

Rivista Italiana di Paleontologia e Stratigrafia	volume 121	no. 1	1 pl.	pp. 49-60	March 2015
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**PALEOBIOGEOGRAPHY AND PALEOECOLOGY OF THE OSTRACOD
HELIOCYTHERE BONADUCE, RUGGIERI & RUSSO, 1988
 WITH RE-DESCRIPTION OF MIDDLE MIOCENE
HELIOCYTHERE MORAVICA (PROCHÁZKA, 1893)
 FROM THE CARPATHIAN FOREDEEP (CZECH REPUBLIC)**

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Received: March 19, 2014; accepted: January 28, 2015

Key words: Ostracoda, Neotype, Miocene, Carpathian Foredeep, Central Paratethys, Mediterranean, Paleobiogeography, Paleocology.

Abstract. Twelve species attributed to the genus *Heliocythere* have been recorded from the epineritic/neritic and circalittoral/epibathyal deposits of Cenozoic subtropical 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). *Heliocythere* profited of a marine connection between the Mediterranean and the Paratethys through the Slovenian corridor during the latest Burdigalian (Karpatian) and settled in Central Europe and Balkan Peninsula marine biotopes, but a paleogeographic and paleoecologic change during the late Serravallian caused an extinction of Paratethyan *Heliocythere*. In Late Miocene times, *Heliocythere* 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 *Heliocythere*. No *Heliocythere* 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 herewith a neotype for the early Badenian (early Langhian) *Cythere moravica* Procházka, 1893 from the Carpathian Foredeep, referred to in this work as *Heliocythere moravica* (Procházka, 1893). We discuss its paleoecology and position within the genus *Heliocythere*.

Introduction

Procházka (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 & Jiríček (1978) considered as doubtful the generic assignment of *C. moravica* within the genus *Cythere* and used only open nomenclature “Gen. Indet.” *moravica* (Procházka), 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 Procházka’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 Židlochovice, sev-

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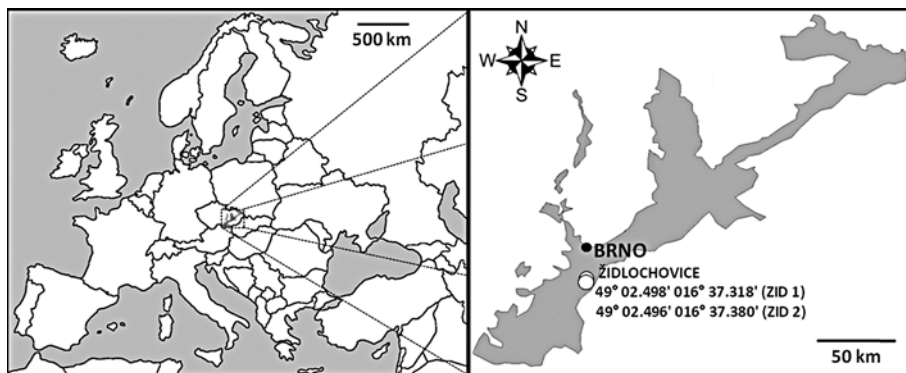


Fig. 1 - Geographical/geological position of locality Židlochovice (Carpathian Foredeep, Czech Republic) with boreholes 49° 02.498' N, 16° 37.318' E (ZID 1), 230 m above sea level and 49° 02.496' N, 16° 37.380' E (ZID 2), 246 m above sea level.

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 *Heliocythere* 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 paleoecological data on *Heliocythere*.

Geological and biostratigraphic framework

The marine deposits around the small city Židlochovice (Fig. 1) in the Carpathian Foredeep (Moravia, Czech Republic) originated in front of the forehead of the Carpathian Paleogene nappes (Chlupáč 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, anthozoa, 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 Židlochovice 1 (ZID1) and Židlochovice 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 NN5 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 Židlochovice 1 and Židlochovice 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 specimens; $\bar{\varphi}$, average; ♀, female; ♂, 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 *Heliocythere moravica* (Procházka, 1893).

