A Silurian myodocope with preserved soft-parts: cautioning the interpretation of the shell-based ostracod record

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Ostracod crustaceans are the most abundant fossil arthropods. The Silurian Pauline avibella gen. et sp. nov., from the Herefordshire Lagerstätte, UK, is an extremely rare Palaeozoic example with soft-part preservation. Based on its soft-part morphology, especially the exceptionally preserved limbs and presence of lateral eyes, it is assigned to the myodocopid myodocopes. The ostracod is very large, with an epipod on the fifth limb pair, as well as gills implying the presence of a heart and an integrated respiratory–circulatory system as in living cylindroleberidid myodocopids. Features of its shell morphology, however, recall halocyprid myodocopes and palaeocopes, encouraging caution in classifying ostracods based on the carapace alone and querying the interpretation of their shell-based fossil record, especially for the Palaeozoic, where some 500 genera are presently assigned to the Palaeocopida.

1. Introduction

The shells of ostracods occur profusely throughout the stratigraphic record from the Early Ordovician onwards [1–3] in a wide range of aqueous environments [4]. The overwhelming majority of the estimated 33 000 living and fossil species [5] are benthic/nektobenthic. Pelagic forms, exclusively members of the Myodocopa, one of the two major living ostracod groups, arose via an ecological shift in the Silurian [6,7]. Myodocopes typically have weakly calcified valves and, consequently, a scant fossil record [8–11], which begins in the Late Ordovician [12]. The soft-parts of ostracods are rarely fossilized [13,14]. From the Palaeozoic a single ostracod-type limb is known from the Late Cambrian [15]; a podocopid specimen with some soft-parts [16] and an undescribed, partially open carapace with poorly preserved limbs [17] from the Devonian; and three myodocope species, each based on an essentially completely preserved specimen, from the Herefordshire (Silurian) Konservat-Lagerstätte, UK [18–20]. Here, we describe a new ostracod with soft-parts from the Herefordshire deposit, Pauline avibella gen. et sp. nov. (Myodocopa), based on two specimens.

2. Material and methods

The Herefordshire fossils occur as three-dimensional calcitic in-fill within calcareous nodules hosted in a volcaniclastic layer [26]. The ostracods are reconstructed...
as ‘virtual fossils’ using the custom SPIERS software suite [27,28]. The original datasets resulting from serial grinding are housed at the University Museum of Natural History, Oxford (OUMNH). The fossils were 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 ray tracing.

3. Systematic palaeontology

Phylum Arthropoda, Subphylum Crustacea, Class Ostracoda.
Subclass: Myodocopa Sars [29].
Order: Myodocopida Sars [29].
Family: Cylindroleberididae Müller [30].
Genus: Pauline gen. nov.

Derivation of name: for Pauline Siveter, in memoriam. Gender: feminine.

Diagnosis: large cylindroleberid. Carapace elongate with an adductor sulcus, an anterior lobe complex, a prominent wing-like posteraloral lobal structure and a simple anterior gape. Exopod of second antenna has about 20 long setae distally. Type species: Pauline aubella sp. nov.

Derivation of name: Latin aubella, bird + bella, beautiful; fancied resemblance of the posterodorsal lobal structure to a bird’s wing.

Diagnosis: as for the genus (monotypic).

Material: two carapaces with soft-parts. The holotype, OUMNH C.29614 (figure 1a), reconstructed in three-dimensions (figure 1a–k–n–t); and the slightly less completely preserved OUMNH C.29613 (figure 2a), reconstructed in three-dimensions with some loss along the plane of cut (figure 2a–c–i).

Locality and stratigraphy: Herefordshire, UK; Wenlock Series, Silurian (further locality information by application to OUMNH).

