

Research



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Palaeontology

A well-preserved respiratory system in a Silurian ostracod

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Ostracod crustaceans are diverse and ubiquitous in aqueous environments today but relatively few known species have gills. Ostracods are the most abundant fossil arthropods but examples of soft-part preservation, especially of gills, are exceptionally rare. A new ostracod, *Spiricopia aurita* (Myodocopa), from the marine Silurian Herefordshire Lagerstätte (430 Mya), UK, preserves appendages, lateral eyes and gills. The respiratory system includes five pairs of gill lamellae with hypobranchial and epibranchial canals that conveyed haemolymph. A heart and associated vessels had likely evolved in ostracods by the Mid-Silurian.

1. Introduction

Ostracod crustaceans, originated about 500 Mya [1], are abundant as fossil shells from the Ordovician to the Holocene and have colonized all aquatic environments. Most are benthic/nektobenthic, with pelagic species (exclusively Myodocopa) known from the Silurian onwards ([2] and references therein). Of the respiratory strategies [3–6] in living species only one involves respiration by gills. Only eight ostracod species (six Myodocopa) with soft parts preserved are known from the Palaeozoic, most documented from single specimens ([7] and references therein). The Herefordshire Konservat-Lagerstätte (approx. 430 Mya), UK, has yielded unparalleled evidence of the palaeobiology and evolutionary significance of diverse Silurian invertebrates, including four ostracod species ([8] and references therein). Here, we report a new Herefordshire ostracod that reveals the ancestry of the respiratory/circulatory system within the group.

2. Material and methods

Herefordshire Lagerstätte fossils occur as three-dimensional calcitic in fills in calcareous concretions within volcanoclastics [9]. The fossil (OUMNH C.36063) was ground and photographed at 20 µm intervals. SPIERS software [10] was used to remove extraneous material digitally, resolve fossil–matrix ambiguities and generate a colour-coded three-dimensional virtual reconstruction for study by interactive visualization, stereo-pairs and animation.

3. Systematic palaeontology

The single, holotype specimen (Oxford University Museum of Natural History: OUMNH C.36063) is classified as Euarthropoda, Crustacea, Ostracoda, Myodocopa, Myodocopida, Cyndroleberididae, *Spiricopia aurita* gen. et sp. nov. Latin,

