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 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.

L’examen détaillé de la morphologie des valves de Typhlocypris, en combinaison avec l’étude de la morphologie des appendices permet de distinguer Typhlocypris des lignées phylogénétiques non apparentées possédant elles-aussi des carapaces de forme triangulaire. Il est montré que la description appropriée des taxons de ce genre doit se baser conjointement sur la microscopie optique par transparence et électronique à balayage.

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 & Savatenalinton, 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 presently their semantic content has become totally confused (compare inter alia the systematics of Candoninae proposed by Krstić & 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. Šoštarić (1888) raised the subgenus to the generic rank. Neither Vejdovský (1882) nor Šoštarić (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. Šoštarić (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. Šoštarić (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 & Savatenalinton, 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 & Savatenalinton, 2011). Although the genus has an almost worldwide distribution, the vast majority of species occurs in the Palaearctic Region (Martens & Savatenalinton, 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 & Savatenalinton, 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 Krstić, 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
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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). Krstić & Guan (2000) and Krstić (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. Krstić (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 (Krstić, 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, Sokač (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 Krstić (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 Krstić (2006) assigned to the tribe Advenocyprini. On the other hand, the living species *Candona pannonicola* Löfler, 1960, also considered to be closely related with the *eremita*-species group (Meisch, 2000; Namiotko & Danielopol, 2004), was assigned to the new genus *Pannonocandona* Krstić, 2006 by Krstić (2006), for which the Pliocene species *P. farkasi* Krstić was designated as type species. Unlike *Cavernocandona*, *Pannonocandona* was assigned to the tribe Pseudocandonini described by Krstić & Guan (2000).

**MATERIAL AND METHODS**

The material used for the redescription of *Typhlocypris eremita* (Vejdovský, 1882) comes from Čečelice, 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 (j uv) 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 Hennersdorf, 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 & Savatenalinton (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)
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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.

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 Čečelice 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 Křemencova street (Praha 1, Nové Město, 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 sand-gravel 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 Radotin (i.e., at about 11 km from the type location mentioned by Vejdovský, 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 Vejdovský. 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 redescrip-
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 Vejdovský (1882) by Řeháčková (1956) and illustrated by Jančařík (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 Čečelice (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 Čečelice as the name-bearing type of *T. eremita*. The Čečelice 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 Čečelice, 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 Čečelice and the illustrations of valves given by Vejdovský (1882), Vávra (1891a), Jančařík (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 Vejdovský (1882) and Jančařík (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 Čečelice 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 Jančařík
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 Jančařík (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, Jančařík (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, Jančařík (1952: fig. 2) = 1 and Vejdovský (1882: pl. 7, fig. 1) = 2. Delta vectors in C and D are 2.5× enlarged.

(1952) documented *T. eremita* only with juvenile valves, what was indeed affirmed in the latter paper (Jančařík, 1952).

From the Čečelice 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 Čečelice 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. 3. Typhlocypris eremita (Vejdovský, 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 Vejdovský (1882: Plate 7, fig. 1) = 1; D, Superposition in the standardised for equal surface mode of Ad LV No. 8354 from Čečelice = 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. 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
Fig. 5. A-C, *Typhlocypris eremita* (Vejdovský, 1882) specimens from Čečelice, 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.

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

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

Diagnosis.— Carapace of medium length (mostly \( \leq 1.1 \) 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 \( \leq 10\% \) of the valve length and \(< 2\times \) 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 \( G_1 \geq 2.2\times \) and \( G_M \geq 1.8\times \) the length of the penultimate segment, in males \( G_2 \geq 2.0\times \) and \( G_M \geq 1.6\times \) the length of the 3\(^{rd}\) and 4\(^{th}\) endopodial segments combined (E II + III); male \( z_1 \) claw relatively short, usually \(< 3/4 \) of G2. Second segment of mandibular palp with 3 setae in the setal group, and with externo-distal (\( \gamma \)) 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

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).
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


*Typhlocypris eremita* and the closely related species *T. danubialis*, *T. pannonicola*, *T. serbani*, *T. szoecsí* 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. szoecsí* 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 Sokač (1978) from Quaternary deposits at Vinkovci in Slavonia, Croatia and *Typhlocypris* cf. *serbani* described by Krstić (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.

Krstić & 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 phylogentically 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 pechelbronnnensis* (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 Tuchorice, 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.


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., Čečelice, also Czech Republic).