Description: maximum length, height and width (in dorsal view) of the carapace are 6400 μm, 3000 μm and 4500 μm (holotype), and 10200 μm, 5300 μm and 5500 μm (OUMNH C.29613). Valves gape at about 70° (holotype) and 25° (OUMNH C.29613) (figures 1c and 2e), and outline an ovoid posterior gape (figures 1k and 2i). The valve is bordered by a narrow marginal ridge that is less prominent posteriorly (figures 1a,c,g and 2r,g). A wide, thin, incomplete lamella-like feature of uncertain interpretation (contact margin structure?) extends adaxially from the ventral to posterior regions of the marginal ridge of the right valve, and indicates some measure of left over right valve overlap (figures 1g and 2g). A large, globose anterior lobe is gently rounded dorsally; its crest reaches just above the hinge line in the holotype, but is more subdued in OUMNH C.29613 (figures 1a and 2a). A smaller, more weakly developed node occurs between the anterior lobe and the hinge line (figures 1h and 2c). An adductorial sulcus occurs at mid-length; it is weakly Z-shaped, widest dorsally, and extends to just below valve mid-height (figures 1a,h and 2e,c). The ventral two-thirds of the valve behind the adductorial sulcus are gently inflated; above this a prominent wing-like lobal structure curves gently above the hinge line with posterior projections at mid-height and dorsally (figures 1a,h,k and 2r,c,i). The external surface of the valve of the holotype is smooth; in OUMNH C.29613, it is finely reticulate with a few weakly developed narrow costae close and parallel to the anterior margin of the valve (figures 1a and 2a,e,g).

The first antenna (i.e. antennula; figures 1a–j,n and 2a,c,e–h,j) originates close to the sagittal plane. It consists of two parts of similar length, separated by a geniculation (probable articulation) that is strongly compressed transversely. The distal part of the limb projects beyond the carapace and bears two long setae ventrally, which may correspond to separate podomeres; it terminates in three or four long setae. Exsagittal to the first antenna a pedunculate, ovoid, presumed compound lateral eye (ommatidia not discernible) lies in the anterior lobe of the valve (figures 1b,fj and 2f,h). A medial eye is not evident. The basipod of the second antenna (i.e. antenna; figures 1a–j–o and 2f–h,j) is large, globose and almond-shaped with a marked lateral axial depression. The exopod is long, stout, ovoid in cross section, curved and slightly wider in the distal one-quarter, which bears about 20 long, fine, closely set and parallel setae; podomeres are not discernible (as in Recent cylindroleberids, the distribution of setae may reflect individual podomeres, including multiple setae on the terminal podomere). The right exopod of the holotype projects beyond the carapace, whereas the left is preserved curving ventrally and posteriorly inside the domicilium (figure 1c,g). The endopod arises just below the exopod. It is stout, about half the length of the exopod, and consists of a proximal part that is geniculate with a longer distal part bearing a very long terminal seta that is preserved only on one limb in OUMNH C.29613 and preserved as a small stub in the holotype (figures 1b,g,i and 2a,c,e–h,j).

The mandible (figures 1b,g,i,p and 2f–h,j) has a broadly triangular-shaped limb base (presumed basipod and coxa) sited just over the atrium oris and adjacent to the conical-shaped labrum (figure 1e). The inner edge of the limb base bears a few weakly developed, presumed enditic processes. The endopod is stout, gently tapered and consists of a proximal part separated from a distal part of similar length by a geniculum. The exopod (evident in the holotype only in the left limb) arises adjacent to the endopod and is of similar length to the proximal part of the endopod but much narrower. The limb base (presumed basipod and proximal endite) of the first maxilla (i.e. maxillula) is large, broad, with 2–3 long, well-developed enditic processes along its inner edge adjacent to the atrium oris (figure 1b,g,i,q). The ramus (presumed endopod) is large, blade-like and comprises subequal proximal and distal parts (podomer?) separated by a marked geniculation (figures 1b,i and 2b,j). As seen in the holotype, the ramus has at least three fine setae distally (best evident in the right limb; figure 1b) and a long fine seta that originates ventrally near the geniculum.

