

Towards objectivity in Ostracoda species definition

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Abstract – The problem of consistent identification of unornamented fossil ostracod taxa, especially species, is reviewed in an historical context. The solution lies in modern imaging and image storage and handling technologies combined with a careful but pragmatic (heuristic) approach to identification and taxonomy.

Keywords: taxonomy / species / imaging

Résumé – Vers l'objectivité dans la définition des espèces d'ostracodes. On examine, dans son contexte historique, le problème de l'identification cohérente des ostracodes non ornementés. La solution réside dans l'utilisation des techniques modernes de digitalisation d'images et leur traitement, et d'une approche prudente et pragmatique de l'identification et de la taxonomie.

Mots clés : taxonomie / espèces / images

1 Introduction

A common remark to ostracod specialists even from fellow palaeontologists' is "Oh, ostracods, little beans!" with the implication that they are essentially unidentifiable and not very useful. While it is true that ostracods are not usually as abundant as foraminifera in marine sediments and are extremely difficult to identify in thin-section, nonetheless, the importance of the group for palaeoenvironmental analysis and biostratigraphy especially of non-marine sequences is well-established (e.g. chapters in Holmes and Chivas, 2002; Park and Smith, 2003; Horne, 2002; Whittaker and Hart, 2009). Living ostracods occur in all aquatic environments from the deep ocean to temporary pools and ground water, their geological record and evolutionary history is long, rich and varied from at least Ordovician to Recent (Oakley *et al.*, 2012; Siveter *et al.*, 2014), and their low-magnesium calcite shells record chemical and isotopic data from the host water (chapters in Holmes and Chivas, 2002; Park and Smith, 2003). Many ostracods have distinctive external ornament and complex internal structures as keys to identification (see Horne *et al.*, 2002), however, in the fossil record there are many taxa that lack external surface ornament, where internal features when observable are simple, and there is only three-dimensional shape to work with. Even with unornamented "beans" it is important to understand that beginners with ostracods can

quickly learn how to orientate them: as an introductory student exercise the author gave classes a monospecific assemblage of the smooth Early Jurassic Maticopina species *Ogmoconchella aspinata* (Drexler) and equipped with very basic knowledge of the animals mode of life within an hour students could orientate the specimens, work out left valve > right valve overlap, and reach the conclusion that the collection of adult and juvenile carapaces and valves probably represents a single species. However, despite this promising start there are fundamental problems with logical and consistent identification of unornamented extinct ostracod taxa, much of which results from poor original material, poor description and/or illustration and subsequent taxonomic adjustments.

Meisch *et al.* (2019) estimate that there are 2330 "subjective" species of extant non-marine ostracods assigned to 270 genera. Meisch and colleagues use the word "subjective" advisedly as the 2330 named/described species were defined at different times by many different workers and most have not been validated *via* genetic characterization. The number of living marine and brackish water ostracod species is currently being evaluated *via* the WoRMS database (World Register of Marine Species) (Simone Brandão, personal communication, 9 July 2019), but in 2000 an estimated figure was 9500 living species and 15 500 fossil marine and brackish water species (Koen Martens, OSTRACON, 28 March 2000). Horne *et al.* (2002) give an estimate of 33 000 living and fossil species. These figures are certainly underestimates, as Rodriguez-Lazaro and Ruiz-Muñoz (2012, p. 1) comment "Only about half of the estimated 20 000 living species have

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been described formally, the majority from marine and transitional waters”.

