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Redefinition of the Genus *Typhlocypris* Vejdovský, 1882 (Ostracoda, Candonidae)

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Abstract

The taxonomy of the genus *Typhlocypris* Vejdovský, 1882 is reviewed. New morphological information on *Typhlocypris eremita* (Vejdovský, 1882), the type species of the genus, is provided, and a new reference material is presented. The generic diagnosis is emended with details derived from the developmental trajectory of the valves, from the juvenile stage A-3 to the adult. Those criteria clearly differentiate *Typhlocypris* from the related genus *Pseudocandona* Kaufmann, 1900. As here redefined, *Typhlocypris* is a phylogenetic lineage of the subfamily Candoninae containing extant species presently living in aquatic subterranean habitats and fossil species recovered from non-marine Late Palaeogene to Neogene and Quaternary deposits in Europe and western Asia. The type species of *Typhlocypris* is considered a metaspecies, taxonomically treated as *T. eremita* (*sensu lato*), which includes populations resembling the newly designated reference material. The homeomorphic triangular valve shape of the Candoninae is discussed. Careful examination of the valve morphology of *Typhlocypris* combined with the analysis of limb traits helps to distinguish representatives of this genus from unrelated phylogenetic groups presenting similar triangularly shaped valves. It is emphasised that for a useful description of *Typhlocypris* taxa both transmitted light and scanning electron microscopy are necessary.

Introduction

Candoninae Kaufmann, 1900 is a very species-rich group, widely distributed in non-marine habitats, especially in the Palaearctic Region. In this zoogeographic domain it is documented by a high number of both fossil and extant taxa (Kempf, 1980a, b, c, d, 1997a, b, c, d; Martens et al., 2008; Martens & Savatienalinton, 2011). Unfortunately, a number of groups of the subfamily, like the genera *Candona* Baird, 1845 and *Pseudocandona* Kaufmann, 1900, are poorly defined and need to be reviewed (Danielopol et al., 2011). Some taxa, like *Typhlocypris* Vejdovský, 1882, were used by ostracodologists in such different ways that

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presently their semantic content has become totally confused (compare *inter alia* the systematics of Candoninae proposed by Krsti & Guan, 2000 with that of Karanovic, 2012). Even worse, it has become practically impossible to use *Pseudocandona* and *Typhlocypris* when dealing with topics of wider interest, e.g., for biogeographic studies at regional or global scales. Therefore ostracodologists (*inter alia* Prof. K. Martens, message on 9 Jan. 2009 to D.L.D. and C.M.) requested taxonomic clarification of such groups.

Recently, for a review of the taxonomy of Candoninae it has been proposed (Danielopol et al., 2011) to re-examine the original diagnoses of critical taxa, the genus *Typhlocypris* included, to look for new criteria in order to better define both the genus- and species-group taxa and to try to harmonise the systematics used by palaeontologists with those of neontologists. The latter ostracodologists are in a better situation to improve critical taxonomies because they could use morphological traits of both the carapace and limbs. In the present study we first present a review of the different ways along which zoologists and palaeontologists integrated the taxonomic position of *Typhlocypris* within the general systematics of Candoninae. We then present new data on the morphology of *T. eremita* (Vejdovský, 1882), the type species of the genus. We point out the inaccuracy of the original description of the type species and therefore great difficulty in using that description as a stable reference for further comparative taxonomic studies. To improve that situation we present information on a new reference material for the type species *T. eremita*. Once solved the problem of the fixation of an objective reference system we will propose new criteria to differentiate the closely related genera *Typhlocypris* and *Pseudocandona*. We continue with the fossil record of *Typhlocypris* taxa and discuss the homeomorphism of the triangular carapace shape within the Candoninae. All this information is then used to present a redefinition of the genus *Typhlocypris*. The present contribution is intended to provide ostracodologists, both neontologists and palaeontologists, a new and sound basis for future research. One should note that this contribution is an expanded version of our communication to the 14th International German Ostracodologists' Meeting in Cologne (11-14 Oct. 2012), which honoured Professor Eugen Kempf (Namiotko et al., 2012).

Taxonomic problems encountered by zoologists

The taxon *Typhlocypris* was introduced by Vejdovský (1882) as a subgenus of the genus *Cypris* O. F. Müller, 1776 for the unique species *Cypris eremita* Vejdovský, 1880. Šoštari (1888) raised the subgenus to the generic rank. Neither Vejdovský (1882) nor Šoštari (1888) presented a diagnosis for the then monotypic (sub)genus *Typhlocypris*. Following the "International Code of Zoological Nomenclature" (ICZN, 1999), in cases of the genus-group names published before 1931 without an accompanying description or a definition, the first species name (in this case we have a monotypic genus) mentioned in combination with the new generic name is considered the type species of the genus and the descriptive traits of the species act as diagnostic features for the genus. Šoštari (1888), who proposed the generic status for *Typhlocypris*, uncritically translated into Croatian selected parts of the German text of Vejdovský's (1882) publication, including also some of the erroneous traits existing in Vejdovský's text. Šoštari (1888) presented the description of *T. eremita* from Prague as relying on the material he had sampled in wells at Zagreb (for details see Appendix A). Vávra in his monograph (1891a) offered for the first time a short diagnosis of the genus

Typhlocypris and showed that *T. eremita* is a representative of the Candoninae closely related to the species of the genus *Candona*. In another publication Vávra (1891b) noted that the only major character which validates the generic rank of *Typhlocypris* is the lack of eyes. It is now known that all candonines lack any black eye pigment (Meisch, 2000). Müller (1912) considered this trait an adaptive convergency occurring in many subterranean organisms and therefore regarded *Typhlocypris* as a junior synonym of the genus *Candona*. Ostracodologists in the first half of the 20th century followed Müller's (1912) opinion. More recently, *T. eremita* and the related species were included in the genus *Pseudocandona* (cf. Danielopol, 1978; Meisch, 2000; Namiotko & Danielopol, 2004; Martens & Savatnalinton, 2011; but see Karanovic, 2005, 2012). *Pseudocandona* comprises some 84 extant and 28 fossil species (Kempf, 1980a, b, c, d, 1997a, b, c, d; Martens & Savatnalinton, 2011). Although the genus has an almost worldwide distribution, the vast majority of species occurs in the Palearctic Region (Martens & Savatnalinton, 2011). The genera *Typhlocypris*, *Pseudocandona* and *Candona* have a rather tortuous and interwoven taxonomic history, of which only the most significant steps are reported here.

Typhlocypris* versus *Pseudocandona

The genus *Pseudocandona* was established by Kaufmann (1900) for a single species *Candona pubescens* (Koch, 1837), a species in which the males were known to possess sexually non-dimorphic antennae (A2), i.e., (a) with 5 (versus 6) segments (penultimate segment undivided), and (b) lacking the so-called male bristles (those bristles are now known to be transformed t-setae; Danielopol, 1978; Meisch, 2000). Initially, *Pseudocandona pubescens* (Koch, 1837) — now considered an unused older synonym of *Pseudocandona insculpta* (G. W. Müller, 1900) (see Hartwig, 1901 and Meisch, 2000 for synonymy) — was the unique species assigned to *Pseudocandona*.

Subsequently, both *Typhlocypris* and *Pseudocandona* were put into synonymy with *Candona* s. l. by the most influential authors of the first half of the 20th century (e.g., Müller, 1912; Alm, 1915; Klie, 1938). Bronstein (1947) maintained the genus *Pseudocandona* and, relying on Kaufmann's (1900) diagnostic character (i.e., the non-sexually-dimorphic male A2), included eight species collected from Lake Baikal in the previously monospecific genus. The same author (Bronstein, 1947) also put the genus *Metacandona* Bronstein, 1930 in synonymy with *Pseudocandona*.

In a milestone publication, Triebel (1963), a palaeontologist, treated the systematics of the Candoninae within a bright framework including both palaeontological and zoological information. His treatment was largely followed by a series of zoologists (see below). Triebel (1963) brought the taxonomic knowledge of the lineages *Typhlocypris* and *Pseudocandona* a big step forward. First, he correctly pointed out that the male A2-feature is not a useful taxonomic character at the generic and subgeneric levels, this because it leads to the grouping of otherwise very diverse and therefore not closely related species (for instance, *P. insculpta* and Bronstein's Baikal species). Triebel (1963: 165) therefore redefined *Pseudocandona*, the 'reticulate' surface of the juvenile valves becoming the main differentiating character of the taxon. He consequently transferred the species of the *rostrata*- and *compressa*-groups of the genus *Candona* into *Pseudocandona*, which he classified as a

subgenus of *Candona*. Triebel (1963: 162) similarly revived *Typhlocypris*, putting forward the triangular shape of the carapace as the main differentiating character, the larger valve (in this case the left one) being approximately triangular and the smaller one approximately trapezoidal in shape. Triebel (1963) assigned *Typhlocypris* the rank of a subgenus of *Candona*. Subsequently, Petkovski (1969a, b) reintroduced *Pseudocandona* as a separate genus to include the *rostrata*- and *compressa*-groups of species. *Typhlocypris eremita*, the type species of *Typhlocypris*, was considered to belong to the *rostrata*-group. *Typhlocypris* was therefore sunk into synonymy with *Pseudocandona*, becoming an unused older synonym of *Pseudocandona*. This view was adopted by the majority of zoologists up to the present time (e.g., Danielopol, 1978; Martens, 1984; Marmonier, 1988; Meisch, 2000; Namiotko & Danielopol, 2004; Martens & Savatnalinton, 2011).

Danielopol (1978: 27) provided an additional diagnostic character of *Pseudocandona*, i.e., the shape of the M-process of the hemipenis, a process which usually appears flat and proximally only weakly sclerotised in the males of the genus. Meisch (1996) introduced two important 'new' differentiating characters which each on its own permits easy distinction of the extant species of *Pseudocandona* from those of the related genera *Candona* s. str., *Fabaeformiscandona* Krsti, 1972 and *Schellencandona* Meisch, 1996: (a) the presence of dense, long, stiff and perpendicularly attached setae on the valves, and (b) the existence of three setae (d1, d2 and dp) on the protopodite of the cleaning leg (L7) (there are only two such setae, d1 and dp in three other genera mentioned above).

