An exceptionally preserved myodocopid ostracod from the Silurian of Herefordshire, UK

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An exceptionally preserved new ostracod crustacean from the Silurian of Herefordshire, UK, represents only the third fully documented Palaeozoic ostracod with soft-part preservation. Appendages, gills, gut system, lateral compound eyes and even a medial eye with a Bellonci organ are preserved, allowing assignment of the fossil to a new genus and species of cylindroleberidid myodocene (Myodocopida, Cylindroleberididae). The Bellonci organ is recorded for the first time in fossil ostracods. The find also represents a rare occurrence of gills in fossil ostracods and confirms the earliest direct evidence of a respiratory-cum-circulatory system in the group. The species demonstrates remarkably conserved morphology within myodocopids over a period of 425 Myr. Its shell morphology more closely resembles several families of myodocopids other than the Cylindroleberididae, especially the Cypridinidae and Sarsiellidae, thus questioning the utility of the carapace alone in establishing the affinity of fossil ostracods.

Keywords: cylindroleberidid; exceptional preservation; Herefordshire Lagerstätte; Myodocopa; Ostracoda; Silurian

1. INTRODUCTION

Ostracods are by far the most common arthropods in the fossil record, with thousands of species and countless valves known from at least the basal Ordovician onwards (Siveter 2008; Williams et al. 2008). The group has successfully invaded a range of marine, non-marine and, rarely, terrestrial habitats (Horne 2003). Ostracod species are valuable indicators of paleosalinity and other palaeoenvironmental variables, and can be used as an independent test of palaeogeography at palaeocontinental to local scales. The fossilized soft parts of ostracods are extremely rare (Smith 2000), especially in Palaeozoic rocks, from which only two specimens (species) have been documented in detail (Siveter et al. 2003, 2007a), both from the Silurian Herefordshire Konservat-Lagerstätte, England (Briggs et al. 1996). Here we describe a third specimen, Nasunaris flata gen. et sp. nov., from the same deposit, which, like the two previously described species, is a myodocene ostracod. Myodocopes and podocopes are the two major groups of ostracods today (Horne et al. 2002, 2005). The monophyly of (myodocene and podocene) ostracodes has been questioned in molecular phylogenies (e.g. Yamaguchi & Endo 2003; Regier et al. 2005) and supported by the use of a morphological approach (e.g. Cohen et al. 1998; see Horne et al. 2005). The fossil record of myodocopes, which begins with one (latest) Ordovician species (Gabbott et al. 2003), is generally poor, in part due to their typically weakly calcified carapace.

The Herefordshire Konservat-Lagerstätte is of Wenlock Series, mid-Silurian age (approx. 425 Myr BP) and is one of only four major Konservat-Lagerstätte known from the Silurian (Briggs et al. 1996; von Bitter et al. 2007). Since its discovery in the 1990s, it has yielded a wide range of exquisitely preserved three-dimensional invertebrate fossils from a few millimetres to several centimetres in dimension (Briggs et al. 2008). The fossils preserve extraordinary detail of soft parts and furnish remarkable palaeobiological and evolutionary data. They include a polychaete worm (Sutton et al. 2001c), an aplacophoran-like mollusc (Sutton et al. 2001a,b, 2004), a gastropod (Sutton et al. 2006), a pycnogonid (Siveter et al. 2004), a stem-group chelicerate (Orr et al. 2000b; Sutton et al. 2002), a marrellomorph (Siveter et al. 2007b), a stem-group crustacean (Siveter et al. 2007c), ostracods (Siveter et al. 2003, 2007a), a barnacle (Briggs et al. 2005), a phyllocardid (Briggs et al. 2004), a brachiopod (Sutton et al. 2005a), a stem-group asteroid (Sutton et al. 2005b) and a large variety of unpublished forms.

