its posterior part. This selvage is placed far away from the external valve margin and runs parallel to the outer margin. This remarkable structure is visible in *H. asymmetricus* too (VICTOR & FERNANDO 1981: 146-147, figs 4-7). More over the marginal fused zone of *H. madarászi* is very reduced and traversed by short simple canals (Text-fig. 2B). Only the inner lamella is digitiform and connected to the outer lamella by dark island-shaped structures (Text-fig. 2B), which does not exist in the Pannonian “*Hungarocypris*”.

The Pannonian species “*H. auriculata*” has a very poorly developed selvage, practically not visible, which runs closely to the outer margin (Text-figs. 3 B-E). The valves of the adults have a wider fused marginal zone with dense marginal

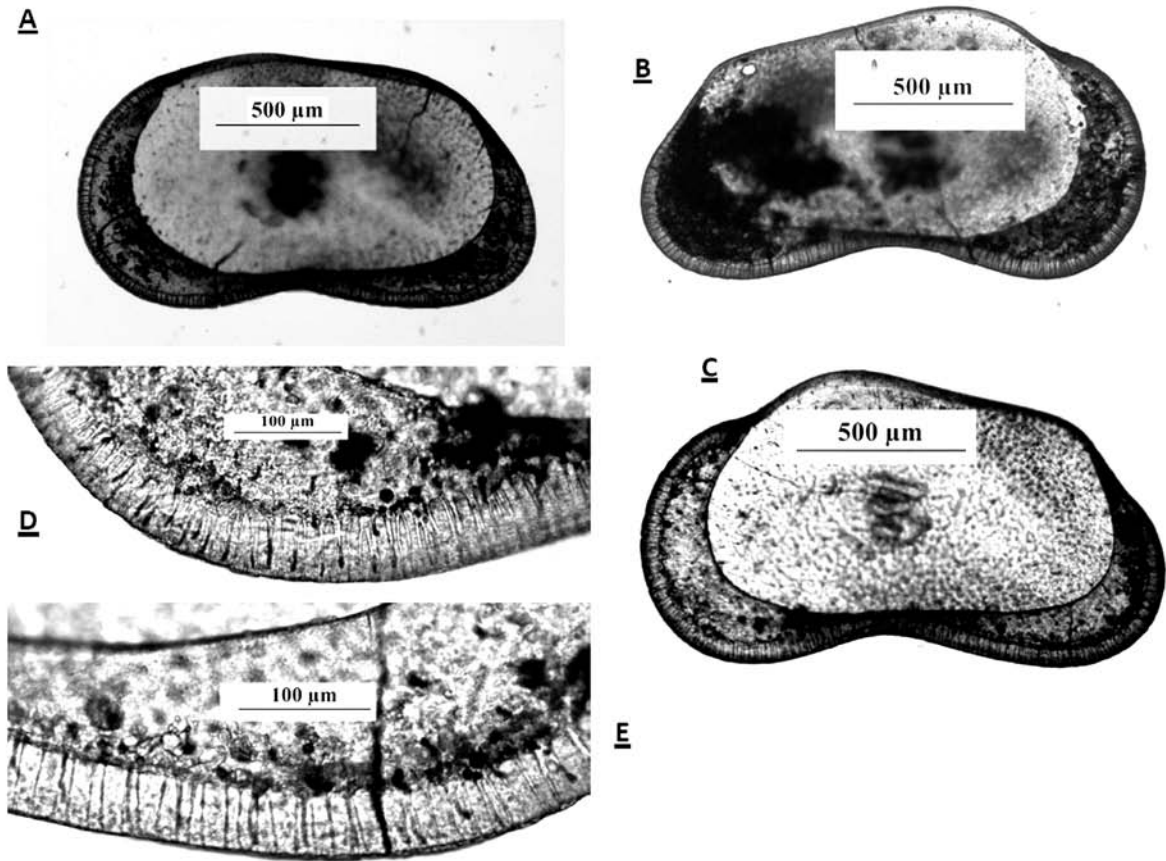
canals, some are furcated (Text-figs. 2D, 3E, 4 D-E). These latter morphological characters are not visible in the last juvenile stage (A-1), where the fused zone is reduced and the marginal canals are short and unbranched (Text-fig. 10C).

H. mongolica has a poorly developed selvage, practically not visible; the marginal fused zone is large and traversed by long canals (BRONSHTEIN 1947). These aspects are visible on the photographed valves published by KRSTIĆ (2006: plate 52, figs 7, 8). In this respect, they differ markedly from the details described above from *H. madarászi*.

The Pannonian “*Hungarocypris*” display valves with a shape and size very similar to those of *H. mongolica*. The length of the valves varies between 1.5 and 2 mm like *H. mongolica* (cf. BRONSHTEIN 1947); this is markedly different from the valves of *H. madarászi*, which are longer than 3 mm (Text-fig. 2A). Both Pannonian “*Hungarocypris*” and *H. mongolica* display asymmetrical valves, the left one is smaller and more rounded than the right valve (BRONSHTEIN 1947, KRSTIĆ 2006). In *H. madarászi*, at least the male has larger and more angular left valves. When the valves of “*H. auriculata*” are superimposed on those of *H. mongolica* (Text-figs. 5A-B) we noticed a good fit between both species. From the data and the argumentation presented above we propose, as a phylogenetical hypothesis (we use this term with the connotation given by BAUM 1998, HEY et al. 2003), to consider the Pannonian “*Hungarocypris*”



Text-fig. 3. A–E: *Herpetocyprilla auriculata*, Sankt Margarethen; A–left valve, outer view; B–E–right valves, inner view: B–male (cf. traces of spermatic tubes); C–female, inner view; D–anteroventral detail; E–postero-ventral detail (arrow point to a bifid marginal pore canal).