The limb base of the second maxilla (i.e. fifth limb) bears at least five setiferous enditic processes arranged in one or (as evident on the left limb of the holotype) two rows that lie just outside, and project towards, the atrium oris (figure 1b,g,i,r). A large, posteriorly concave, lamellar epipod projects laterally from the limb base (figure 1r), which also bears a single short tapered ramus (conventionally the exopod in myodocopids, but see Bosshard [32], figure 1i,r). The second maxilla and sixth limb in OUMNH C.29613 cannot be fully resolved due to preservational factors. The sixth limb in the holotype is also poorly preserved; it is small, with a stout, tapered ramus projecting posterolaterally from a lamellar limb base that bears five long, medial enditic processes, evident on the best preserved (right) limb, the more distal of which project less anteromedially and more ventrally (figure 1b,g,i,s). The body
Figure 1. (a–l, n–t) Holotype of Pauline avibella, carapace with soft-parts (OUMNH C.29614): (a–k, n–t) ‘virtual’ reconstructions; (l) specimen in rock. The exact boundary between structures such as body and limbs, as indicated by colour changes, is somewhat arbitrary. (a) External right lateral view (stereo-pair). (b) Right lateral view (stereo-pair), valves omitted. (c) Anterior view. (d) Right lateral view (stereo-pair) of gut system. (e) Oblique ventral view of labrum and atrium oris. (f) Anterior view (stereo-pair), valves omitted. (g) Ventral view. (h) Dorsal view. (i) Ventral view (stereo-pair), valves omitted. (j) Dorsal view (stereo-pair), valves omitted. (k) Posterior view. (l) Lateral oblique section. (n–t) Oblique posterior approximately medial view of left limbs: (n) first antenna, (o) second antenna, (p) mandible, (q) first maxilla. (r) second maxilla. (s) sixth limb. (t) seventh limb. (m) Halocyprid myodocope Discoconchoecia pseudodiscophora (Rudjakov [31]), carapace, right lateral view (OUMNH RY.37); Recent, Sea of Japan, depth 320 m. All scale bars 1 mm. a1, first antenna; a2ba, a2en, a2ex, basipod, endopod and exopod of second antenna; a6, sixth limb; a7, seventh limb; alo, anterior lobe; an, anus; ao, atrium oris; as, adductorial sulcus; co, costa(e); cm?, contact margin structure?; ec?, epibranchial canal?; fs, finger-like structure; fu, furca; gi, gills; hl, hinge line; is, isthmus; la, labrum; le, lateral eye; lv, left valve; maba, maen, maex, basipod, endopod and exopod of mandible; mr, marginal ridge; mx1, first maxilla; mx1ba, mx1en, basipod and endopod of first maxilla; mx2, second maxilla; mx2ba, mx2ep, mx2r, basipod, epipod and ramus of second maxilla; no, node; oe, oesophagus; pg, posterior gape; ri, rostral incisure; ro, rostrum; rv, right valve; s-s, line of section through specimen (h–l); st, stomach.
The seventh limb is vermiform and over 3000\,\mu m long; it arises from the body just behind the isthmus and is similar in width throughout with a spanner-shaped termination (figures 1b,i–k,t and 2d,h,j).

Flanking the hind body region in OUMNH C.29613 (figure 2d,h,j) there are at least four paired sets of thin overlapping lamellae interpreted as gills. The outer edge of the outer right lamella is thickened, possibly representing the site of an (efferent) epibranchial canal. Two small, short, curved finger-like projections of unknown function originate from the body area between the seventh limb and the gills (evident on the right side in OUMNH C.29613; figure 2d,h,j). The posterior part of the body is poorly preserved in the holotype. The furca protrudes from the carapace (figure 1a,b,g,i). Each furcal lamella preserves a row of at least three to four long curved claws, though the large size of the furca suggests that more were probably present. The preserved gut includes oesophagus and stomach (figures 1d and 2d). The gender of the specimens cannot be determined.

4. Discussion

Lateral eyes and a vermiform seventh limb occur only in myodocopid ostracodes, and gills are known only in the Cylindroleberididae, to which \textit{P. avibella} is assigned. The
morphology of most of the other limbs, including the presence of an epipod only on the second maxilla, is also compatible with that assignment, as is the large size. Furthermore, the seventh limb of *P. avibella* has an indented distal termination as that in Recent cylindroleberids [33, fig. 15], but the associated comb of fine bristles found in living representatives is not evident, there is no setae comb on the second maxilla, and the (poorly resolved) sixth limb is not flap-like. *Pauline avibella* differs from almost all cylindroleberids in lacking a rostrum and rostral incisure and in having a long, well-defined adductor sulcus. Specimen OUMNH C.29613 differs from the holotype in being larger and preserving gills; other, minor differences in lobation (e.g. more acute posterior wing-like structures) and valve ornament may represent ontogenetic variation. At around 1 cm long, the larger specimen is comparable in size to adults of many Recent and fossil myodocopid species, which range up to about 30 mm in length [5,9,34].