Sywula (e.g., 1973, 1974) was the first to draw the attention to the fact that the generic name *Typhlocypris*, as revised by Vávra (1891a), has priority over the name *Pseudocandona*. Therefore Sywula in his monograph (Sywula, 1974) used *Typhlocypris* instead of *Pseudocandona* assigning it the rank of a subgenus within the genus *Candona*. This scheme, though in a slightly different variant, was also used more recently by Karanovic (2005) (see the following subsection).

Meisch (2000: 152) pointed out that *Typhlocypris* is an unused older synonym of *Pseudocandona* and that, if the species of the *eremita*-group of *Pseudocandona* would later be considered to belong to a separate genus, then *Typhlocypris* would be the valid name of that genus. This statement foreshadowed the reassessment and redefinition of the genus *Typhlocypris* as proposed in the present contribution.

The *eremita*-group of *Pseudocandona*

Danielopol (1971: 182) introduced the *eremita*-group of species within *Pseudocandona* s. l. for the species around *Pseudocandona eremita*. More recently Namiotko & Danielopol (2004) and Namiotko et al. (2004) presented a detailed review of the species of the *eremita*-group of *Pseudocandona*, assigning 11 extant species to that group. Iepure et al. (2007) discussed the evolutionary morphology of the species of the *eremita*-group and described two new species. The present work uses many results of the latter three studies. It should be noticed that Karanovic (2005, 2012) proposed an alternative taxonomic scheme: upon recognising *Typhlocypris* as an older, albeit currently unused synonym of *Pseudocandona*, she decided to apply the nomenclatural priority rule. Consequently, Karanovic (2005) put both names into synonymy, with priority given to *Typhlocypris* and subdivided the genus

Typhlocypris into two subgenera: (1) *Typhlocypris* (*Pseudocandona*) with the species of the *compressa*-group, and (2) the nominotypical subgenus *Typhlocypris* (*Typhlocypris*) for the remaining species groups formerly assigned to *Pseudocandona*. For both taxonomic and phylogenetic reasons presented in the present paper, this view is not adopted here.

Here we recognise the species around *P. eremita* to form a separate evolutionary lineage and we therefore propose to extract the *eremita*-group of species from the genus *Pseudocandona* Kaufmann to elevate it to the genus level under the name *Typhlocypris* Vejdovský. A redefinition of *Typhlocypris* is given and the evolutionary trajectory of the lineage is discussed.

Taxonomic schemes used by palaeontologists

Héjjas (1894) described a new genus and species, *Kochia trigonella*, from Miocene deposits of (palaeo)Lake Pannon, a site which today is situated in Transylvania, Romania. This ostracod has asymmetric valves, the left one being triangular and displaying a strong umbo. With these traits it resembles the species of the genus *Typhlocypris*. Schneider (in Mandelstam & Schneider, 1956) described from Miocene deposits in the Caucasus another candonine genus with triangular left valves — *Advenocypris* Schneider, 1956. Because of the triangular shape of the carapace, Schneider (in Lubimova et al., 1960) created for this taxon the subfamily Advenocyprinae, which still nowadays is accepted by some specialists (cf. Vekua, 1975). Krsti & Guan (2000) and Krsti (2006) lowered Schneider's (1960) subfamily Advenocyprinae to the status of a tribe (Advenocyprini). Mandelstam & Schneider (1963) described a series of new species from the Miocene and Pliocene, which they assigned to *Advenocypris*. Krsti (2000), however, considered those triangular candonines to belong to a new tribe (Typhlocyprini), for which she did not offer any diagnosis.

Triebel (1963) imposed the idea that both *Kochia* and *Advenocypris* are junior synonyms of *Candona* (*Typhlocypris*). This taxonomic scheme was widely followed by palaeontologists from Central and Western Europe and Turkey (Krsti, 1972, 1993; Freels, 1980; Pokorný, 1988; Gross, 2004). *Kochia trigonella* Héjjas, 1894 was also mentioned as belonging to *Typhlocypris* by various specialists, *inter alia* Freels (1980) and Stoica (in ter Borgh et al., 2013). It should be noted that *Kochia* was already a preoccupied name used by botanists for the Chenopodiaceae genus *Kochia* Roth (cf. Chu & Sanderson, 2008). More importantly, the living triangular candonid *Candona trigonella* Klie, 1931 (a potential species for the genus *Typhlocypris*, cf. Namiotko & Danielopol, 2004 and additional information in the section “Notes on living and fossil species assigned to the genus *Typhlocypris* Vejdovský” of this contribution) uses a preoccupied name (see above) and as such is a junior homonym. Moreover, Soka (1978) assigned a fossil Quaternary ostracod resembling the extant *eremita* species to the genus *Typhlocypris*. Other palaeontologists assigned their fossil triangular candonids either to the genus *Candona* (e.g., Absolon, 1973, 1978) or to *Pseudocandona* (e.g., Pipík & Bodergat, 2008), without the recognition of a subgenus *Typhlocypris*.

Finally, we have to mention the taxonomic scheme proposed by Krsti (2006) for the triangular candonines. This author uses taxonomic names that zoologists pointed out to be synonyms of other taxa. This is the case of the monotypic genus *Cavernocandona* Hartmann,

1964 (type species *C. dispar* Hartmann, 1964 considered to be a representative of the *eremita*-species group of *Pseudocandona* by Namiotko & Danielopol, 2004), which Krsti (2006) assigned to the tribe Advenocyprini. On the other hand, the living species *Candona pannonicola* Löffler, 1960, also considered to be closely related with the *eremita*-species group (Meisch, 2000; Namiotko & Danielopol, 2004), was assigned to the new genus *Pannonocandona* Krsti, 2006 by Krsti (2006), for which the Pliocene species *P. farkasi* Krsti was designated as type species. Unlike *Cavernocandona*, *Pannonocandona* was assigned to the tribe Pseudocandonini described by Krsti & Guan (2000).

Material and Methods

The material used for the redescription of *Typhlocypris eremita* (Vejdovský, 1882) comes from the locality, a locality situated about 30 km north of Prague, Czech Republic. It consists of fossil valves collected by Dr. A. Absolon (Prague) and given as a present to D.L.D. in 1971. The sampling site is an outcrop of ‘Sumpfkreide’ (lake marl deposited in swamps) dated as ‘Altholozän’ (Early Holocene) in Absolon (1973: 50 and 1978: 40). Our sample contains five valves registered under the four figure photo-catalogue numbers of the Ostracoda collection of D.L.D. housed until January 2013 in the Department of Geology and Palaeontology, Institute of Earth Sciences, Karl-Franzens University Graz, and then transferred and deposited in the Department of Invertebrate Zoology, Natural History Museum, Vienna and registered under five figure NHMW crustacean collection numbers: (1) adult (Ad) left valve (LV) specimen (Spec) 1, here designated as a new valve reference material for *T. eremita* (photo-catalogue no 8354, NHMW-25481); (2) Ad LV Spec 2 (8355, NHMW-25482); (3) Ad right valve (RV) (8356); (4) A-2 juvenile (juv) RV Spec 1 (8357) both kept in one micropalaeontological cell (as NHMW-25483); and (5) A-2 juv RV Spec 2 (8358, NHMW-25484).

We compared our adult valves with the illustrated material of Absolon (1978, fig. 25). Additional valves came from a well at Hotarele, a village located about 30 km south of Bucharest in the Judeţ Ilfov, Romania. The material originates from the sample of living individuals and empty valves used for the study of the developmental trajectory and life cycle of *T. eremita* (*sensu lato*) published by Danielopol (1980). We used the following valves listed with their photo-catalogue numbers: Ad LV (8299), Ad RV (8300), A-1 juv LV (8301), A-1 juv RV (8302), A-2 juv LV (8303), A-2 juv RV (8304), A-3 juv LV Spec 1 (8305), A-3 juv LV Spec 2 (8306), A-3 juv RV Spec 1 (8307) and A-3 juv RV Spec 2 (8308). This material was also deposited at the Natural History Museum of Vienna (Austria), Department of Invertebrate Zoology under numbers NHMW 25485-25489.

Additionally, we used for comparison fossil specimens of Late Miocene age from the Lake Pannon collected at Mataschen, Styrian Basin (regional stage Pannonian, “Zone B”) and Hennesdorf, Vienna Basin (regional stage Pannonian, “Zone E”), which two of us (D.L.D. and M.G.) intensively sampled for ostracods during a number of years. For the first site one should consult the monograph of Gross (2004), whereas for the second one the information can be found in Danielopol et al. (2011).

Valves were photographed by transmitted light microscopy (TLM) with a Nikon DS-5 M digital camera fitted to a Nikon E-200 microscope as well as with a JEOL 6610 scanning electron microscope (SEM). In this latter case we examined the external side of the same valve which was previously photographed in TLM. Microphotographs were stored as tiff and jpg files and used for the digitised outline analysis using the software tps-dig, version 1.37 (Rohlf, 2003). In this way we realized a much more detailed analysis of valves as compared with classic descriptions where generally either TLM or SEM is used. In our case we examined for the same valve its shape, the inner and outer surface and structural elements of the calcified layer, the inner lamellae as well as the marginal pore canals.

For comparative analysis of the valve shapes we used the computer software Morphomatica (Linhart et al., 2007) with protocols for geometric morphometrics superposition using two modes, the standardised and non-standardised for surface. The former mode was used to avoid differences due to the valve size. For the mathematical reconstruction of outlines (the approximation of the B-spline curve) we used 24 (12×2) control points. This algorithm slightly differs from that used by Iepure et al. (2007) where 16 (8×2) control points defined the outline shape. However, in our case an excellent approximation of the mean and maximum error of the fitted mathematical curve to the digitised outline was obtained with 24 control points. For comparative purposes, especially for the geometric morphometrics analysis, we used a number of illustrations taken from the existing literature. The precise origin of the data is given in the captions to the corresponding figures.

