First record of preserved soft parts in a Palaeozoic podocopid (Metacopina) ostracod, *Cytherellina submagna*: phylogenetic implications

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The metacopines represent one of the oldest and most important extinct groups of ostracods, with a fossil record from the Mid-Ordovician to the Early Jurassic. Herein, we report the discovery of a representative of the group with three-dimensionally preserved soft parts. The specimen—a male of *Cytherellina submagna*—was found in the Early Devonian (416 Ma) of Podolia, Ukraine. A branchial plate (Bp) of the cephalic maxillula (Mx), a pair of thoracic appendages (walking legs), a presumed furca (Fu) and a copulatory organ are preserved. The material also includes phosphatized steinkerns with exceptionally preserved marginal pore canals and muscle scars. The morphology of the preserved limbs and valves of *C. submagna* suggests its relationship with extant Podocopida, particularly with the superfamilies Darwinuloidea and Sigillioidea, which have many similar characteristic features, including a large Bp on the Mx, the morphology of walking legs, Fu with two terminal claws, internal stop-teeth in the left valve, adductor muscle scar pattern, and a very narrow fused zone along the anterior and posterior margins. More precise determination of affinities will depend on the soft-part morphology of the cephalic segment, which has not been revealed in the present material.

Keywords: soft-part preservation; bacteria-like organisms; Podolia; Metacopina; Ostracoda; Early Devonian

1. INTRODUCTION

The ostracods are the best-represented group of arthropods in the fossil record. More than 65 000 living and extinct species of ostracods have been described. However, knowledge of ostracod relationships in the Early Palaeozoic still remains inadequate. The systematics of living ostracods are based principally on the soft-part anatomy, which is almost unknown in the fossil record.

Here, we describe a single metacopine ostracod specimen of *Cytherellina submagna* [1] from the Lower Devonian (Lochkovian) of Podolia in the Ukraine, with partly preserved soft-part anatomy. The material also contains many specimens of the species with exceptionally preserved muscle scars, marginal structures and phosphatized marginal pore canals. The species belongs to the Podocopida (Metacopina)—one of the three major Palaeozoic ostracode groups. This taxonomic assignment is based on the hard-part characteristics.

The Lower Devonian sediments in Podolia also yield other Palaeocopida and Podocopida ostracod species. Preservation of the fossils in the locality is generally very good. Even the original colour pattern of the valves of some of the brachiopods is preserved [2].

Metacopine ostracods occur in the fossil record from the Mid-Ordovician to the Early Jurassic. They survived the end-Permian extinction, and were diverse and relatively abundant in the Triassic and Early Jurassic. The

extinction of the metacopines in the Early Toarcian time coincided with the onset of the Early Toarcian Oceanic Anoxic Event and a global eustatic sea-level rise. However, the metacopines probably lost in competition with more advanced cytheroidean ostracods in unfavourable environments [3].

In the Palaeozoic, examples of soft-part preservation of ostracods are extremely rare. Myodocopid ostracod species with soft parts preserved were described from the Lower Silurian Herefordshire Konservat-Lagerstätte in England [4–6]. A single specimen of a kirkbyacean ostracod (Palaeocopida) with poorly preserved appendages has been described from the Upper Devonian of Italy [7]. Ostracods with soft-part preservation occur very rarely in Mesozoic and Cenozoic deposits (e.g. [8]).

2. GEOLOGICAL SETTING

The described specimen was found in the uppermost part of the marine Lochkovian succession cropping out in the right escarpment of the River Dniester near the village Ivanye Zlote, Podolia, Ukraine (coordinates: 48°42′21.7″ N, 25°39′12.5″ E). The deposits belong to the upper part of the Ivanye Horizon of the Tyver Series (see map and section, figs 1, 2 and 4 in [9]) and are composed of shallow-marine argillites interbedded with argillaceous carbonates. They contain abundant fish remains, ostracods, brachiopods, some bivalves, conodonts and scolecodonts. Upwards, they pass gradually into the Old Red Sandstone facies. The described

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specimen occurred in a carbonate layer located about 5 m below the Old Red deposits.