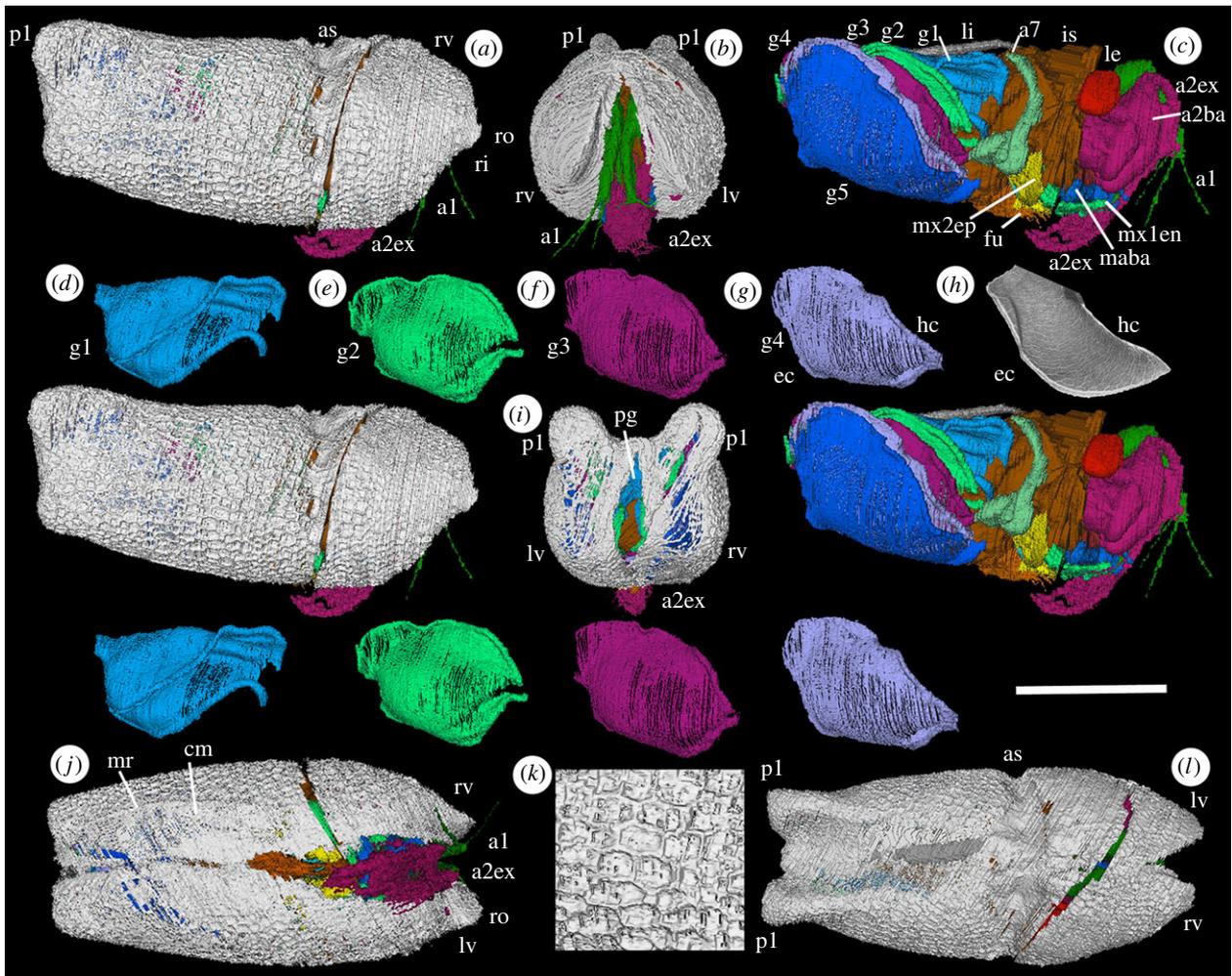


Figure 1. (a–g,i–l) *Spiricopia aurita*: ‘virtual’ reconstructions (a,c–g: stereo-pairs). (a) Right lateral view. (b) Anterior view. (c) Right lateral view, valves omitted. (d–g) Inner right gill lamellae. (i) Posterior view. (j) Ventral view. (k) Valve ornament. (l) Dorsal view. (h) Holocene cylindroleberidid *Leuroleberis surugaensis* [11], gill lamella (from [5]). Scale bar: (a–i,l) 2.5 mm; (k) 1.3 mm. a1, first antenna; a2ba, a2ex, basipod and exopod of second antenna; a7, seventh limb; as, adductor sulcus; cm, contact margin; ec, epibranchial canal; fu, furca; g1–5, gill lamellae; hc, hypobranchial canal; is, isthmus; le, lateral eye; li, ligament; lv, left valve; maba, limb base of mandible; mr, marginal ridge; mx1en, endopod of first maxilla; mx2ep, epipod of second maxilla; pg, posterior gape; pl, posterodorsal lobe; ro, rostrum; rv, right valve.

spiritus, breath of life, plus *copia*, abundance, alluding to the gills; *auritus*, eared, fancied resemblance of the posterodorsal lobes. From the Wenlock Series, Herefordshire, England.

Diagnosis: Cylindroleberidid with an elongate, reticulate carapace with a rostrum, adductor sulcus, posterodorsal lobe, second maxilla bearing an epipod and five pairs of gills.

Description: Carapace maximum length is 7500 μm ; maximum height (2950 μm) and width (3200 μm) lie anterior of an adductor sulcus (figure 1a,l; as). There is a beak-like rostrum above a gently concave rostral incisure (figure 1a,j; ro, ri). Valves gape at about 20°; a posterior gape is present (figure 1i; pg). The narrow adductor sulcus occurs at one-third valve length and curves gently forward to below valve mid-height. Each valve has a prominent posterodorsal lobe (figure 1a,b,i,j; pl). A weak marginal ridge occurs in the right valve, demarcating the reticulate lateral surface from the smooth ventral (contact margin) surface (figure 1j,k; cm, mr); valve overlap was probably left over right.