- Class **Ostracoda** Latreille, 1802
- Subclass **Podocopa** Sars, 1866
- Order **Podocopida** Sars, 1866
- Suborder **Cytherocopina** Baird, 1850
- Superfamily Cytheroidea Baird, 1850
- Family Hemicysteridae Puri, 1953
- Subfamily Thaerocytherinae Hazel, 1967
- Genus *Heliocythere* Bonaduce, Ruggieri & Russo, 1988
- Type species: *Hemicythere magnei* Keij, 1955

Heliocythere 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 & Jiříček, p. 437, pl. 8, fig. 9.

2010 *Cythere moravica* Procházka, 1893 - Zorn, p. 285, pl. 3, figs. 33-35.

2012 “Gen. Indet.” *moravica* (Procházka, 1893) - Seko et al., p. 120, fig. 7].

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

Other material: MSRP-1-8, RV♀(ZID2, 9.7-9.8 m), Pl. 1, Fig. 2; MSRP-1-7, RV♂(ZID2, 9.7-9.8 m), Pl. 1, Fig. 3; MS-2-16, LV♀(ZID1,

2.3–2.4 m), Pl. 1, Fig. 4; MSRP-1-5, LV♂(ZID1, 2.3–2.4 m), Pl. 1, Fig. 5; MS-2-17, RV♀ (ZID2, 9.7–9.8 m), Pl. 1, Fig. 6; MSRP-1-4, LV♂ (ZID1, 2.3–2.4 m), Pl. 1, Fig. 7; MSRP-1-2, LV♀ (ZID1, 2.3–2.4 m), Pl. 1, Fig. 8–9; MSRP-1-6, RV♀ (ZID1, 2.3–2.4 m), Pl. 1, Fig. 10–11; MSRP-1-9, C♀ (ZID2, 9.7–9.8 m), Pl. 1, Fig. 12; MSRP-1-3, C♀ (ZID1, 2.3–2.4 m), Pl. 1, Fig. 13.

Locus typicus of the neotype: core ZID1, Židlochovice, Vejhon hill, Moravia, Czech Republic, co-ordinates: 49° 02.498' N, 16° 37.318' E (ZID 1), sample No. 3 (2.3–2.4 m)

Stratum typicum: Middle Miocene, early Badenian – Moravian (Mediterranean Stage: early Langhian).

Diagnosis: The largest among all known species referred to the genus *Heliocythere*; the radial ribs arranged from the centre to outer margin; narrow sagittate posterior and deltaic outline visible in the dorsal view; prominent ala and elliptical fossae.

Description. LV ♀ (Neotype): AM widely rounded; DM sloping toward posterior and overlapped by postero-dorsal rib; ADM and PDM angles rounded; PM oblique with prominent postero-ventral process; VM concave in the first third and overlapped by ala; outline rectangular, maximum height at anterior.

RV♀: AM widely rounded; DM sloping toward posterior and overlapped by postero-dorsal rib; ADM and PDM widely rounded or almost not visible; PM oblique with postero-ventral process; VM strongly concave in the first third than widely rounded; outline sub-rectangular; maximum height at anterior.

Sexual dimorphism: males longer than females.

Muscle scars: not well visible, consisting of vertical row of four semi-circular scars; frontal muscle scar strong and elongated; dorsally, elliptical scars visible on the prolongation of the central muscle scars and frontal muscle scars axis.

Normal pore canals: open.

Hinge: amphidont; the hinge of the RV is composed of rounded tooth. It continues to shallow socket and smooth groove. Elongate tooth in posterior into three lobes. The elements of the LV opposite to RV.

Ornamentation: the carapace has dominant alae and significant eye tubercles; the surface is formed by radially arranged ribs; six ribs are visible in ventral view at the ventral side. Circular and semi-circular fossae are the largest on centro-ventral area and towards the AM and PM shrinks to a size of punctae.

Marginal zone: inner lamella 0.08 mm large at AM, slightly shorter (0.06–0.07 mm) at VM and PM and almost fused with outer lamella; vestibulum very narrow or almost invisible; inner margin parallel to outer margin; MPC numerous, straight, thin and dense on AM, their density is slightly lower at VM and PM; bifurcated MPC visible at AVM; zone of fusion almost of the same size as inner lamella; line of conrescence parallel with inner margin.

