PALEOBIOGEOGRAPHY AND PALEOECOLOGY OF THE OSTRACOD
HELIocythere BONADUCE, RUGGERI & RUSSO, 1988
WITH RE-DESCRIPTION OF MIDDLE MIocene
HELIocythere MORAVICA (PROCHÁZKA, 1893)
FROM THE CARPATHIAN FOREDEEP (CZECH REPUBLIC)

MICHAL SEKO¹, RADOVAN PIPÍK¹, JEAN-PAUL COLIN²,
MAHBOUBEH TARIGHATI¹, MARTINA SYKOROVÁ¹
& JAHANBAKHSH DANESHIAN³

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Abstract. Twelve species attributed to the genus Heliocthere have been recorded from the epineritic/neritic and circalittoral/epibathyal deposits of Cenozoic sub-tropical seas. The oldest species is from the Lower Oligocene deposits of the northwest Indian Ocean. The youngest species are confirmed from the Late Miocene (Messinian) of the Mediterranean area and one stratigraphically uncertain record from the Early Pliocene of Vejer de la Frontera (southern Spain). Heliocthere profited of a marine connection between the Mediterranean and the Paratethys through the Slovenian corridor during the latest Burdigalian (Karpian) and settled in Central Europe and Balkan Peninsula marine biotopes, but a paleoecographic and paleoecologic change during the late Serravallian caused an extinction of Paratethyan Heliocthere. In Late Miocene times, Heliocthere spread through the entire Mediterranean area and extended its biogeographic range to the eastern Atlantic Ocean. This was a period of maximum species diversity of Heliocthere. No Heliocthere species has been described from present-day marine ostracod associations and we suppose that this fully marine genus is extinct.

Due to the loss of the type material and the necessary correction of genus attribution, we designate here a neotype for the early Badenian (early Langhian) Cythere moravica Prochážka, 1893 from the Carpathian Foredeep, referred to in this work as Heliocthere moravica (Prochážka, 1893). We discuss its paleoecology and position within the genus Heliocthere.

Introduction

Prochážka (1893) described seven new species of ostracods from the Miocene deposits of the Carpathian Foredeep, among which is Cythere moravica. This oldest established genus for marine ostracods has been used in the past as generic name for all marine cytherid species (van Morkhoven 1963). Brestenská & Jiříček (1978) considered as doubtful the generic assignment of C. moravica within the genus Cythere and used only open nomenclature “Gen. Indet.” moravica (Prochážka), which is also the latest used generic assignment for this species. Zorn (2010) summarized the ostracod type specimens deposited in the Geological Survey of Austria in Vienna, including Prochážka’s collection, and noted the loss of the type material of Cythere moravica.

In spite of the numerous micropaleontological investigations in the Central Paratethys, no new record of C. moravica was reported from the original locality and thus the taxonomic position of the species is still open.

In a work of Seko et al. (2012) focused on the paleoecologic analysis of ostracod assemblages from the early Badenian parastratotype at Žilchovice, sev-

¹ Geological Institute, Slovak Academy of Sciences, Ďumbierska 1, 974 01 Banská Bystrica, Slovakia.
E-mail: michal.seko47@gmail.com, pipik@savbb.sk; sykorova@savbb.sk
² University of Lisbon, Faculty of Sciences, Centre of Geology, Campo Grande, C6, 3, 1749-016 Lisboa, Portugal and 3 Impasse des Biroulbres, 33610, Cestas, France.
³ Kharazmi University, Faculty of Science, Department of Geology, Tehran, Iran. E-mail: matarigiti@yahoo.com
eral tens of specimens of “Gen. Indet.” *moravica* (Procházka, 1893) were identified. This discovery allows a neotype designation for *Cythere moravica* and its generic attribution to the genus *Helicythere* Bonaduce, Ruggieri & Russo, 1988, rarely occurring in fossil marine ostracod associations. To better understand the evolution and paleobiogeography of the Central Paratethys marine ostracod fauna in relation to the Mediterranean bioprovince in Miocene times we summarized the occurrences and palaeoecological data on *Helicythere*.