Text-fig. 4. A–E: *Herpetocyrella auriculata*, Stavěšice, female; A–left valve, inner view; B–E—two right valves; B—general view valve 1, outer side; C–E—valve 2, inner side; C–D—anteroventral detail; E—postero-ventral detail.

members of the genus *Herpetocyrella* DADAY. Hence, this taxonomic transfer will affect the nomenclature used through this paper.

Description of *Herpetocyrella auriculata* (REUSS, 1850) and consideration on the validity of *Herpetocyrella hieroglyphica* (MÉHES, 1907)

The original description of *H. auriculata* is very poor. It took more than 100 years until KRSTIĆ (1960) briefly mentioned it again. REUSS (op. cit.) placed this species in the genus *Cytherina*. His material originated from several localities. The first two mentioned are relevant for our study, unnamed place between Atzgersdorf and Altmannsdorf, today in Vienna and Sopron, Hungary. MÉHES (1907) studied ostracods from Sopron and mentioned that he could not recognise *C. auriculata*. Due to this fact, MÉHES (op. cit.) described *H. auriculata* under the names: *Candona sieberi* n. sp., *Candona sieberi* var. *nodosa* n. var. and *Iliocypris gracilis* n. sp. It took again more than 50 years until ostracodologists recognised that the species of MÉHES were synonyms of the REUSS' *auriculata* (SOKAČ 1972).

It is still of relevance to understand what was the material described and figured by REUSS and MÉHES. Are we dealing

with one widely distributed and morphologically plastic species or with a cluster of closely related species? In the following, we will try to answer these questions through a comparative analysis of the original figures of these two authors compared with our own data.

General traits of *H. auriculata*: Valves of asymmetric shape, left one more rounded than the right one, which has a biangular dorsal side (Text-figs. 2 C, D, 3 A, C, 4 A–C, 10 D, E). The length of the valves varies between 1.4–1.7 mm with mean value 1.6 mm; right valve slightly longer than the left valve (Tab. 2). Anterior and posterior margins with fused zone traversed by simple and/or branched long marginal pore canals (Text-figs 2D, 3D, E, 4D, E); posterior outer margin seldom with small denticles of variable number and size (Text-fig. 3E) surface of the valve covered by fossae.

The initial descriptions of *H. auriculata*: Did REUSS (1850) and MÉHES (1907) recognise the adults of this species or are their descriptions based on juvenile specimens? To answer this question we digitised the outline of the REUSS' figure 8a on plate 3 and superimposed it on the A-1 juvenile mean outline from Stavěšice (Text-fig. 6A). One notices that shape and size match rather well hence one can say that REUSS used juveniles for his new species *auriculata*. We supposed that the same situation applies to MÉHES' original description too. To test for this hypothesis we compared an A-1 juvenile valve from Sankt Margarethen with the mean outline of the

Tab. 2. *Herpetocyrella auriculata*, Stavěšice – Length of the valves from the adult to the A-4 juvenile stage (arithmetic mean and standard deviation in microns); L, R–left and right valves; n–number of valves; SD–standard deviation; CV–coefficient of variation.

Stage	Adult		A-1		A-2		A-3		A-4	
Valve	LV	RV	LV	RV	LV	RV	LV	RV	LV	RV
n	19	21	12	8	6	26	16	18	9	7
Mean (µm)	1584	1609	1245	1265	994	989	773	752	606	606
± S.D.	52	57	42	47	28	27	18	15	17	15
CV	3.27	3.56	3.39	3.72	2.86	2.75	2.33	2.03	2.77	2.41

A-1 from Stavěšice and with those from MÉHES' publication (*C. sieberi*). Text-figs. 6 A-C demonstrate that they are similar in size and shape. Therefore, in this case we deal with an A-1 juvenile too, respectively MÉHES did not recognised the adult of this species.

We found in the REUSS collection an adult right valve (Text-fig. 2C), which we wanted to know if it closely resembles those of the other adults belonging to populations like those from Sankt Margarethen and Drassburg. Text-fig. 2D shows a good superposition between the REUSS specimen and the mean shape of the adult valves from Sankt Margarethen. However, we noticed differences in the ventral part of the outline that we hypothesized that could be due to a sexual dimorphism. This aspect was unknown until now.

Sexual dimorphism of *H. auriculata* valves: On the Text-figs. 2D, 3B and 10D one can distinguish the imprints of the testes tubes (= seminiferous tubules) in right and left male valves. Females are recognizable due to the ovary imprints (Text-figs. 3C, 4A, 4C, 10E). Further, we superimposed the outline of some of these valves or mean of outlines. Text-figs. 5D, 7C, 7D show that the male valve is more elongated in the posteroventral side, while the female for the same area is more rounded. If we turn back to the REUSS' adult valve and we superpose it on the outline of the male valve from Drassburg (Text-figs. 7A, 7B), one notices the close similarity, especially in the standardised mode. Hence, one has a good reference of adult valves for *H. auriculata*. So, the next step is to explore the variability of the adult valves, especially of the right valve, which is used commonly for the identification of herpetocyprid species.