Fossil species now assigned to *Typhlocypris* are mentioned from lacustrine sediments (e.g., Lutz, 1965; Carbonnel, 1969; Vekua, 1975; Sokač, 1978; Freels, 1980; Pokorný, 1988; Krstić, 2006; Pipik & Bodergat, 2008). Species of *Typhlocypris* are also known from brackish water environments in basins linked to the Paratethys domain. For instance, Krstić (1972) mentioned *T. beogradica* (Krstić, 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 Mikulić, 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 Palaearctic 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 Palaearctic 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.

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MEISCH, C., 1996. 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, 97: 211-237.


Panel A of fig. A1 reproduces the L7 of Cryptocandona vavrai Kaufmann, 1900, published by that author in his monograph “Cypriden und Darwinuliden der Schweiz” (KAUFMANN, A., 1900. Revue Suisse de Zoologie, 8, pl. 26 fig. 14). One should note in this figure that a transversal septum between two endopodial segments E II and EIII does not exist, which allows a long muscle to extend through the whole E II + III segment being attached on one side to the septum between E I and E II + III, and on the other side to the septum between E II + III and E IV. The second short muscle inserted on the lateral side of the E II + III wall is also visible. This anatomical configuration of the muscles differs from that existing within the endopodial segment E I, where a septum exists at both extremities between which two muscles are inserted.

Panel B in fig. A1 presents female L7 of the stygobite species Mixtacandona pietrosanii Danielopol & Cvetkov, 1979, collected in a well of the village Lumina, near Constanța in Romania (DANIELOPOL, D. L. & L. CVETKOV, 1979. Hydrobiologia, 67: 249-266). With TLM, one of us (D. L. D.) observed a transversal ring near the insertion of the seta f (the thin arrow points to it). The endopodial wall seen laterally is thinner there than in the surrounding area. One should also notice a well-developed arthrodial membrane (the thick arrow points to it) between the segment E I and the next endopodial segment. The above mentioned intersegmental ring in M. pietrosanii could not be detected in TLM in the case of Mixtacandona sp. aff. chappuisi (Klie, 1943), a small stygobitic species collected from a well at Cuhea, a village in the north-eastern part of Romania. The L7 depicted here in panel C belongs to a small adult female of Mixtacandona sp. with poorly calcified valves (cf. fig. 2A and 2B in DANIELOPOL, D. L. & L. CVETKOV, 1986. Hydrobiologia, 143: 143-157) and weakly sclerified limbs. When examined at high magnification with SEM techniques (cf. panel D, scale = 0.05 mm, and panel E, scale = 0.025 mm), an external annulation becomes visible.

Fig. A1.
(the thin arrow points to it). The shallow depression at the limit between so-called E II and E III differs markedly from the intersegmental arthrodial membrane and the articulation (the thick arrow points to them) existing between the endopodial segment E I and the next segment, where also a transversal septum exists.

THE LOCATION OF THE FIRST SAMPLING SITES IN PRAGUE FOR *T. EREMITA* BY VEJDOVSKÝ (1882) AND VÁVRA (1891A), AS WELL AS THE FIRST DOCUMENTATION OF THIS SPECIES AS BELONGING TO CANDONINAE BY VÁVRA (1891A)

In fig. A2, note the vicinity between the two streets Kremencova (where Vejdovský sampled) and Spálená (formerly Brenntegasse, where Vávra mentioned the species), both belonging to the district Praha 1 — Nové Město. The site of Vávra’s well on Spálená street is placed with approximation, as the original house does not exist anymore as mentioned in our paper.

Vávra (1891a) described for the first time, with useful details, the adult female of *T. eremita* and allocated correctly this species to the subfamily Candoninæ, considering the characteristics of the 2nd antenna, and of the 5th and 7th limbs (fig. A3 is a reproduction of fig. 15 from Vávra, 1891a).

THE PROBLEMATIC CONTRIBUTION OF D. ŠOŠTARIĆ (1888) TO THE DEFINITION OF THE GENUS *TYPHLOCYPRIS* VEJDOVSKÝ, 1882

Here, for the first time it is documented that a part of the description of *T. eremita* from Croatia made by Šoštarić (1888) is a free translation of a text from Vejdovský’s (1882) publication. Below, the documentation for this allegation is presented:

Šoštarić (1888) published a long report, in Croatian, on the aquatic crustaceans from the Zagreb and from the surroundings of Varaždin (cf. “Contribution to the knowledge on freshwater fauna of crustaceans in Croatia”). This work was published by the Yugoslav Academy of Arts and Sciences. On page 153, Šoštarić (1888) mentions that he collected in two wells two specimens of *T. eremita* that he considered juveniles. The exact formulation is: “The two animals that I collected were relatively young and the carapace was not so convex on the dorsal edge as in adults”. The phrase before
mentions the exact sites in Zagreb: “Locality: Two wells at the following address: Demetrovoja ulica 7 (27 September 1885), Pivarska ulica 3 (30 October 1885). The wells were over 30 m deep and had clean water”. In our opinion the specimens collected could not be juveniles, but adults of a species belonging to the *T. eremita* lineage. Our supposition is based on the fact that the juveniles display a more triangular valve shape as compared to the adult (cf. the data presented in this present publication). We hypothesize that Šoštarić took as reference the valve figures from Vejdovský (1882, pl. 7 fig. 4), considered at that time as belonging to an adult female. We documented here that the valves figured by Vejdovský (1882) belong to juveniles.

