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 median eye with a Bellonci organ are preserved, allowing assignment of the fossil to a new genus and species of cylindroleberidid myodocope (Myodocopa, 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 myodocopes over a period of 425 Myr. Its shell morphology more closely resembles several families of myodocopes 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 palaeosalinity 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 myodocope ostracod. Myodocopes and podocopes are the two major groups of ostracods today (Horne *et al.* 2002, 2005). The monophyly of (myodocope and podocope) ostracods 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 some 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 aplousobranch-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 phyllocarid (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

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Figure 1. (*Caption opposite.*)

concretions that occur in a volcanoclastic 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. (*Opposite.*) (*a–k, m–r*) Holotype of *Nasunaris flata*, carapace with soft parts: (*a–c, e–k, m–r*) ‘virtual’ reconstructions (a slight diagonal break across the left valve and gaps in the first antenna left exopod and right endopod represent missing data; and the exact boundary between structures such as body and appendages, as indicated by colour changes, is arbitrary); (*d*) specimen in rock. (*a*) External right lateral view, $\times 11$. (*b*) Anterior view (stereo-pair) showing the eyes and first and second antennae, with valves and other features omitted, $\times 9.9$. (*c*) Ventral view (stereo-pair), with right valve omitted, $\times 10.9$. (*d*) Oblique posterior section, $\times 9.9$. (*e*) Right lateral view (stereo-pair) of gut system, $\times 7$. (*f*) Internal right lateral view (stereo-pair), with right valve omitted, $\times 11$. (*g*) Anterior view (shadow-casting of valves turned off for clarity), $\times 9.9$. (*h*) Anterior oblique view (stereo-pair) of eyes, $\times 15$. (*i*) Dorsal view (stereo-pair), with left valve omitted, $\times 10.9$. (*j*) Posterior view, $\times 10.9$. (*k*) Gut contents, $\times 7$. (*m–r*) Oblique posterior medial view of right limbs, $\times 11.5$: (*m*) first antenna; (*n*) second antenna; (*o*) mandible; (*p*) first maxilla; (*q*) second maxilla; (*r*) seventh appendage. (*l*) *Cylindroleberidid* myodocopid, type-species *Cylindroleberis mariae* (Baird, 1850), male (Department of Zoology, Natural History Museum, London, no. 1973.159), external right lateral view; Recent, Isles of Scilly, $\times 30$. All scale bars, 1 mm. Abbreviations: a1, first antenna; a1cb, c-bristle of first antenna; a1fb, f-bristle of first antenna; a2ba, basipod of second antenna; a2en, endopod of second antenna; a2ex, exopod of second antenna; a7, seventh appendage; am, adductor muscle area; ao, atrium oris; as, adductor sulcus; bo, Bellonci organ; bu, bulb; cs, caudal siphon; fu, furca; gc, gut content; gi, gill; hi, position of hinge line; hp, hemipenis; is, isthmus; le, lateral eye; lv, left valve; maba, basipod of mandible; maen, endopod of mandible; maex, exopod of mandible; me, medial eye; mx1, first maxilla; mx2, second maxilla; mx2ep, epipod of second maxilla; oe, oesophagus; ri, rostral incisure; ro, rostrum; rv, right valve; st, stomach.

from the serial grinding are housed at The University Museum of Natural History, Oxford (OUM).

3. SYSTEMATIC PALAEONTOLOGY

Phylum Arthropoda, Subphylum Crustacea, Class Ostracoda.

Subclass: Myodocopa Sars, 1866

Order: Myodocopida Sars, 1866

Family: Cylindroleberididae Müller, 1906

Genus: *Nasunaris* gen. nov.

Derivation of name: Latin *nasus* (nose) + *naris* (nostril); alluding to the prominent rostrum and rostral incisure. Gender, feminine.

Diagnosis: Cylindroleberididae with a well-developed elongate rostrum and ovoid rostral incisure and a prominent caudal siphon. Pedunculate lateral eyes and a medial eye bearing a short Bellonci organ.

Species: *Nasunaris flata* sp. nov.

Derivation of name: Latin *flatus* (breath of life); alluding to its respiratory system.

Diagnosis: as for the genus (monotypic).

Holotype: Oxford University Museum of Natural History OUM C.29 612; the only known specimen. A carapace and soft parts (figure 1*d*), reconstructed in three-dimensions (figure 1*a–c, e–k, m–r*).

Locality and stratigraphy: Herefordshire, England; Wenlock Series, Silurian.

The carapace is preserved with valves slightly agape. Maximum length (excluding rostrum), height and width (at mid-length) are 5050, 4850 and 3370 μm , respectively. The carapace is subcircular in lateral outline, with a long, tapering rostrum above an ovoid rostral incisure, and a short, tapering caudal siphon with an ovoid gape (figure 1*a*). In lateral outline, the position of the hinge is marked by a straight line running posteriorly from the highest point of the carapace, which is just in front of mid-length; in dorsal view the area adjacent to the hinge line is slightly depressed (figure 1*i, j*). Each valve is gently inflated, with a bulb immediately behind the rostral incisure, a shallow adductor sulcus running obliquely posterodorsally from valve centre to just behind dorsal mid-length, and a narrow flattened admarginal zone from the rostral incisure to the caudal siphon. Along the rostral incisure the valve-free margin is flexed gently inwards (figure 1*g*).

The first antenna is long, slender, weakly tapered and projects forward adaxial to the second antenna (figure 1*b, 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 abaxial and just above the base of the first antennae (figure 1*b, f, h*). Sagittally, a small medial eye bears a short, elongate, forward projecting structure, interpreted as a Bellonci organ (figure 1*h*). The second antenna (figure 1*b, c, f, g, i, n*) arises below the lateral eye; its large, globose, almond-shaped basipod is sited 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 podmeres. 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 1*c, 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 1*c, f, p*). The second maxilla (figure 1*c, 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 posteroventally (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 adductor sulcus (figure 1*a,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 1*i*). The seventh appendage is vermiform, about 4 mm long, slender, tapers weakly and may have a bifid-shaped termination (evident in right limb; figure 1*f,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 1*c,f,g*); individual lamellae and claws are not discernible. The posteroventral body area behind the seventh appendage is flanked by delicate lamellae (figure 1*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 large, broadly curved stomach mostly in-filled with darker (phosphatized?) material—presumed food (figure 1*e,f*). 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 Cyndroleberididae, to which *N. flata* is therefore assigned. The first to fifth appendages are also compatible with the limb morphology of cyndroleberidids, 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 1*g,l*; 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 cyndroleberidids. 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 cyndroleberidids, whereas it is relatively long in sarsiellid, philomedid and rutidermatid myodocopids. A caudal siphon occurs in sarsiellids and many cypridinid myodocopids, but (notwithstanding *N. flata*) is rarely and only weakly developed in cyndroleberidids.

The position and alignment of the isthmus along the adductor 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 cyndroleberidid *Colymbosathon eplecticos* Siveter *et al.*, 2003 from the Herefordshire Lagerstätte are the only fossil Ostracoda that preserve gills (evidence for gills in the myodocopids *Triadocypris 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. eplecticos* and the site of hypobranchial and epibranchial canals in Recent cyndroleberidids. Ventilation in *N. flata* was presumably facilitated by the second maxilla epipod, which drew water into the domiciliar 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 *et al.* 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 cyndroleberidid affinity, but, as with *C. eplecticos*, its shell morphology appears to be anomalous, especially when compared with the type genus of the family, for example (cf. figure 1*a,l*). 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 bolbozoids 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 myodocope 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 cyndroleberidid myodocopids are basal to cypridinid and sarsiellid myodocopids.

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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