# Ontogeny of the ostracod *Conchoprimitia osekensis* (Přibyl, 1979) from the Darriwilian of the Prague Basin (Czech Republic)

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Abstract. The ontogeny of the species *Conchoprimitia osekensis* (Přibyl, 1979) from the Šárka Formation (lower and middle Darriwilian) is evaluated. Eight ontogenetic stages (A-8 to A-1) and one adult specimen are described and illustrated. This study displays that another common species of the same stratigraphical unit, *Conchoprimitia? dejvicensis* Přibyl, 1979, represents early instars of *C. osekensis*. It clearly demonstrates the importance of such ontogenetic studies for understanding real taxonomy and diversity of fossil ostracods.

Key words: Ostracoda, ontogeny, Ordovician, Darriwilian, Šárka Formation, Bohemia, Prague Basin.

### INTRODUCTION

Ostracods are small crustaceans with a well-documented fossil record from the Early Ordovician (Tinn & Meidla 2004; Salas et al. 2007; Williams et al. 2008b; Salas & Vaccari 2012). A major species diversification of ostracods took place during the Middle Ordovician, in the time span between the Floian and Darriwilian (Tinn & Meidla 2004). Since then, ostracods have continued their diversification and colonized almost the entire aquatic ecosystem from the ocean abyssal planes to damp leaf litter. They are also the most abundant arthropods in the fossil record and are widely used in palaeoecology and as additional tools in biostratigraphy (Tinn et al. 2006). The systematics of modern ostracods is mostly based on soft body anatomy. Except for rare examples of soft anatomy preservation (Siveter et al. 2003; Siveter 2008; Williams et al. 2008a; Wilkinson et al. 2010; Olempska et al. 2012), the identification of fossil ostracods is possible only through the morphologies of the calcified carapace.

Ostracods are one of the major components of the fossil assemblages in the Ordovician of the Prague Basin (Barrandian area, Bohemian Massif, Czech Republic). They are very abundant in the Šárka Formation (Darriwilian), however, their species diversity is very low. Three species have been mentioned in recent papers. *Brephocharieis? ctiradi* Schallreuter & Krůta, 1988, previously often recorded under the name *Cerninella complicata* (Salter, 1848) (in Phillips & Salter, 1848), is

c never described or figured. (The species is valid but occurs in the upper Katian Králův Dvůr Formation.) Přibyl (1979) revised Barrande's material for his monograph on Ordovician ostracods and distinguished the two new species mentioned above. They are both characterized by simple morphology. According to Přibyl's (1979) diagnoses, one of critical features of identification was the size of the carapace. The specimens that were smaller than the smallest *Conchoprimites osekensis* were referred to *Conchoprimita? devicensis*.

identification was the size of the carapace. The specimens that were smaller than the smallest *Conchoprimites osekensis* were referred to *Conchoprimitia? dejvicensis*. Both forms were mentioned in later studies on Ordovician ostracods of Bohemia by Schallreuter & Krůta (1988) and Lajblová (2010). They were originally attributed to different genera but the generic name *Conchoprimites* was later considered a synonym of *Conchoprimitia* Öpik, 1935 by Schallreuter (1993, p. 126; see also Schallreuter & Krůta 2001, p. 100).

uncommon. Two other species, *Conchoprimites osekensis* Přibyl, 1979 and *Conchoprimitia? dejvicensis* Přibyl,

1979, are very abundant. These two species were dis-

tinguished in the revision by Přibyl (1979), both being

previously attributed to a single taxon Primitia prunella

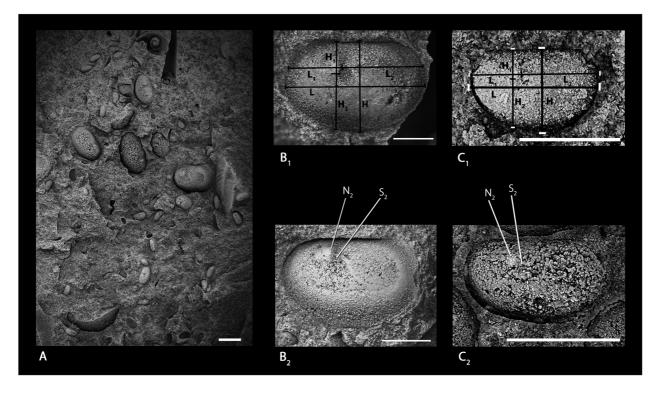
Barrande, 1872 (for original type specimen see Fig.  $1C_2$ ).

*Primitia prunella* has been mentioned several times in lists of fauna from the Šárka Formation (Holub 1908;

Bassler & Kellett 1934; Havlíček & Vaněk 1966) but

The common co-occurrence of both of Přibyl's species in the Šárka Formation (with the overall prevalence of smaller *Conchoprimitia*? *dejvicensis*), the similar morphological features of the valves of these species

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**Fig. 1. A.** Siliceous nodule with ostracods, NM L 36446, locality Osek. **B**<sub>1</sub>, **B**<sub>2</sub>, specimens representing the growth stage classified formerly as *Conchoprimites osekensis* Přibyl, 1979. B<sub>1</sub>, biometric features, NM L 35977, left valve, locality Osek; B<sub>2</sub>, morphological features, NM L 42166, originally designated paratype, left valve, locality Osek. **C**<sub>1</sub>, **C**<sub>2</sub>, specimens mentioned previously as *Conchoprimitia*? *dejvicensis* Přibyl, 1979. C<sub>1</sub>, biometric features, NM L 36020, left valve, locality Ejpovice near Rokycany; C<sub>2</sub>, morphological features, NM L 8861, holotype, left valve, locality Osek. S<sub>2</sub> = sulcus; N<sub>2</sub> = preadductorial node (node-like lobe); L = maximum length of the valve; L<sub>1</sub> = length from the preadductorial node (N<sub>2</sub>) to the anterior margin; L<sub>2</sub> = length from the N<sub>2</sub> to the posterior margin; H = maximum height; H<sub>1</sub> = height from the N<sub>2</sub> to the dorsal margin; H<sub>2</sub> = height from the N<sub>2</sub> to the ventral margin. Scale bars equal 1 mm.

and the absence (by definition) of younger ontogenetic stages of *Conchoprimites osekensis* raised the question about their probable conspecific nature. The purpose of this study is to evaluate the potential affinity between these two species and to describe the ontogeny of *Conchoprimitia* from the Šárka Formation by assessing the size, shape and convexity of the valves at different stages of growth.