**Geological and biostratigraphic framework**

The marine deposits around the small city Žižlochovice (Fig. 1) in the Carpathian Foredeep (Moravia, Czech Republic) originated in front of the forehead of the Carpathian Paleogene nappes (Chlupčič et al. 2002). Based on biostratigraphy, these deposits were selected as a parastratotype for the early Badenian – Moravian for their rich fossil record of nannoplankton, foraminifers, ostracods, molluscs, bryozoans, anthozoans, and fishes, which corresponds to the early Langhian in the Mediterranean stratigraphic scale (Cicha 1978; for correlation of the Mediterranean and Paratethys stages, see Fig. 2).

The cores Žižlochovice 1 (ZID1) and Žižlochovice 2 (ZID2) were drilled to revise the Middle Miocene marine ecosystems of the Central Paratethys. A composite lithological profile of these cores consists, at the base, of gray sandy and silty calcareous clay (known as Tegel), fine yellowish sand and algal limestone layers with a top layer of Pleistocene loess a few metres thick (Seko et al. 2012). The sedimentary succession was biostratigraphically correlated with the NN9 Zone (14.9–13.9 Ma), namely with the initial time of the Middle Miocene Climatic Transition (Doláková et al. 2014).

**Abbreviations**

Institutional abbreviation: No. MSRPxx-yy and MSxx-yy: catalogue number of specimens deposited in the Slovak National Museum in Bratislava (Slovakia); ZID1 and ZID2: short names of boreholes Žižlochovice 1 and Žižlochovice 2.

Other abbreviations: A, adult; LV, left valve; RV, right valve; AM, anterior margin; ADM, antero-dorsal margin; DM, dorsal margin; PDM, postero-dorsal margin; PM, posterior margin; PVM, postero-ventral margin; VM, ventral margin; AVM, antero-ventral margin; l, h, w, length, height and width of the valve in mm; h/l, height / length ratio; MPC, marginal pore canals; N, number of measured specimen; φ, average; ½, female; 3, male.

**Systematic Paleontology**

Based on the newest findings, neotype designation, morphological description and comparisons, in this work, *Cythere moravica* Procházka, 1893 is re-described as *Helicythere moravica* (Procházka, 1893).

Class **Ostracoda** Latreille, 1802  
Subclass **Podocopa** Sars, 1866  
Order **Podocopida** Sars, 1866  
Suborder **Cytherocopina** Baird, 1850  
Superfamily **Cytheroidea** Baird, 1850  
Family **Hemicytheridae** Puri, 1953  
Subfamily **Thaerocytherinae** Hazel, 1967  
Genus *Helicythere* Bonaduce, Ruggieri & Russo, 1988  
_Type species:* _Hemicythere magni_ Reiji, 1955

*Helicythere moravica* (Procházka, 1893)  
Pl. 1, Figs 2-13.

1893 *Cythere moravica* nov. spec., Procházka, p. 54-55, pl. 1, figs. 10 a-c.  
1978 “Gen. Indet.” _moravica_ (Procházka) - Brestenská & Jiřiček, p. 437, pl. 8, fig. 9.  
2010 *Cythere moravica* Procházka, 1893 - Zom, p. 285, pl. 3, figs. 33-35.  
2012 “Gen. Indet.” _moravica_ (Procházka, 1893) - Seko et al., p. 125, fig. 7.  

Neotype for *Cythere moravica* Procházka, 1893, designated here: MSRP-1-1, LV (ZID1, 2.3-2.4 m); Pl. 1, Fig. 1.

**Other material:** MSRP-1-8, RV(2) (ZID2, 9.7-9.8 m), Pl. 1, Fig. 2; MSRP-1-7, RV(3) (ZID2, 9.7-9.8 m), Pl. 1, Fig. 3; MS-2-16, LV(ZID1,
Locus typicus of the neotype: core ZID1, Žílochovice, Veihon hill, Moravia, Czech Republic, co-ordinates: 49° 02.498' N, 16° 37.318' E (ZID 1), sample No. 3 (2.3-2.4 m).

