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An Ostracode Crustacean with Soft Parts from the Lower Silurian

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An exceptionally well-preserved ostracode from the Silurian of Herefordshire, United Kingdom, provides a rare view of the fossilized soft-part anatomy of this important group of living crustaceans and confirms that Ostracoda were extant in the Paleozoic. The fossil has striking similarity to the extant myodocopid family Cylindroleberididae, to which it is assigned, and demonstrates remarkable evolutionary stasis over 425 million years. The fossil is identified as a male on the basis of its copulatory organ.

Ostracodes are small bivalved crustaceans, known from an estimated 33,000 living and extinct marine, nonmarine, and even terrestrial species (*1*). They are by far the most abundant arthropods in the fossil record, known globally from millions of their valves, which were biomineralized in life and therefore readily preserved. The shells of supposed ostracodes occur from at least the basal Ordovician [about 500 million years ago (Ma)] onward (*2*) and are important in biostratigraphy. Examples of ostracodes with preserved soft parts are, however, extremely rare and are virtually confined to post-Paleozoic deposits: a few species in the Mesozoic, and four in the Quaternary (*3*). The nature of the many small Paleozoic bivalved arthropods assigned to the ostracodes has hitherto been uncertain [previous evidence is essentially confined to an undescribed, partially open carapace with appendages from the Upper Devonian of Italy (*4*)].

The Lower Silurian (425 Ma) Herefordshire Konservat-Lagerstätte, in England (*5*), yields exquisitely preserved invertebrates as three-dimensional calcite infills in nodules hosted within a volcanic ash (*6*–*8*). Here we describe the soft parts of an ostracode from this biota, reconstructed by grinding the specimen at 20-μm intervals, digitally capturing the serial images, digitally removing extraneous material, resolving fossil versus matrix ambiguities, and then rendering a three-dimensional colored virtual fossil (*9*, *10*).

The Herefordshire ostracode belongs to the Myodocopa, one of the two major living ostracode groups (*1*). Myodocopes occur worldwide, from depths of a few meters to 6000 m, and are among the most abundant macroinvertebrates on some continental shelves (*11*). The valves are generally thin and weakly calcified, and their assumed fossil record, which includes Silurian and an Ordovician species (*12*, *13*), is generally poor. DNA sequence data indicate that the Myodocopa probably existed in the Cambrian and that the monophyly of Ostracoda remains ambiguous (*14*).

The specimen described here is classified as Arthropoda, Crustacea, Ostracoda, Myodocopa, Myodocopida, Cylindroleberididae, *Colymbosathon ecplecticos* gen. et sp. nov. **Name:** *Kolymbos* (swimmer) + *sathon* (with a large penis); *ekplektikos* (astounding). **Material:** A carapace with preserved soft parts, Oxford University Museum of Natural History specimen number OUM C.295670 (holotype). The specimen (Fig. 1 H) has been reconstructed in three dimensions (Fig. 1, A to C, E to G, and I to P). **Locality and stratigraphy:** Herefordshire, England; Wenlock Series, Silurian. **Diagnosis:** Cylindroleberidid with well-developed adductorial sulcus and long, simple gape; six pairs of posteriorly attached gills; second maxilla lacks setose "comb." **Description:** The bivalved carapace is large (maximum length, height, and width, 5210, 3100, and 3150 μm, respectively) and smooth (Fig. 1, F and I). In lateral view, the anterior, posterior, and ventral outlines of the valve are gently curved. A gape extends from the anterior cardinal corner to just behind mid-length. An adductorial sulcus curves forward slightly, to about mid-height. A weak anterior lobe and evenly curved postadductorial dorsal margin extend just above the hinge line.

The first antenna (Fig. 1, A to C, J, and I) is slender, has a long, broad-based, and tapering proximal part (podomere?) geniculate with a slightly longer distal part (articulations of the podomeres are not discernible) bearing a forwardly directed seta near mid-length (preserved only on the right antenna) and a pair of widely spaced divergent setae distally. The second antenna (Fig. 1, A to C, K, and I) has a large, globose, almond-shaped basipod. The exopod is long, slender, and flexed outward and backward. It has possibly two long proximal podomeres (indicated by flexure) composing about half its length, distal of which a sequence of at least six or seven closely set, long, subparallel setae originate along the outer edge of presumed separate podomeres. The endopod is curved, one-third as long as the exopod, and lacks discernible podomeres.