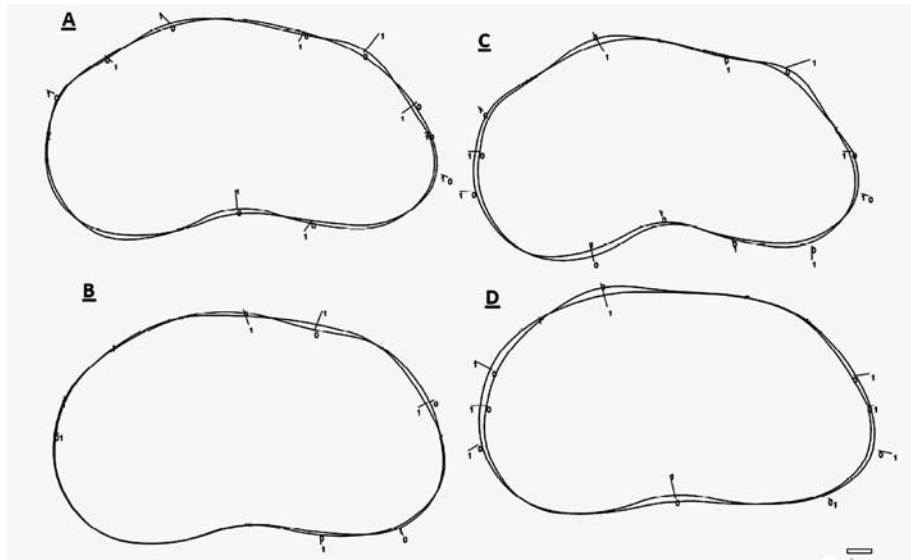
Variability of adult valves in size and shape: We analyse first the length of the valves of the population from Stavěšice (Tab. 2). We note that the right valve displays a higher coefficient of variation than the left one, 3.56 against 3.27. If we compare the size of valves between various sites, we notice the following differences: within the Styrian Basin the valve from Eisengraben is very large (length = 1.65 mm), while those from Unterbuchberg are smaller than the mean value (length = 1.47 mm). The largest valve measured comes from Stavěšice (length = 1.71 mm). The REUSS' valve (a male) measures 1.56 mm, much similar to the values of the valves from Sankt Margarethen and Drassburg (1.54–1.60 mm). Text-fig. 9C is a N-MDS plot for the disparity data in non-standardized for size mode. It demonstrates the wide variability of the Stavěšice population and the extreme position of the Unterbuchberg valve.

The shape variability of valves is also important within the Stavěšice population. Compare for instance the dorsal contour

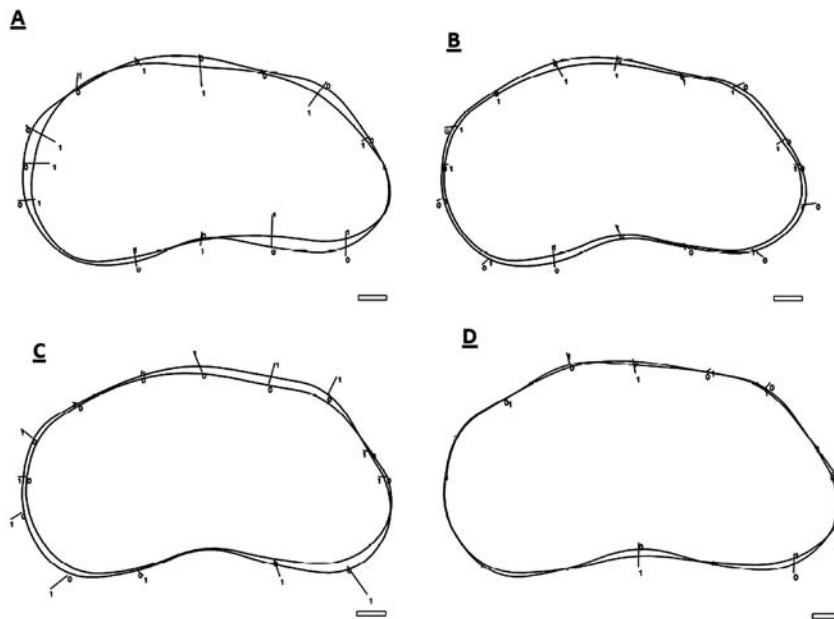
of right valves in Text-figs. 4B, 4C and the same superimposed in standardized for size in Text-fig. 5C. This latter figure shows differences not only in the dorsal part of the valve but also in the antero- and anteroventral sides, a detail that we do not perceive by comparing the previous figures. The N-MDS plot (Text-fig. 5D) gives us a synthetic image of the extent of the shape disparity as well the extent of the variability of the population of Stavěšice and those of Sankt Margarethen; there is no visible morphological separation between them. Hence, these data stress out the wide variability of *H. auriculata* and its wide geographical distribution.