Stratigraphic and geographical range. This species has been found so far only in clay and marl of the early Badenian (early Langhian) parastratotype at Žílochovice (Carpathian Foredeep, Czech Republic).

Paleobiogeography of genus Heliocythere

In the Ashawq Formation (ca. 17°N, 54°E, southernmost Oman) dated by the occurrence of the larger foraminifer Nummulites fichteli to the Rupelian (Early Oligocene), Guernet et al. (1991) identified the species Malzella? sp. 2 (p. 305, pl. 3, fig. 3). The individual has a conspicuous eye tubercle, radial ribs outgoing from the central area towards the margins and 1 to 2 postero-dorsal protrusions, which are not typical for the genus Malzella (Hazel 1983), but for Heliocythere. Therefore, we conclude that Guernet et al. (1991) documented the oldest fossil record of Heliocythere, still in open nomenclature.

A connection between the Mediterranean and the Indian Ocean existed during the Early Miocene, through the area of today's Iran, Iraq, and Syria (Rögl 1999). This connection during the Aquitanian and early Burdigalian allowed the migration of molluscs, larger foraminifers and marine benthic ostracods, among them Heliocythere, into the Mediterranean region.

H. magni (Keij, 1955) with pronounced ala, radial ribs and sub-trapezoidal shape, thus possessing all characters typical for the genus, was originally considered as the oldest Heliocythere. The first record of this species is from the Early Atlantic Miocene (Late Aqui-
tanian) in the Aquitanian Basin (France) (Bonaduce et al. 1988). Moyes (1965) identified *H. magnesi* (originally as *Aurula magnesi*) from two outcrops of SW France, which were dated as Aquitanian. *H. magnesi* (Pl. 1, Fig. 17 in this paper) discovered near the Qom city in the Iranian mountain range Kuh-e-Dochah in the lower Burdigalian sediments of the Qom Formation (Reuter et al. 2009). This finding documents a large geographic extension of *Helicythere* from the western Mediterranean up to the northwestern Indian Ocean in the Early Miocene.

A closure of the connection between the Mediterranean and the Indian Ocean (Rögl 1999) during the late Burdigalian (Ottangian) could be the reason why other findings of *Helicythere* are restricted to the Mediterranean and Paratethys areas.

*Helicythere* profited of a marine connection between the Mediterranean and the Central Paratethys during the latest Burdigalian (Karpattian); this confirms the finding of *H. leobendorfensis* Zorn, 1998 in the Korneuburg Basin (Austria) (Zorn 1998) and the spatial distribution of *H. vejehonensis* in the Middle Miocene. This later, geographically and stratigraphically most widespread species in the genus *Helicythere*, occurred in the upper Burdigalian deposits of the Porto Torres Basin (Sardinia, Italy) (Bossio et al. 2006) and during the early Badenian it migrated and successfully settled in the marine ecosystems of the Carpathian Foredeep and the Vienna Basin (Procházka 1893; Zorn 1999, 2004; Bretenšká & Jiřiček 1978; Zelenka 1985; Gross 2006; Seko et al. 2012).

Whereas *H. leobendorfensis* has an elliptical outline in dorsal view without alae, *H. vejehonensis* is highly variable in shape and ornamentation, possibly linked with its large geographic range, different water chemistry among the basins, or a combination of these factors.

In the lower Badenian sediments of the Carpathian Foredeep, *H. moravica* has been identified in the marine ostracod associations (Procházka, 1893; Bretenšká & Jiřiček 1978; Seko et al. 2012 and this paper). Procházka (1893) recorded *H. moravica* (= *C. moravica*) as a relatively common species in the sediments of the Carpathian Foredeep, but this information was not confirmed by later studies. Currently, this species is known from the latest Badenian parastratotype Židlochovice only.

During the late Badenian, marine conditions persisted in the Central Paratethys, but a closure of the Slovenian corridor (Rögl 1999) caused an isolation of *Helicythere* from the Mediterranean populations. *H. vejehonensis* settled the Vienna Basin (Austria, Czech Republic) and extended up to the Balkans (Rundić 1992; Rundić et al. 2000).