The limb stem (presumed basipod and coxa) of the mandible is a wide structure bearing some 8 to 10 small, pointed enditic procesess (Fig. 1, A, C, L, and I). The endopod consists of two subequal parts (podomeres?) geniculate at about 90° (there may be another, much shorter podomere). The exopod is about half the length of the proximal part of the endopod. The limb stem (presumed basipod and coxa) of the first maxilla has pointed enditic processes, including two long ones distally, projecting adaxially in the outer part of the atrium oris (Fig. 1, A, C, and M). The slender tapered ramus (presumed endopod) consists of two subequal parts (podomeres?) geniculate at almost 90°; an exopod is not discernible.

The second maxilla consists of a short stout ramus (traditionally, the exopod in myodocopids) with a large, basally attached, laterally projecting and slanting lamelliform epipod (Fig. 1, A, C, and N). The epipod appears to have at least 16 long, slender, marginal processes, but this could reflect impersistent preservation distally. Podomeres are not discernible in the main ramus, which has several stout setiferous medial endites and terminates distally in a cluster of about five tiny processes. The sixth appendage is relatively short; its limb stem arises in near contact with the posterior base of the second maxilla and is stout and narrow and bears a distal lamelliform splay of five or six elongate processes (Fig. 1, A, C, and O). The seventh appendage is vermiform and flexed around the body immediately posterior to the isthmus (Fig. 1, A, C, H, and P). At the base of the seventh appendage, there is a short, slender, gently curved, forwardly projecting "ramus" forming a possible biramous arrangement.

The copulatory organ is large and stout, projects anteriorly, and has lobelike flanks distally (Fig. 1, A, C, and G). The furca protrudes out of the valves; both furcal lamellae have a row of at least four (up to perhaps six or seven) curved claws (Fig. 1, A, C, F, G, and I). A sinuous fingerlike process of unknown homology projects from the proximal posterior part of the furca. Six tightly nested pairs of broad, curved, thin lamellae (gills) are attached to the posteroventral part of the trunk and wrap around its posterior one-third (Fig. 1, A, C, and H); they

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are better preserved on the right side. The free edges of each lamella are ridgelike. The isthmus is well developed. A pair of elongate compound lateral eyes occurs posterodorsally above the basipod of the second antenna (Fig. 1, A, B, G, and H). A small anteriorly directed sagittal process is interpreted as the medial eye (Fig. 1B).

Tuberclelike processes occur together with longer processes on the margins of the labrum and lower lip adjacent to the atrium oris (Fig. 1G). The gut is preserved through sediment infilling. The oesophagus is long, and the stomach is wider, elongate, and curved (Fig. 1, E and H); the hindgut is short, and the anus is sited between the furca and the copulatory appendage (Fig. 1, E and G).

The prominent copulatory appendage indicates that the specimen is a sexually mature adult male. The two distal setae on the first antenna also have homologs in Recent male cylindroleberidids (Fig. 1D) (*15*).

Discussion: *C. ecplecticos* lived in outer shelf–shelf slope marine waters at a depth of