Šoštarić (1888) mentions: “The valves are smooth, without ornamentation, but have strong bristles”. This assertion does not fully conform to the diagnostic characteristics of the species belonging to the *T. eremita* lineage, which have a central ornamentation as figured in this publication and a moderate density of thin and flexible setae (cf. for this latter detail: Danielopol, 1982, fig. 5A and B). We compared the Šoštarić assertion with the text of Vejdovský (1882: 64) where it is written: “Die Schalen entbehren einer besonderen Sculptur, dagegen sind sie mit zahlreichen und starken Borsten besetzt.”
For the antennae Šoštarić (1888) writes: “The anterior antennae 7-articulated, bearing on the last article a dense fascicle of strong and long bristles. The second pair of antennae is 4-articulated. The last two articles bearing many long and strong bristles, while the second has some hairs”. As it is well known, the Candonininae have generally on the distal segment of the 1st antenna only two long setae, one claw-like seta, and one aesthetasc (cf. for species of T. eremita lineage the description of Danielopol, 1982). Hence, this description is inadequate. Now if we read Vejdovský (1882: 64) we find: “die Anntennen des ersten Paares (Taf. VII, Fig. 2 an1), die 7gliedrig sind und am Endgliede mit einem dichten Büschel von langen Borsten besetzt sind. Die übrigen Glieder sind nur mit einzelnen kürzeren Borsten versehen. Das zweite Antennenpaar ist 4gliedrig (Taf. VII, Fig. 2. an2). Die zwei letzten Glieder sind dicht mit ungemein langen und kräftigen Borsten bewaffnet, während das 3. Glied mit einigen schwächeren Borsten besetzt ist”. As we documented in this contribution, the Candonininae have no such long setae as in Vejdovský’s fig. 2 and in the mentioned text. However, the similarity between the Šoštarić formulations (1888) and that of Vejdovský (1882) is surprising.

Considering the L7 limb and the uropodal rami (the so-called furca) Šoštarić (1888) writes: “Second pair bent between articles 2 and 3 knee-shaped upwards and armed with a long and a short bristle. Posterior part of the body ending with two appendages, similar to legs. They correspond to a furca”. As we showed in the present publication, the Candonininae in general and the T. eremita lineage anyway, have three distal setae on the last endopodial segment. In Vejdovský (1882: 64) we find the following description for the above-mentioned appendages: “…die Füsse des zweiten Paares zwischen dem 2. und 3. Gliede knieartig nach oben gebogen und mit einer langen und einer kürzeren Endklauen versehen sind (Taf. VII. fig. 6 p2) . . . Der hintere Körperteil endet mit einem Paar beinartige Anhänge (Taf. VII, Fig. 2, 6 fca), welche den bekannten Furcalgliedern entsprechen”.

Šoštarić (1888), strangely enough, after the description of the posterior part of this ostracod species, continues with the anterior part: “Anterior part of the body decorated by a pair of special frontal appendages, which are not present in any other known species. It may be, that these are special sense organs”.

The presentation of the so-called anterior sense organs follows exactly Vejdovský’s text (1882: 64), that is, after the description of the posterior part of the body this author continues with the anterior part, and with similar details for a sense-organ that does not exist: “Der vordere Körpertheil dieses interessanten Muschelkrebses ist durch ein Paar besonderer Stirnfortsätze ausgezeichnet, welche ich bei keiner anderen einheimischen Art gefunden habe. Es sind dies vielleicht eigenthümliche Sinnesorgane…”.

We consider similarities of the style and form for phrases of Šoštarić text (1888) with those existing in Vejdovský (1882) a case of “mild plagiarism” (see for this concept GREENE, S. P., 2002. Plagiarism, norms and the limits of theft law: some observations of the use of criminal sanctions in enforcing intellectual property rights, available online at http://faculty.law.lsu.edu/stuartgreen2/J-greene2.pdf).

Note that at no time Šoštarić mentions the origin of his information, and the details presented contain exactly the inadequate aspects which exist in Vejdovský’s text, too. Therefore, following Greene’s (2002) logic, Šoštarić (1888) infringed the so-called “norm of attribution”.

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