# GEOLOGICAL AND PALAEONTOLOGICAL SETTINGS

The ostracods studied here occur in the Šárka Formation, which represents a significant unit within the volcanosedimentary infill of the Prague Basin (Havlíček 1981, 1998). This basin was located in the peri-Gondwanan realm (e.g. Havlíček et al. 1994). The Šárka Formation is typified by dark grey to black shales. Ferrolites (iron ore deposits) are locally developed at its base or may represent the whole thickness of the unit in some parts of the basin (Havlíček 1998). The shales are usually monotonous and partly bioturbated and contain early diagenetic siliceous nodules. These richly fossiliferous nodules are well known for their palaeontology (Havlíček & Vaněk 1966; Chlupáč 1993; Havlíček 1998) and sedimentology (Kukal 1962; Mikuláš 2003) and have attracted the attention of numerous geologists and palaeontologists because of their unique invertebrate fauna (Fig. 1A).

The Šárka Formation is of early to middle Darriwilian age (Oretanian in the regional stratigraphy of the European Variscides, equivalent to the latest Arenig to middle/late Llanvirn of the British regional chronostratigraphic scheme that has been applied in the Barrandian area in the past). Two graptolite biozones have been established in the formation: *Corymbograptus retroflexus* in its lower and middle parts and *Didymograptus clavulus* in the upper part. The nodules are mostly collected on farmed fields where they accumulate in soil where the shales are denuded. Thus, the exact stratigraphic horizon of the nodules, with the exception of those containing graptolites, is unclear. However, based on the occurrence of graptolites in the nodules at the localities listed below, almost all studied specimens come from the *Corymbograptus retroflexus* Biozone.

The fauna of the Šárka Formation occurs both in shales and in nodules. It belongs to the Euorthisina-Placoparia Community (Havlíček & Vaněk 1990; = Euorthisina-Placoparia Association according to Budil et al. 2007), characterized by the predominance of benthic organisms. Trilobites are the most diversified and abundant component of the Euorthisina-Placoparia Assemblage; brachiopods, bivalves, hyolithids, gastropods and echinoderms are also very common but their diversity is variable. Ostracods are a significant component of the assemblage. Although very abundant, their diversity is very low. In this respect the assemblage is comparable to the very early (latest Floian-earliest Dapingian) ostracod assemblage from the mid-ramp carbonate succession in Estonia (Meidla et al. 1998). Assemblages that are coeval to the Euorthisina-Placoparia Assemblage in the Prague Basin are mostly much more diverse in the Baltoscandian area (see Tolmacheva et al. 2001, 2003; Tinn et al. 2006). The assemblages of equally low diversity are known also in the Ordovician of Baltoscandia but they are confined exclusively to non-calcareous mudstone (argillite) units (basal Mossen Formation, Fjäcka Formation – Meidla 1996). Vannier et al. (1989) demonstrate that the diversity of Ordovician ostracods was generally lower in siliciclastic environments. This suggests that the very low diversity of ostracods in the Šárka Formation is likely related to overall environment, as reflected in the shale-dominated lithofacies.

Fossil preservation depends on lithology: shells are deformed (broken and/or flattened to a different degree) in the shales because of the compaction of sediment; specimens in the nodules are preserved in full 3-D relief and original shape. The use of material from nodules is thus essential for our study.

#### MATERIAL AND METHODS

The ostracods studied are mainly from siliceous nodules (locally called Rokycany or Šárka Balls) rather than from shales. Thus, most specimens come from famous nodule localities including Osek (originally called Wosek by Barrande 1872), Rokycany, Díly near Rokycany, Těškov and Pětidomky near Zbiroh. The total number of the studied ostracod specimens exceeds 500. It is a mixture of isolated valves and complete carapaces occurring separately, in clusters or in larger accumulations. The quality of the material is variable as the specimens are preserved only as internal and external molds. This type of material cannot be successfully processed by any disintegration or dissolution method. The mode of

the material preservation (internal and external molds) has put some limits on the selection methods of the study. Only a part of the diagnostic features could be used, although the most important aspects of carapace morphology could still be considered.

Latex casts were made in order to analyse the morphological features properly. The casts were mounted on stubs and sputter-coated in gold and photographed using the scanning electron microscope Jeol JSM-6380. Other specimens were coated with ammonium chloride and photographed digitally (Leica DFC495 and Olympus DP72). The material studied is mostly deposited in public collections of the National Museum in Prague (prefix NM) and the Museum of Dr Bohuslav Horák in Rokycany (MBHR). Some of the specimens used for morphometric analysis are deposited in the private collection of V. Kozák (the material will be moved to public collections in the future).

Our study is based on the examination of the size, shape and convexity of the carapace. For the purpose of quantitative ontogenetic analysis we measured four basic morphological characters (Fig. 1B<sub>1</sub>, 1C<sub>1</sub>) and plotted them against each other to trace relative trends against size. The different rates of growth of parts of the ostracod carapace are well coordinated with respect to each other, in accordance with observations by Raup & Stanley (1978). Ontogenetic stages were tentatively identified in the morphometric dataset.

#### MORPHOLOGY

The abbreviations used herein are as follows:  $S_2$  = sulcus, sulcament;  $N_2$  = preadductorial node (node-like lobe); L = maximum length of the valve, L<sub>1</sub> = length from the preadductorial node (N<sub>2</sub>) to the anterior margin, L<sub>2</sub> = length from the N<sub>2</sub> to the posterior margin; H = maximum height, H<sub>1</sub> = height from the N<sub>2</sub> to the dorsal margin, H<sub>2</sub> = height from the N<sub>2</sub> to the ventral margin; L : H = length : height ratio. Measurements are given in millimetres.

In many beyrichiocope species, which are generally characterized by a long and straight dorsal margin (from a lateral view), the valve surface is modified by lobes (elevations) and sulci (depressions) that are also reflected internally. The number and shape of the lobes and sulci are considered significant for the classification of Palaeozoic ostracods without preserved soft parts (e.g. Kesling 1952; Tinn & Meidla 2003, 2004). The function of sulci has been ascertained through comparative study of Recent ostracods to correspond to muscular attachments inside the valves (Pokorný 1998). Although Přibyl (1979) used the abbreviations  $L_2$  (= lobe 2; note the different meaning of the abbreviation used here) and  $S_2$  in his descriptions of the species considered here, most of the subsequent authors (e.g. Schallreuter 1993; Tinn et al. 2010a) describe the valves of *Conchoprimitia* as being non-lobate and use the terms 'preadductorial node' and 'sulcal depression' or 'sulcament' (Schallreuter 1967, p. 626; Meidla 1996, p. 18).