2 The problem

With living ostracods anatomical features of body parts and appendages, including hemipenes, and genetic data together with carapace characteristics are available to aid species recognition. Only exceptionally are soft body parts preserved in the fossil record, as in the very special case of the Silurian Herefordshire Lagerstätte, UK (e.g. [Siveter et al., 2012](#)). Thus, of three potential approaches to taxonomy, viz. genetics, appendages, calcified carapace, only the latter is usually available to palaeontologists. In the background is another problem: what is a species? The old idea of a species representing a unique interbreeding group is now very old-fashioned and there is no clear agreement on how to define a biological species, it depends what you mean and where you are coming from. [Martens et al. \(1998\)](#) in discussing ostracod species with mixed reproduction, sexual and asexual, cite [Mayden \(1997\)](#) who listed 25 different species concepts ([Martens et al., 1998](#), Box 11.2). More recently [Pante et al. \(2015\)](#), discussing problems of species recognition and connectivity in living marine organisms, comment (p. 527) “described taxa are not facts, but testable hypotheses about the structure of biodiversity. This is true not only for higher taxonomic ranks, generally considered as arbitrary ranks, but also for the species rank, which is the only taxonomic category for which a “biological reality” is recognized by most scientists”. Unlike [Pante et al. \(2015\)](#), the palaeontologist also has the time dimension to consider when defining a species in a phylogenetic context, where the species diagnosis is of critical importance. From the palaeontological point-of-view we are simply dealing with “morphospecies” and individual judgement and experience come into play in assessing the variation in morphocharacters permissible in a single (fossil) species. With fossil ostracods it is usually possible to recognise juveniles from adults and often adult males and females from carapace characteristics, but the specimens occur in death assemblages that represent varying distance from the original living population of a species. Why is this important? In simple terms the species is the basic building block for applications ranging from biostratigraphy to environmental interpretation and monitoring to reconstruction of evolutionary processes and patterns through time, and is therefore of fundamental importance.

Key for identification of fossil species are carapace features, i.e.:

- **A. External:** 1. Three-dimensional shape in dorsal, ventral, left-lateral, right-lateral, anterior and posterior views. 2. Valve overlap and over-reach. 3. Surface morphology including ocular structures, subcentral tubercles or depressions, lobation, contact margin features, caudal process. 4. Surface ornament. 5. Normal pore canals. 6. Marginal rims and spines. 7. Sexual dimorphism features. 8. Juvenile moult stages *cf.* adults.
- **B. Internal:** 1. Shape of outer margin viewed internally especially in relation to A.1 and A.2. 2. Relationship of dorsal margin to free margins. 3. Nature of dorsal hinge structures or contact groove in larger valve. 4. Nature of

adductor, frontal, mandibular and other muscle scars. 5. Nature of marginal zone: shape, width, vestibulae, marginal pore canals. 6. Internal morphology reflecting external surface morphology (A.3). 7. Internal nature of normal pore canals. 8. Sexual dimorphism features (A.7). 9. Juvenile moult stages *cf.* adults (A.8).

At first sight numerous criteria from the calcified carapace are thus available for species definition and recognition, however, not all are routinely available, especially with fossil material. Many Palaeozoic and early Mesozoic taxa have relatively simple internal structures and muscle scars are only occasionally preserved and visible.

3 Visualisation and comparison

As the list below will demonstrate, in a few decades palaeontologists have moved from free-hand or camera-lucida drawings and simple light photographs of fossils to technologies that not only image but also allow precise comparison of shapes and surfaces with the ability to apply a confidence factor to the comparisons. Of course, with fossil material lacking soft parts and genetic information, close comparison of shells does not necessarily give evidence of a biological closeness or relationship.

2D: 1. Line drawings—some are very good (e.g. [Müller, 1894](#); [Sars, 1922–1928](#); [Benson, 1964](#); [Maddocks, 1966](#)) but many others are a less helpful guide to reliable species identification. It is worth commenting that the preparation of line drawings helps the “artist” to understand the structures and therefore to highlight key elements in the drawing. 2. Photographic and digital images *via* light microscopy (LM) and scanning electron microscopy (SEM)—LM, until the advent of modern digital imaging with computer graphics few publications rivaled the transmitted and reflected light figures of [Triebel \(e.g. 1941\)](#); SEM, particularly important for ostracods where all important carapace taxonomic features except for marginal pore canals for visible on the shell surface. 3. Carapace outline geometry—[Herrig \(1979a\)](#) applied a geometrical approach to analyzing the lateral outlines of Lower Jurassic *Bairdia* species, and similarly [Forel and Grădinaru \(2018\)](#) measured the relative lengths and angles of dorsal margin elements in Triassic species of *Acratia*, *Bairdia*, *Kempfina* and *Paracypris* to provide objectivity in describing these smooth taxa; the software package “MORPHOMATICA” facilitates comparison of valve outlines (e.g. [Danielopol et al., 2014](#); [Gitter et al., 2015](#)), further developed as Geometric Morphometrics by [Wrożyna et al. \(2016\)](#), and *cf.* image analysis of sediment grains (e.g. [Klosa, 1991](#)).