Discussion. The radially arranged ribs allow us to attribute this unique, probably largest species to the

	N	l	h	w
LV♀, neotype, MSRP-1-1	1	1.051	0.57	-
LV♀	3	1.00–1.017	0.558–0.583	-
RV♀	3	1.017	0.542–0.567	-
LV♂	2	1.00–1.067	0.533–0.575	-
RV♂	1	1.050	0.567	-
C♀	2	1.00	-	0.600

Tab. 1 - Dimensions (in mm) of *Cythere moravica* Procházka, 1893, neotype, MSRP-1-1 and several individuals of *Heliocythere moravica* (Procházka, 1893), Židlochovice. Abbreviations: see text.

genus *Heliocythere*. A pronounced deltoid shape in dorsal view is the principal character of *H. moravica*, caused by a presence of alae. This character is well visible also in *H. vejhonensis* (Procházka, 1893) in Bonaduce et al. (1988, pl. 4, figs. 6–8) here supposed as new species (see chapter Paleobiogeography of genus *Heliocythere*), but both species differ at posterior and anterior which are sagittate in *H. moravica*. *H. vejhonensis* occurs in association with *H. moravica* in the Carpathian Foredeep, but the latter is robust, larger, with ala and lacking the postero-dorsal protrusions.

Stratigraphical and geographical range. This species has been found so far only in clay and marl of the early Badenian (early Langhian) parastratotype at Židlochovice (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 outcoming 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. magnei (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 Aqu-

tanian) in the Aquitanian Basin (France) (Bonaduce et al. 1988). Moyes (1965) identified *H. magnei* (originally as *Aurila magnei*) from two outcrops of SW France, which were dated as Aquitanian. *H. magnei* (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 *Heliocythere* 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 *Heliocythere* are restricted to the Mediterranean and Paratethys areas.

Heliocythere profited of a marine connection between the Mediterranean and the Central Paratethys during the latest Burdigalian (Karpatian); this confirms the finding of *H. leobendorfensis* Zorn, 1998 in the Korneuburg Basin (Austria) (Zorn 1998) and the spatial distribution of *H. vejhonensis* in the Middle Miocene. This later, geographically and stratigraphically most widespread species in the genus *Heliocythere*, 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; Brestenská & Jiříček 1978; Zelenka 1985; Gross 2006; Seko et al. 2012).

Whereas *H. leobendorfensis* has an elliptical outline in dorsal view without alae, *H. vejhonensis* 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; Brestenská & Jiříček 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 early 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 *Heliocythere* from the Mediterranean populations. *H. vejhonensis* 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. vejhonensis* in the Badenian sediments of the NW Bulgaria, identifying it as *Mutilus (Aurila) magnei* (Keij).

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

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 *Heliocythere* 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. vejhonensis* 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; Conesa & Babinot 1999; Faranda et al. 2008). It is also known from early Messinian deposits in southern Italy, northern Algeria, and Skyros Island (Miculan 1992; Babinot & Boukli-Hacene 1998; Guernet 2005), but ornamentation and outline start to differentiate from the Middle Miocene *H. vejhonensis*. It is still possible to recognize the radial ribs, but *H. vejhonensis* has a restricted postero-ventral process (pl. 4, fig. 9, Bonaduce et al. 1988).