Comparison of diagnoses of Conchoprimitia? dejvicensis and Conchoprimites osekensis provided by Přibyl (1979) is given in Table 1. Přibyl (1979) characterized C.? dejvicensis as a medium-sized ostracod (1.0-1.3 mm in length) with a small but recognizable rounded  $N_2$  in the anterior half of the valve (Fig. 1C<sub>2</sub>), which is less visible or lacking in early ontogenetic stages. Valves of C. osekensis, according to Přibyl (1979), attained by contrast a larger size from 1.30 mm in juvenile to 3.56-3.90 mm in adult specimens. Based on length measurements he recognized five instars of C. osekensis; his intervals typical of individual instars are shown in Table 2 for comparison. A distinct N<sub>2</sub> in the anterior half of the valve near the dorsal margin was mentioned in Přibyl's description of C. osekensis, as well as a short, straight and prominent S2, perpendicular to the dorsal margin (Fig. 1B<sub>2</sub>).

### ONTOGENY

The ontogeny of Ostracoda is important for understanding their evolution. As in all crustaceans, ostracods grow in discontinuous stages called instars through the process of ecdysis. When the body of an instar has grown too large for its exoskeleton, the rigid chitinous and calcareous valves are moulted. During ecdysis the ostracod approximately doubles its volume (Martinsson 1962), along with possible changes in soft body anatomy.

In Recent ostracods a complete ontogenetic series contains 5-9 larval stages but it depends on the systematic unit. Modern myodocopes with a more advanced metanauplius have usually 5-6 ontogenetic stages (e.g. Kornicker et al. 2010). On the other hand, podocopes have been observed to have passed through 8-9 stages (e.g. Baltanás et al. 2000; Smith & Martens 2000; Smith & Kamiya 2003). In fossil ostracods the exact number of ontogenetic stages is difficult to indentify but the general ontogenetic pattern known in Recent ostracods occurred already in the Ordovician (Tinn & Meidla 2003). Eight moulting stages are identified in ctenonotellid Brezelina palmata from the mid-Dapingian of Estonia (Tinn & Meidla 2003). Martinsson (1962) described nine ontogenetic stages (including adults) in Craspedobolbina (Mitrobeyrichia) clavata from the Silurian. The same number of instars was found by Cooper (1945) in the Permian Ectodemites plummeri. Spjeldnaes (1951) discovered even 11 growth stages (including adults) in the Silurian Beyrichia jonesi, and even more than 11 growth bands (that reflect the number of growth stages) were recognized in some eridostracan species (Olempska 2012 and references therein). The highest known number of moulting stages was 15 in the Devonian Cryptophyllus sp. 18 sensu Becker & Bless (1974). Based on such differences, Hartmann (1963) pointed out that the number of growth stages in Recent ostracods (max. 9) indicates most likely loss of instars during the evolution, evidently due to the appearance of more mature embryonic nauplius larvae starting their ontogenetic development already in the egg. At the same time, the number of juvenile stages in each species may also vary with climatic conditions (Pokorný 1998).

The ontogeny of Middle Ordovician ostracods is poorly investigated. There are cases in the history of

Table 1. Comparison of critical features of *Conchoprimites osekensis* and *Conchoprimitia? dejvicensis* used by Přibyl (1979) in his diagnoses

Species	Outline	Shape	Dorsal margin	Cardinal angles	Ventral margin	N <sub>2</sub>	S <sub>2</sub>	Surface
Conchoprimites osekensis	Postplete	Oval to elliptical	Straight, 5/7 (= 71%) of the whole length	Obtuse; anterodorsal 125°–135°, posterodorsal 125°–140°	Convex; posterior half wider, higher and con- siderably more arched than anterior half	Small, oval	Well defined	Smooth
Conchoprimitia? dejvicensis	Postplete	Oval to suboval	Straight, $6/8$ to 7/10 (= 75- 70%) of the whole length	Obtuse; anterodorsal 115°–120°, posterodorsal 125°–130°	Convex; posterior half wider than anterior half	Small, oval, indistinct or lacking in juveniles	Absent	Smooth

	A-8	A-7	A-6	A-5	A-4	A-3	A-2	A-1	Adults
Length, mm Maximum height, mm	0.38–0.70 0.437	0.71–0.89 0.607	0.91–1.13 0.676	1.14–1.34 0.969	1.37–1.62 1.112	1.69–2.15 1.495	2.22–2.67 1.830	2.74–3.41 2.266	3.46–3.95 2.491
Přibyl's specimens length, mm					1.30-2.00	2.01-2.60	2.67-3.10	3.11-3.55	3.56-3.90

Table 2. Instars of Conchoprimitia osekensis (Přibyl, 1979) and their size ranges

ostracod research when different growth stages of a species were described as different taxa (e.g. Fox 1964), causing confusion in taxonomy. Thus, identifying juveniles is necessary for taxonomic studies but also for studies on population dynamics and life cycles of certain communities and species (Smith & Martens 2000). Another set of problems arises from the fact that valves of very simple morphology can effectively serve for establishing a very large number of species according to minor random, ecophenotypic, taphonomic or diagenetic differences (Tinn et al. 2010a).