Growth of valves and developmental trajectory of valve-shapes: Text-figs. 8A, 8B document the growth and the change of shape for left and right valves. We note a gradual increase of size from the A-4 juvenile stage to the adult one and this is additionally, well represented in Tab. 2. We note in this latter that the left and right valves in the A-4 juvenile stage have similar mean sizes, while with each molt up to the adult one we assist to a slightly stronger growth of the right valve as compared to the left one. This causes the asymmetry between the valves mentioned previously. If we standardise for size the outlines of the 5 stages (from A-4 to the adult), we note that the differences in shape are minimal between the A-1 and the adult valves and more important between A-4 and A-3 ones. This is visible optically by superimposition of outlines (Text-figs. 8C, 8D) as well as in a N-MDS plot when one looks to the distance between the points representing the disparity range of the different stages (Text-figs. 9A). An interesting aspect comes out when we examine the change of shapes in Text-figs. 8A, 8B and in the group-average dendrogram of the Text-fig. 9B based on the pair-wise dissimilarities between the mean shapes of the left and right valves for the five stages. We note that left and right valves in the A-4 stage are very similar, while in the more advanced stages valves become more dissimilar and therefore cluster differently (A-1 - Adult and A-2–A-3 cluster as couples of left or right valves).

Morphological differences between *H. auriculata* and *H. hieroglyphica*: MÉHES (1907) described *H. hieroglyphica* for specimens who were larger than those named *Candona sieberi* and had more prominent anterior and posterior marginal denticles. He attributed this species to the genus *Cypris* O. F. MÜLLER, 1776 and noted that in his sample occur valves with two different lengths, 1.95 mm and 1.55 mm. He considered the larger ones as males and the smaller ones, as females. *C. sieberi*, that we showed and that represents an A-1 juvenile of *H. auriculata* had a length of 1.36 mm (MÉHES 1907). The two characteristics mentioned by MÉHES for *H. hieroglyphica*, the large size of the valves and the prominent marginal denticles



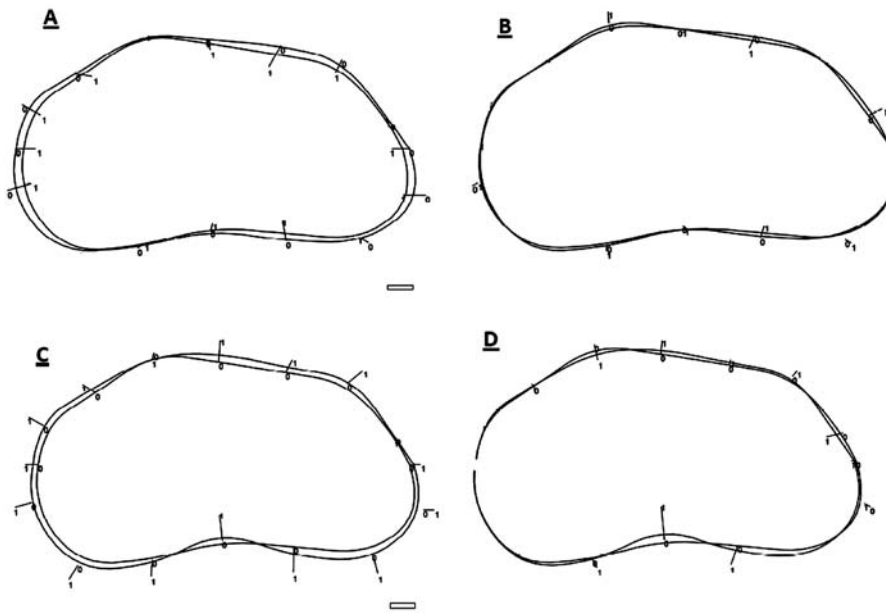
Text-fig. 5. Superimposition of outlines in standardised (A–C) and non-standardised (D) modes: A, C – right valves; B, D – left valves; A–B: *H. auriculata*, Stavěšice, mean shape outline (1) on *H. mongolica* (0); C – two superimposed outlines of *H. auriculata*, Stavěšice; D – superimposed left valves of *H. auriculata*, Stavěšice, female (1) on male (0) (scale bar – 0.1 mm; outlines of *H. mongolica* from KRSTIĆ 2006: 357, Pl. 62, Figs. 8, 9).



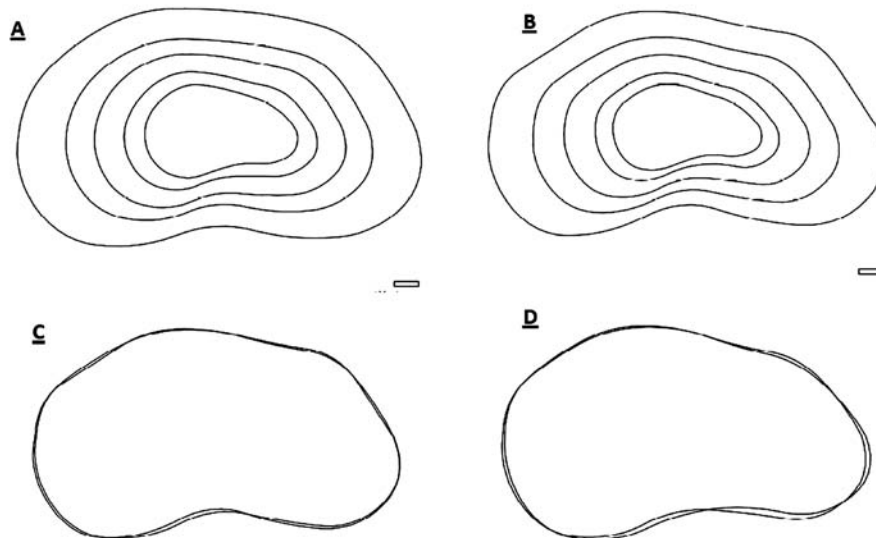
Text-fig. 6. Superimposition of outlines, *H. auriculata* right valves, in non-standardised mode: A – A-1 outline of REUSS 1850, Pl. 3, Fig. 8a (1) on Stavěšice A-1 mean shape outline (0); B – A-1 Sankt Margarethen (1) on A-1 Stavěšice mean shape outline (0); C – outline of MÉNES 1907, Pl. 5, Fig. 21 (1) on A-1 Sankt Margarethen (0); D – adult valve Atzgersdorf-Altmanndorf (1) on mean shape outline Sankt Margarethen (0); (scale bars – 0.1 mm).