3D: 1. Line drawings of serial sections aimed at a 3D impression (e.g. [Lethiers, 1972](#), Fig. 4). 2. Stereopairs—stereopair visualisation of photographic images followed quickly after the early development of photography, but in the context of micropalaeontology the technique was rejuvenated by the ease with which stereo images can be made in the SEM ([Sylvester-Bradley, 1973](#)), and stereo effect can also be achieved by red/green false colouring available in modern SEMs (e.g. [Swanson, 2012](#)). 3. Computer graphic reconstruction of ground or sliced images (Herefordshire Lagerstätte—[Sutton et al., 2001, 2014](#); [Siveter et al., 2012](#)).

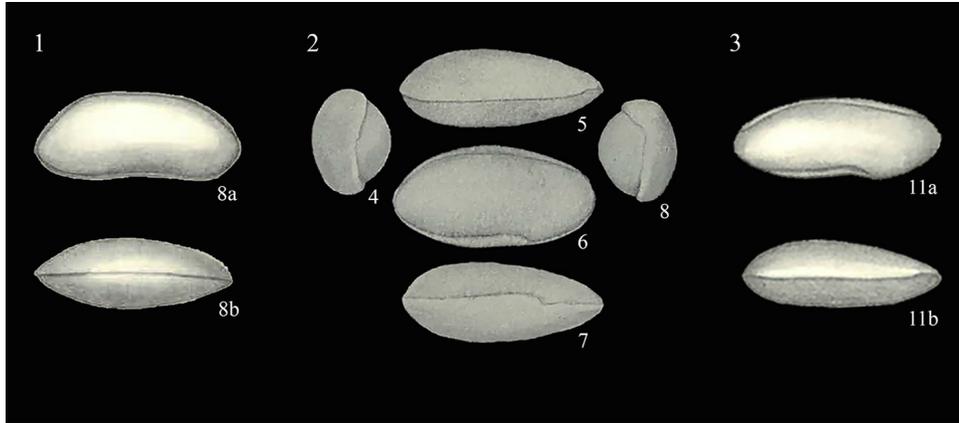


Fig. 1. Original illustrations of *Bairdiacypris* and *Fabalicypris*.

1. *Bairdiacypris deloi* Bradfield (1935).

Fig. 1. Plate 7, figs. 8a and 8b of Bradfield: type species of genus, Holotype; Locality 13 of Bradfield, Ardmore, Ardmore Basin, Oklahoma, USA; Hoxbar Formation, Pennsylvanian, Upper Carboniferous.

Fig. 8a: carapace right lateral view; 8b: carapace dorsal view. Dimensions: (text, p. 93) L=1.32, H=0.54, W=0.45; (figure caption, p. 160, magnification factor x27) L=1.26, H=0.52, W=0.41.

2. *Fabalicypris wileyensis* Cooper (1946).

Plate 6, figs. 4–8 of Cooper: type species of genus, Holotype; Locality 13 of Cooper, Illinois, USA; Wiley “zone”, Cherokee Group, Pennsylvanian, Upper Carboniferous.

Fig. 4: carapace posterior view; 5: carapace dorsal view; 6: carapace right lateral view; 7: carapace ventral view; 8: carapace anterior view. Dimensions: (text, p. 61) L=1.02, H=0.53, W=0.42; (figure caption, p. 138, magnification factor x30) L=1.06, H=0.53, W=0.42.