The chaetotaxic scheme used here follows Broodbakker & Danielopol (1982) as revised for the second antenna by Martens (1987) and extended to the walking and cleaning legs by Meisch (1996). For a review see Meisch (2000) and for the nomenclature of valves and limbs we followed Horne et al. (2002) as well.

Here we introduce a rectification to the nomenclature of the endopodial segments of the 7th limb (the cleaning leg L7) for the Candoninae. One of us (D.L.D.) noticed that the endopodial segment 2 (E II) is not separated by an intersegmental septum from the next endopodial segment (E III); therefore, one has to consider them as one compound segment, named here E II + III. By combining the observation in TLM with that obtained with SEM it is possible to deduce that the so-called septum between the endopodial segments E II and E III is just an external annulation which varies in its expression depending on the thickness of the outer cuticular layer of the endopodite. Arguments for the present assertion are offered in the Appendix A which is added to this publication.

The following abbreviations are used: A2, second antenna; Ad, adult; juv, juvenile; L5, fifth limb (= first thoracopod transformed into a maxilliped); L7, seventh limb (= third thoracopod forming a cleaning leg); LV, left valve; RV, right valve. For endopodial segments of L7 we use the codes E I, E II + III and E IV following a scheme of Broodbakker & Danielopol (1982) and as mentioned above.

Hierarchical taxonomic position of the genus *Typhlocypris* follows Martens & Savatnalinton (2011).

Results and Discussion

Morphology of *Typhlocypris eremita* (Vejdovský, 1882), new aspects On the accuracy of the description of *Typhlocypris eremita* in Vejdovský's (1882) monograph

We mentioned above that Vejdovský (1882) proposed *Typhlocypris* as a subgenus of the at that time well-known but vaguely defined genus *Cypris*. Originally, the subgenus *Typhlocypris* included only one species (*Cypris eremita*) which name was first introduced in Vejdovský's earlier paper (Vejdovský, 1880) without any description or illustration, and as such was a nomen nudum. The same name (*Cypris eremita*) was made available later for the same concept when Vejdovský (1882) provided a description, thus the name takes the authorship and date of that act of establishment, not from the earlier publication.

In his description and figures, Vejdovský (1882) starts with the description of the carapace in lateral view (his fig. 1 of Plate VII is reproduced here in fig. 1A) and says that the carapace in lateral view is triangular in shape. However, Vejdovský's (1882) description of limbs is inadequate. As we do not have either the original reference material (no name-bearing type specimen is believed to be extant) or a good diagnosis of the species, ostracodologists encounter serious problems with the accurate identification of *T. eremita*-like individuals coming from populations located outside Prague. This conundrum will be solved here for the first time and inaccuracies of Vejdovský's (1882) description are here clarified.

Vejdovský (1882) figured a juvenile of *T. eremita* with surprising traits (fig. 1 here). First, it is easy to recognise that the juvenile in question is the A-3 stage, as indicated by the "Anlage" of the L7 limb (arrowed in fig. 1B here). Vejdovský's juvenile has anterodorsally a roundly shaped structure, which he suggested be a rudimentary eye (fig. 1B), although he considered the eye to be absent from adult specimens. As pointed out by Namiotko et al. (2012) a similar structure was not seen in controlled experiments with *T. eremita* (*sensu lato*) from the groundwater at Hotarele, southern Romania (details in Danielopol, 1980). Additionally, the juvenile figured by Vejdovský (op. cit.) displays long endopodial setae on A2 (arrow in fig. 1C here), which are equivalent to the swimming setae seen in the genus *Cypris* and many species of the family Cyprididae Baird, 1845 in general. However, as representatives of the subfamily Candoninae are all devoid of swimming setae (Meisch, 2000), in our opinion the supposed swimming setae of *T. eremita* figured by Vejdovský (1882) are most probably not shown inserted in the correct place on the correct podomere, and thus it can be argued that they are in fact not swimming setae and the drawing is mistaken. Finally, in fig. 1D (arrow) we point out the distal setae of L7 illustrated by Vejdovský (1882). In contrast to the Cyprididae, both the adults and A-1 juveniles of the Candoninae usually have three well developed setae there (Kovalenko, 1983). The L7 in Vejdovský's (1882) figure (here reproduced in fig. 1D) belongs to an adult female with a well developed *receptaculum seminis* and an ovocyte inside, but only two distal setae are figured. We consider that Vejdovský did not see the 3rd long seta, typical of the Candoninae.

Typhlocypris eremita from the elice and designation of a new reference material

Vejdovský (1882) sampled *T. eremita* in a house-well used for drinking water in Prague at the address 183 K emencova street (Praha 1, Nové M sto, 50°4'43.489"N 14°25'1.582"E).

The site is located about 230 m away from the bank of the Vltava River and the well most probably was dug in alluvial sandygravel sediments. As this house-well does not exist anymore, on 15 September 1969 one of us (D.L.D.) tried to collect *T. eremita* in alluvial sediments of the so-called hyporheal of the bank of the Vltava River in the southern part of Prague, at Radotín (i.e., at about 11 km from the type location mentioned by Vejvodský, 1882), but only *Fabaeformiscandona wegelini* (Petkovski, 1962) was found. Additionally, D.L.D. addressed an inquiry to the National (Natural History) Museum in Prague, Department of Invertebrate Zoology for a possible location of the holotype and/or other type material left by Vejvodský. The following message was received on 21 February 2013 from Dr. Petr Dolejš: “I checked databases and inspected the collections as well and found no type material of *Cypris* (*Typhlocypris*) *eremita*”. Also the well from where Vávra (1891a) got specimens used for his redescription of *T. eremita*, namely Brenntegasse 22, nowadays Spálená 22 (Praha 1, Nové Město), disappeared as we were informed by P. Dolejš, who wrote on 21 February 2013 to D.L.D.: “I am afraid that number 22 does not exist any more because there is a metro-station (currently in reconstruction so I cannot check the situation). The last building has number 18 and the following 30 (numbers 20-22-24-26-28 were probably demolished)”. It seems that also a house-well at the address Spálená 64 does not exist anymore, from where *T. eremita* was re-sampled after Vejvodský (1882) by Čecháková (1956) and illustrated by Janáček (1952).

Considering the above presented inadequacy of the original description coupled with the lack of the type material, we decided to designate a selected valve of a series of valves from the elice (described in detail below) as a new reference material which for the moment is proposed as a standard for *T. eremita*. Although the new reference material meets qualifying conditions for designation of a neotype, in the absence of the soft parts we were disinclined to formally designate the Holocene valve from the elice as the name-bearing type of *T. eremita*. The elice valve is the best characterised material we have nowadays which came as nearly as practicable from the original type locality. We decided to adopt this pragmatic solution because it is absolutely necessary to have a fixed reference material for future studies dealing with the taxonomic status of this species. The designed here new reference valve material should be abandoned once new material of living *T. eremita* is collected in Prague, and when valves are correctly described.

Absolon (1978) provided excellent figures of the valves of *Typhlocypris eremita* sampled at the elice, ca. 30 km north of the type locality in Prague. His description is useful in order to complement the scarce and sometimes incorrect information existing on this species. This is done here with the help of the material of A. Absolon offered to one of us (D.L.D.) and listed in the Material and Methods section. By the superposition of the valve outlines we compared the material from the elice and the illustrations of valves given by Vejvodský (1882), Vávra (1891a), Janáček (1952) and Absolon (1978) using geometric morphometric techniques in standardised and non-standardised for surface modes.

Vávra's (1891a) and Absolon's (1978) descriptions clearly deal with adult females. When we superposed on these valves the outlines of the valves figured by Vejvodský (1882) and Janáček (1952) it can be shown that the latter two valves belong to juvenile stages (consult fig. 2A-D). In fig. 3A-B the superposition of the outlines of adult and juvenile valves

illustrated by Absolon (1978) allowed us to identify the developmental stage of the valves illustrated by Vejdovský (1882). We also noted (fig. 2A, C) that the adult left valve figured by Vávra (1891a) is similar to that of Absolon (1978). Our left valves No. 8354 and No. 8355 from the elice closely fit Absolon's figures (fig. 4). When the outline given by Vejdovský (1882) in his fig. 1 of Plate 7 is superposed on the outline of the A-2 juvenile figured in Absolon (1978, fig. 25, juv.) we notice a close resemblance (fig. 3C). Therefore we can now say with confidence that Vejdovský (1882) and Janáček (1952) documented *T. eremita* only with juvenile valves, what was indeed affirmed in the latter paper (Janáček, 1952).

From the elice sample (cf. above, Material and Methods) we chose as the new reference material a left adult valve No. 8354, here illustrated in figs. 4A-B and 5A-B, catalogued at the Natural History Museum in Vienna under the number NHMW-25481. The remaining valves of our material from the elice offer additional information on *T. eremita*, especially on the diagnostic morphological traits existing on the adult right valve and on the juvenile valves. Hence, we illustrate here the specimens of this series with both TLM and SEM pictures. Figs. 4A and 5A depict the general aspect of the new reference material. They show the triangular shape of the left valve, as well as the reduced extension of the dorsal umbo and of the inner lamella. The anterior marginal pore canals of this valve are short (fig. 4C); the central surface of the valve is covered with foveolae well visible in TLM (fig. 4B) and better documented with SEM pictures (fig. 5A-B). The adult right valve (fig. 4E) is only slightly triangular and the intercardinal dorsal margin has an oblique position. As in the left adult valve, the inner lamella is reduced. The juvenile A-2 right valves (figs. 4F-G and 5C) have a triangular shape with a rounded dorsal margin and a stronger expression of the central ornamentation.

Finally, we have to mention that the modern systematics of *Typhlocypris*, as here discussed, uses mainly details of the valve morphology. Therefore, the valve material from a site near Prague (as near as possible to the original type locality) as the reference for *T. eremita* is the alternative solution we offer. Indeed, groundwater ostracods are hard to sample in the Prague area, this mainly because Vejdovský's and Vávra's wells have disappeared (cf. also Appendix A) and also because no other sites in Prague and surroundings have yielded material of *T. eremita* so far.