remain until the present-day the diagnostic traits for this species. One of us (R.O.) could confirm the validity of these traits in his material from Groși (Banat), where the valves have a size of 1.87–1.98 mm and are denticulate (OLTEANU 1971). We analysed two right valves (Text-figs. 10A, 10B) from Turislav Valley, at Soceni (Banat), in order to look for possible new diagnostic traits, which should better define *H. hieroglyphica*. Looking to the extension of the marginal fused zone and at the

shape and length of the marginal canals, we can say that the large valve is an adult while the smaller one is an A-1 juvenile. Apparently, when we compare Text-figs. 4B, 4C with 10A, the former coming from Stavěšice, we immediately notice that the dorsal part of the valves is different. Thus, the form of this valve area could be used for diagnosing herpetocyprid species. In Text-fig. 11A the two Turislav valves are superimposed in non-standardized mode on the mean outline of the adult from



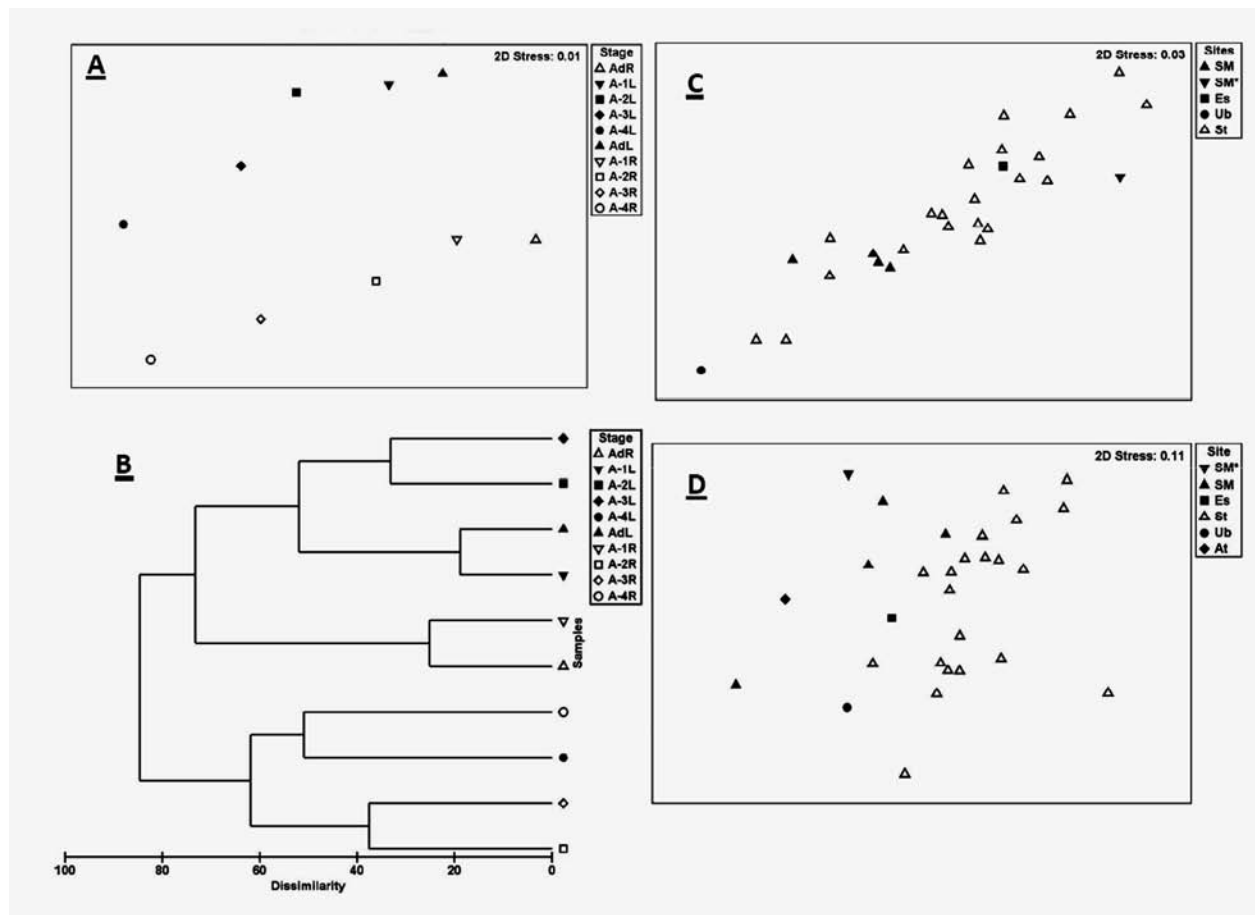
Text-fig. 7. Superimposition of outlines, *H. auriculata* right adult valves, in no-standardised (A, C) and standardised (B, D) modes: A, B—Drassburg, male (1) on Atzgersdorf-Altmanndorf valve (0); C, D—Stavěšice, female (1) on male (0); (scale bars—0.1 mm).