Stancheva (1962; p. 38-39, pl. 5, fig. 6) found *H. vejehonensis* in the Badenian sediments of the NW Bulgaria, identifying it as *Matilus (Aurula) magnesi* (Keij).

Gross (2006; p. 61; pl. 35, figs 9-10) documented juveniles of *Helicythere* sp. 1 from the Vienna Basin with rounded postero-ventral process, which is usually pointed in juveniles and adults of *Helicythere*.

It is likely that the salinity reduction and chemism change of sea water on supersaturated carbonic water with high alkalinity (Pisera 1996) caused the extinction of *Helicythere* in the Central Paratethys area during the late Serravallian. Later, the genus survived in marine conditions in the Mediterranean during the Late Miocene.

Only *H. vejehonensis* is known from the Tortonian after the extinction of Paratethyan species. This species occurred in coral reef complexes in the Eastern Mediterranean (Crete), Italy, Sicily and Spain (Bonaduce et al. 1988; Comesa & Babinot 1999; Paranda et al. 2008). It is also known from early Messinian deposits in southern Italy, northern Algeria, and Skyros Island (Miculcan 1992; Babinot & Boukli-Hacene 1998; Guernet 2005), but ornamentation and outline start to differentiate from the Middle Miocene *H. vejehonensis*. It is still possible to recognize the radial ribs, but *H. vejehonensis* has a restricted postero-ventral process (pl. 4, fig. 9, Bonaduce et al. 1988).

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**PLATE 1**

LV - left valve; RV - right valve; C - carapace.

**Fig. 1** - *Cylthere moravica* Procházka, 1893, locality: Židlochovice, Czech Republic. 1) LV; 2) ZID1, 2.3-2.4 mm, external lateral view.

**Figs 2-13** - *Helicythere moravica* (Procházka, 1893), locality: Židlochovice, Czech Republic. 2) RV, ZID2, 9.7-9.8 mm, external lateral view; 3) RV, ZID2, 9.7-9.8 mm, external lateral view; 4) LV, ZID2, 9.7-9.8 mm, external lateral view; 5) RV, MS-2-16, ZID1, 2.3-2.4 mm, external lateral view; 6) LV, MS-2-16, ZID1, 2.3-2.4 mm, external lateral view; 7) LV, ZID2, 2.3-2.4 mm, external lateral view; 8) RV, ZID2, 2.3-2.4 mm, external lateral view; 9) ZID2, 2.3-2.4 mm, external lateral view; 10) RV, ZID1, 2.3-2.4 mm, external lateral view; 11) ZID2, 2.3-2.4 mm, external lateral view; 12) RV, ZID2, 2.3-2.4 mm, external lateral view; 13) RV, ZID2, 2.3-2.4 mm, external lateral view.

**Figs 14-16** - *Helicythere vejehonensis* (Procházka, 1893), locality: Židlochovice, Czech Republic. 14) LV, ZID2, 9.7-9.8 mm, external lateral view; 15) RV, MS-2-39, ZID2, 9.7-9.8 mm, external lateral view; 16) MS-2-39, ZID1, 9.7-9.8 mm, external lateral view; 17) MS-2-39, external oblique lateral view.

**Fig. 17** - *Helicythere magnesi* (Keij, 1955), locality: Kuh-e-Dochah, Northwest Qom, Iran. 17 C, MT 167, external oblique lateral view.
Fig. 2 - Paleogeography and stratigraphical distribution of Heloiothere.
A heavy and distinctive ornamentation with prominent alae distinguishes the early Messinian *H. vejho- nensis* of Malta (Bonaduce et al. 1988, pl. 4, figs. 6-8) from the specimens from the Carpathian Foredeep (Procházka 1893; see also Gross 2006, pl. 35, pl. 36, fig. 5; this paper, Pl. 1, Figs 14-16). The specimens from Malta may represent a new species of *Helioicythere* (Fig. 2), morphologically close to *H. moravica* regarding a deltoid outline and ribs visible in dorsal and ventral views.