The first antenna (antennule: figures 1a–c and 2a–d; a1) originates close to the sagittal plane. It has a long, stout proximal part (presumed podomere) geniculate with a shorter stout middle part (presumed podomere) and a transversely compressed, longer, weakly curved distal section

(podomeres not evident). Two slender setae project ventrally, at the junction of the proximal and middle podomeres and from the distal section, respectively. Four other setae, preserved only in the right limb, project from the distal podomere. A pair of pedunculate lateral eyes originate posterodorsally to the first antenna (figures 1c and 2b,c,l; le). A tiny projection between the lateral eyes may represent a medial eye (figure 2c; me?).

The second antenna (antenna: figures 1a–c and 2a–c,e; a2) arises laterally to the first. The basipod is large, almond-shaped, globose; a lateral depression demarcates an anterior and a smaller posterior part. The exopod is stout, strongly curved to the posterior and projects beyond the carapace. An array of long, closely spaced curved setae in the distal half of the ramus (more evident in the right limb) may reflect the podomere distribution in living cylindroleberidids (in which podomere 1 lacks setae; podomeres 2–8 each bear one seta and podomere 9 has multiple setae; figure 2o). The endopod is stout and a quarter as long as the exopod. It is strongly geniculate proximally, at a presumed podomere boundary. The longer distal part terminates in a long, straight seta and a shorter tightly reflexed seta.