3. MATERIAL AND METHODS

The material comprises rare complete carapaces, isolated pyritized valves and numerous phosphatized steinkerns showing well-preserved muscle scars, pore canals and marginal structures. One specimen preserves soft parts in the posterior part of the carapace.

The material was extracted from limestone by processing the samples with acetic acid using a method commonly applied for the search of conodonts. As a result, most of the specimens are preserved as phosphatic coatings of the originally calcitic valves, presumably because any remaining calcite was dissolved by the acetic acid. The internal phosphate layer is usually preserved, and therefore the internal morphological features of the carapace are preserved in the phosphate layer as negative reliefs. The pore canals within the valves have been cast in phosphate. The material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (ZPAL O.60).

4. SYSTEMATIC PALAEONTOLOGY

Phylum: Arthropoda, Subphylum: Crustacea, Class: Ostracoda, Subclass: Podocopa, Order: Podocopida, Suborder: Metacopina, Superfamily: Healdiidae.

Family: Healdiidae [10].

Genus: *Cytherellina* [11].

Type species: Beyrichia siliqua Jones [12], p. 90, pl. 5, fig. 22; by original designation of Jones & Holl [11]; Late Silurian, late Ludlow Series, England.

Remarks: The genus *Cytherellina* is currently known from more than 45 species [13]. The specific differentiation in many descriptions of the *Cytherellina* species may be incorrect, which is caused by the lack of distinctive external morphological characters or insufficient knowledge on the interior valve morphology. The most distinctive feature of *Cytherellina* is the presence of an adductorial recess on the interior surface of the valves, reflected as an inflation bordered by two depressions ('undulated contours' of Jones & Holl [11]) on steinkerns of the type species *Cytherellina siliqua* from the Ludlow Series of England and a Scandinavian erratic boulder from the Wrocław area, Poland (Jones & Holl [11], pl. 14: 6a–e). Two specimens illustrated by Jones & Holl ([11], pl. 14: 2, 5) as *C. siliqua* have been referred to the new species *Cytherellina ruperti* [14]. The adductorial recess has been documented only in *Cytherellina decliva* [15] from the Early Devonian of Moldavia, *Cytherellina oleskoiensis* [16] from the Early Devonian of Podolia [17,18] and *Cytherellina crepiduloides* [19] from the Late Silurian of central New York, USA.

Stratigraphic and geographical range of the species known from internal morphology: Late Silurian–Early Devonian of Europe and USA.

Cytherellina submagna [1] (figures 1–3c).

1963 *Healdianella submagna* sp. nov. [1], p. 99 (part), pl. 10, figs 1, 2, 4 (not pl. 9, fig. 10).

1971 *Cytherellina? submagna*; [17], p. 113, pl. 37, figs 13–16.

Holotype: Institute of Geology and Geochemistry, NAS Ukraine, Kyiv, no. 32/10 [1].

Type locality and stratigraphy: Kasperovcy village, left border of the river Seret, Podolia, Ukraine; Chortkov Horizon, Early Devonian.

Material: Several tens of steinkerns, of which one preserves soft parts, and some isolated valves.

Description: Carapace subovate in lateral view, moderately inflated posteriorly; maximum length 1.3 mm; greatest length below mid-height; greatest height at posterior cardinal angle. Dorsal margin asymmetrically arched with highest point in posterior part; anterior part of dorsal margin inclined anteriorly. Anterior margin narrowly and sharply rounded; posterior margin broadly rounded; ventral margin weakly concave. Left valve (LV) overlaps right valve (RV). LV with narrow ventral lip (i.e. 'bow-shaped projection' of Adamczak [20,21]). External surface smooth, lacking any lobal/sulcal structures. Sexual dimorphism not observed.

Internally, valves with deep adductorial recess in antero-median part, anteriorly and posteriorly bordered by two transverse ridges, posterior ridge best developed. Ridges distinguishable as depressions on steinkerns.