The highest number of *Helioicythere* species yet known is from the Messinian of the Melqart Formation (Gulf of Gabes, Tunisia) (Bonaduce et al. 1992). There have been identified *H. brontotherium* Bonaduce et al. 1988, also known from Sicily, *H. simplicissima* Bonaduce, Ruggieri, Russo & Bismuth, 1992 and *Helioicythere anura* Bonaduce, Ruggieri, Russo & Bismuth, 1992 (Bonaduce et al. 1992). The oldest but unconfirmed occurrence of *H. simplicissima* and *H. anura* is assumed from the Burdigalian of Corsica (Ferrandini et al. 2002).

*H. brontotherium* has the most bizarre ornamentation with variable development of tubercles (Bonaduce et al. 1988, pl. 4, figs. 12-14) typical for anomohalin *Cyprideis torosa* (Jones, 1850) living in different ranges of salinity. *H. simplicissima* is similar to *H. leóbendorfensis*, but differs in development of the radial ribs and size of fossae (Gross 2006). The radial ribs of *H. anura* suggest a taxonomic position within *Helioicythere*, but its outline from lateral and dorsal views are unusual in comparison with *H. vejhoennis*, *H. magnei* and *H. moravica*. In conclusion, all Melqart Formation *Helioicythere* species have unusual or abnormal characters which are on a limit for clear determination of *Helioicythere* genus. Due to the absence of radial ornamentation on the anterior area, which is a primary character of genus, *H. latebrata* Bonaduce, Ruggieri, Russo & Bismuth, 1992 from the Melqart Formation (Bonaduce et al. 1992) is here not regarded as belonging to *Helioicythere*.

The ostracod species identified in the Messinian Porites limestone of Algeria as Gen. 1 sp. (Cytherididae?) (Guéret et al. 1984, pl. 2, fig. 1) is here supposed as *H. vejhoennis* with postero-dorsal protrusion, but without postero-ventral process; this suggest that this species is close to *H. vejhoennis* from Sicily (Bonaduce et al. 1988, pl. 4, fig. 9).

The westernmost occurrence of *Helioicythere* was recorded from the Azores in the Atlantic Ocean in the Messinian NN11b zone (Meireles et al. 2012, pl. 3, figs. 7-9). *H. magnei* has very developed radial ribs, rounded and oblique postero-ventral margin terminated by pointed process and weak alae. We suppose that this species is new and different in outline from the Early Miocene *Helioicythere*. Bossio et al. 1996 identified *H. magnai* in the Messinian of Livornesi Mountains ("off reef talus-slope facies", Rosignano reef complex, Central Italy p. 283) and in the Messinian (T. quinqueloba Zone) of Calcarenits di Androano Formation, Apulia, Italy (Bossio et al. 2005, p. 44). We cannot confirm these identifications, because *Helioicythere* is not figured. Aranik et al. (1992) described a new Early Pliocene subspecies of *H. vejhoennis moravica* from southern Spain, which would imply that the genus survived the Messinian crisis. An attribution of the Vejer de la Frontera section to the Pliocene is based on unpublished nannoplankton data (Aranik et al. 1992), Giannelli et al. (1982) and Foresi et al. (2002) attribute the Vejer de la Frontera section largely to the Tortonian based on planktonic foraminifers and nannoplankton, except for the upper part of the section, which is Messinian. Based on these facts, a Pliocene record of *Helioicythere* is uncertain.

In contrast to the unusual Messinian and Tortonian *Helioicythere described in this article, *H. vejhoennis moravica* conserved characters of the Early and Middle Miocene heliocysts – radial ribs, postero-ventral process and postero-dorsal protrusions. It differs in outline at anterior, ventral and postero-ventral and development of ventral ribs from the typical *H. vejhoennis* from the Carpathian Foredeep (Aranik et al. 1992, pl. 1, fig. 17, 18; this paper, Pl. 1, Figs 14-16) and in this view, the rank of *H. vejhoennis moravica* should be changed from subspecific to specific.