Supposed myodocopids recorded from the fossil record number many tens of species, of which some 20 have been assigned to the Cylindroleberidae; however, only six, including five cylindroleberids, are confirmed as myodocopids based on preserved soft-parts ([9,10] and references herein). Of the six species, the carapace morphology of the two post-Palaeozoic forms, the cylindroleberids *Triolyaspis spitzbergensis* Weischat ([35] Triassic) and *Juraleberis jubata* Vannier & Siveter ([36] Jurassic), accords with that of Recent myodocopids. The overall carapace morphology of *P. avibella*, with its sub-oblong shape, long straight dorsal margin, well-developed lobation and long, prominent adductor sulcus is unlike that of other extant or supposed fossil myodocopids. It may represent the shell form of the cylindroleberid stem, in which a rostrum and rostral incisure had yet to develop, or perhaps belong more basally and indicate that the cylindroleberid soft-anatomy is relatively primitive. The carapace morphology of *P. avibella* in many respects recalls that of certain halocypridid Halocyprida myodocopes, such as *Discoconecha* (figure 1m) [37,38], a group unknown from the fossil record. However, the limb morphology and lateral eyes of *P. avibella* clearly place it within the Myodocopida and not the Halocyprida. A marked adductor sulcus and prominent lobation are features typical of Palaeocopida [39], the diverse and abundant Palaeozoic ostracod group that is known from carapaces alone and comprises some 500 genera (D. J. Siveter 2008, unpublished data), although the majority of palaeocopes characteristically have an adventral structure(s), which is lacking in *P. avibella*. *P. avibella* and the three other known Palaeozoic myodocope species with soft-parts, *Nymphatella gnawda*, *Nasunaris infilata* and *Colymbosathon ecplecticos* (figure 2n, k–m; [18–20]), show a diversity of carapace morphologies even though their soft-parts indicate that all four are myodocopids and all but *Nymphatella* are cylindroleberids (these assignments receive independent support from molecular/morphological analysis of fossil and Recent ostracods [40]). This confirms that carapace morphology alone is an inadequate basis for suprageneric assignment of (Recent) myodocopids [41]. The discovery of *P. avibella* with a soft-part morphology that is at odds with the appearance of the carapace encourages caution in interpreting the affinities of Palaeozoic ostracods based merely on shell morphology [1,19,20]. The current taxonomic assignment of many fossil ostracods, especially Palaeozoic forms, may be flawed.

The depositional setting of the Herefordshire Lagerstätte within the Welsh Basin included water depths of 150–200 m [21], a niche favoured by Silurian myodocopids [7,34]. The two powerful anterior limbs and especially the large basipod of the second antenna suggest that *P. avibella* was a swimmer. Its limited known distribution and its morphology suggest a nektobenthic lifestyle, similar to most Recent myodocopids [42]. In lacking a setae comb on the second maxilla, *P. avibella* apparently differed from living cylindroleberids in not being a filter (comb)-feeder. With mandibles and first maxillae bearing endites and a furca with well-developed claws, *P. avibella* would have been capable of a feeding strategy similar to other Recent myodocopids, which scavenge, prey or are detritivores on or near the substrate [42]. *P. avibella*, a very large ostracod with gills and epipods, likely had a respiratory-circulatory system with a heart similar to that of living cylindroleberids [43,44].

We thank the Natural Environment Research Council (grant no. NE/F017227/1) and English Nature for support; Carolyn Lewis for technical work; Robin Smith, John Whittaker and Hataruika Museum, Toyama Prefecture, Japan, for Recent material; Mark Williams, David Horne and an anonymous reviewer for comments on the manuscript; T. H. Oakley and co-workers for a preprint of their manuscript; David Edwards and the late Roy Fern for general assistance.

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