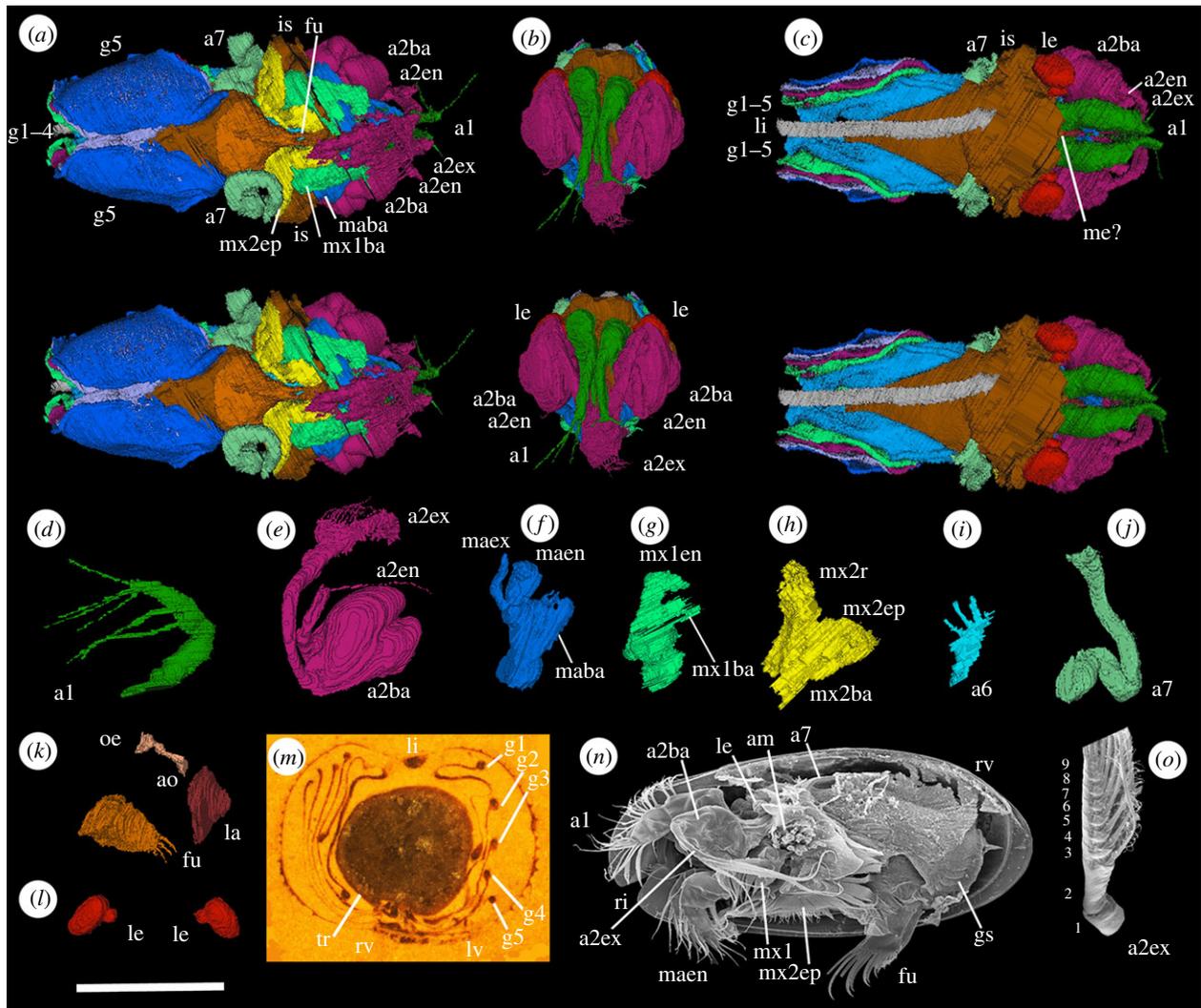


Figure 2. (a–m) *Spiricopia aurita*: ‘virtual’ reconstructions (a–c. stereo-pairs). (a) Ventral view, valves omitted. (b) Anterior view, valves omitted. (c) Dorsal view, valves omitted. (d) Right first antenna, adaxial face. (e) Right second antenna, anterior oblique view. (f) Right mandible, posterior oblique view of abaxial face. (g) Right first maxilla, adaxial face. (h) Left second maxilla, posterior oblique view of adaxial face. (i) Left sixth limb, adaxial face. (j) Right seventh limb, posterior view. (k) Oesophagus, labrum, furca, right lateral view. (l) Eyes, anterior view. (m) Specimen in rock. (n,o) Holocene cylindroleberid *Asterope mariae* [12]: (n) internal view, juvenile (courtesy V. Perrier); (o) left second antenna exopod (distal part omitted; Natural History Museum, London, no. 1973:160); Sillily Isles. Scale bars: (a–l) 2.5 mm; (m) 2 mm; (n) 600 μm ; (o) 300 μm . Additional abbreviations: a2en, endopod of second antenna; a6, sixth limb; am, adductor muscle; ao, atrium oris; gs, gills; la, labrum; maen, maex, endopod and exopod of mandible; me?, medial eye?; mx1, first maxilla; mx1ba, limb base of first maxilla; mx2ba, mx2r, limb base and ramus of second maxilla; oe, oesophagus; tr, trunk; 1–9, podomeres.

The mandible (figures 1c and 2a,f; ma) has a broad flat limb base (presumed basipod and coxa) positioned over a small conical labrum and the presumed site of the atrium oris. Its inner edge, although poorly preserved, is serrated, suggesting enditic processes. Only a stout, proximal part (possible podomere) of the endopod is preserved. The exopod is slender, geniculate at about mid-length (possible podomere boundary) and slightly longer than the preserved part of the endopod.

The limb base (presumed basipod and proximal endite) of the first maxilla (maxillula: figures 1c and 2a,g; mx1) is broad, flat and projects adaxially over the presumed site of the atrium oris; its inner edge is poorly preserved. The ramus (presumed endopod) is large, blade-like, and consists of subequal proximal and distal parts (possible podomeres) joined at a marked geniculation. An exopod is not discernible.

The second maxilla (fifth limb: figures 1c and 2a,h; mx2) is poorly preserved. The limb base bears a stout ramus (conventionally the exopod in myodocopids; but see [13]) and a large

laterally projecting lamellar epipod with a curved ventral margin. A small sixth limb lies against the inner base of the fifth appendage; it consists of a short, flat ramus bearing a row of three short setae (figure 2i; a6). A seventh limb arises below mid-height anterior of the gills. It is vermiform, about 3500 μm long with a v-shaped termination (figures 1c and 2a,c,j; a7).

Five pairs of thin, overlapping gill lamellae flank the trunk (figures 1c–g and 2a,c,m; g1–5). A narrow subcylindrical swelling follows the margin of each lamella. Lamella 1 is folded, forming an outer drape posterodorsally (figures 1c,d and 2c; g1). Lamellae 4–5 are elongate, paddle-like, with a gently curved ventral margin.