**Paleoecology of genus Helioicythere**

No post-Pliocene occurrence has been identified to the present day, making thus *Helioicythere* an extinct marine genus; therefore, paleoecological interpretation has to be done basing on all accessible geologic, sedimentologic and paleobiologic data from the fossil record. However, such data are sporadic and insufficient.

**Helioicythere in the locality Židlochovice**

A quantitative analysis of the ostracod assemblages from the early Badenian of Židlochovice locality indicates that *Helioicythere* was a rare genus within ostracod associations (maximum dominance of *H. moravica* 5.9 %, *H. vejhoennis* 6.8 %) and lived in marine environment which evolved from circalittoral/epibathyal to shallow infralittoral (Seko et al. 2012). Well-preserved and numerous *Helioicythere* valves and carapaces without any evidence of transport occur in two subsidiary cores; this allows us to constrain the bathymetrical preferences of both *Helioicythere* species (Fig. 3).

*H. moravica* firstly occurs in sample 12 (1 individual) in association with circalittoral /? epibathyal os-
tracods, such as 

Buntonia subulata
subulata Ruggieri, 1954, 

Cytherella pessens
postdenticulata Oertli, 1961, 

Henrybouwella asperima
(Reuss, 1850), and 

Bosquetina
carnella (Reuss, 1850) (Fig. 3 – B). The abundance of 

H. moravica
is low (0-4 individuals per sample) in samples 

13 to 8 representing deeper marine environment; this 

leads to the interpretation that this environment was 

not optimal or that the individuals were transported 

into this environment.

A high abundance of 

H. moravica
(18 individuals) in 

sample 3 (ZID1) and in samples of the stratigraphically 

superposed core ZID2 (samples 18, 16 and 14-16, 

23, 20 individuals) was observed in the samples where 

marine littoral taxa became abundant and dominant 

along with taxa tolerating decrease of salinity e.g. Aurla 

spp., 

Cnestocythere lamellicosta Triebel, 1950, 

Loxocorenculum hastatum (Reuss, 1850), 

Pokornyna deformis (Reuss, 1850), 

Seneisiphiili (Reuss, 1850) and 

Tenedocythere suctatopunctata (Reuss, 1850). An increase in 

abundance of 

H. moravica
individuals in these samples together with change of assemblage structure (Seko et al. 2012) indicates that 

H. moravica
preferred shallower infralittoral conditions. This assumption on bathymetric preference is supported by an increase in 

abundance of ostracod carapaces toward a top of the drills indicating higher sedimentary rate (Seko et al. 2012). 

H. moravica
carapace distribution follows the same trend along both cores too (Fig. 3-A).

In core ZID1 (Fig. 3 – B), which partially overlaps 

core ZID2, the maximum of abundance of 

H. vejbornensis
is in sample 11 (11 individuals) in which 

H. vejbornensis
associates with circalittoral/?epibathyal marine taxa such as 

Bosquetina carnellaa, 

Cytherella pessens
postdenticulata, 

Henrybouwella asperima
and 

Krithe sp. From this level, the abundance of 

H. vejbornensis
individuals decreased towards the top in both cores, where 

marine species tolerating a salinity decrease dominated, 

e.g. 

Aurla cicatrica (Reuss, 1850), A opaca (Reuss, 

1850), 

Grimioneis hadingeri (Reuss, 1850), 

Cnestocythere lamellicosta Triebel, 1950, 

Loxocorenculum punctata (Reuss, 1850) (Seko et al. 2012).

The presence of Platycopida in assemblages of 

cores ZID1 and ZID2 (Fig. 3 - C) does not exceed 

11.5%. This, according to Whateley et al. (2003) and 

the Platycopid Signal Hypothesis (PSH), indicates very 

well oxygenated environment containing 

O2> 5 ml/l. 

Brandão & Horne (2009) maintain that the modern data 
do not support the PSH, but neither do they disprove it. 

Paleontological analysis of foraminifers and molluscs from 

Židlochovice indicate a poorly oxygenated environment 
(Doláková et al. 2014). It follows, that the 

O2
level parameter cannot be clearly defined for 

Heliocythere from the lower Badenian sediments of 

Židlochovice.