Typhlocypris eremita (sensu lato)* from Hotarele and Tekovské Lužany (Nagysalló): their interest for redefinition of the genus *Typhlocypris

Iepure et al. (2007) defined *T. eremita* (as *Pseudocandona eremita* in their paper) as a metaspecies, with the meaning of an entity which has a rather arbitrary definition for the moment and within which one can insert populations or even nominal taxa which are commonly difficult to characterise. Considering the parthenogenetic population from Hotarele in southern Romania studied first by Danielopol (1982) and, more recently, by Iepure et al. (2007), it was not possible to find clear morphological traits permitting to classify those ostracods as belonging to a new species different from *T. eremita* from Bohemia as characterised by Vávra (1891a) and Absolon (1978). Therefore, the population from Hotarele was considered to belong to a metaspecies termed *T. eremita (sensu lato)*, for

which in addition to the existing morphological information, details on the life cycle traits are also available (Danielopol, 1980). Here we present information on the developmental stages of the valves starting from the A-3 stage to that of the adult. Fig. 6 displays images in TLM where several important aspects of the development trajectory of this species are seen: (1) the left valves (fig. 6A-G) change from a pronounced triangular shape and a well-developed umbo in the A-3 stage to an attenuated triangular outline and a slightly developed dorsal umbo in the adult. (2) The right valves (fig. 6H-K) show changes from a triangular shape with a round dorsal margin in the A-3 stage to a trapezoidal shape in the A-2 and A-1 stages. (3) The anterior fused zone with the marginal pore canals and the inner lamella are reduced and their extension does not change substantially from one stage to the next ones. (4) The number of the marginal pore canals increases from the A-3 stage towards the adult stage. (5) When the outlines of the A-3 left valves are superposed onto those of the subsequent stages (fig. 7A), the triangularity remains preserved. (6) However, if we look at the same valves superposed and standardised for equal surface (fig. 7B) a gradual decrease of the triangular shape from the A-3 stage to the adult is seen. In the A-3 the maximum height is placed in the middle or slightly behind the middle of the valve (fig. 7B). This pattern is also seen in the adult right valve (fig. 7D).

When the left adult valve from Hotarele was superposed onto that from the elice and standardised for equal surface (fig. 7C), the Bohemian valve displays a greater height as compared to that from southern Romania. Both the left and right valves of *T. eremita* from Tekovské Lužany (Nagysalló) in Slovakia illustrated by Farkas (1958, fig. 51A-B) are higher than those from the elice and from Hotarele (figs. 3D and 7D). Similar differences were described by Iepure et al. (2007) for the closely related species *T. danubialis* Iepure, Namiotko & Danielopol, 2007 and *T. transylvanica* Iepure, Namiotko & Danielopol, 2007. Hence, a re-investigation of local populations originally identified as *Typhlocypris eremita* (or *Candona eremita* and *Pseudocandona eremita*) from Europe is needed in order to better understand the extent of intra- and/or interpopulational variability of valves, as well as microevolutionary aspects related to them. We have in mind *inter alia* the re-examination of the *Typhlocypris* material published by Klie (1936, 1940) and Löffler (1964).

Redefinition of the genus *Typhlocypris* Vejdovský, 1882

Class: OSTRACODA Latreille, 1802

Subclass: PODOCOPA G. W. Müller, 1894

Order: PODOCOPIDA Sars, 1866

Suborder: CYPRIDOCOPINA Baird, 1845

Superfamily: CYPRIDOIDEA Baird, 1845

Family: CANDONIDAE Kaufmann, 1900

Subfamily: CANDONINAE Kaufmann, 1900

Tribe: Candonini Kaufmann, 1900

Genus *Typhlocypris* Vejdovský, 1882

Diagnosis of the genus *Typhlocypris* Vejdovský, 1882

We use the diagnosis provided by Namiotko et al. (2012: 42), which was compiled from Danielopol (1982), Namiotko & Danielopol (2004), Namiotko et al. (2004) and also from additional information based on the new reference material from the elice.

Type species.— *Cypris eremita* Vejdovský, 1882.

New reference material (here designated).— One left adult valve from the Early Holocene deposits of an outcrop at the elice, 30 km north of Prague, Czech Republic (see Material and Methods for more details) registered under NHMW-25481.

Diagnosis.— Carapace of medium length (mostly 1.1 mm), approx. triangular in lateral view, with the greatest height at or just behind mid-length (at 50–60% of the length), and height to length ratio > 50%. Left valve dorsally with a hump (umbo) that overlaps the right valve. Valves thin, with a fine ornamentation consisting of shallow pits mostly located in the central valve area. Calcified inner lamella narrow, anteriorly usually 10% of the valve length and <2× as wide as posteriorly. Inner and outer margins more or less parallel. Valve shape, ornamentation and the relative width of the inner lamella remain almost unchanged throughout the last four stages of the postembryonic development. Sexual dimorphism in size and shape of the carapace weakly expressed; male carapace slightly larger than that of the female. A2 in both sexes with long apical claws: in females G1 2.2× and GM 1.8× the length of the penultimate segment, in males G2 2.0× and GM 1.6× the length of the 3rd and 4th endopodial segments combined (E II + III); male z1 claw relatively short, usually <3/4 of G2. Second segment of mandibular palp with 3 setae in the setal group, and with externo-distal (γ) seta smooth (not plumose). L5 with rudimentary exopodial branchial plate bearing two filaments. L7 with protopodite bearing three setae (d1, d2, dp), penultimate segment (E II + III) lacking the medial f seta and bearing long distal g seta, the terminal segment set with two long h2 and h3 setae and one short curved h1 seta. Female genital lobe with two fine folds separated by a flat depression or weakly developed and evenly rounded. Hemipenis: three lobes (a, b, h) well developed; M-process with a broad proximal plate, central part contracted and distal part weakly sclerotised, variously shaped and often crenulated; bursa copulatrix cornet-shaped. Zenker organ with five whorls of spines and two terminal cap-like structures.

Additional diagnostic valve differences between *Typhlocypris* Vejdovský and *Pseudocandona* Kaufmann

Namiotko & Danielopol (2004) offered a synthetic view on the diagnostic traits of the main living species of *Pseudocandona* subdivided at that time into six groups: *carribeana*, *compressa*, *eremita*, *prespica*, *rostrata* and *zschokkei*. The *eremita*-group is what we here define as the genus *Typhlocypris* Vejdovský. The *compressa*- and *rostrata*-groups form the genus *Pseudocandona* Kaufmann (*sensu stricto*). For the *zschokkei*-group Danielopol et al. (2012) proposed a new genus, *Marmocandona* Danielopol, Namiotko & Meisch, 2012. However, we will not discuss here the affinities and differences of *Typhlocypris* and *Marmocandona* (this will be published elsewhere). Further, Namiotko & Danielopol (2004)

pointed out that the *carribeana*- and *prespica*-groups need to be reviewed as their affinities with the other species-groups of *Pseudocandona* are still unclear. Therefore, we here tentatively consider *Pseudocandona* to comprise only the species of the *compressa*- and *rostrata*-groups.

Most of the European species of *Pseudocandona* display a more or less rectangular shape in the adult stage (Meisch, 2000). Absolon (1978), Kovalenko (1983) and Namiotko & Danielopol (2004) provided information on the carapace shape of the last three juvenile stages of the species of both the *rostrata*- and *compressa*-groups, showing that the juveniles down to the juvenile stage A-3 keep a more or less rectangular shape. Fig. 8, with superposed outlines of the A-3 shape of the left valve onto the adult valve shows clear differences between *Pseudocandona sarsi* (Hartwig, 1899) (fig. 8A), *Pseudocandona albicans* (Brady, 1864) (fig. 8B) and *Typhlocypris eremita* (*sensu lato*) (fig. 8C). It should be noticed that in *Pseudocandona* the right valves of adults and A-3 juveniles are also more or less rectangular, while in *Typhlocypris eremita* (*sensu lato*) the A-3 valve is triangular to become quasi-rectangular in the adult stage (fig. 8D). We therefore would like to point out that details of the valve shapes of juvenile stages combined with those observed in the adults help to complement the differential diagnosis of *Typhlocypris* and *Pseudocandona*.

Notes on living and fossil species assigned to the genus *Typhlocypris* Vejdovský

There are currently 14 nominal living species of the genus *Typhlocypris* (see Danielopol, 1978; Namiotko & Danielopol, 2004; Namiotko et al., 2004; Karanovic, 2005; Iepure et al., 2007): *Typhlocypris cavicola* (Klie, 1935), *T. danubialis* (Iepure, Namiotko & Danielopol, 2007) comb. nov., *T. dispar* (Hartmann, 1964), *T. eremita* (Vejdovský, 1882), *T. marmonieri* (Danielopol & Namiotko, 2004) comb. nov., *T. pannonicola* (Löffler, 1960), *T. pretneri* (Danielopol, 1978) comb. nov., *T. puteana* (Klie, 1931), *T. serbani* (Danielopol, 1982) comb. nov., *T. skadari* Karanovic, 2005, *T. sywulai* (Namiotko, Danielopol & Ra a, 2004) comb. nov., *T. szoecsi* (Farkas, 1958), *T. transylvanica* (Iepure, Namiotko & Danielopol, 2007) comb. nov. and *T. trigonella* (Klie, 1931).

Typhlocypris eremita and the closely related species *T. danubialis*, *T. pannonicola*, *T. serbani*, *T. szoecsi* and *T. transylvanica* have left valves with a reduced umbo and a widely rounded postero-ventral margin. Their morphological similarity suggests close phylogenetic affinities. This observation led Meisch (2000) and Karanovic (2012) to suggest that the names of some of these species, mainly of *T. pannonicola* and *T. szoecsi* are synonyms of *T. eremita*.

Typhlocypris cavicola and *T. pretneri* are closely related species (Klie, 1935; Danielopol, 1982; Mori et al., 2011). Their left valves generally possess umbos larger than those seen in other species of the genus. Also, the pitted (foveolated) central valve area is larger. The taxonomic status of both species should be checked after a careful redescription. This is a current project in which two of us (C.M. and N.M.) are involved.