PLATE 1

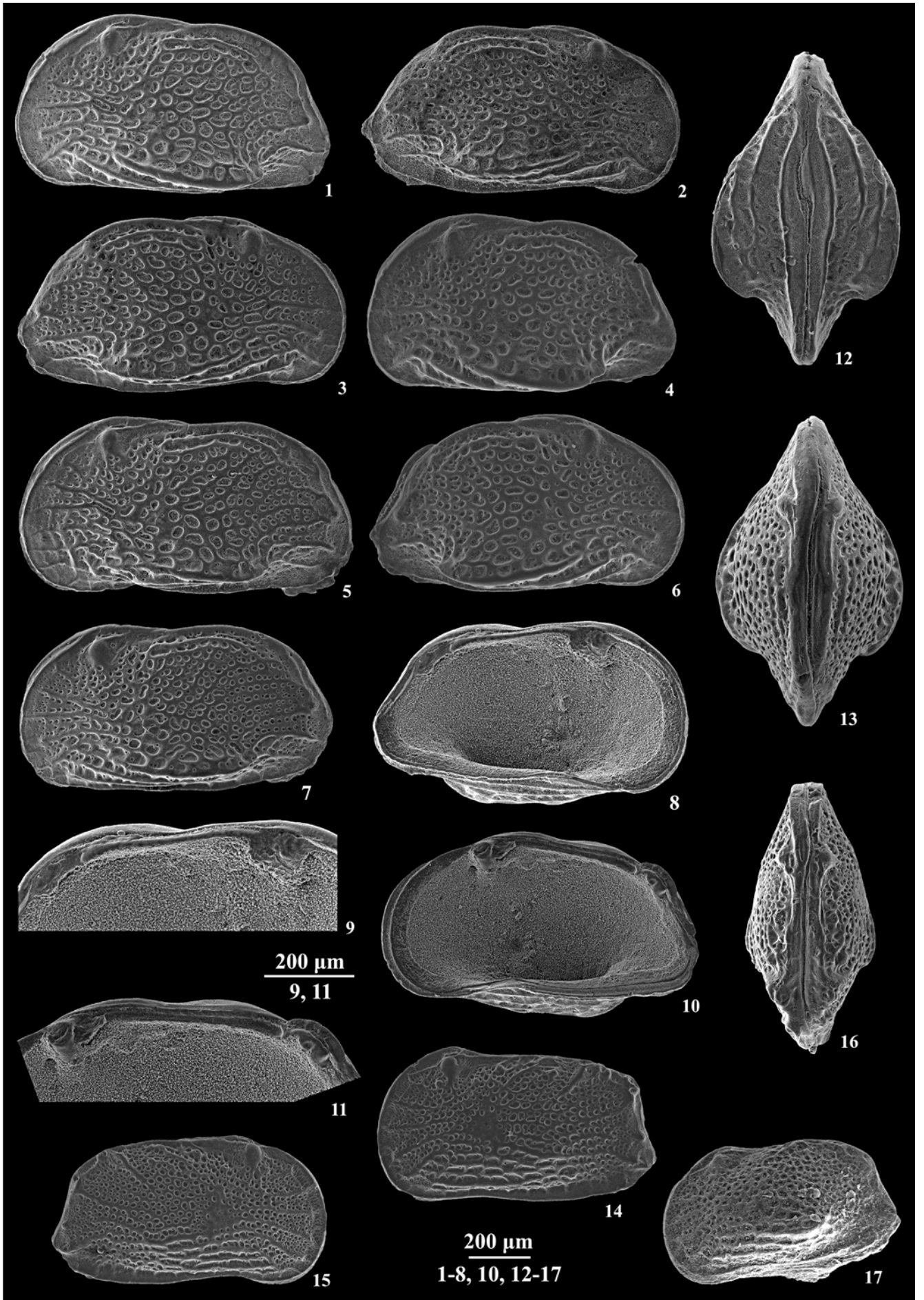
LV - left valve; RV - right valve; C - carapace.

Fig. 1 - *Cythere moravica* Procházka, 1893, locality: Židlochovice, Czech Republic. 1) LV♀, neotype, MSRP-1-1, ZID1, 2.3-2.4 m, external lateral view.

Figs 2-13 - *Heliocythere moravica* (Procházka, 1893), locality: Židlochovice, Czech Republic. 2) RV♀, MSRP-1-8, ZID2, 9.7-9.8 m, external lateral view; 3) RV♂, MSRP-1-7, ZID2, 9.7-9.8 m, external lateral view; 4) LV♀, MS-2-16, ZID1, 2.3-2.4 m, external lateral view; 5) LV♂, MSRP-1-5, ZID1, 2.3-2.4 m, external lateral view; 6) RV♀, MS-2-17, ZID2, 9.7-9.8 m external lateral view; 7) LV♂, MSRP-1-4, ZID1, 2.3-2.4 m, external lateral view; 8, 9) LV♀, MSRP-1-2, ZID1, 2.3-2.4 m, 8 - internal lateral view, 9 - detail of the hinge; 10, 11) RV♀, MSRP-1-6, ZID1, 2.3-2.4 m, 10 - internal lateral view, 11 - detail of the hinge; 12) C♀, MSRP-1-9, ZID2, 9.7-9.8 m, ventral view; 13) C♀, MSRP-1-3, ZID1, 2.3-2.4 m, dorsal view.