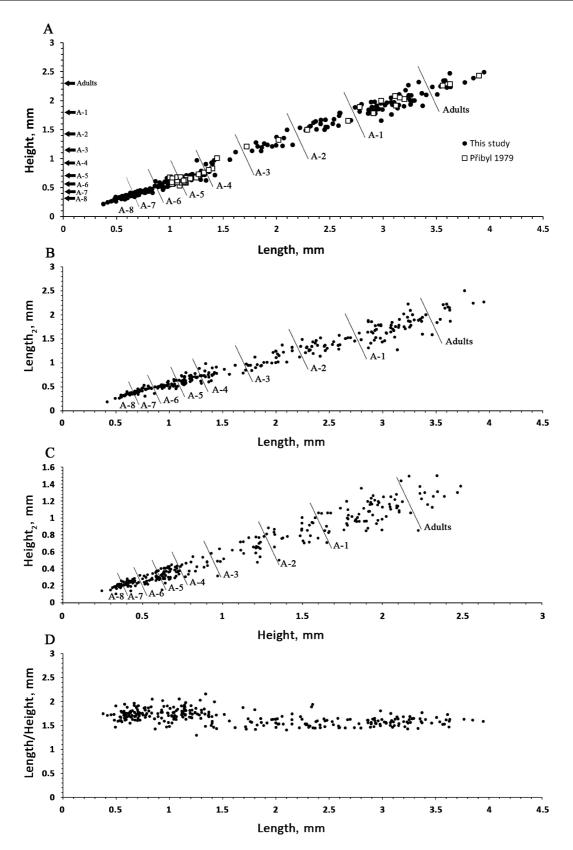
The valves of ostracod instars increase progressively in size and become thicker and more heavily calcified. These changes may be accompanied by modifications in shape and gradual development of macrosculpture (ridges or nodes - sometimes also summarized under the term 'valve structure' - see Hinz-Schallreuter & Schallreuter 1999). Some authors (e.g. Pokorný 1998) state that the L:H ratio is lowest in the earliest larval stages, as these have a small number of appendages and consequently a shorter body. In Ostracoda ontogenetic changes are also seen in the increasing complexity of hinge, duplicature (calcification becomes broader), marginal pore canals and in the pattern of muscle scars (early larval stages of some genera have a smaller number of muscle scars than the later larval stages and adults). Studies of ostracod population dynamics (e.g. Martinsson 1955; Whatley 1988; Frentzel & Boomer 2005) suggest that size distribution of carapaces is the most important factor in recognizing palaeoecologic characters of ostracod assemblages. It is obvious that in natural conditions the early instars have a lower preservation potential due to weakly calcified and fragile carapaces (Tinn & Meidla 2003).

#### RESULTS

About 300 specimens preserved and visible in full, nondeformed outline were measured. The available specimens range from 0.38 mm to 3.95 mm in length. The material includes both morphotypes, *Conchoprimitia? dejvicensis*  and *Conchoprimites osekensis*, and the data are plotted together. Scatter plots show uniform trends of growth and a linear distribution of the data points (Fig. 2A–D). This demonstrates that the ontogeny of two species distinguished by Přibyl (1979) follows the same trend, including the specimens examined by him (Fig. 2A). As the development of N<sub>2</sub> and L<sub>2</sub> is gradual and size-dependent, the valve surface is smooth in both species and other distinguishing features are lacking, we infer that *C*.? *dejvicensis* and *C. osekensis* represent different growth stages of one species, which should be called *Conchoprimitia osekensis* (Přibyl, 1979), as this is the senior synonym.

The scatter plot of length versus height (Fig. 2A) shows no appreciable gaps between the data points, i.e. the instars do not cluster into very clear moult stages. This is typical of fossil assemblages because of seasonal changes in populations, time averaging and later deformations. The separating lines dividing the instar data points into adults and eight instars are drawn according to Brooks' rule (Brooks 1886); the respective size range and proportions of the instar carapaces are shown in Table 2. Additional plots of L versus L<sub>2</sub> (Fig. 2B) and H versus H<sub>2</sub> (Fig. 2C) were constructed to demonstrate the gradual development of morphological features of the valves shown in Fig. 3. Both ratios (Fig. 2B, C) do not reveal any distinctive size groups similarly to the L:H ratio (Fig. 2A), and the application of Brooks' rule has the same results. The shape of this species does not change significantly during ontogeny (Fig. 2D).

The morphological development of the instar valves characterized in Table 3, the overall morphology of different instars in Fig. 3 and their dimensions in Table 2 show that juveniles acquired the typical morphological features of the adult valves in the A-3 stage (formerly typical *Conchoprimites osekensis*) of ontogeny. According to Tinn & Meidla (2003), the A-3 stage in early Middle Ordovician ctenonotellids (*Brezelina palmata*) and tetradellids (*Ogmoopsis bocki*) marks the first appearance of dimorphic admarginal structures (distinction of preadult heteromorphs possible for the first time). The



**Fig. 2. A–D**. Scatter plots of *Conchoprimitia osekensis* showing instars and adults. Instar heights inferred from Brooks' rule are marked with arrows on the *y*-axis (beginning of the mean height of instar A-8, each subsequent arrow being located 1.26 times the previous height). Dividing lines separating instars in A–C were calculated based on Brooks' rule.

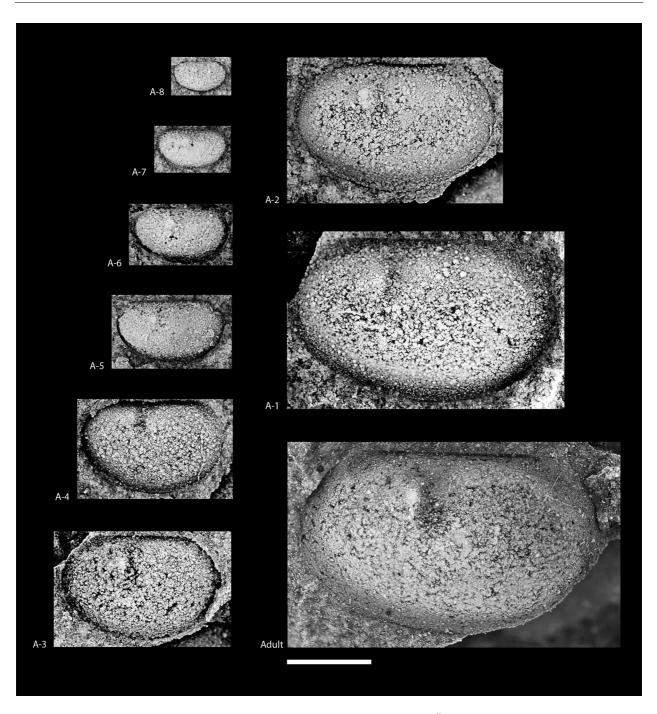


Fig. 3. Ontogenetic stages of *Conchoprimitia osekensis*, (Přibyl, 1979). Ordovician, Šárka Formation. Left valves. A-8. NM L 35974, locality Osek. A-7. NM L 36025, locality Osek. A-6. MBHR 9852, locality Těškov. A-5. NM L 36020, locality Ejpovice near Rokycany. A-4. MBHR 18781, locality Díly. A-3. MBHR 18831, locality Díly near Rokycany. A-2. MBHR 6339, locality Osek. A-1. MBHR 15492, locality Díly near Rokycany. Adult. MBHR 9851, locality Díly. Scale bar equals 1 mm.