The assemblages from Židlochovice suggest that 

there was a difference in bathymetric preferences 

between 

H. moravica
and 

H. vejbornensis. From quantitative 
terms it is evident that larger 

H. moravica
preferred an infralittoral zone and smaller 

H. vejbornensis
lived in a deeper, circalittoral/?epibathyal environment.

Heliocythere from other Cenozoic regions

The late Aquitanian 

H. magnei
from Villandraut 

(Aquitaine Basin) was described from coastal-epineritic 

facies (Moyses 1965). Conversely, the occurrence of this 

species in the early Burdigalian of Iran was recorded in 

association with marine deep-water genera, such as 

Cytherella, Krithe and Paracypris, from silty clay deposits 

originated in a cold upper bathyal zone (250-300 m) 

with euhaline salinity and low O2 content (2-2.5 ml/l). 

H. magnei
was represented by only one carapace in this 

assemblage and therefore an autochthonous origin 
cannot be confirmed herein. 

H. loebendorfensis Zom, 

1998, discovered in Leobendorf (Korpatin; Korneburg 

Berg, Lower Austria) is associated with 21 other 

ostracod species (Zorn 1998, tab. 2, p. 217), e.g. 

Aurla spp., 

Barodopilata sp., 

Loxocorenculum hastatum, 

Cnestocythere truncata (Reuss, 1850), which occurred in 
in warm (tropical/subtropical) shallow marine paleoenvironment without brackish water influx.

H. vejbornensis
was the most widespread of all 

Heliocythere species in space and time. In the ostracod 

assemblage from the late Burdigalian of the Porto Torres Basin (N. Sardinia, Italy), 

H. vejbornensis
was associated with outer neritic/upper epibathyal 

Bairdia
conformis Terquem, 1878, 

Cytherella spp., Ruggieria 

spp., Costa spp., deeper marine 

Henrybouwella asperima, infra/circalittoral 

Cnestocythere truncata. Bossio et al. (2006) infer that a dominance of open shelf environment 
taxa and reduced occurrence of littoral taxa is in 

accordance with the foraminiferal P/B ratio; they 
suppose a depositional setting referable to the intermediate 

part of the outer neritic zone and this is in agreement 

with the occurrence of 

H. vejbornensis
in the Židlochovice ostracod association.

However, other Cenozoic occurrences of 

H. vejbornensis
indicate a preference for shallower marine environment.

Zelenka (1985) recorded 

H. vejbornensis
in the Vienna Basin in association with several marine shallow-water species, such as 

Cytheridea acuminate acuminate
Bosquet, 1852, 

Pokornyna deformis, 

Urocysthes kostelensis (Reuss, 1850) and shallow-water foraminifers, such as 

stenoaline epiphytic 

Asterigerinata planorbis (d’Orbigny, 1846), 

Elphidium macellum (Fichtel & Moll, 1798), and 

E. fichtelidsanum (d’Orbigny, 1846). These findings indicate that 

H. vejbornensis
occurred in a shallow marine water of the near-shore zone (inner sublittoral).
Fig. 3 - ZID1 and ZID2 core profiles: A) Valves/Carapaces distribution of H. moravica along cores; B) H. moravica and H. vejehonensis distribution of individuals (valves + carapaces) along cores; C) Distribution and percentage of Platycopida in ostracod assemblages along cores. For methodological approach, see Seko et al. (2012).
Zorn (2004) observed *H. vejbonensis* in an association of 61 species in the early Badenian Grund Formation of the Molasse Basin and concluded that this species lived in warm shallow-water environment not exceeding 100 m depth. In the late Badenian ostracod assemblages from the Vienna Basin, Gross (2006) ranked *H. vejbonensis* and *Helicythere* sp. 1 among the elements of epiteritic fauna which lived in shallow marine (<50 m depth) tropical/subtropical paleoenvironments.