Adductor muscle scar (Ad) located in ventral part of adductorial recess, developed as closely packed cluster with up to 40 polygonal scars. Cluster outline transversely extended, asymmetric, with slightly concave anterior margin and curved posterior margin. Two elongated mandibular scars (Md) located antero-ventrally to Ad. Frontal muscle scar (Fr) transversely elongated, located antero-dorsally to Ad.

Hinge of LV consists of groove (crenulated?) and lists. LV with contact groove interrupted in the middle part of the ventral margin. Three inner stop-teeth (antero-ventral, postero-ventral and caudo-ventral) developed in LV by thickening of inner list. Antero-ventral and postero-ventral teeth located in front of ventral lip and behind it. Caudo-ventral tooth developed in posterior part of inner list, below mid-length and is best developed. Stop-teeth preserved as elongate depressions on surface of steinkerns.

Fused zone very narrow in the anterior and posterior parts of the carapace.

Marginal pore canals straight, comparatively short along anterior and posterior margins; canals crossing ventral lip simple, long. Adult specimens with 15–20 marginal pore canals along anterior margin, less canals along posterior margin.

Carapace with soft parts preserved with valves closed. Branchial plate (Bp) of left maxillula (Mx), three-dimensionally preserved pair of walking legs, presumed furca (Fu) and hemipenis (Hp) preserved in posterior part of carapace.

Bp large, with up to 24 feathered rays, of which 19 definitely belong to the Mx Bp because in most cases their proximal point of attachment can be seen, and the rest are evident only by their distal ends protruding from under the inner lamella (In). These last five could belong to an L5 or sixth limb (L6) Bp.

Pair of presumed L6 is preserved in the postero-ventral part of the carapace. Endopodite of left limb with two complete visible segments: first visible segment (proximal) with a dorsal apical seta. Second visible segment elongate, with a ventral sub-apical seta and a very long, slender, slightly curved terminal claw. Right limb poorly visible behind the left, showing distal segment

Figure 1. *Cytherellina submagna*: (a) LV, internal view (stereo pair), internal teeth (arrows), ZPAL O.60/60; (b,c) LV, internal view and close up of caudo-ventral tooth, ZPAL O.60/62; (d) RV, lateral external view, ZPAL O.60/76; (e,f) antero-ventral, postero-ventral and caudo-ventral teeth visible as depressions on external surface of steinkern, ZPAL O.60/81; (g–i) steinkern, left lateral view, (g,h) marginal pore canals in anterior and posterior parts, (i) negative relief of adductorial recess and stop-teeth, ZPAL O.60/002; (j,k) central muscle field, anterior to left, ZPAL O.60/003, ZPAL O.60/043; (l,m) ventral view on steinkern and close up of marginal pore canals in antero-ventral and ventral parts, ZPAL O.60/038; (n,o) steinkern with bacterial-like phosphatized organisms in anterior and posterior part of fused zone, ZPAL O.60/033.

and terminal claw. The distal end of a third (more proximal) segment of the left L6 is visible in some views.

Presumed seventh limb (L7) represented by a proximal endopodite segment on the left side, hidden behind the triangular ventral tip of the Hp, with an oval cross-section (visible in figure 2c); distal segments and setae missing, presumed broken off.

Hp large, triangular-ovate in outline, occupying a large part of the posterior part of carapace, with a rounded triangular ventral tip overhanging the L6 and L7 on the left side, and a complex structure protruding about halfway along the posterior side.

Fu a pair of elongate, lamellar rami extending anteriorly from the posterior body extremity; the distal (anterior) end of the left one is broken off, but that of the right one (much of which is hidden behind the left) bears distally two large terminal claws/setae with a slender seta in between, and the broken stub of a fourth seta posterior to these, all directed ventrally.

Posterior body showing possible traces of abdominal segmentation and bearing a small, posteriorly directed seta at the distal extremity.

Abundant phosphatized bacteria-like elongate organisms, each 3–4 μm in diameter and 10–15 μm in length, preserved in anterior and posterior marginal part of one specimen (figure 1n,o).