general characters of *C. osekensis*, such as the shape (change from elongate to suboval) and outline (from amplete to postplete), change markedly in the A-5 and A-4 stages. On the valve surface,  $N_2$  that appears in A-7 becomes more prominent in the succeeding stages and

 $S_2$  is recognizable from A-6. The ctenonotellid species *B. palmata* has no distinct  $N_2$  but the appearance of sulci begins in stage A-7 with intersection of  $S_2$ . This suggests that ontogenetic modification of the valve surface may follow the same temporal (age) pattern in

Instar	Outline	Shape	Cardinal angles	Convexity	$N_2$	$S_2$
A-8	Amplete	Elongate	Rounded	Small	Lacking	Lacking
A-7	Amplete-postplete	Elongate	Less rounded	Small	Faint	Lacking
A-6	Amplete-postplete	Elongate	Distinctly obtuse	Small	Pronounced	Faint
A-5	Amplete-postplete	Elongate	Distinctly obtuse	Small	Distinct	Distinct
A-4	Postplete	Oval-suboval	Distinctly obtuse	Distinct	Distinct	Distinct
A-3	Postplete	Oval-suboval	Distinctly obtuse	More distinct in posterior part	Distinct	Distinct
A-2	Postplete	Oval-suboval	Distinctly obtuse	Distinct in posterior part	Distinct	Distinct
A-1	Postplete	Oval-suboval	Distinctly obtuse	Distinct in posterior part	Distinct	Distinct
Adult	Postplete	Oval-suboval	Distinctly obtuse	Distinct in posterior part	Distinct	Distinct

Table 3. Development of valve characters during the Conchoprimitia osekensis (Přibyl, 1979) ontogeny

different suborders of Ostracoda, taking place through growth stages A-7 to A-4. Convexity in *C. osekensis* increases in the posterior portion of the valves from stage A-4.

It is worth mentioning that most specimens of *Conchoprimitia osekensis* are dominated by early growth stages (i.e. instars formerly classified as *Conchoprimitia? dejvicensis*) in the fossil record of the Šárka Formation. Hundreds or even thousands of specimens of these early instars predominate over less abundant older instars (former *Conchoprimites osekensis*). This is in contradiction with the cases of juvenile carapaces preserved less often than valves of the adults as described and explained e.g. by Whatley (1988) and Tinn & Meidla (2003). Note that the total number of measured specimens plotted in our graphs does not correspond to natural ratios in the sample, because of selective sampling of measurable specimens representing individual instars.

#### DISCUSSION

The genus Conchoprimitia was erected by Öpik (1935). It is characterized by simple morphology: postplete outline, a long hinge line, more or less convex carapace without distinct lobes and sulci. Specimens may attain a relatively large size (up to 4 mm). Such simple, almost 'featureless' morphology is the reason why large numbers of specimens have been assigned to numerous different species of this genus or, on the other hand, some species of Conchoprimitia were classified in various genera. Many species of Conchoprimitia have been described and recorded from the Baltoscandian Palaeobasin from Estonia (Öpik 1935; Sarv 1959; Meidla et al. 1998; Tinn & Meidla 1999, 2001; Tinn 2002; Tinn et al. 2006, 2010a, 2010b), Norway (Henningsmoen 1954), Sweden (Hessland 1949), Latvia (Ainsaar et al. 2002), Lithuania (Sidaravičienė 1992, 1996) and from erratic boulders of northern Germany (Schallreuter 1993 and references therein). Other *Conchoprimitia*-like species have also been recorded from the Ordovician of Poland (Olempska 1994), Argentina (Salas & Vaccari 2012), the British Isles (Siveter 2009) and North America (Landing et al. 2013). These belong to a few valid species, whilst almost 20 former Baltoscandian 'species' are, according to Tinn et al. (2010a), assigned to a polymorphic species *Conchoprimitia socialis* (Brøgger, 1882) and other collections have not been revised. However, except for the material considered in this paper, only one species, *Conchoprimitia transiens* (Barrande, 1872), has been recorded by Schallreuter & Krůta (2001) in the Prague Basin. It comes from the Dobrotivá Formation, the unit overlying the Šárka Formation.

Both eridostracan 'species' described by Přibyl (1979), *Conchoprimitia? dejvicensis* and *Conchoprimites osekensis*, share the same simple morphology: postplete to slightly amplete outline, long dorsal margin, convex carapace with a simple node and sulcus and the absence of marginal structures. Along with size, the main differences between the species were the distinctiveness of the sulcus and node on the surface of the valves. However, such distinction between the species is arbitrary, with 'differences' arising, for example, from taphonomic and preservational effects. In addition, the comparison of the morphological features (compiled in Table 1) by Přibyl (1979) revealed no clear distinction between *Conchoprimitia? dejvicensis* and *Conchoprimites osekensis*.

Ostracod ontogenetic stages can be difficult or impossible to distinguish in the fossil record. This blurring may result from mixture or time averaging of specimens from different environments and/or seasons: when ostracods tend to be smaller in spring than in autumn (Whatley & Stephens 1977). Brooks' rule (Brooks 1886) is useful for recognizing instars and adults of ostracods and may provide insight into the timing of such ontogenetic changes that reflect the addition of appendages and development of sexual maturity (Retrum & Kaesler 2005). This particular rule suggests that crustaceans double their volume through each moult stage with an increase showing a linear relationship by approximately the cube root of two (resulting in the coefficient 1.26) with each moult (Brooks 1886, see also Przibram 1931; Teissier 1960). The rule is a general observation of crustacean growth but is not in every case applicable to all ostracod ontogenies. The degree of adherence to Brooks' rule during ontogeny bears on the importance of heterochrony in evolution (Martinsson 1962). As we did not know the exact number of moult stages, we used the coefficient mentioned above (1.26)and started the numbering of moult stages from the adult. The results show that Conchoprimitia osekensis follows Brooks' rule quite closely. The number of ontogenetic stages falls into the range observed in modern and fossil ostracods, being identical to that in modern podocopes (e.g. Smith & Kamiya 2003).