Figs 14-16 - *Heliocythere vejhonensis* (Procházka, 1893), locality: Židlochovice, Czech Republic. 14) LV, MS-2-40, ZID1, 9.7-9.8 m, external lateral view; 15) RV, MS-2-39, ZID1, 9.7-9.8 m, external lateral view; 16) C) MSRP-3-1, ZID2, 12.7-12.8 m, dorsal view.

Fig. 17 - *Heliocythere magnei* (Keij, 1955), locality: Kuh-e-Dochah, Northwest Qom, Iran 17 C, MT 167, external oblique lateral view.



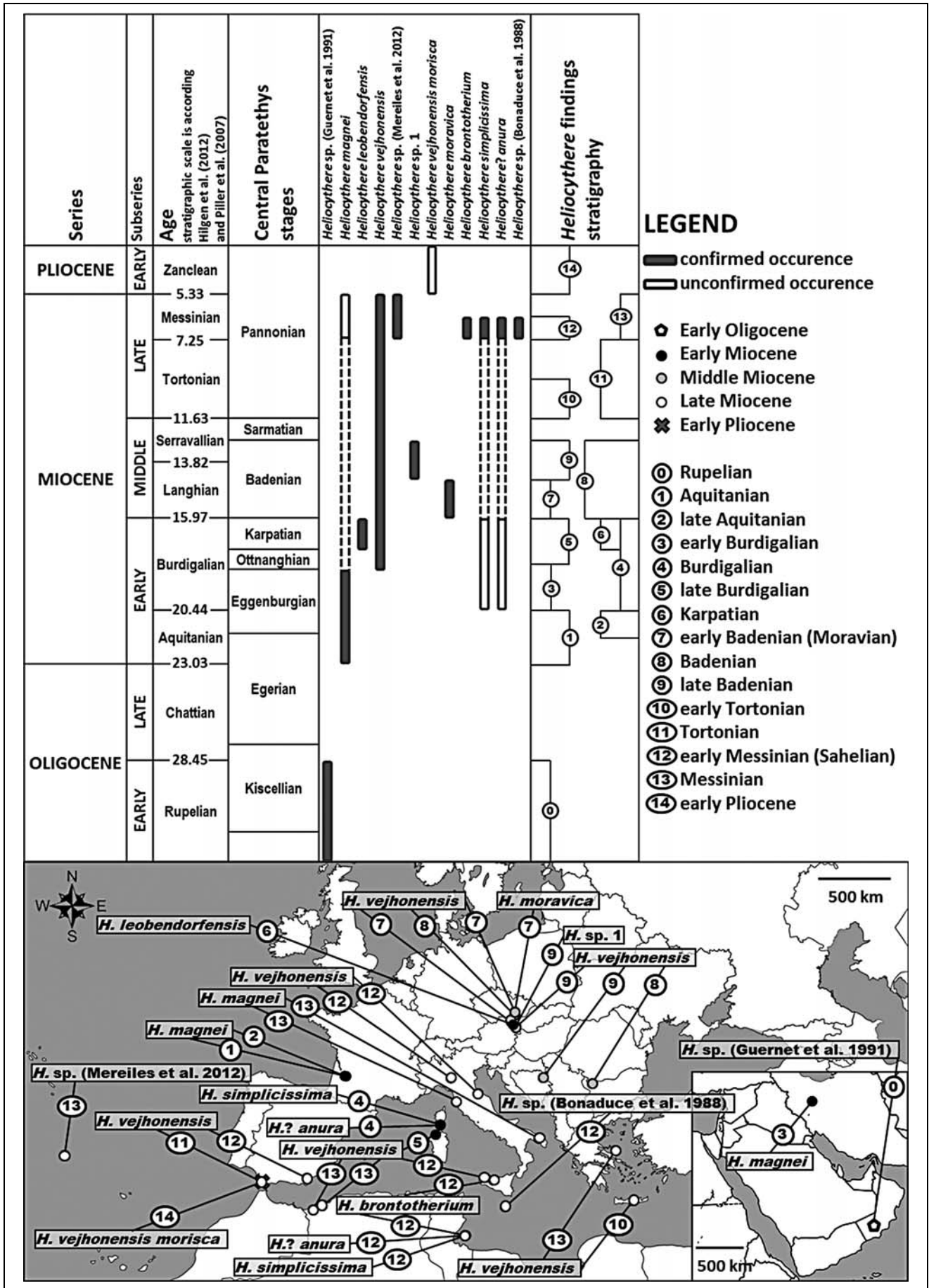


Fig. 2 - Paleogeography and stratigraphical distribution of *Heliocythere*.