Remarks: *C. submagna* is closely related to *C. oleskoien-sis* [16] from the Early Devonian of Podolia (Borshchiv and Lower Chortkiv horizons), from which it can be distinguished by a more elongate and slightly angular anterior margin, and by weaker LV–RV overlap along the ventral margin. The outline and negative relief of the adductorial recess in steinkerns of *C. submagna* are very similar to those in the specimen of *C. siliqua* from the erratic border from Poland illustrated by Jones & Holl [11].

Stratigraphic and geographical range: Early Devonian, Lochkovian, Chortkiv–Ivanye horizons, Podolia, Ukraine.

Figure 2. (a–e) *Cytherellina submagna*: (a) left lateral view of steinkern (stereo pair) with soft anatomy in posterior part, ZPAL O.60/001; (b) close-up view of soft parts showing Bp of Mx, walking legs, Hp and presumed Fu; (c) posterior oblique view of walking leg (L6) and the remnant of a basal podomere or proximal endopodite podomere of L7; (d) close-up of walking legs and presumed Fu (stereo pair), right appendage hidden behind the left one; (e) close-up (stereo pair) of soft parts in ventral part.

5. PHYLOGENETIC IMPLICATIONS

The evolution of the soft-part features was very slow in the ostracode lineages; in some cases, an evolutionary stasis has been recorded for more than 400 Myr (e.g. [4]). Therefore, the preservation of soft parts in fossil specimens is extremely important for the reconstruction of the phyletic continuity between Recent and fossil fauna.

As in Recent podocopids, the large Bp of the Mx of *C. submagna* was probably associated with respiration, being used to produce an oxygenated water current through the internal space of the carapace, and is interpreted as a modified exopod [22,23]. The morphology of the legs preserved in *C. submagna*, similar to the trunk walking legs in Recent podocopine ostracods, suggests that these appendages were used mainly for locomotion.

In general morphology of the preserved soft parts, *C. submagna* is relatively similar to some extant Podocopida, especially to members of the superfamilies Darwinuloidea and Sigillioidea (figure 3). The walking appendages of *C. submagna* may be compared with those of the Recent Podocopida. In the L6 and L7 walking legs of the Cytheroidea, Bairdioidea, Darwinuloidea and Sigillioidea, the endopodite is well developed with a terminal claw, but the exopodite is reduced [22]. The thoracic appendages of living platycopid ostracods differ from those of other ostracods [30]. In *C. submagna*, the Hp is large and with traces of complex structures.

We interpret the visible soft-part morphology as indicating a close affinity with living Sigillioidea (e.g. the genus *Saipanetta*), although there are also some interesting similarities with living Darwinuloidea. The Ad pattern, L7 long terminal seta, Fu with large distal setae and the possible trunk segmentation are all indicative of sigillioidean affinities. Olempska [31] reported the mero-dont hingement, numerous Ads and narrow calcified inner lamella in the Palaeozoic *Microcheilinella* species, which makes them similar to the Mesozoic to Recent sigillioidean ostracods. The metacopine affinities of *Microcheilinella* have been suggested by some authors (e.g. [32]). The sigillioidean affinities of *C. submagna*, which on the basis of hard-part morphology is clearly a metacopine healdoid, are particularly interesting because the sigillioidean genus *Saipanetta* was originally considered to be a living metacopine ostracod [33], a view challenged by other authors (e.g. [34]). Our new evidence suggests that a reconsideration of *Saipanetta* as a living metacopine may not be out of the question, but it would be premature to draw conclusions without the evidence of the anterior appendages of *C. submagna*.

Recent darwinuloideans are ancient asexual ostracods (e.g. [35–37]) that brood their eggs internally; they probably derived, however, from bisexually reproducing ancestors that became extinct. Sexual reproduction in darwinuloidean ostracods probably disappeared after the

Figure 3. Diagrams showing comparative anatomy of (a) a darwinuloidean, (b) a sigillioidean and (c) *Cytherellina submagna*, with only one of each pair of limbs shown for clarity; (a) and (b) are 'general arrangement' diagrams that are not intended to represent single species and are based on illustrations published by (a) Rossetti & Martens [24] and Smith *et al.* [25], and (b) McKenzie [26], Maddocks [27], Schornikov & Gramm [28] and Wouters [29].

end-Permian mass extinction and they are considered to have been asexual for over 200 Myr (e.g. [38]). They were diverse in the Late Palaeozoic, but recently darwinuloids are represented by only one family, the Darwinulidae, with five genera and 28 extant species [39]. Since the Carboniferous, the darwinuloids have been non-marine ostracods (e.g. [40]).