Přibyl (1979) studied the material of 'Conchoprimities osekensis' and distinguished five instars (see Table 2). He referred the smallest specimens (length 1.30–2.00 mm) to our A-4 (his numbering was different) and suggested that no younger stages were present in the material. The largest recorded specimens of 'Conchoprimitia? dejvicensis' were of maximum length up to 1.30 mm. That size corresponds to our A-5 where a short and poorly defined  $S_2$  (just behind the  $N_2$ ) can be observed. However, it is not mentioned in Přibyl's (1979) original description. Přibyl's (1979) smallest specimens referred to C.? dejvicensis reached 1.00 mm in length. These correspond to A-6 here. As our smallest specimens are 0.38 mm long, we could complete the ontogenetic sequence up to A-8 as the earliest instar. In this larval stage the L:H ratio is approximately 1.73, whilst in the adults it is 1.59.

As mentioned above, early instars predominate in abundance over the late growth stages, possibly due to higher natural mortality during the early breeding season. When considering problems in distinguishing growth stages, it should be taken into account that the material originates from various stratigraphic levels and does definitely contain a mixture of populations of slightly different age. Thus a very good fit to the theoretical model could not be expected.

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#### REFERENCES

- Ainsaar, L., Meidla, T., Tinn, O. & Stinkulis, G. 2002. The "Volkhov Collector" in western Latvia – a siliciclastic turbidite bed in the Ordovician epeiric carbonate basin. In Basin Stratigraphy – Modern Methods and Problems; The Fifth Baltic Stratigraphical Conference, Vilnius (Satkunas, J. & Lazauskiene, J., eds), pp. 11–13. Vilnius University, Vilnius.
- Baltanás, A., Otero, M., Arqueros, L., Rossetti, G. & Rossi, V. 2000. Ontogenetic changes in the carapace shape of the non-marine ostracod *Eucypris virens* (Jurine). *Hydrobiologia*, **419**, 65–72.
- Barrande, J. 1872. Systême silurien du centre de la Bohême. Iere Partie: Recherches Paléontologiques 1 (Supplément) [Trilobites, Crustacés divers et Poissons]. Prague & Paris, 647 pp.
- Bassler, R. S. & Kellett, B. 1934. Bibliographic index of Paleozoic Ostracoda. *Geological Society of America* Special Papers, 1, 1–500.
- Becker, G. & Bless, M. J. M. 1974. Ostracode stratigraphy of the Ardenno-Rhenish Devonian and Dinantian. In *International Symposium on Namur 1974, Belgian Micropaleontological Limits from Emsian to Viséan*, pp. 1–52. Ministry of Economic Affairs, Brussels, Belgium.
- Brøgger, W. C. 1882. Die Silurischen Etagen 2 und 3 im Kristianiagebiet und auf Eker, ihre Gliederung, Fossilien, Schichtenstorungen und Contactmetamorphosen. Universitets-Program, 2. Semester, A.W. Brøgger. Kristiania, 376 pp.
- Brooks, W. K. 1886. Report on the scientific results of the voyage of H.M.S. *Challenger. Report, Zoology*, **16**(45), 1–116.
- Budil, P., Kraft, P., Kraft, J. & Fatka, O. 2007. Faunal associations of the Šárka Formation (Middle Ordovician, Darriwilian, Prague Basin, Czech Republic). Acta Palaeontologica Sinica, 46 (Supplement), 64–70.
- Chlupáč, I. 1993. Geology of the Barrandian. A Field Trip Guide. Senckenberg-Buch 69. Frankfurt am Main, 163 pp.
- Cooper, C. L. 1945. Moult stages of the Pennsylvanian ostracode *Ectodemites plummeri*. *Journal of Paleontology*, 19, 368–375.
- Fox, H. M. 1964. On the larval stages of Cyprids and on Siphlocandona (Crustacea, Ostracoda). Proceedings of the Zoological Society of London, 142, 165–176.

- Frentzel, P. & Boomer, I. 2005. The use of ostracods from marginal marine, brackish waters as bioindicators of modern and Quaternary environmental change. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **225**, 68–92.
- Hartmann, G. 1963. Zur Phylogenie und Systematik der Ostracoden. Zeitschrift f
  ür Zoologische Systematik und Evolutionsforschung, 1, 1–154.
- Havlíček, V. 1981. Development of a linear sedimentary depression exemplified by the Prague Basin (Ordovician– Middle Devonian; Barrandian area – central Bohemia). Sborník geologických věd, Geologie, 35, 7–48.
- Havlíček, V. 1998. Ordovician. In Palaeozoic of the Barrandian (Cambrian to Devonian) (Chlupáč, I. & Turek, V., eds), pp. 41–79. Czech Geological Survey, Praha.
- Havlíček, V. & Vaněk, J. 1966. The biostratigraphy of the Ordovician of Bohemia. Sborník geologických Věd, Paleontologie, 8, 7–69.
- Havlíček, V. & Vaněk, J. 1990. Ordovician invertebrate communities in black-shale lithofacies (Prague Basin, Czechoslovakia). Věstník Ústředního ústavu geologického, 65, 223–236.
- Havlíček, V., Vaněk, J. & Fatka, O. 1994. Perunica microcontinent in the Ordovician (its position within the Mediterranean Province, series division, benthic and pelagic associations). *Sborník geologických věd, Geologie*, 46, 23–56.
- Henningsmoen, G. 1954. Lower Ordovician Ostracods from the Oslo Region, Norway. Norsk Geologisk Tidsskrift, 33, 41–68.
- Hessland, I. 1949. Investigations of the Lower Ordovician of the Siljan District, Sweden, I. Lower Ordovician Ostracodes of the Siljan District. *The Bulletin of the Geological Institution of Uppsala*, **33**, 97–408.
- Hinz-Schallreuter, I. & Schallreuter, R. 1999. *Ostrakoden*. Ferdinand Enke Verlag, Stuttgart, 168 pp.
- Holub, K. 1908. Příspěvek ku poznání fauny pásma Dd ly [Contribution to the Knowledge of Fauna in the Dd ly Zone]. Česká akademie císaře Františka Josefa pro vědy, slovesnost a umění (Třída II) 17(10), Praha, 19 pp. [in Czech].
- Kesling, R. V. 1952. A study of Ctenoloculina cicatriosa (Warthin). Contributions from the Museum of Paleontology, University of Michigan, 9, 247–290.
- Kornicker, L. S., Humphreys, W. F., Danielopol, D. L. & Harrison-Nelson, E. 2010. Ontogeny of an anchialine ostracod from Western Australia and comments on the origin and distribution of Halocyprididae. *Crustaceana*, 83, 715–752.
- Kukal, Z. 1962. Petrografický výzkum vrstev šáreckých barrandienského ordoviku [Petrographical investigation of the Ordovician Šárka beds in the Barrandian area]. *Sborník ústředního ústavu geologického, oddíl geologický*, 27, 175–214 [in Czech, with English summary].
- Lajblová, K. 2010. Předběžná zpráva o revizi ostrakodů klabavského a šáreckého souvrství (pražská pánev, spodní a střední ordovik) [Preliminary report on revision of ostracods from the Klabava and Šárka formations (Prague Basin, Lower and Middle Ordovician)]. Zprávy o geologických výzkumech v roce 2009, 154–155 [in Czech, with English summary].