2. MATERIAL AND METHODS

The Herefordshire Konservat-Lagerstätte yields three-dimensional fossils as calcitic void in-fills in carbonate
concretions that occur in a volcaniclastic host deposit (Orr et al. 2000a). The ostracod was reconstructed as a ‘virtual fossil’: the specimen was serially ground and photographed at 20 μm intervals; extraneous material was removed digitally; fossil/matrix ambiguities were resolved prior to generating a colour-coded reconstruction using the custom SPIERS software suite, implementing the methods of Sutton et al. (2001d, 2002). Images in figure 1 were generated by ray-tracing. The specimen was studied using an interactive stereo-capable viewer. The datasets resulting

Figure 1. (Caption opposite.)
The first antenna is long, slender, weakly tapered and projects forward adaxial to the second antenna (figure 1b,f,g,i,m). It consists of a long proximal part (podomere?) that is markedly geniculate with a slightly longer distal part (podomeres not discernible); the forked termination of the latter (evident in the right limb only) is presumed to be the proximal parts of two setae. A pair of pedunculate, elongate ovoid lateral eyes (presumed compound; ommatidia not discernible) arise abaxially and just above the base of the first antennae (figure 1b,f,h). Sagittally, a small medial eye bears a short, elongate, forward projecting structure, interpreted as a Bellonci organ (figure 1h). The second antenna (figure 1b,c,f,g,i,n) arises below the lateral eye; its large, globose, almond-shaped basipod is situated within the bulb of the carapace. The exopod is long, slender and curves anterolaterally through the rostral incisure and flexes backwards. It consists of two long subequal parts delimited at a weak flexure (a possible podomere boundary), the distal part bearing at least four closely spaced subparallel setae along the outer edge (more clearly evident on the right limb) of presumed separate podomeres. The endopod is curved, about one-quarter the length and one-third the width of the exopod; podomeres are not discernible. The gaps in the left exopod and right endopod represent missing data.

The mandible (figure 1c,f,g,o) arises below and adaxial of the second antenna, and abaxial of the labrum. The limb base (presumed basipod and coxa) is elongate, but details of any enditic processes cannot be resolved. The presumed endopod is separated from the limb base by a geniculation; it is straight, short, elongate, tapering distally and it projects anteroventrally. A tiny narrow elongate structure, projecting dorsally from the limb base/endopod boundary, is interpreted as the proximal part of an exopod (it is better preserved on the right limb). The right first and second maxillae are intact, but only the base of each corresponding left limb is preserved. The first maxilla has a short limb base (presumed basipod and proximal endite) with a few poorly defined possible enditic processes, and a presumed endopod consisting of a proximal part (podomere?) that is geniculate with a shorter, tapering distal part (figure 1c,f,p). The second maxilla (figure 1c,f,q) lies aside the atrium oris and projects below the first maxilla. The limb base appears to bear a lateral lamelliform
projection of equal size directed posteroventrally (a presumed epipod), and an elongate ramus (conventionally, the exopod in myodocopids; reinterpreted as the endopod by Boxshall 1998) consisting of a long distal part flexed at about 90° to a much shorter proximal part. The sixth limb has not been identified.

The body isthmus forms a posterodorsally inclined ridge coincident with the adductorial sulcus (figure 1a,c,f,i); a flattened area of the ventral part of the isthmus represents the adductor muscle attachment (most clearly evident on the left side; figure 1f). The seventh appendage is vermiform, about 4 mm long, slender, tapers weakly and may have a bifid-shaped termination (evident in right limb; figure 1f,i,r). This appendage arises below and posterior to the isthmus, curving behind the latter and over the posterodorsal body area. The furca is large and elongate, extending slightly outside the carapace ventrally (figure 1c,f,g); individual lamellae and claws are not discernible. The posteroventral body area behind the seventh appendage is flanked by delicate lamellae (figure 1a,c,f,i); parts of two lamellae with slightly thickened edges are preserved on the left side and one incomplete lamella on the right side (there may be multiple pairs, but this area is difficult to resolve). Such lamellae are presumed gills: they do not occur elsewhere over the body area and in position and morphology they are similar to the gills of the Silurian myodocopid Colymbosathon. The labrum is evident medially but its lateral margins are difficult to resolve. A well-developed atrium oris leads to a short oesophagus and a highly developed secondary atrium. The gut terminates bluntly in the presumed anus in front of the furca. Preservation of the ventral body area is not adequate to allow gender to be determined.