Typhlocypris trigonella (Klie) is so far only known from one single, 0.55-mm-long individual collected from the Postojna cave in Slovenia (Klie, 1931). The species was not found in the samples taken from that cave or from any other locality in Slovenia since 1931.

T. trigonella has the typical morphological traits of *Typhlocypris*: a triangular left valve with a strongly developed dorsal umbo and foveolae in the central valve area (Klie, 1931: figs. 9 and 10). However, the distal segment of L7 displays a long h1 seta, which does not conform to the short, hook-like seta that characterises *Typhlocypris*. Note that also the setal equipment of the basal segment of that limb, which is important for the generic assignment (Klie, 1931) remains unknown. Therefore, the exact taxonomic status of *T. trigonella* remains to be elucidated.

Typhlocypris puteana displays the left valve dorsally less prominent and more elongated, resembling that of the species of the genus *Cryptocandona* Kaufmann, 1900 (Danielopol, 1982, fig. 14F) and the central valve area displays only a faint ornamentation (Namiotko, unpubl.). The endopodite of L7 was figured by Klie (1931) as having 4 segments. As pointed out above in the Material and Methods section we consider that the endopodite E II + III displays a well expressed annulation. In our opinion this species may belong to a separate lineage within the genus *Typhlocypris*.

A number of fossil species closely resemble the living stygobitic species of *Typhlocypris*. This is the case of *T. eremita* illustrated by Soka (1978) from Quaternary deposits at Vinkovci in Slavonia, Croatia and *Typhlocypris* cf. *serbani* described by Krsti (1993) from Quaternary deposits at Bačka in Serbia. The latter species resembles *T. serbani* described from the groundwater habitats in the Olt Valley in Romania. More recently, Pipík and Bodergat (2008) mentioned *Pseudocandona* aff. *eremita* from Miocene deposits of the palaeolake Turiec in Slovakia. The latter species is clearly similar to *T. eremita* from Bohemia. *Candona* (*Typhlocypris*) *eremita* in Freels (1980), from limnic Pliocene deposits in Turkey, clearly also belongs to *Typhlocypris* and closely resembles extant *T. eremita*. All these fossil species were found in sediments deposited in freshwater habitats. They all have a very small umbo of about 2.5% of the maximal height of the left valve; the dorsal angle of that valve is about 120° for both the Recent living species and the fossil ones. They all come from central and south-eastern Europe and Anatolia. We therefore hypothesise that the extant hypogean species are related to the fossil taxa mentioned above.

Krsti & Guan (2000) noted that the tribe Advenocyprini, which they introduced as new, comprises two groups of species: (1) species with very high and triangular carapaces, grouped in the genus *Advenocypris* (type species *A. alpherovi* Schneider, 1956), and (2) species with more roundly shaped carapaces belonging to the *eremita*-group. The valves of *Advenocypris schneiderae* Vekua, 1975 resemble those of the living species *Typhlocypris dispar* and in our opinion *A. schneiderae* actually belongs to the genus *Typhlocypris* as defined herein. *Typhlocypris schneiderae* is known from Quaternary freshwater deposits in Abkhazia (Vekua, 1975). The living species *T. dispar* is a stygobitic species collected from a cave near Erekli in Anatolia (Hartmann, 1964). Both species display highly triangular left valves with an umbo of about 7.5-10% of the maximum valve height. The dorsal angle of the left valve varies from 85° (the fossil *T. schneiderae*) to 110° in the cavernicolous *T. dispar*. We therefore hypothesise that both these species known from the same geographic area are phylogenetically linked.

We point out the similarity in the carapace shape of the Recent subterranean species *T. marmonieri* from the karstic Massif des Causses in the department of Tarn, southern France (Namiotko & Danielopol, 2004) and the fossil Miocene species *Cavernocandona roaixensis* Carbonnel, 1969 recorded from the department of Vaucluse, also in southern France. The carapaces of both species are very high, with a height reaching about 70% of the length, and we therefore suggest a close phylogenetic relationship between the two species. *T. marmonieri* also appears similar to *Typhlocypris pechelbronnensis* (Stchepinsky, 1960). The latter species is geologically the most ancient species of the genus. It was originally assigned to the subgenus *Kochia* of the genus *Candona*, then redescribed and placed in the subgenus *Typhlocypris* by Triebel (1963), and in the genus *Typhlocypris* by Carbonnel (1969). The species was found in non-marine Oligocene/Early Miocene deposits at Keffenach and Entzheim (France) and Nieder-Ingelheim (Germany). Additionally to the triangular carapace shape and the presence of an umbo on the left valve, the species presents foveolae in the central valve area as well as short anterior marginal pore canals (Triebel, 1963: Plate 26, figs. 12a, 14).

The fossil *Typhlocypris ratisbonensis* (Lutz, 1965) occurred in Central Europe. First identified by Lutz (1965) in a sample of Middle Miocene age (Badenian, Upper Freshwater Molasse) from near Regensburg in Bavaria, it was rediscovered by Pokorný (1988) in Bohemia, at Tucho ice, in a species rich sample of Early Miocene age. The latter author provided for the first time a detailed description of *T. ratisbonensis*, including details of the left and right valves belonging to both adults and the last four juvenile stages. The juvenile left valves display the typical triangular shape and the central ornamentation with foveolae. The adult left valve is approximately triangular, but instead of an umbo, it displays an antero-dorsal plication. Because of the latter character, *T. ratisbonensis* occupies an isolated position within the genus *Typhlocypris*.

There are several taxa commonly assigned to *Typhlocypris*, but which might not belong there. (1) *Candona* (*Typhlocypris*) aff. *eremita*, described by Gross (2004) from Mataschen, located in the area of (palaeo)Lake Pannon in the Styrian Basin (Late Miocene, Pannonian B). The left valve is triangular in shape and displays an umbo (fig. 9A and B). However, the surface of the valves is smooth. It is not clear if this morphotype belongs to *Typhlocypris* or if it displays a homeomorphic shape evolved through convergence (see next section). For such unresolved taxonomic cases we suggest to use the generic name “*Typhlocypris*” *incertae sedis* until new information will become available. (2) *Caspiocypris schneiderae* Livental, 1961 and *Caspiocypris ola* Markova, 1961 described in the monography of Agalarova et al. (1961) dealing with Pliocene and Quaternary ostracods from Azerbaijan. Both species possess triangular adult left valves with a dorsal umbo and the central valve area is covered with foveolae (fig. 10A and C). Juveniles of *C. schneiderae* are also triangular (fig. 10B). However, the carapace of both species is conspicuously inflated and the ventral margin is convex, traits that are not seen in the well established *Typhlocypris* taxa. Moreover, *Caspiocypris ola* seems to display long anterior marginal pore canals (fig. 10D), a trait atypical for *Typhlocypris*. We propose to consider these species as “*Typhlocypris*” *incertae sedis*, hoping that new data allowing one to resolve the question of their generic assignment will soon be available.

Hou et al. (2002) mentioned the following fossil *Typhlocypris* species from China: *Typhlocypris acuminata* Ho, 1978, *T. arrecta* (Chen & Ho, 1982), *T. brevialis* (Shi & Ho, 1963), *T. camerata* (Bojie, 1978), *T. definita* (Tsao, 1959), *T. dorsicurta* (Bojie, 1978), *T. gibbosa* (Chen & Ho, 1982), *T. sinensis* (Bojie, 1978) and *T. truncata* (Ho, 1978). All the above mentioned species do not belong to *Typhlocypris* as defined here and are therefore not discussed here.

Brief review of the ecological and geographical distribution of the species of *Typhlocypris*

Living species of *Typhlocypris* mainly occur in the interstitial habitats of alluvial aquifers, in the hyporheic zone along rivers and in cavernicolous habitats in central and south-eastern Europe (*Pseudocandona eremita* included in the checklist of Recent non-marine ostracod species of China by You et al., 2002 most probably constitutes an erroneous record that needs verification). They were occasionally collected in surface waters of irrigation ditches fed by underground waters (Namiotko, 1990; Namiotko & Sywula, 1993). In Slovenia, *T. pretneri* and *T. cavicola* were found in karstic outflows, and the latter species also in caves and in the hyporheic zone (Danielopol, 1982; Mori et al., 2011; Mori & Meisch, 2012). At present it is unclear if they are capable of maintaining stable populations in those springs.

Absolon (1973) reported *T. eremita* from Holocene marl sediments, rich in calcium carbonate, which were either deposited close to springs forming travertine substrates (e.g., Hurichův Dolec in Czech Republic) or in shallow bogs (e.g., e elice, also Czech Republic).

Fossil species now assigned to *Typhlocypris* are mentioned from lacustrine sediments (e.g., Lutz, 1965; Carbonnel, 1969; Vekua, 1975; Soka , 1978; Freels, 1980; Pokorný, 1988; Krsti , 2006; Pipik & Bodergat, 2008). Species of *Typhlocypris* are also known from brackish water environments in basins linked to the Paratethys domain. For instance, Krsti (1972) mentioned *T. beogradica* (Krsti , 1972) from sediments of Lake Pannon dated from the Middle Pannonian (Late Miocene). Gross (2004) recorded *Typhlocypris* aff. *eremita* from the Styria Basin during the Early Pannonian, Late Miocene. Minati and Danielopol (unpubl.) found one single juvenile of *Typhlocypris* sp. at Hennersdorf in Austria (Pannonian E, Late Miocene) (fig. 5D). In our opinion, the latter specimen had been drifted from the nearby non-saline, limnic habitats into the brackish Lake Pannon.

Tunoglu (2003) mentions two *Typhlocypris* species (left in open nomenclature) sampled from a Pontian (Early Pliocene) oligohaline environment of the (palaeo) Euxinic Basin, a part of the Eastern Paratethys.