- Landing, E., Mohibullah, M. & Williams, M. 2013. First early Middle Ordovician ostracods from western Avalonia: paleogeographical and paleoenvironmental significance. *Journal of Paleontology*, 87, 269–276.
- Martinsson, A. 1955. Studies on the ostracode family Primitiopsidae. *The Bulletin of the Geological Institution* of Uppsala, 36, 1–33.
- Martinsson, A. 1962. Ostracodes of the Family Beyrichiidae from the Silurian of Gotland. Bulletin of the Geological Institutions of the University of Uppsala, 41, 1–369.
- Meidla, T. 1996. Late Ordovician ostracodes of Estonia. *Fossilia Baltica*, 2, 1–222.
- Meidla, T., Ainsaar, L. & Tinn, O. 1998. Volkhov Stage in North Estonia and sea level changes. *Proceedings of the Estonian Academy of Science, Geology*, 47, 141–157.
- Mikuláš, R. 2003. Ichnological aspect of fossiliferous nodules of the Šárka Formation (Ordovician, Llanvirnian, Czech Republic). *Bulletin of the Czech Geological Survey*, 78, 83–88.
- Olempska, E. 1994. Ostracods of the Mójcza Limestone. In Ordovician Carbonate Platform Ecosystem of the Holy Cross Mountains, Poland (Dzik, J., Olempska, E. & Pisera, A., eds), Paleontologia Polonica, 53, 129– 212.
- Olempska, E. 2012. Morphology and affinities of Eridostracina: Palaeozoic ostracods with moult retention. *Hydrobiologia*, **688**, 139–165.
- Olempska, E., Horne, D. J. & Szaniawski, H. 2012. First record of preserved soft parts in a Palaeozoic podocopid (Metacopina) ostracod, *Cytherellina submagna*: phylogenetic implications. *Proceedings of the Royal Society*, *Series B, Biological Sciences*, 279(1728), 564–570.
- Öpik, A. 1935. Ostracoda from the lower Ordovician Megalaspis-limestone of Estonia and Russia. Publications of the Geological Institutions of the University of Tartu, 44, 1–12.
- Phillips, J. & Salter, J. W. 1848. Palaeontological appendix to Professor John Phillips' memoir on the Malvern Hills, compared with the Palaeozoic districts of Abberly, etc. *Memoir of the Geological Survey of Great Britain*, 2, 331–386.
- Pokorný, V. 1998. Ostracodes. In Introduction to Marine Micropaleontology (Haq, B. U. & Boersma, A., eds), pp. 109–149. Elsevier Science.
- Přibyl, A. 1979. Ostrakoden der Šárka bis Králův Dvůrschichtengruppe des böhmischen Ordoviziums. Sborník Národního Muzea, Řada B, 33(1977, 1/2), 53–145.
- Przibram, H. 1931. Connecting Laws in Animal Morphology. Four lectures held at the University of London, March 1929. University of London Press, London, 62 pp.
- Raup, D. M. & Stanley, S. M. 1978. Principles of Paleontology. W. H. Freeman and Company, San Francisco, 481 pp.
- Retrum, J. B. & Kaesler, R. G. 2005. Early Permian Carbonitidae (Ostracoda): ontogeny, affinity, environment and systematics. *Journal of Micropalaeontology*, 24, 179–190.
- Salas, M. J. & Vaccari, N. E. 2012. New insights into the early diversification of the Ostracoda: Tremadocian ostracods from the Cordillera Oriental, Argentina. *Acta Palaeontologica Polonica*, **57**, 175–190.
- Salas, M. J., Vannier, J. M. C. & Williams, M. 2007. Early Ordovician ostracods from Argentina: their bearing on

the origin of binodicope and palaeocope clades. *Journal of Paleontology*, **81**, 1384–1395.