Text-fig. 8. Superimposition of outlines, *H. auriculata*, Stavěšice, in non-standardised (A, B) and standardised (C, D) modes: A - left valves; B—right valves; A—B: female mean outlines from A-4 (inner outline) to adult; C—A-1 on adult; D—A-4 on A-3; (scale bars—0.1 mm).

Sankt Margarethen. We notice the close fit of the smaller valve when compared with the adult of Sankt Margarethen and the large difference of the adult Turislav valve compared to reference (Sankt Margarethen). When we superimpose the outline of the large (2.03 mm length) Turislav valve on the mean outline shape of the Sankt Margarethen (Text-fig. 11B) we note again a good fit. The same can be seen for the standardised shapes of the large and small standardised valves of Turislav (Text-fig. 11C) and the mean outline shape of the ostracods

from Sankt Margarethen and Stavěšice (Text-fig. 11D). From this permutation of outlines we conclude that the shape of *H. hieroglyphica*, which initially appeared quite different from those of *H. auriculata*, does not represent a valid discriminant trait. The same applies for the marginal denticles. We found in various populations individuals with and without denticles. Therefore, *H. hieroglyphica* as compared to *H. auriculata* remains poorly defined. But, still it is a valid species through its difference in size when compared to *H. auriculata*.



Text-fig. 9. *H. auriculata*: A–B: Stavěšice, developmental trajectory of the ostracod shape (mean outlines) from the A-4 to the adult stage, for the left (L) and right valves (R) in standardised mode; A – N-MDS plot; B – Hierarchical clustering with group-average linking dendrogram; C–D: N-MDS plots, disparity right valves, adult females, in non-standardised (C) and standardised (D) modes; (SM–Sankt Margarethen, St–Stavěšice, Es–Eisengraben, Ub –Unterbuchberg).