3. *Fabalicypris warthini* (Bradfield, 1935).

Plate 5, figs. 11a and 11b of Bradfield: presumed Holotype; original x 27 slightly enlarged here; Locality 98 of Bradfield, Deese, Ardmore Basin, Oklahoma, USA; Deese Formation, Pennsylvanian, Upper Carboniferous.

Fig. 11a: carapace right lateral view; 11b: carapace dorsal view. Dimensions (text, p. 83) L=1.07, H=0.41, W=0.34; (figure caption, p. 156, magnification factor x27) L=1.04, H=0.41, W=0.33. Abbreviations: L=length, H=height, W=width. Dimensions in mm.

The future: Computed tomography and magnetic resonance imaging, see Ziegler *et al.* (2018) on Mollusca, combined with publicly available databases of images of type specimens.

4 Case study: *Bairdiacypris* Bradfield (1935) and *Fabalicypris* Cooper (1946)

Bairdiacypris was described from the Pennsylvanian (Upper Carboniferous) of Oklahoma by Bradfield (1935) established on the new species *B. deloi* (Fig. 1, fig. 1; Fig. 2, figs. 1a and 1b). Later, Cooper (1946) erected the new genus *Fabalicypris* based on his new species *F. wileyensis* (Fig. 1, fig. 2) from the Upper Carboniferous of Illinois. Subsequently, Sohn (1960) reviewed these taxa and placed the species *Bairdia warthini* Bradfield (1935) into *Fabalicypris* (Fig. 1, fig. 3). The genera are similar only in as much as both are elongate with a concave ventral margin, are unornamented and lack strong surface morphological features, and both have left valve > right valve overlap; they differ in the geometry of the lateral valve outlines and nature of valve overlap ventrally. Internal features were not mentioned in either case in the original descriptions.

Kozur (1971) placed two new Triassic species in *Bairdiacypris*, citing Belousova (1965) as a source. The first use of the genus *Bairdiacypris* in the Jurassic was by Donze (1966—who cites Elmi and Mouterde (1965) but without giving the reference) for *B. sartriensis* Donze (1966) from the

Hettangian of Ardèche, France and was followed in this generic designation by Lord (1971) for specimens from the Hettangian of Yorkshire, UK, in both cases without meaningful discussion of the use of a Palaeozoic genus for Mesozoic species. Similarly Donze (1966) recognised a new species as *Fabalicypris praelonga* without comment. Drexler (1958) placed Lower Jurassic (Hettangian) species in the Palaeozoic genera *Healdia* Roundy (1926) and *Krausella* Ulrich (1894). These appear to be the first applications of names of Palaeozoic genera to post-Palaeozoic species.

Herrig (1979a) describing material from the Lower Jurassic of eastern Germany placed new species in both *Bairdiacypris* and *Fabalicypris*, and although the new taxa were thoroughly described and figured there was again no discussion of the generic assignments. This pattern was followed by later workers, for examples, Harloff (1993) carefully describes and figures one species each of *Bairdiacypris* and *Fabalicypris* but without comment on the genera, and similarly Beher (2004) describes and figures seven species of *Bairdiacypris* and five of *Fabalicypris*, in both cases from the Lower Jurassic of SW Germany. The use of *Bairdiacypris* for Lower Jurassic species is now well-established.

5 Discussion

Personal experience and anecdotal information indicate that few workers now visit collections to compare type material, despite enlightened funding *via* programmes such as