Rundić (1992) described the paleoenvironment of *H. vejbonensis* from the late Badenian locality Gornja Trnava (NE Bosnia) as tropical/subtropical sea with depth of water not exceeding 50 m, with higher O2 level and normal salinity, which formed favourable conditions for rich littoral-neritic bioenesis. Along with *H. vejbonensis*, the sporadic occurrence of the dinoflagellate *Semseya lamellata* was recorded in the upper Badenian (NN6 zone) sediments from Bogutovo Selo (NE Bosnia) which suggest a shallow and protected sea with some terrigenous influx (Rundić et al. 2000).

Meireles et al. (2012) recorded *H.* sp. (originally *H. magni*) as a frequent species in the Late Miocene association dominated by littoral *Loxoconcha stellifera* Mueller, 1894, *Dameriella aff. dameriacensis* (Keij, 1958)? *Quadracythere* sp., brackish infralittoral *Xestoleberis* cf. *pasi* Nascimento, 1989 and the thermophilic taxa of other phyla (brachiopods, gastropods, bivalves, sea-urchins); the authors inferred warm waters and epiteritic habitats with vegetated bottom.

*H. vejbonensis morisca* from Vejer de la Frontera (southern Spain) is associated with dominant Bairdiidae, Loxoconchidae, Xestoleberididae and Hemicytheridae. The occasional occurrence of deeper water ostracods, such as *Paraknithe, Henryhowella,* and *Acantocythereis,* suggests that these were transported upwards by wave surges during (seasonal) storms. *H. vejbonensis morisca* lived as a marine benthos in the nearshore and the shallow sea with paleodepth around 50 m (Aranki et al. 1992).

Conclusions

We designated a neotype for *Cythere monavica* Prochážka, 1893 and re-described *Helicythere monavica* (Prochážka, 1893). After more than one century of paleontological investigations in the Paratethys this large deltoid species is known only from the early Badenian (early Langhian) parastratotype at Židlochovice in the Carpathian Foredeep. This species, probably endemic to the Central Paratethys, is most abundant in the infralittoral association, but occurs in circalittoral/epibathyal deposits too.

The stratigraphic range of the extinct marine genus *Helicythere*, which includes 12 species (of which 4 are in open nomenclature), is longer than previously recorded and extends from the Early Oligocene (Rupelian) to the Late Miocene? Early Pliocene. The occurrences of *Helicythere* in Lower Oligocene (Rupelian) deposits of Oman, *H. magni* in the lower Burgudjian sediments of Iran, and *H. monavica* from the early Badenian of Central Paratethys provide further details on the paleobiogeographic and stratigraphic distribution and paleoenvironmental interpretation of this genus.

**Taxa currently referred to Helicythere**

- *H. magni* (Keij, 1955)
- *H. lebedevi* nov. sp. Zorn, 1998
- *H. vejbonensis* (Prochážka, 1893)
- *H. vejbonensis morisca* Aranki et al., 1992. – This subspecies differs from the nominotypical subspecies of *H. vejbonensis* (Prochážka, 1893) in outline at anterior, ventral and postero-ventral and development of ventral ribs. These marked differences suggest that *H. vejbonensis morisca* should be ranked at species level.
- *H. monavica* (Prochážka, 1893), re-described, this article
- *H. brontotherium* Bonaduce, Ruggieri & Russo, 1988
- *H. simplicicosta* Bonaduce, Ruggieri, Russo & Bismuth, 1992
- *H.? aurata* Bonaduce, Ruggieri, Russo & Bismuth, 1992 – this species has a very unusual outline from lateral and dorsal views for *Helicythere*, and for this reason its position within *Helicythere* is unclear.

**Helicythere sp. 1** nov. Gross, 2006

**Helicythere sp.** – determined in Guemet et al. (1991) as *Malzella* sp. 2.

**Helicythere sp.** – determined in Meireles et al. (2012) as *H. magni* (Keij, 1955). Basing on the valve outline and ornamentation, this could represent a new species.

**Helicythere sp.** – determined in Bonaduce et al. (1988) as *H. vejbonensis* (Prochážka, 1893). Different in outline in dorsal view, presence of alae and heavy ornamentation of original description, also this taxon could represent a new species.

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