- Sarv, L. 1959. Ostrakody ordovika Estonskoj SSR [Ordovician Ostracodes in the Estonian S.S.R.]. Eesti NSV Teaduste Akadeemia Geoloogia Instituudi Uurimused 4, Tallinn, 211 pp. [in Russian].
- Schallreuter, R. 1967. Neue Ostracoden aus ordovizischen Geschieben. *Geologie*, **16**, 615–631.
- Schallreuter, R. 1993. Ostrakoden aus ordovizischen Geschieben II. Beiträge zur Geschiebekunde Westfalens 2. Geologie und Paläontologie in Westfalen, 27, 1–273.
- Schallreuter, R. & Krůta, M. 1988. Ordovician Ostracodes of Bohemia. Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg, 67, 99–119.
- Schallreuter, R. & Krůta, M. 2001. Ostracodes from the Dobrotivá Formation (Ordovician, Bohemia). Acta Musei Nationalis Pragae, Series B - Historia Naturalis, 56[2000](3–4), 95–103.
- Sidaravičienė, N. 1992. Ostrakody ordovika Litvy [Ordovician Ostracodes of Lithuania]. LitNIGRI, Vilnius, 251 pp. [in Russian].
- Sidaravičienė, N. 1996. Ordovician Ostracodes of Lithuania, Biostratigraphy. Lithuanian Institute of Geology, Vilnius, 81 pp. [in Lithuanian, with English summary].
- Siveter, D. J. 2008. Ostracods in the Palaeozoic? Senckenbergiana lethaea, 88, 1–9.
- Siveter, D. J. 2009. Ordovician. In Ostracods in British Stratigraphy (Whittaker, J. E. & Hart, M. B., eds), The Micropalaeontological Society, Special Publications, 15–44.
- Siveter, D. J., Sutton, M. D. & Briggs, D. E. G. 2003. An ostracode crustacean with soft parts from the lower Silurian. *Science*, **302**(5651), 1749–1751.
- Smith, R. J. & Martens, K. 2000. The ontogeny of the cypridid ostracod *Eucypris virens* (Jurine, 1820) (Crustacea, Ostracoda). *Hydrobiologia*, **419**, 31–63.
- Smith, R. J. & Kamiya, T. 2003. The ontogeny of Loxoconcha japonica Ishizaki, 1968 (Cytheroidea, Ostracoda, Crustacea). Hydrobiologia, 490, 31–52.
- Spjeldnaes, N. 1951. Ontogeny of *Beyrichia jonesi* Boll. Journal of Paleontology, 25, 745–755.
- Teissier, G. 1960. Relative growth. In *The Physiology of Crustacea, Vol. 1: Metabolism and Growth* (Waterman, T. H., ed.), pp. 537–560. Academic Press, New York and London.
- Tinn, O. 2002. Early Ostracode Evolution and Palaeoenvironmental Application in the Ordovician of Baltoscandia. Dissertationes Geologicae Universitatis Tartuensis 13, Tartu University Press, Tartu, 145 pp.
- Tinn, O. & Meidla, T. 1999. Ordovician ostracodes from the Komstad Limestone. Bulletin of the Geological Society of Denmark, 46, 25–30.
- Tinn, O. & Meidla, T. 2001. Middle Ordovician ostracods from the Lanna and Holen Limestones, south-central Sweden. *GFF*, **123**, 129–136.
- Tinn, O. & Meidla, T. 2003. Ontogeny and thanatocoenosis of early Middle Ordovician ostracode species *Brezelina*

palmata (Krause, 1889) and Ogmoopsis bocki (Sarv, 1959). Journal of Paleontology, 77, 64–72.

- Tinn, O. & Meidla, T. 2004. Phylogenetic relationships of Early Middle Ordovician ostracodes of Baltoscandia. *Palaeontology*, 47, 199–221.
- Tinn, O., Meidla, T. & Ainsaar, L. 2006. Arenig (Middle Ordovician) ostracodes from Baltoscandia: fauna, assemblages and biofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 241, 498–514.
- Tinn, O., Meidla, T. & Sohar, K. 2010a. Intraspecific variation and polymorphism in the ostracode *Conchoprimitia socialis* (Brøgger, 1882) from the early Middle Ordovician Baltoscandian Palaeobasin. *Bulletin of Geosciences*, **85**, 603–616.
- Tinn, O., Meidla, T., Ainsaar, L. & Kivioja, K. 2010b. Rich and heterogeneous fossil ostracod fauna in the Ordovician sediment intrusions at Osmussaar Island, Estonia, reveals an ancient impact event. *GFF*, **132**, 201–211.
- Tolmacheva, T., Egerquist, E., Meidla, T. & Holmer, L. 2001. Spatial variations in faunal composition, Middle Ordovician, Volkhov Stage, East Baltic. *GFF*, **123**, 65–72.
- Tolmacheva, T., Egerquist, E., Meidla, T., Tinn, O. & Holmer, L. 2003. Faunal composition and dynamics in unconsolidated sediments: a case study from the Middle Ordovician of the East Baltic. *Geological Magazine*, 140, 31–44.
- Vannier, J. M. C., Siveter, D. J. & Schallreuter, R. E. L. 1989. The composition and palaeogeographical significance of the Ordovician ostracode faunas of Southern Britain, Baltoscandia and Ibero-Amorica. *Palaeontology*, **32**, 163–222.
- Wilkinson, I. P., Wilby, P. R., Williams, M., Siveter, D. J., Page, A. A., Leggitt, L. & Riley, D. A. 2010. Exceptionally preserved ostracodes from a Middle Miocene palaeolake, California, USA. *Journal of the Geological Society*, 167, 817–825.
- Williams, M., Siveter, D. J., Ashworth, A., Wilby, P., Horne, D. J., Lewis, A. R. & Marchant, D. 2008a. Exceptionally preserved lacustrine ostracods from the Middle Miocene of Antarctica: implications for high latitude palaeoenvironment at 77° south. *Proceedings of the Royal Society, Series B, Biological Sciences*, 275(1650), 2449– 2454.
- Williams, M., Siveter, D. J., Salas, M. J., Vannier, J., Popov, L. E. & Ghobadi Pour, M. 2008b. The earliest ostracods: the geological evidence. *Senckenbergiana lethaea*, 81, 11–21.
- Whatley, R. C. 1988. Population structure of ostracods: some general principles for the recognition of palaeoenvironments. In *Ostracoda in the Earth Sciences* (De Deckker, P., Collins, J.-P. & Peypouquet, J.-P., eds), pp. 245–256. Elsevier, Amsterdam.
- Whatley, R. C. & Stephens, J. M. 1977. Precocious sexual dimorphism in fossil and recent Ostracoda. In Aspects of Ecology and Zoogeography of Recent and Fossil Ostracoda (Löffler, H. & Danielopol, D., eds), pp. 69–91. Dr. W. Junk b.v. Publishers, The Hague.

# Praha basseini (Tšehhi Vabariik) Darriwili ostrakoodi Conchoprimitia osekensis (Přibyl, 1979) ontogenees

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On analüüsitud Šárka kihistus (Alam- ja Kesk-Darriwil) väga sageli esineva ostrakoodiliigi *Conchoprimitia osekensis* (Přibyl, 1979) ontogeneesi. On kirjeldatud ja illustreeritud liigi täiskasvanud isendeid ning kaheksat varasemat kasvustaadiumi. Tulemused osutavad, et samas stratigraafilises intervallis sageli esinev liik *C. osekensis* on kirjeldatud *Conchoprimitia? dejvicensis*'e varasemate kasvustaadiumide alusel ja seda tuleb pidada *C.? dejvicensis*'e sünonüümiks. See tulemus rõhutab ontogeneesiuuringute tähtsust ostrakoodide süstemaatika selgitamisel ja biodiversiteedi hindamisel.