A heavy and distinctive ornamentation with prominent alae distinguishes the early Messinian *H. vejhonensis* 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 *Heliocythere* (Fig. 2), morphologically close to *H. moravica* regarding a deltoid outline and ribs visible in dorsal and ventral views.

The highest number of *Heliocythere* 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 *Heliocythere?* *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. leobendorfensis*, 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 *Heliocythere*, but its outline from lateral and dorsal views are unusual in comparison with *H. vejhonensis*, *H. magnei* and *H. moravica*. In conclusion, all Melqart Formation *Heliocythere* species have unusual or abnormal characters which are on a limit for clear determination of *Heliocythere* 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 *Heliocythere*.

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

The westernmost occurrence of *Heliocythere* 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 *Heliocythere*. Bossio et al. 1996 identified *H.*

magnei 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 Calcareniti di Andrano Formation, Apulia, Italy (Bossio et al. 2005, p. 44). We cannot confirm these identifications, because *Heliocythere* is not figured. Aranki et al. (1992) described a new Early Pliocene subspecies of *H. vejhonensis morisca* 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 (Aranki 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 *Heliocythere* is uncertain.

In contrast to the unusual Messinian and Tortonian *Heliocythere* described in this article, *H. vejhonensis morisca* conserved characters of the Early and Middle Miocene heliocythers – 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. vejhonensis* from the Carpathian Foredeep (Aranki et al. 1992, pl. 1, fig. 17, 18; this paper, Pl. 1, Figs 14-16) and in this view, the rank of *H. vejhonensis morisca* should be changed from subspecific to specific.

Paleoecology of genus *Heliocythere*

No post-Pliocene occurrence has been identified to the present day, making thus *Heliocythere* 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.

Heliocythere in the locality Židlochovice

A quantitative analysis of the ostracod assemblages from the early Badenian of Židlochovice locality indicates that *Heliocythere* was a rare genus within ostracod associations (maximum dominance of *H. moravica* 5.9 %, *H. vejhonensis* 6.8 %) and lived in marine environment which evolved from circalittoral/?epibathyal to shallow infralittoral (Seko et al. 2012). Well-preserved and numerous *Heliocythere* valves and carapaces without any evidence of transport occur in two subsidiary cores; this allows us to constrain the bathymetrical preferences of both *Heliocythere* 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 pestiensis postdenticulata* Oertli, 1961, *Henryhowella asperrima* (Reuss, 1850), and *Bosquetina carinella* (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. *Aurila* spp., *Cnestocythere lamellicosta* Triebel, 1950, *Loxocorniculum hastatum* (Reuss, 1850), *Pokornyella deformis* (Reuss, 1850), *Senesia philippi* (Reuss, 1850) and *Tenedocythere sulcatopunctata* (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. vejhonensis* is in sample 11 (11 individuals) in which *H. vejhonensis* associates with circalittoral/?epibathyal marine taxa such as *Bosquetina carinella*, *Cytherella pestiensis postdenticulata*, *Henryhowella asperrima* and *Krithe* sp. From this level, the abundance of *H. vejhonensis* individuals decreased towards the top in both cores, where marine species tolerating a salinity decrease dominated, e.g. *Aurila cicatricosa* (Reuss, 1850), *A. opaca* (Reuss, 1850), *Grinioneis haidingeri* (Reuss, 1850), *Cnestocythere lamellicosta* Triebel, 1950, *Loxoconcha punctatella* (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 Whatley et al. (2003) and the Platycopid Signal Hypothesis (PSH), indicates very well oxygenated environment containing $O_2 > 5$ 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 O_2 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. vejhonensis*. From quantitative terms it is evident that larger *H. moravica* preferred an infralittoral zone and smaller *H. vejhonensis* 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 (Moyes 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 O_2 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. leobendorfensis* Zorn, 1998, discovered in Leobendorf (Karpatian; Korneuburg Beds, Lower Austria) is associated with 21 other ostracod species (Zorn 1998, tab. 2, p. 217), e.g. *Aurila* spp., *Bairdoppilata* sp., *Loxocorniculum hastatum*, *Cnestocythere truncata* (Reuss, 1850), which occurred in warm (tropical/subtropical) shallow marine paleoenvironment without brackish water influx.