Although the preserved soft parts of *C. submagna* show a general podocopid affinity, the morphology of the shell clearly shows a similarity to the darwinuloids in having the LV–RV overlap (typical of most darwinulid genera except *Darwinula*), narrow fused zones with few straight and short marginal pore canals in the anterior and posterior part of the carapace, the presence of valve internal stop-teeth and a smooth external surface [39]; however, sulcal/lobe structures are not seen in post-Palaeozoic darwinuloideans.

The importance of the inner marginal structures of the carapace for the systematics of Palaeozoic podocopid

ostracods, especially the morphology of the contact groove and the stop-mechanism, was strongly emphasized by Adamczak [20,21,41]. Characteristic features of the metacopines, such as the interrupted contact groove and narrow ventral lip, occur in the early metacopines (*Kuresaaria gotlandica*) from the Silurian of Gotland [21] and also in the late metacopine ostracod *Ogmoconcha ellipsoidea* from the Early Jurassic of England [42].

The inner marginal stop-teeth, interpreted as a blockage for the edge of the smaller valve in tightly closed carapaces, are common in Palaeozoic metacopines [20,41]. Internal stop-teeth on the antero- and postero-ventral margin of larger LV are present in Ordovician and Silurian metacopine genera (e.g. [21,43,44]). Similar structures occur also in the early podocopines (e.g. the bairdioidean *Bairdiocypris marginata* and *Bairdiocypris lamellaris*) [20]. The stop-mechanism in Early Palaeozoic species is a transitional character between the Podocopina and Metacopina [41].

Some freshwater Carbonitoidea species appear to have stop-teeth that closely resemble those described above. For example, stop-teeth preserved as ovate depressions ([45], figs 2.9, 2.11, 5.3) can be seen in the steinkerns of *Carbonita* sp. and *Gutschickia* sp. from the latest Mississippian of Virginia; this structure, however, is not discussed by the author. These ancient carapace features (such as the stop-mechanism) occur in some Recent and fossil darwinulid ostracods (e.g. *Vestalenula*, *Penthesilenula*, *Microdarwinula*) [25,38,39].

The teeth acted as stoppers to prevent the valves from overlapping one another too much ventrally and, therefore, to protect the eggs or juveniles in the brood space against crushing [25,46]. The stop-mechanism is unknown in Recent Cytheroidea. However, the resemblance between the valve stoppers of metacopines and darwinuloideans may also be a case of homeomorphy.

In Recent ostracods, the marginal pore canals bear sensilla that have a sensory function. They are likely to have played a similar role in Palaeozoic ostracods. The well-developed system of marginal pores in the Palaeocopida dates from at earliest the Early Palaeozoic times [47].

The very narrow fused zone with few straight and short marginal pore canals in the anterior and the posterior part of the carapace distinguished *C. submagna* from the Cytheroidea, but is more similar to those in the Darwinuloidea [39].

The Ad pattern of *C. submagna*, composed of many scars, differs from that of most Recent Podocopida, which shows fewer and more discrete scars, developed for example as a row of four scars in the Cytheroidea and arranged in a rosette composed of 9 to 11 elongate scars in the Darwinuloidea. On the other hand, the pattern is very similar to that of the podocopid Sigillioidea. However, the other aspects of the valve morphology of *C. submagna*, especially the hinge, are quite different from those of Sigillioidea. The possible darwinuloidean and sigillioidean affinities of *C. submagna* lend credence to the suggestion of Horne [40] that marine Sigillioidea could possibly be ancestral to the non-marine Darwinuloidea.

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