The problem of homeomorphism in the triangular Candoninae — comparative data related to living species of *Typhlocypris*

Danielopol (1978) showed in a diagram that living Candoninae with triangular carapace shapes are relatively rare in the Palaearctic, with a higher number of species living in hypogean aquatic habitats as compared to those known from surface water systems. In a number of species with triangular carapaces, the generic characters are easily recognised. For instance, in *Mixtacandona tabacarui* Danielopol & Cvetkov, 1979 the distal setae of the L7 and the structure of the hemipenis unambiguously point towards *Mixtacandona* (fig. 11);

the valves are also easily separated from those characteristic of *Typhlocypris* because of the wide calcified inner lamellae, which form the anterior and posterior vestibulae. Two other European species with triangular valves according to characters of both the soft parts and carapace were documented to belong to other genera than *Typhlocypris*:

Fabaeformiscandona aemonae (Klie, 1935) or *Schellencandona triquetra* (Klie, 1936) (see Meisch, 2000). Danielopol (1982) showed that *Pseudocandona inaequivalvis baikalensis* (Bronstein, 1930) displays limbs and the Zenker Organ, which differ from those of *Typhlocypris*. The valves of that species are asymmetric and differ from those of *T. eremita* and the related species in fine details, e.g., the smooth valve surface (Danielopol, unpubl.). Detailed descriptions of the valves of the triangular species belonging to the *neglecta*-group of *Candona* living in Lake Ohrid (see Mikuli, 1961) are so far missing. This is also true for *Candona punctata* Furtos, 1933, the carapace of which is triangular in shape, the left valve being dorsally more developed than the right one. Furtos (1933) showed that the entire surface of the right valve is strongly pitted. No further details of the valve structure were provided by the authors who studied that species (Furtos, 1933; Staplin, 1963; Karanovic, 2006). However, from the original description by Furtos (op. cit.) and the more recent one by Karanovic (2006) it appears that the L5 male endopodite and also the hemipenis differ markedly from those of *Typhlocypris*. Also, the distal h1 seta of L7 in the redescription of Karanovic (op. cit.) is long and flexible, unlike that seen in the European species of *Typhlocypris*, where that seta is curved and conspicuously hook-like. In our opinion, *C. punctata* therefore does not belong to the genus *Typhlocypris* as redefined here.

Conclusion

1. In addition to the morphological traits already discussed by Meisch (1996, 2000), Namiotko & Danielopol (2004) and Iepure et al. (2007), the traits presented here, in particular those of the developmental trajectory of the valve shapes, provide robust evidence for considering *Typhlocypris* Vejdovský, 1882 a valid genus.
2. The generic redefinition presented here permits to allocate a number of Neogene and Quaternary fossil species from the Palaeartic to the genus *Typhlocypris*.
3. The genus *Typhlocypris* is an evolutionary entity with its own history and biogeography.
4. *Typhlocypris* presently appears to form a bundle of evolutionary lineages (species) with slightly diverging trajectories.
5. The origin of the living stygobitic species of *Typhlocypris* has to be sought in limnic ostracods which were spread over the western Palaeartic since the Late Palaeogene.
6. Investigations should be undertaken on living species using geometric morphometrics combined with classic morphological analysis of traits and, if possible, molecular techniques, in order

to clarify the taxonomic status of various populations recognised as *Typhlocypris incertae sedis*.

7.

Fossil Candoninae species presently classified in other genera but presenting similarities to *Typhlocypris* should be re-examined with both SEM and TLM techniques. Future investigators should use a large number of valves in order to treat their morphology with geometric morphometrics and multivariate statistic techniques.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

- Absolon A. Ostracoden aus einigen Profilen spät- und postglazialer Karbonatablagerungen in Mitteleuropa. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie. 1973; 13(1):47–94.
- Absolon A. Die Gattung *Candona* (Ostracoda) im Quartär von Europa. Rozprawy i Sprawozdania Akademii Nauk i Literatury, Oddział Matematyczny i Przyrodniczy. 1978; 88(5):1–76.
- Agalarova, DA.; Kadyrova, ZK.; Kulieva, SA. Ostracoda from Pliocene and Postpliocene deposits of Azerbaijan: 1–420. Azerbaijan State Publishers; Baku: 1961. [In Russian.]
- Alm G. Monographie der schwedischen Süsswasser-Ostracoden nebst systematischen Besprechungen der Tribus Podocopa. Zoologiska Bidrag från Uppsala. 1915; 4(1):1–248.
- Bronstein, ZS. Ostracodes des eaux douces. Faune de l'URSS. Crustacés, Vol. 2, n° 1. Pavlovsky, EN.; Stackelberg, AA., editors. Vol. 31. Institut Zoologique de l'Académie des Sciences de l'URSS, N.S.; Moscou/Leningrad: 1947. p. 1–339.[In Russian.]
- Broodbakker N, Danielopol DL. The chaetotaxy of Cypridacea (Crustacea, Ostracoda) limbs: proposals for a descriptive model. Bijdragen tot de Dierkunde. 1982; 52(2):103–120.
- Carbonnel G. Les ostracodes du Miocene Rhodanien: Systematique, biostratigraphie, ecologique, paleobiologie. Documents des Laboratoires de Geologie de la Faculte des Sciences de Lyon. 1969; 32(1–2):1–469.
- Chu G-L, Sanderson SC. The genus *Kochia* (Chenopodiaceae) in North America. Madro o. 2008; 55:251–256.

- Danielopol DL. Quelques remarques sur le peuplement ostracodologique des eaux douces souterraines d'Europe. Bulletin du Centre de Recherches Pau-SNPA. 1971; 5(Suppl):179–190.
- Danielopol, DL. Über Herkunft und Morphologie der Süßwasser-hypogäischen Candoninae (Crustacea, Ostracoda). Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Abt. 1; 1978. p. 1-162.
- Danielopol DL. Sur la biologie de quelques ostracodes Candoninae épigés et hypogés d'Europe. Bulletin du Musée National d'Histoire Naturelle de Paris, ser. 4, sect. A. 1980; 2(2):471–506.
- Danielopol DL. Nouvelles données sur les Candoninae (Ostracoda) hypogés de Roumanie et Yougoslavie. Bulletin du Musée National d'Histoire Naturelle de Paris, ser 4, sect. A. 1982; 4(3–4):369–396.
- Danielopol DL, Baltanás A, Morocutti U, Österreicher F. On the need to renew the taxonomic system of the Candoninae (non-marine Ostracoda, Crustacea). Reflexions from an analysis of data using the Yule Process. Geo-Eco-Marina. 2011; 17:5–20.
- Danielopol DL, Cvetkov L. Trois nouvelles espèces du genre *Mixtacandona* (Ostracoda, Cyprididae, Candoninae). Hydrobiologia. 1979; 67(3):249–266.
- Danielopol DL, Namiotko T, Meisch C. *Marmocandona* nov. gen. (Ostracoda, Candoninae), with comments on the contribution of stygobitic organisms to micropalaeontological studies. Kölner Forum für Geologie und Paläontologie. 2012; 21:13–16.
- Farkas H. Kagylosrakok — Ostracoda. Fauna Hungariae, Magyarorszag Allatvilaga. 1958; 394(3):1–68. [In Hungarian.].
- Freels D. Limnische Ostrakoden aus Jungtertiär und Quartär der Türkei. Geologisches Jahrbuch, B. 1980; 39:1–169.
- Furtos N. The Ostracoda of Ohio. Bulletin of the Ohio Biological Survey. 1933; 29:411–524.
- Gross M. Zur Ostracodenfauna (Crustacea), Paläoökologie und Stratigraphie der Tongrube Mataschen (Unter-Pannonium, Steirisches Becken, Österreich). Joannea Geologie Paläontologie. 2004; 5:49–129.
- Hartmann G. Asiatische Ostracoden. Systematische und zoogeographische Untersuchungen. Internationale Revue der gesamten Hydrobiologie, Systematische Beihefte. 1964; 3:1–155.
- Hartwig W. Die Arten der Ostracoden-Unterfamilie Candoninae der Provinz Brandenburg. Sitzungs-Bericht der Gesellschaft naturforschender Freunde zu Berlin. 1901; 1901(4):87–129.
- Héjjas E. Neue Beiträge zur fossilen Ostracoden-Fauna Siebenbürgens. Ertesitő az Erdelyi Múzeum-Egylet Orvos-Természettudományi Szakosztályából, Ser. 2. 1894; 19(1):99–112.
- Horne DJ, Cohen A, Martens K. Taxonomy, morphology and biology of Quaternary and living Ostracoda. Geophysical Monograph. 2002; 131:5–36.
- Hou, Y.; Guo, Y.; Chen, D. Fossil Ostracoda of China, (Vol. 1) Superfamilies Cypridacea and Darwinulidacea: 1-1090. Science Press; Beijing: 2002. [In Chinese with Engl. abstract.]
- ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE). International Code of Zoological Nomenclature. 4th ed. Tipografia La Garangola; Padova: 1999. p. 1-126.
- Iepure S, Namiotko T, Danielopol DL. Evolutionary and taxonomic aspects within the species group *Pseudocandona eremita* Vejdovský (Ostracoda, Candonidae). Hydrobiologia. 2007; 585:159–180.
- Jan a fík A. Nový nález lasturnatky *Candona eremita* Vejdovský 1882. Sborník Klubu P írodov deckého v Brn . 1952; 29(1951):232–235. [In Czech.].
- Karanovic I. On the genus *Typhlocypris* Vejdovský, 1892 (Crustacea: Ostracoda: Candoninae), with description of two new species. Systematics and Biodiversity. 2005; 3(4):375–406.
- Karanovic, I. Recent Candoninae (Crustacea, Ostracoda) of North America. Records of the Western Australian Museum, Suppl., 71. 2006. p. 1-75.
- Karanovic, I. Recent freshwater ostracods of the World. Crustacea, Ostracoda, Podocopida. Springer-Verlag; Berlin, Heidelberg: 2012. p. 1-608.
- Kaufmann A. Cypriden und Darwinuliden der Schweiz. Revue Suisse de Zoologie. 1900; 8:209–423.
- Kempf EK. Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln. 1980a; 35:1–188.
- Kempf EK. Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln. 1980b; 36(Part 2: Index B):1–180. 37 (Part 3: Index C): 1-204; 38 (Part 4: Bibliography A): 1-186.