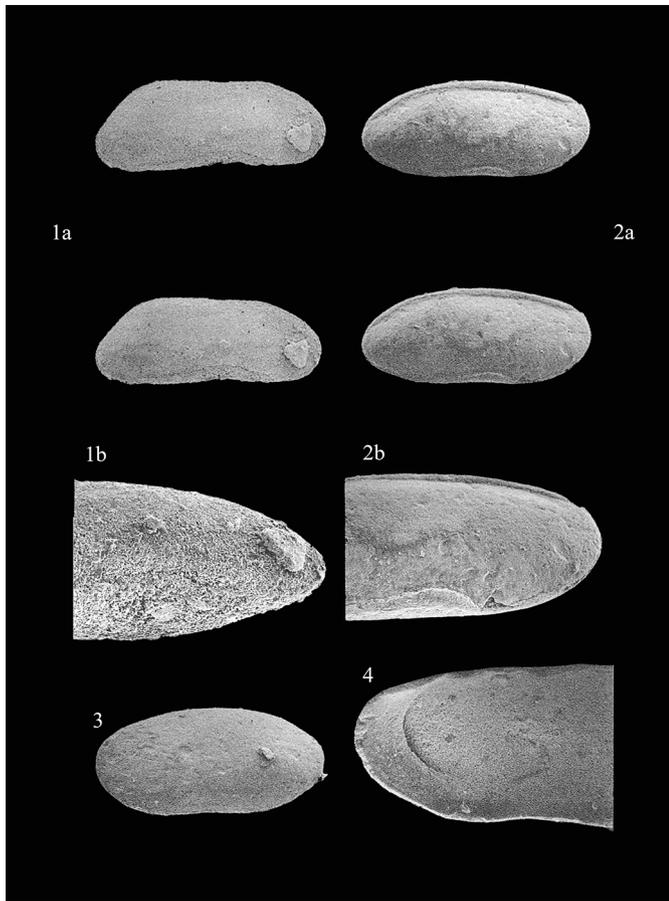


Fig. 2. 1a, b. *Bairdiacypris deloi* Bradfield (1935).

USNM 307374 Carapace (converted to fluorite); topotype of type species of *Bairdiacypris* Bradfield (1935); Locality 13 of Bradfield, south edge Ardmore, Carter County, Oklahoma, USA (Sohn, 1960, p. 57).

1a. Carapace right lateral view, stereopair; L=0.66 mm, H=0.26 mm. 1b. Carapace antero-ventral detail; width 0.48 mm.

2a, b. *Fabalicypris warthini* (Bradfield, 1935) USNM 307375 Carapace; Locality Carter County, Oklahoma, USA (Sohn, 1960, p. 64).

2a. Carapace right lateral view, stereopair; L=0.98 mm, H=0.42 mm; note strong LV dorsal margin overhang and LV ventral margin extension or “step”.

2b. Carapace anterior to show ventral margin “step”.

3. *Fabalicypris warthini* (Bradfield, 1935) USNM 307376 Carapace, left lateral view; L=0.92 mm, H=0.42 mm; Locality as Figure 2.

4. *Fabalicypris warthini* (Bradfield, 1935) USNM 307377 RV, internal lateral view of anterior to show width of marginal zone and vestibule; H=0.39 mm; Locality as Figure 2.

SYNTHESYS, or request loan or comparative material, or SEM images from colleagues, and are therefore relying on published images. In this respect the demise of the pioneering *A Stereo-Atlas of Ostracod Shells* is particularly unfortunate but subscription income no longer supported its publication.

The example of *Bairdiacypris* and *Fabalicypris* demonstrates the difficulties involved with taxonomy based on fossil material. There are numerous cases. It seems unlikely that “*Bythocypris*” from the Jurassic is biologically close or related

to the living genus *Bythocypris* Brady (1880), despite similar carapace characteristics, because of the 190 Ma + time interval involved; some examples: Lower Jurassic: south-west Germany (Drexler, 1958), eastern Germany (Herrig, 1979b), south west Germany (Harloff, 1993), south Germany-western Austria (Harloff and Jäger, 1994), south Germany-north Switzerland (Beher, 2004), Hungary (Monostori, 2008), Argentina (Ballent, 1987); Middle Jurassic: southern Tunisia (Mette, 1995), India (Khosla *et al.*, 2009), Argentina (Ballent, 1991). A parallel but different example concerns the genus *Xestoleberis* Sars (1866), described from living material and with a fossil record from the mid Cretaceous (c. 95 Ma) (Slipper 2009a, p. 353), with an unornamented “bean” carapace but with a characteristic antero-dorsal scar called the *Xestoleberis*-spot present in both living and fossil species, which provides a more convincing case for genus longevity.