The isthmus occurs at the adductor sulcus (figures 1c and 2a,c; is). A non-mineralized dorsal band of soft tissue is interpreted as a ligament (figures 1c and 2c,m; li). Part of the oesophagus is preserved as a narrow sediment infill, projecting posterodorsally from behind the labrum (figure 2k; oe). A furca is preserved between the posterior limbs; each furcal

lamella bears at least six long, slender, gently curved claws only four of which are completely preserved (figures 1c and 2a,k; fu).

4. Discussion

A vermiform seventh appendage and lateral eyes occur only in myodocopids, and gills are known only in *Cylindroleberididae* (figure 2n). The morphology of appendages 1–6, including the presence of an epipod only on the second maxilla, is also compatible with a *cylindroleberidid* placement. Many of the appendages resemble those of the Herefordshire Lagerstätte *cylindroleberidids* *Colymbosathon*, *Nasunaris* and *Pauline* and the associated nymphetelid myodocopid *Nymphetelina* [14–18]. *Spiricopia* is unusual among *cylindroleberidids* in having a prominent adductor sulcus and atypical in apparently lacking a setate comb on the second maxilla. The shell morphology of these five Herefordshire myodocopids is very variable and emphasizes that the carapace alone is an unreliable basis for classifying fossil ostracods [17].

Living *cylindroleberidids* use the setate comb for filter feeding. As a setate comb is not evident in *Spiricopia*, it likely used its furca and appendages for predation, scavenging and detritivory on or near the substrate, as do most living myodocopids [19]. Its powerful antennae suggest effective swimming.

In small ostracods (less than 3 mm long), gas diffusion occurs via the surface of the body integument and the uncalcified inner lamella integument. In larger ostracods (myodocopid and halocyprid *Myodocopa*) simple diffusion for gaseous exchange is supplemented by internal fluid convection via an anastomosing integumental vascular network which forms part of an integrated circulatory system [3–6]. Evidence from external shell ornament suggests that certain Silurian myodocopes had an integumental vascular network [4]. Among myodocopes, *cylindroleberidids* augment this with gills (external integumental folds), typically seven pairs, which, *inter alia*, enhance metabolism. The only fossil ostracods previously known to have gills are *Colymbosathon eplecticos*, which preserves six incomplete gill pairs, and

Nasunaris flata and *Pauline avibella*, which preserve fragmentary gill lamellae [14,16,17]. Gill-like features also occur in the Triassic myodocope *Triadocypris spitsbergensis* [20]. By comparison with living *cylindroleberidids* [4,5] (figure 1h), the swollen margin of each gill lamella in *Spiricopia* can be confidently interpreted as the site of hypobranchial (concave; afferent) and epibranchial (convex; efferent) canals that conveyed haemolymph in life (figures 1c–g and 2m). The ridge-like free edges previously noted in the gills in *Colymbosathon* [14] can be similarly interpreted. As in living *cylindroleberidids* [5], the epipod of the second maxilla likely functioned to rhythmically ventilate the domicilium including the gills, with a water/feeding current entering anteriorly and egressing posteriorly. The gills are posterior, the probable region for preferential oxygen exchange in myodocopids and a position that facilitates grooming by the vermiform seventh limb [4,5]. The lamellae in *S. aurita* provide a total surface area of about 35 mm² for gaseous exchange in an outer shelf/slope, purported 150–200 m deep environment [21]. Whether a diurnal activity rhythm featured in tissue oxygenation, as in some living *cylindroleberidids*, which migrate between the sea bottom and the water column [22], is unknown. The myodocopid *S. aurita* reveals a well-developed branchial system. Likely a heart and associated vascular system had evolved in ostracods by the Silurian.

Data accessibility. The model (VAXML/STL format) of OUMNH C.36063 is at Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.000bq75> [23].

Authors' contributions. David J.S., Derek J.S., D.E.G.B. and M.D.S. designed the research and fieldwork. David J.S. wrote the paper with scientific and editorial input from co-authors. All authors approve the final version of the manuscript and agree to be accountable for its content.

Competing interests. We declare we have no competing interests.

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