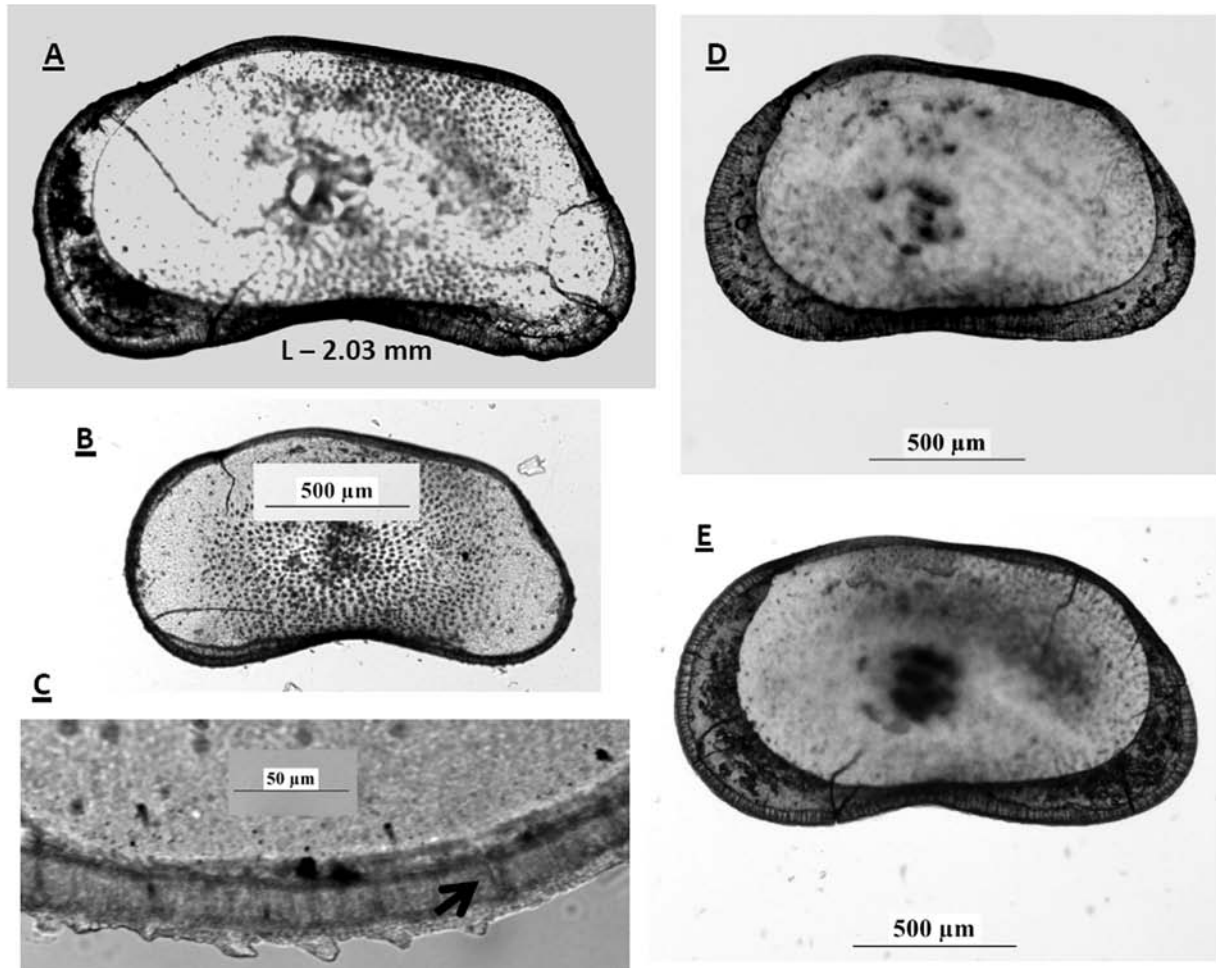
Discussion and conclusion

The most interesting morphological characteristics of fossil *Herpetocyrella* we noticed are the peculiar developmental trajectory of the valve shapes and the sexual dimorphism. There is practically a very slight development of the valve shape between the A-1 and the adult stages in *H. auriculata* and *H. hieroglyphica* when the valves are standardised for size. The shape of the valves in species like *Candona neglecta* SARS, 1887, *Candona candida* (O.F. MÜLLER, 1776), *Eucypris virens* (JURINE, 1820), become more rounded posteriorly after the last moult, (BALTANÁS et al. 2000, DANIELOPOL et al. 2008). The developmental type of *H. auriculata* for the valve shape resemble those of *Cytherissa lacustris* (SARS, 1863), where in the last two stages the shape change minimally too (cf. DANIELOPOL et al. 2008). The sexual dimorphism of the adult right valve of *H. auriculata* with a more rounded ventroposterior outline in the female is also unusual compared to species like *C. neglecta* (HORNE et al. 1998). There is practically no difference in the lengths of female and male valves. Generally, the male with its large male copulatory complex displays larger valves and a more rounded outline in the ventroposterior part of the valves. These peculiar morphological aspects could become additional criteria for the

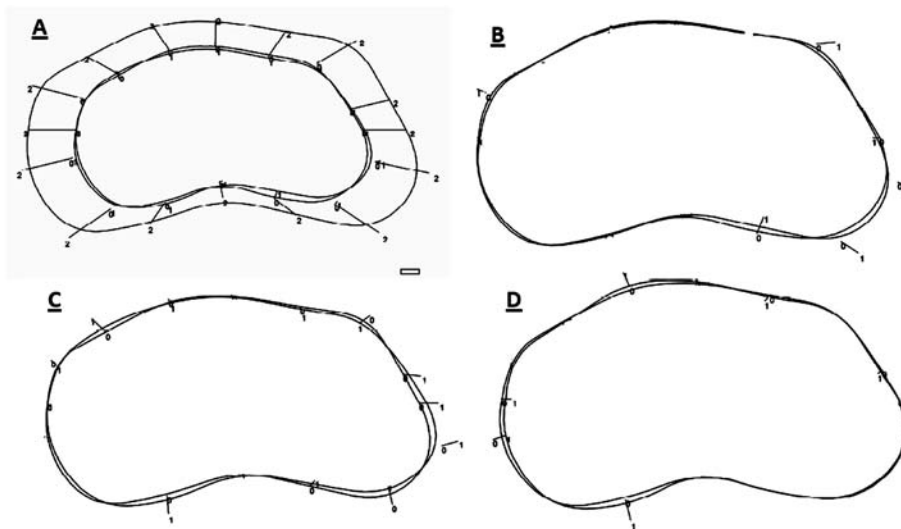
definition of the subfamily Herpetocyrellinae, besides the lack of swimming setae on the second antenna on which this supra-generic taxon was mainly proposed (BRONSHTEIN 1947).

The systematics of Lake Pannon *Herpetocyrella* is also remarkable: *H. auriculata* was described using juvenile stages in various ways (REUSS 1850, MÉHES 1907). This could be the case also for other taxa with small valve sizes (less than 1.5 mm length), now included in this genus respectively, *Herpetocyrella sinkjangia* MANDELSHTAM, 1963, *Herpetocyrella tuberculoalveolata* MANDELSHTAM, 1963 and *Herpetocyrella cornuta* KRSTIĆ, 2006 (MANDELSHTAM & SHNEIDER 1963, KRSTIĆ 2006). The criteria that were used to define the fossil species of *Herpetocyrella* are much reduced as we saw here with *H. hieroglyphica*. Size differences certainly represent an acceptable criterion used also for other species. *Dolerocypris fasciata* (O.F. MÜLLER, 1776) differs from *Dolerocypris sinensis* (SARS, 1903) by the length of their carapaces (MEISCH 2000).

The *Herpetocyrella* valves in the samples we investigated and also published material (e.g. OLTEANU 1971, GROSS 2004), are dominated by juveniles. Only in few cases, as in the Stavěšice sample, we found besides juveniles many adult specimens. This situation could be due to the fact that the valves are not autochthonous. The original habitats of the *Her-*



Text-fig. 10. A–C: *Herpetocyrella hieroglyphica*, Soceni - Turislav Valley, right valves, inner view; A–adult; B–A-1; C–posteroventral detail of A-1 (arrow points to the reduced fused zone and the short simple marginal canal); D–E *H. auriculata*, Stavěšice, left valves; D–male (cf. traces of testes tubes); E–female.