- Kempf, EK. Index and bibliography of nonmarine Ostracoda. Part 3, Index C. Vol. 37. Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln: 1980c. p. 1-204.
- Kempf, EK. Index and bibliography of nonmarine Ostracoda. Part 4, Bibliography A. Vol. 38. Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln: 1980d. p. 1-186.
- Kempf, EK. Index and bibliography of nonmarine Ostracoda. Part 6, Index A, Supplement 1. Vol. 109. Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln: 1997a. p. 1-142.
- Kempf, EK. Index and bibliography of nonmarine Ostracoda. Part 7, Index B, Supplement 1. Vol. 110. Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln: 1997b. p. 1-134.
- Kempf, EK. Index and bibliography of nonmarine Ostracoda. Part 8, Index C, Supplement 1. Vol. 111. Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln: 1997c. p. 1-152.
- Kempf, EK. Index and bibliography of nonmarine Ostracoda. Part 9, Bibliography C. Vol. 112. Sonderveröffentlichungen des Geologischen Instituts der Universität zu Köln: 1997d. p. 1-144.
- Klie W. Zwei neue Arten der Ostracoden-Gattung *Candona* aus unterirdischen Gewässern im südöstlichen Europa. Zoologischer Anzeiger. 1931; 96(7/8):161–168.
- Klie W. Drei neue Höhlenostracoden aus der Umgebung von Laibach. Zoologischer Anzeiger. 1935; 111(7/8):189–198.
- Klie, W. Entomostraken aus der bulgarischen Höhle “Lakatnik”. Mitteilungen aus den Königlichen. Vol. 9. Naturwissenschaftlichen Instituten in Sofia — Bulgarien: 1936. p. 108
- Klie, W. Ostracoda, Muschelkrebse. Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise. Vol. 34. Gustav Fischer Verlag; Jena: 1938. p. 1-230. Teil: Krebstiere oder Crustacea
- Klie W. Zur Kenntnis der Ostracodenarten *Candona eremita* (Vejdovsky) und *Candona reducta* Alm. Mitteilungen über Höhlen- und Karstforschung. 1940; 1940(1):24–29.
- Kovalenko AL. Postembryonic evolution of *Candona parallela* G.W. Müller (Crustacea, Ostracoda). Izvestiya Akademii Nauk Moldavskoy SSR, Seriya Biologicheskikh i Kimicheskikh Nauk. 1983; 1983(1):33–38.
- Krsti N. Serbian Academy of Sciences and Arts, Monographs, 140, Section of Natural and Mathematical Sciences. 1972; 39:1–145.
- Krsti N. Several rare ostracode species of Ba ka Quaternary. Proceedings of Geoinstitute Belgrade. 1993; 28:173–185.
- Krsti , N. Some ostracodes from the Dinaric Alps Neogene and its paleoecology. Geology and metalogeny of the Dinarides and the Vardar Zone. Karamata, S.; Jankovi , S., editors. Vol. 1. Academy of Sciences and Arts of the Republika Srpska, Monographs; 2000. p. 207-214.
- Krsti N. Pliocene ostracodes of the Paludinian Beds in Pannonian plain, Serbian Part. Herald of the Nature History Museum Belgrade. 2006:1–409. Spec. Publ.
- Krsti N, Guan NS. A proposal for the systematics of the subfamily Candoninae (Ostracodes) with the description of the *Macedocandona*, new genus. Geologica Macedonica. 2000; 14:25–48.
- Linhart, J.; Brauneis, W.; Neubauer, W. Morphomatica, version 1.6.0.1. Graz: 2007. available online at <http://palstrat.uni-graz.at/methodsinostracodology.htm> Graz
- Löffler H. Wissenschaftliche Arbeiten aus dem Burgenland. 1964; 31:156–169.
- Lubimova, PS.; Mandelstam, MI.; Schneider, GF. Ostracoda: Nadsemeystwo Cypracea. Osnovy Paleontologii. Orlov, JA., editor. Vol. 8. Nauka, Moskva; 1960. p. 264-421. [In Russian.]
- Lutz AK. Jungtertiäre Süßwasser-Ostracoden aus Süddeutschland. Geologisches Jahrbuch. 1965; 82:271–329.
- Mandelstam MI, Schneider GF. Materialien zur Paläontologie: Neue Familien und Gattungen. Trudy Vsesoyuznogo Nauchno-issledovatel'skogo Geologicheskogo Instituta (VSEGEI) Ministerstva Geologii i Ochrany Nedr SSSR, NS. 1956; 12:87–144. [In Russian.].
- Mandelstam, MI.; Schneider, GF. Fossil Ostracoda of the USSR: family Cyprididae. Trudy Vsesoyuznogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Neftyanogo Instituta (VNIGRI), NS. Vol. 203. In Russian, English translation 1968 by National Lending Library of Science and Technology; Boston Spa: 1963. p. 1-331.

- Marmonier, P. Biocénoses interstitielles et circulation des eaux dans le sous-écoulement d'un chenal aménagé du Haut-Rhône français. Ph.D. Thesis; University Claude Bernard Lyon I, Lyon: 1988. p. 1-317.
- Martens K. Annotated check-list of non-marine ostracods (Crustacea, Ostracoda) from African inland waters. Musée Royal de l'Afrique Centrale Tervuren, Documentation zoologique. 1984; 20:1–51.
- Martens K. Homology and functional morphology of the sexual dimorphism in the antenna of *Sclerocypris* Sars, 1924 (Crustacea, Ostracoda, Megalocypridinae). Bijdragen tot de Dierkunde. 1987; 57(2):183–190.
- Martens K, Savatnalinton S. A subjective checklist of the Recent, free-living, non-marine Ostracoda (Crustacea). Zootaxa. 2011; 2855:1–79.
- Martens K, SchöN I, Meisch C, Horne DJ. Global diversity of ostracods (Ostracoda, Crustacea) in freshwater. Hydrobiologia. 2008; 595:185–193.
- Meisch C. Contribution to the taxonomy of *Pseudocandona* and four related genera, with the description of *Schellencandona* nov. gen., a list of the Candoninae genera, and a key to the European genera of the subfamily (Crustacea, Ostracoda). Bulletin de la Société des naturalistes luxembourgeois. 1996; 97:211–237.
- Meisch, C. Freshwater Ostracoda of Western and Central Europe. Die Süßwasserfauna von Mitteleuropa. Schwoerbel, J.; Zwick, P., editors. Vol. 8/3. Spektrum Akademischer Verlag; Berlin, Heidelberg: 2000. p. 1-522.
- Mikuli F. Neue Arten Candona aus dem Ohridsee. Bulletin du Muséum d'Histoire Naturelle Belgrade, Ser B. 1961; 17:87–107. [In Serbo-Croatian with German abstract.].
- Mori N, Meisch C. Contribution to the knowledge on the distribution of Recent free-living freshwater ostracods (Podocopida, Ostracoda, Crustacea) in Slovenia. Natura Sloveniae. 2012; 14:5–22.
- Mori N, Meisch C, Brancelj A. Morphology, ecology and distribution of *Typhlocypris cavicola* (Klie, 1935) and *Fabaeformiscandona aemonae* (Klie, 1935), two triangular shaped ostracods from Slovenia. Joannea Geologie und Paläontologie. 2011; 11:144–146.
- Müller GW. Crustacea: Ostracoda. Das Tierreich. 1912; 31:1–434.
- Namiotko T. Freshwater Ostracoda (Crustacea) of Zuławy Wi lane (Vistula Fen Country, Northern Poland). Acta Zoologica Cracoviensia. 1990; 33(19):459–484.
- Namiotko T, Danielopol DL. Review of the *eremita* species-group of the genus *Pseudocandona* Kaufmann (Ostracoda, Crustacea), with the description of a new species. Revista Española de Micropaleontologia. 2004; 36:117–134.
- Namiotko T, Danielopol DL, Ra a T. *Pseudocandona sywulaj* sp. nov., a new stygobitic ostracode (Ostracoda, Candonidae) from Croatia. Crustaceana. 2004; 77(3):311–331.
- Namiotko T, Danielopol DL, Meisch C, Gross M, Mori N. Reassessment of the genus *Typhlocypris* Vejdovský (Ostracoda, Candoninae), with a brief reflexion on the social role of the “Kempf Database”. Kölner Forum für Geologie und Paläontologie. 2012; 21:48–50.
- Namiotko T, Sywula T. Crustacean assemblages from the irrigation ditches near Szymankowo (Vistula Delta). Zeszyty Naukowe Uniwersytetu Gdańskiego. Biologia. 1993; 10:159–162. [In Polish with Engl. abstract.].
- Petkovski TK. Einige neue und bemerkenswerte Candoninae aus dem Ohrid-See und einigen anderen Fundorten in Europa (Crustacea, Ostracoda). Acta Musei Macedonici Scientium Naturalium. 1969a; 11(5):81–111.
- Petkovski, TK. Über die Notwendigkeit einer Revision der Süßwasser-Ostracoden Europas. The taxonomy, morphology and ecology of Recent Ostracoda. Neale, JW., editor. Oliver & Boyd; Edinburgh: 1969b. p. 76-81.
- Pipf R, Bodergat A-M. Nouvelle faune d'ostracodes d'eau douce du Miocène supérieur de la région Carpatho-Pannonienne et description d'espèces appartenant aux genres *Pseudocandona*, *Fabaeformiscandona* et *Candonopsis*. Palaeontographica Abt A. 2008; 286(4–6):89–121.
- Pokorný V. Freshwater ostracodes from the Lower Miocene of Tucho ice (Bohemia, Czechoslovakia). Acta Universitatis Carolinae, Geologica. 1988; 3(1986):281–315.
- ehá ková V. Hydrobiology of 4 wells in the city of Prague. Acta Societatis Zoologicae Bohemoslovenicae. 1956; 20(2):162–176. [In Czech with Engl. abstract.].