In principle there is no reason why a genus-level taxon should not have survived from the Palaeozoic, through the catastrophic Permian extinction event, and be represented in the Mesozoic by successor species. Above it is argued here that the long time intervals involved militate against this happening in nature, but the real problem, discussed above, is reliable comparative taxonomy.

Most workers looking at a fossil assemblage consciously or unconsciously refer to literature relating to the relevant timeframe for taxonomic precedent or inspiration and use taxa previously recognized, which is a comfortable and comforting procedure but may not advance science. *Isobythocypris* Apostolescu (1959) described from Early Jurassic sediments of the Paris Basin is a reasonably consistently recognised genus that appears to be restricted to the late Triassic-Early Jurassic, but what are its ancestors and descendants? Few workers now look at samples vertically (to use a wine tasting analogy), *i.e.* looking at genera and their included species over extended timescales, yet this is essential to understand evolutionary patterns and hopefully process – what are “real” clades and can we ever get close to them with most fossil material?

Two further examples of problematic genus names follow, in the first case a Palaeozoic taxon applied to post-Palaeozoic material, and in the second a Mesozoic taxon confusingly similar to other Palaeozoic and Mesozoic genera:

- 1 *Krausella* Ulrich (1894) (Lower Silurian, Minnesota), a name used by both Drexler (1958) and Apostolescu (1959) but no longer recognized in the Lower Jurassic.
- 2 *Pontocyprrella* Mandelstam, 1955 (*in* Luebimova 1955) (type species *Bairdia harrisiana* Jones; Cretaceous). Confusingly the genus is attributed to Mandelstam in the publication but the only species actually described is *P. aureola* Luebimova (1955) from the Callovian-Oxfordian; some *Pontocyprrella* are very similar to Palaeozoic *Fabalicypris*, *e.g.* *P. harrisiana* figured in Slipper (2009b, Pl.1, fig. 15) and to *Isobythocypris*.

Taking a broader perspective, “taxonomic harmonisation” is a term recently applied to a practical approach to consistent species identification, particularly in the context of ostracod distributional databases applied to climate reconstruction (Horne *et al.*, 2011a, b), especially in circumstances where it may be difficult to conclusively demonstrate conspecificity

between specimens from different regions. Danielopol *et al.* (2015) develop this idea, introducing the term “consensus species” and using the expression “a heuristic solution”. The word “heuristic” has two meanings (Oxford English Dictionary): 1. enabling a person to discover or learn something for themselves, and 2. (IT) reaching a solution by trial and error or rules that are loosely defined. Definition 2. is applicable but I am also attracted by Definition 1. In contrast, Wikipedia defines “heuristic” as: “any approach to problem solving or self-discovery that employs a practical method that is not guaranteed to be optimal, perfect or rational, but instead sufficient for reaching an immediate goal”. For the palaeontologist, the solution to achievable consistency in ostracod species definition lies in modern imaging and image storage and handling technologies combined with a careful but pragmatic (heuristic) approach to identification and taxonomy in a time context.

6 Conclusions

The problems of consistently identifying fossil species, in this case ostracods, is discussed in terms of them being morphospecies which may or may not have had biological reality. It is worth reminding ourselves of the comment of Pante *et al.* (2015, p. 527) discussing living species: “described taxa are not facts, but testable hypotheses”.

In a generation we have moved from subjective drawings and usually poor quality light micrograph illustrations of living and fossil ostracod species to the vast potential of digital imaging, analysis, manipulation and storage. There is therefore no excuse for poor or minimal illustration of any figured species, but especially those described as new. Publications with species lists but no illustrations are of very limited value. Image capture, storage, manipulation and comparison technologies improve at an ever increasing rate and provide the support for a careful, consistent but pragmatic approach to species description and identification, in a time context, and thereby to enhanced applications.

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