Text-fig. 11. Superimposition of outlines, right valves of *H. auriculata* and *H. hieroglyphica*, in non-standardised (A) and standardised (B–D) modes: A–*H. hieroglyphica*, Soceni - Turislav Valley, A-1 juvenile (1) and adult female (2) on *H. auriculata* female mean adult outline, Sankt Margarethen (0); B–*H. hieroglyphica* adult, female (1) on *H. auriculata*, female mean adult outline, Sankt Margarethen (0); C–*H. hieroglyphica* Soceni–Turislav Valley A-1 (1) on adult female (0); D–*H. auriculata*, adult female mean outlines, Stavěšice, (1) on Sankt Margarethen (0) (scale bar–0.1 mm).

herpetocyrella species could be shallow inland waters from where living animals or valves were transported into Lake Pannon. Therefore, if our hypothesis is correct, there are low chances to find fossilized material in the true habitats of those species. This hypothetical scenario is enforced by the existence of two fossil *Herpetocyrella* species mentioned by MANDELSHTAM & SHNEIDER (1963) as occurring in freshwater Pliocene deposits, in the Tyan-Shan depression and in Kirghizia. However, it is not corroborated by our experience (R.P.) and the published Ostracoda data from various palaeolimnic systems (cf. CARBONNEL 1969, CARBONNEL & RITZKOVSKI 1969, CARBONNEL et al. 1985, OLTEANU 1989, 1995, JANZ 1992, WITT 1999, 2000, GLIOZZI et al. 2007) nor it was found in the estuarine facies of the Central Paratethys (PIPIK et al. 2004, PIPIK & BODERGAT 2004). *H. auriculata* appears suddenly in the brackish ostracod associations of Lake Pannon, in the early phase of this lake (R.P.). One of us (R.O.) found valves of this species at Soceni and in the Mehădia Basin, Banat (Romania), in deposits dated as Sarmatian. Therefore, we accept also the idea that herpetocyrellids could live, respectively tolerate saline water, and form autochthonous populations, documented in Lake Pannon, during the so-called Phase 1 (sensu HARZHAUSER & MANDIĆ 2008), in many places (cf. information presented in previous sections on *H. auriculata* and *H. hieroglyphica*). The rich population of Stavěšice with many juveniles and adults would be an additional argument for this view. Note that *H. mongolica* was repeatedly found in the saline Lake Issyk-Kul (cf. BRONSHTEIN 1947, SCHORNIKOV pers. comm. to D.L.D.). Lake Issyk-Kul seems to be an ancient lake (RICKETTS et al. 2001). Therefore, a stepping-stone migration of herpetocyrellids from Lake Pannon eastwards reaching finally Issyk-Kul should be also possible. Such cases were documented for various cytheroid groups (PIPIK 2007). Hence, we propose as alternatives to the (palaeo-)biogeographical model of VICTOR & FERNANDO (1981) two possible scenarios. (1) Herpetocyrellids could colonise from inland waters of the Palearctic independently saline limnic systems like Lake Pannon and Lake Issyk-Kul during the Neogene. (2) Herpetocyrellids from Lake Pannon spread eastwards in the early phase of the lake formation through a stepping-stone process and without the need to change their halophilic specialisation. This latter scenario differs from those of VICTOR & FERNANDO (1981) in which one needs to postulate a spread of the ostracods eastwards after their adaptation to freshwater environment.

In conclusion, for the near future we propose to further look for sampling sites with rich populations of fossil Pannonian *Herpetocyrella* in order to better delineate their morphological variability, to look for new morphological traits, which could better discriminate these populations and eventually to improve the systematics of this ostracod group. Moreover, it will be necessary to understand better the palaeoecological environment, the palaeosalinity and the chemical composition, under which those herpetocyrellids lived.

In order to better understand the origin and evolution of the Pannonian herpetocyrellids one should look to ostracod groups existing in Asia, Africa or Australia, which display analogies in general valve morphology and/or (palaeo)ecological distribution. We have for instance detailed data on the morphology and systematics for the giant ostracod group Mytilocyprini DE DECKKER 1974 (HALSE & MCRAE 2004). Two species belonging to *Australocypris bennetti* HALSE & MCRAE,

2004 and *Australocypris beaumonti* HALSE & MCRAE, 2004 display superficial similarities of the valve shapes with the Pannonian *Herpetocyrella*. We have also information on the (palaeo)ecology of Australian ostracods from shallow saline water-bodies (cf. DE DECKKER 1982, MARTENS 1985). This type of information should be further used for comparative studies with our Pannonian cypridids.

Finally, we want to stress that geometric morphometrics combined with multivariate statistics is a powerful method to compare valves and to observe subtle morphological differences of shape that otherwise would remain unnoticed. Following this way, we hope to arrive to use herpetocyrellids not only for palaeoecological reconstructions but also for biostratigraphical purposes, an idea already foreseen by the pioneer of the Upper Miocene Lake Pannon stratigraphy, Professor A. PAPP (PAPP & TURNOVSKY 1950).

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