- Rohlf, FJ. Department of Ecology and Evolution. State University of New York; Stony Brook, NY: 2003. Tps-dig, Program, Version 1.37. available online at <http://Life.Bio.SUNYSB.edu/morph/morph/html>
- Soka A. Pleistocene ostracode fauna of the Pannonian Basin in Croatia. *Palaeontologia Jugoslavica*. 1978; 20:1–51.
- Šoštarić, D. Prilog poznavanju faune slatkovodnih korepnjaka hrvatske. *Rad Jugoslavenske Akademije znanosti i umjetnosti. Matematičko-prirodoslovni razred 9*. Vol. 92. Ostracoda; 1888. p. 103–214. p. 103–112. p. 144–153. p. 207–214.
- Staplin FL. Pleistocene Ostracoda of Illinois. Part 1. Subfamilies Candoninae, Cyprinae, general ecology, morphology. *Journal of Paleontology*. 1963; 37:757–797.
- Sywula T. Notes on Ostracoda. 13. General plan of structure of the penis in the subgenera *Candona* Baird, *Eucandona* Daday and *Typhlocypris* Vojd. of the genus *Candona* Baird. *Bulletin de l'Académie Polonaise des Sciences, Série des Sciences Biologiques*, Cl. 2. 1973; 21:123–125.
- Sywula T. Małzorzaczki (Ostracoda). *Fauna Słodkowodna Polski*. 1974; 24:1–315.
- Ter Borgh M, Vasiliev I, Stoica M, Knežević S, Matenco L, Krijgsman W, Rundi L, Cloetingh S. The isolation of the Pannonian Basin (Central Paratethys): new constraints from magnetostratigraphy and biostratigraphy. *Global and Planetary Change*. 2013; 103:99–118.
- Triebel E. Ostracoden aus dem Sannois und jüngeren Schichten des Meinzer Beckens: I. Cyprididae. *Senckenbergiana lethaea*. 1963; 44(3):157–207.
- Tunoglu C. Systematics and biostratigraphy of the Pontian Candonidae (Ostracoda) from the eastern Black Sea region (Northern Turkey). *Geologica Carpathica*. 2003; 54(1):21–40.
- Vávra W. Monographie der Ostracoden Böhmens. *Archiv der naturwissenschaftlichen Landesdurchforschung von Böhmen*. 1891a; 8(3):1–116.
- Vávra W. Kritisches Verzeichniss der Ostracoden Böhmens. *Sitzungsberichte der Königlichen Böhmischen Gesellschaft der Wissenschaften*. 1891b; 1891:159–168.
- Vejdovský F. Über den Ursprung der Brunnenfauna. *Jahresbericht der königlich-böhmischen Gesellschaft der Wissenschaften*. 1880; 1880:49–56. [In Czech.].
- Vejdovský F. Thierische Organismen der Brunnenwässer von Prag. 1882:1–70. (Ostracoda: 64–65, table 7).
- Vekua, ML. The ostracods of the Kimmerian and Kuyalnikian deposits of Abkhazia and their stratigraphic significance. *Akademia Nauk Gruzinskoy SSR*; Tbilisi: 1975. p. 1–137. [In Russian.]
- Yu N, Zhao Q, Li E, Chen S, Chen L. An updated and annotated checklist of recent nonmarine ostracods from China. *Zootaxa*. 2009; 2067:29–50.

Fig. 1. Reproduction of morphological details of *Typhlocypris eremita* (Vejdovský, 1882) from Vejdovský (1882: Plate 7, figs. 1, 2 and 6). A, Individual with carapace and limbs; B, A-3 juv stage with “Anlage” of L7 (arrow); C, A2 of juv figured in B, with presumed swimming setae (arrows); D, Posterior part of Ad, with details on the distal setae on L7 (arrow). Not to scale.

Fig. 2.

Typhlocypris eremita (Vejdovský, 1882), viewed from the left side. A, Carapace reproduced from Vávra (1891a: fig. 15/1); B, LV in outer lateral view from Jan a ík (1952: fig. 2); C, Superposition in standardised for equal surface mode of Ad valve-shapes in lateral views from illustrations of Vávra (1891a: fig. 15/1) — indicated as 0, Jan a ík (1952: fig. 2) = 1 and Absolon (1978: fig. 25) = 2; D, Superposition of valve-shapes, standardised for equal surface, from illustrations of Absolon (1978: fig. 25) = 0, Jan a ík (1952: fig. 2) = 1 and Vejdvský (1882: pl. 7, fig. 1) = 2. Delta vectors in C and D are 2.5× enlarged.

Fig. 3. *Typhlocypris eremita* (Vejnovský, 1882). A-B, Superposition of LV-shapes in lateral views of Ad and juv stages A-1 and A-2. A, non-standardised for equal surface and B, standardised for equal surface outlines from Absolon (1978: fig. 25), Ad indicated as 0, juv A-1 = 1 and A-2 = 2; C, Superposition in the standardised for equal surface mode of A-2 LV from Absolon (1978: fig. 25) = 0 and the outline from Vejnovský (1882: Plate 7, fig. 1) = 1; D, Superposition in the standardised for equal surface mode of Ad LV No. 8354 from e elice = 0 and the outline from Farkas (1958: fig. 51/A) = 1. Scale bar in A, 0.1 mm. Delta vectors in B-D are 2.5× enlarged.

Fig. 4.

Typhlocypris eremita (Vejdovský, 1882), specimens from the elice. A, Ad LV No. 8354 (new reference material) in outer lateral view; B, Ad LV No. 8354 as in A but with visible foveolae in the central surface; C, enlarged anterior end of LV No. 8354 (new reference material) with details on the fused zone and the short and straight marginal pore canals; D, Ad LV No. 8355 outer lateral view; E, Ad RV No. 8356, reversed outer lateral view; F, A-2 RV No. 8357, reversed outer lateral view; G, same as F but with visible foveolae in the central surface; H, superposition in non-standardised for equal surface mode of Ad LV-shapes of specimens No. 8354 (new reference material) = 0 and 8355 = 1; I, superposition in standardised for equal surface mode of LV No. 8354 (new reference material) = 0, LV no. 8355 = 1 and Absolon's (1978) LV from fig. 25 = 2. Scale bars: A, B, D-G, 0.2 mm, C and H, 0.1 mm. Delta vectors in H and I are 2.5× enlarged.

Fig. 5.
A-C, *Typhlocypris eremita* (Vejdovský, 1882) specimens from e elice, SEM microphotographs. A, Ad LV No. 8354 (new reference material) outer lateral view; B, detail from A of central surface with enlarged foveolae; C, juv A-2 RV No. 8358 outer lateral view; D, *Typhlocypris* sp. juv? A-3 LV No. 3915 outer lateral view from Hennersdorf near Vienna (Late Miocene, Pannonian E) in the layer Na (cf. Danielopol et al., 2011, fig. 6). Scale bars: A-C, 0.1 mm, D, 0.2 mm.

Fig. 6.

Typhlocypris eremita (Vejdovský, 1882) (*sensu lato*), valves of living specimens from Hotarele, south of Bucharest. A-G, LVs outer lateral view; H-K, RVs reverse outer lateral view; A-C, female Ad valve No. 8299; A, general view; B, detail of the dorsal margin with slightly developed umbo; C, detail of the anterior margin with the short marginal pore canals; D, juv A-1 valve No. 8301, E, juv A-2 valve No. 8303; F, juv A-3 valve No. 8306; G, detail of the dorsal margin of juv A-3 valve No. 8305; H, Ad valve No. 8300; I, juv A-1 valve No. 8302; J, juv A-2 valve No. 8304; K, juv A-3 valve No. 8307. Scale bars: 0.2 mm, except B, C and G, 0.1 mm.

Fig. 7.

Typhlocypris eremita (Vejdovský, 1882) (*sensu lato*). A and B, superposition of valve outlines of Ad female indicated as 0 and juv A-1 (=1), A-2 (=2) and A-3 (=3) stages of living individuals from Hotarele; A, in non-standardised for equal surface mode; B, in standardised for equal surface mode; C, superposition of Ad LV No. 8354 from the elice (0) and Ad LV No. 8299 from Hotarele in standardised for equal surface mode; D, superposition of Ad RV-shapes in standardised for equal surface mode of the specimens from the elice in Absolon (1978: fig. 25R) indicated as 0, our valve No. 8356 from the elice (=1), valve No. 8300 from Hotarele (2), and valve from Farkas (1958: fig. 51B) (3). Scale bar in A, 0.1 mm. Delta vectors in B-D are 2.5× enlarged.

Fig. 8.

Superposition of valve-shapes of Ad (0) and juv A-3 stage (1) in standardised for equal surface mode. A-C, LVs; D, RVs; A, *Pseudocandona sarsi* (Hartwig, 1899), valve outline from Absolon (1978: fig. 6); B, *Pseudocandona albicans* (Brady, 1864) data from Kovalenko (1983: fig. 1); C-D, *Typhlocypris eremita* (Vejdovský, 1882) (*sensu lato*) from Hotarele; C, valve No. 8299 (Ad) and valve No. 8306 (juv A-3); D, valve No. 8300 (Ad) and valve No. 8307 (juv A-3).

Fig. 9.

Typhlocypris incertae sedis, *Candona* (*Typhlocypris*) aff. *eremita* (Vejdovský, 1882) in Gross (2004); A, LV outer view from Gross (2004: Plate 3, fig. 13); B, same specimen as in A but inner view from Gross (2004: Plate 4, fig. 1). Length 0.8 mm.

Fig. 10.

Fossil *Caspiocypris* species from Azerbaijan (Apsheonian), LVs presenting some of the typical traits of *Typhlocypris*. A-B, *Caspiocypris schneiderae* Lival, 1961; A, Ad outer view; B, juv outer view; C-D, *Caspiocypris ola* Markova, 1961 Ad valves; C, outer view; D, inner view. From Agalarova et al. (1961: Plate 6, figs. 1, 2a, 2b, 3).

Fig. 11.

Mixtacandona tabacarui Danielopol & Cvetkov, 1979. A, Ad male LV inner view; B, Ad male RV and limbs; C-D, details of the umbo in inner view; C, Ad female; D, juv A-1. From Danielopol & Cvetkov (1979: figs. 8, A, B, D, E) reproduced with permission from Springer Publishers, Dordrecht.