4. DISCUSSION

The anterior sensory ‘Bellonci organ’ of the medial eye, known only in Myodocopa, is here recognized for the first time in the fossil record. Within Ostracoda, a vermiform seventh limb and lateral eyes are unique to Myodocopida, and gills are known only from the Family Cylindroleberididae, to which N. flata is therefore assigned. The first to fifth appendages are also compatible with the limb morphology of cylindroleberids, including the presumed two setae borne distally on the first antenna, which may represent the c-bristle (on 7th podomere) and f-bristle (on 8th podomere) of Recent myodocopids (figure 1g, i.e.g. Kornicker 1981). That the sixth appendage has not been resolved in N. flata may reflect the fact that the limb is much reduced in cylindroleberids. A medial eye, a caudal siphon and the presence of an epipod on the second maxilla only, are also characteristic of myodocopid (and not halocyprid) myodocopes. The short length of the Bellonci organ in N. flata is consistent with some cylindroleberids, whereas it is relatively long in sarsiellid, philomedid and rutidermatid myodocopes. A caudal siphon occurs in sarsiellids and many cypridinid myodocopes, but (notwithstanding N. flata) is rarely and only weakly developed in cylindroleberids.

The position and alignment of the isthmus along the adductoral sulcus provides good evidence that the sulcus in other (especially Palaeozoic) ostracods represents the site of the isthmus and adductor muscle. N. flata and the cylindroleberidid Colymbosathon ecplecticos Siveter et al., 2003 from the Herefordshire Lagerstätte are the only fossil Ostracoda that preserve gills (evidence for gills in the myodocopids Triacorys spitzbergensis Weitschat, 1983 from the Triassic and the Jurassic species Juraleberis jubata Vannier & Siveter, 1995 is inconclusive), and they provide the earliest direct evidence of a respiratory-cum-circulatory system in the group. The gills indicate the presence of branchial circulation and, therefore, an integrated vascular circulatory system with a heart (Vannier et al. 1996). The slightly thickened edges of the gill lamellae are also comparable to those in C. ecplecticos and the site of hypobranchial and epibranchial canals in Recent cylindroleberids. Ventilation in N. flata was presumably facilitated by the second maxilla epipod, which drew water into the domiciliary cavity and, as in many myodocopids (Vannier et al. 1996), water was expelled via the caudal siphon, which is sited directly below the gills. A similar function can be inferred for the caudal siphon (‘process’) of several groups of Palaeozoic myodocopes, such as cypridinids, cypridinelliformids and entomoconchids. The clearly defined dark area in the extended stomach is interpreted as food content; it has the same shape and size as a faecal pellet of Recent myodocopids (Vannier 1998).

Carapace shape converges between extant myodocope families, and the accuracy of suprageneric assignment of species depends on knowledge of their body and limb morphology (Cohen & Morin 2003). The soft parts of N. flata indicate its cylindroleberid affinity, but, as with C. ecplecticos, its shell morphology appears to be anomalous, especially when compared with the type genus of the family, for example (cf. figure 1a,f). The subcircular lateral outline combined with a long, tapered rostrum and associated well-developed rostral incisure, together with the presence of a well-developed caudal siphon, recall other myodocopid families, especially cypridinids (supposed Silurian to Recent) and others such as bolbozooids and entomoconchids, which are known only from the Palaeozoic (Siveter & Vannier 1990; Kornicker & Sohn 2000). In limb morphology, subcircular lateral valve outline and the presence of a caudal siphon, N. flata is also like the Sarsiellidae (no known fossil representatives), but such a prominent rostrum and especially a deep rostral incisure are not typical of that family. The discovery of the soft parts of N. flata demonstrates the need for caution in interpreting the affinities of other fossil presumed myodocopes based solely on shell morphology. The current higher taxonomic assignment of many fossil myodocop shell genera may be suspected. The presence of a cypridinid-like (or sarsiellid-like) carapace shape in N. flata is consistent with the hypothesis (Horne et al. 2005) that cylindroleberidid myodocopes are basal to cypridinid and sarsiellid myodocopes.

Nasunaris flata lived in outer shelf to basin slope marine waters at some 150–200 m depth (Briggs et al. 1996). The majority of Recent myodocopes are nekto-benthic, feeding as predators, scavengers or detritivores, and N. flata probably occupied a similar niche and feeding strategy. The substantial basipod of its second
antenna and its well-developed rostral incisure, which would allow protrusion of frontal appendages, suggest that *N. flata* was a proficient swimmer. However, its dispersal capacity was probably limited, as it is unknown outside the type locality in the well-studied Welsh Basin. The origin of pelagic ostracods is recorded in an ecological shift in myodocopes in the late Silurian (Siveter 1984; Siveter et al. 1991).

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REFERENCES