H. vejhonensis 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. vejhonensis* was associated with outer neritic/upper epibathyal *Bairdia conformis* Terquem, 1878, *Cytherella* spp., *Ruggieria* spp., *Costa* spp., deeper marine *Henryhowella asperrima*, 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. vejhonensis* in the Židlochovice ostracod association.

However, other Cenozoic occurrences of *H. vejhonensis* indicate a preference for shallower marine environment.

Zelenka (1985) recorded *H. vejhonensis* in the Vienna Basin in association with several marine shallow-water species, such as *Cytheridea acuminata acuminata* Bosquet, 1852, *Pokornyella deformis*, *Urocythereis kostelensis* (Reuss, 1850) and shallow-water foraminifers, such as stenohaline epiphytic *Asterigerinata planorbis* (d'Orbigny, 1846), *Elphidium macellum* (Fichtel & Moll, 1798), and *E. fichtelianum* (d'Orbigny, 1846). These findings indicate that *H. vejhonensis* occurred in a shallow marine water of the near-shore zone (inner sublittoral).

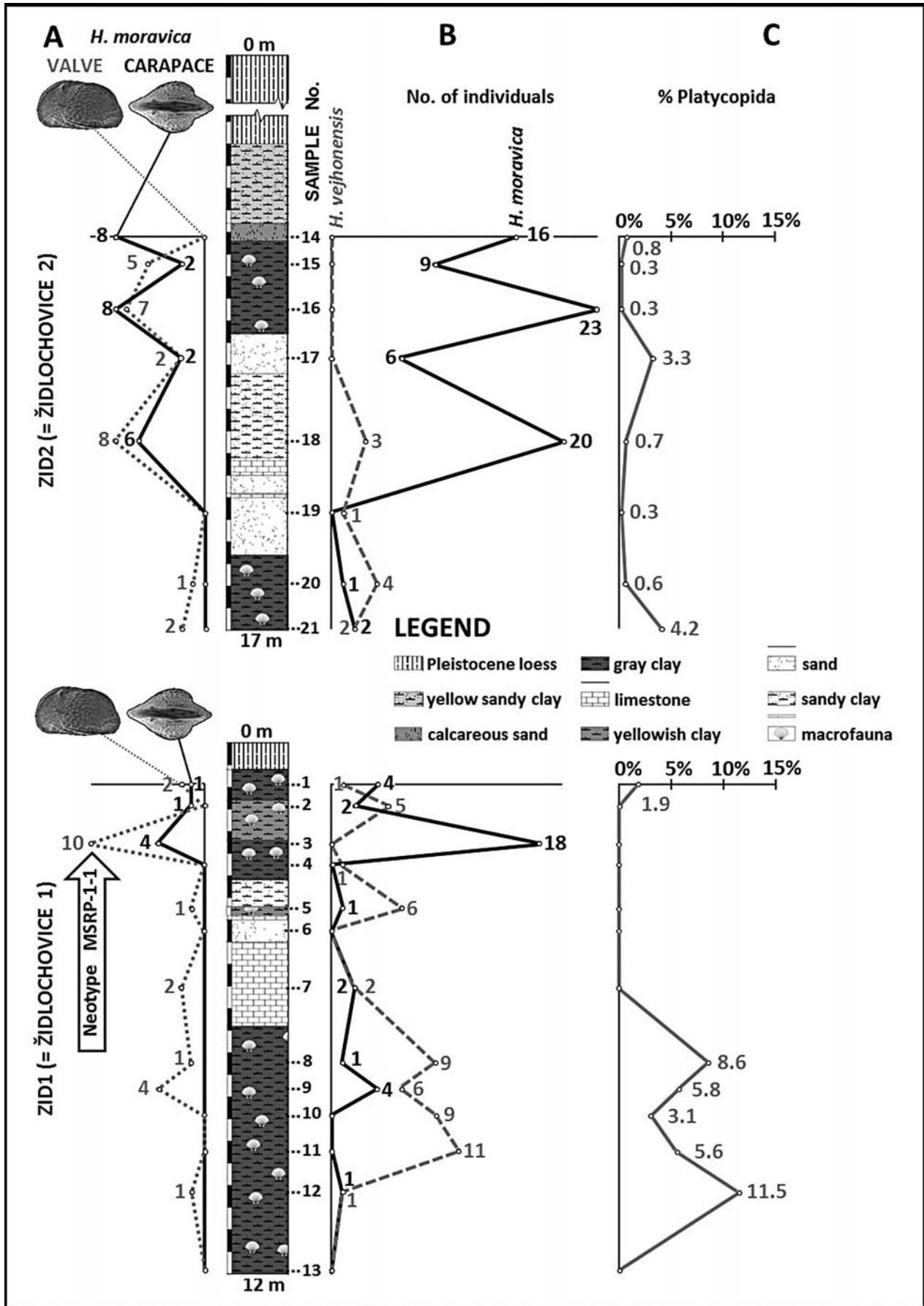


Fig. 3 - ZID1 and ZID2 core profiles: A) Valves/Carapaces distribution of *H. moravica* along cores; B) *H. moravica* and *H. vejhonensis* distribution of individuals (valves + carapaces). along cores; C) Distribution and percentage of Platycopeida in ostracod assemblages along cores. For methodological approach, see Seko et al. (2012).

Zorn (2004) observed *H. vejhonensis* 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. vejhonensis* and *Heliocythere* sp. 1 among the elements of epineritic fauna which lived in shallow marine (<50 m depth) tropical/subtropical paleoenvironments.

Rundić (1992) described the paleoenvironment of *H. vejhonensis* 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 biocoenosis. Along with *H. vejhonensis*, the sporadic occurrence of the dinoflagellate *Semseya lamellata* was recorded in the upper Badenian (NN6 zone) sediments from Bogutovo Selo (NE Bosnia) which suggests a shallow and protected sea with some terrigenous influx (Rundić et al. 2000).

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

H. vejhonensis 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 *Parakrithe*, *Henryhowella*, and *Acantocythereis*, suggests that these were transported upwards by wave surges during (seasonal) storms. *H. vejhonensis 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 moravica* Procházka, 1893 and re-described *Heliocythere moravica* (Procházka, 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 *Heliocythere*, 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 *Heliocythere* in Lower Oligocene (Rupelian) deposits of Oman, *H. magnei* in the lower Burdigalian sediments of Iran, and *H. moravica* 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 *Heliocythere*

H. magnei (Keij, 1955)

H. leobendorfensis Zorn, 1998

H. vejhonensis (Procházka, 1893)

H. vejhonensis morisca Aranki et al., 1992 – This subspecies differs from the nominotypical subspecies of *H. vejhonensis* (Procházka, 1893) in outline at anterior, ventral and postero-ventral and development of ventral ribs. These marked differences suggest that *H. vejhonensis morisca* should be ranked at species level.

H. moravica (Procházka, 1893), re-described, this article

H. brontotherium Bonaduce, Ruggieri & Russo, 1988

H. simplicissima Bonaduce, Ruggieri, Russo & Bismuth, 1992

H.? *anura* Bonaduce, Ruggieri, Russo & Bismuth, 1992 – this species has a very unusual outline from lateral and dorsal views for *Heliocythere*, and for this reason its position within *Heliocythere* is unclear.

Heliocythere sp. 1 sensu Gross, 2006

Heliocythere sp. – determined in Guernet et al. (1991) as *Malzella?* sp. 2.

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

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

Acknowledgements. In memory of the unexpectedly deceased co-author, Prof. Jean-Paul Colin. We thank Prof. Dr. Ljupko Rundić from University of Belgrad, Dr. Irene Zorn from the Geologische Bundesanstalt für Österreich, Dr. Martin Gross from the Universalmuseum Joanneum, and doc. RNDr. Katarína Holcová, CSc. from the Institute of geology and paleontology, Charles University in Prague for their help and support. We also thank the editor Prof. Johannes Pignatti (Sapienza University of Rome), and the reviewers Prof. Antonio Russo (University of Modena and Reggio Emilia), and Dr. Ilaria Mazzini (IGAG, National Research Council, Rome) for their help and constructive improvements. This work was realized in the frame of the project Centre of Excellence for Integrated Research of the Earth's Geosphere (ITMS: 26220120064), which is co-financed through the European Regional Development Fund. The work was co-financed by project VEGA 2/180/12 and APVV_0109_07.

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