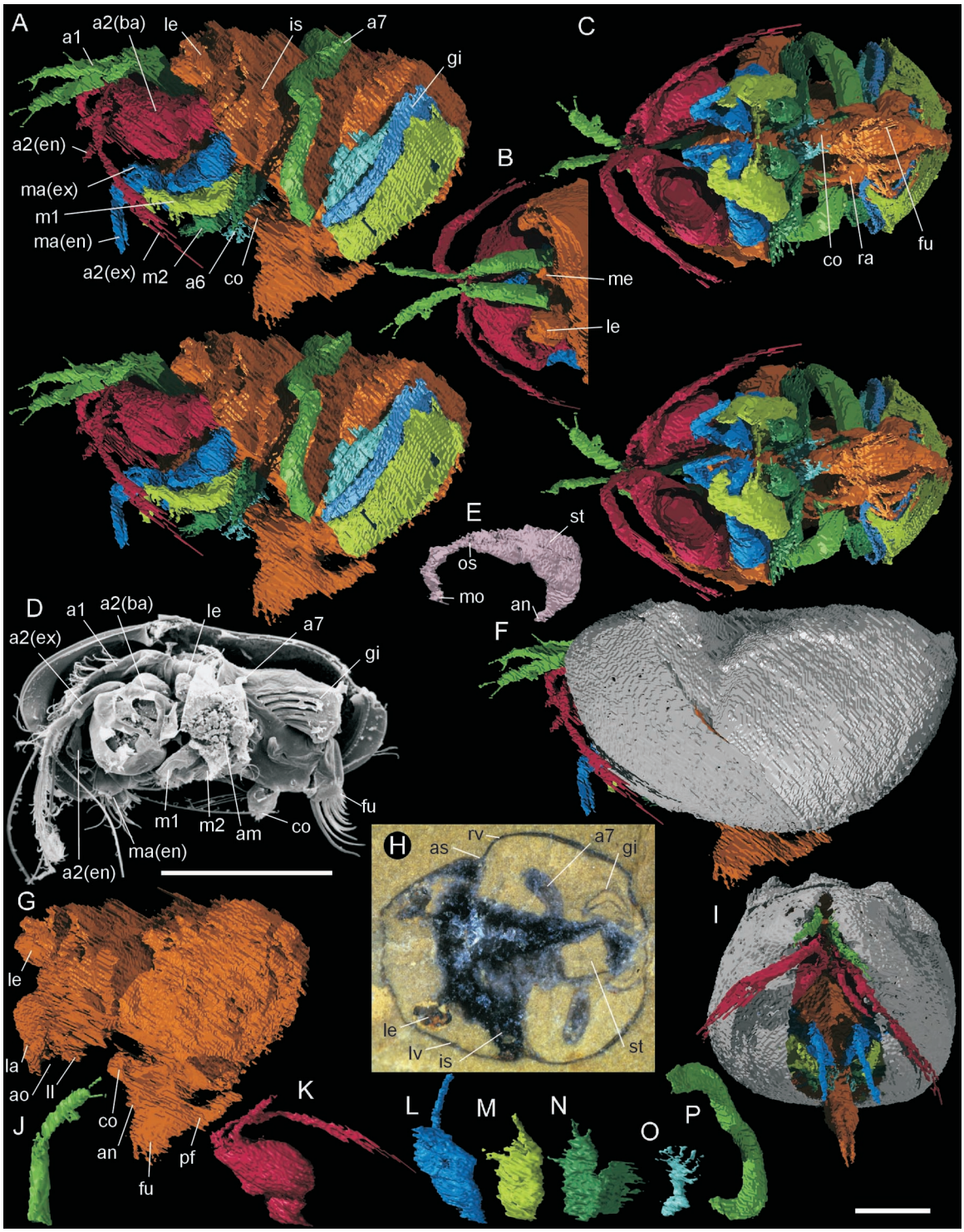


Fig. 1. [(A) to (C) and (E) to (P)] Holotype of *C. ecplecticos*, Wenlock Series, Herefordshire, England. [(A) to (C), (E) to (G), and (I) to (P)] "Virtual" reconstructions; (H) specimen in rock. (**A**) Left lateral view (stereo pair), (**B**) dorsal view of anterior part of head, and (**C**) ventral view (stereo pair); all with carapace omitted. (**E**) Gut, left lateral view. (**F**) Left lateral view. (**G**) Left lateral view with carapace, appendages, and gills omitted. (**H**) Oblique anterior-posterior section. (**I**) Anterior view. (**J** to **P**) First antenna, second antenna, mandible, first maxilla, second maxilla, sixth appendage, and seventh appendage; all are oblique posterior views of left appendages except (**O**), which is an oblique medial view of the right sixth appendage. (**D**) Cylindroleberidid *Xenoleberis yamadai* (*22*), male (length, 2125 μm); Recent, found at a depth of 3 to 5 m in the Japan Sea, Oshoro, Hokkaido, Japan (Department of Zoology, Natural History Museum, London, specimen number NHM 2003.702). Left lateral view, left valve removed. The scale bar for each species is 1000 μm. Abbreviations are as follows: a1, first antenna; a2(ba), a2(en), and a2(ex), basipod, endopod, and exopod of second antenna; a6, sixth appendage; a7, seventh appendage; ao, atrium oris; an, anus; as, adductorial sulcus; co, copulatory organ; fu, furca; gi, gills; is, isthmus; la, labrum; le, lateral eye; ll, lower lip; lv, left valve; m1, first maxilla, m2, second maxilla; ma(en) and ma(ex), endopod and exopod of mandible; me, medial eye; mo, mouth; os, oesophagus; pf, posterior fingerlike process; ra, ramus; rv, right valve; st, stomach. The exact point of color changes shown here, denoting different structures such as body and appendages, is somewhat arbitrary.

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150 to 200 m (*5*). It was probably a nektobenthic scavenger and predator, like most Recent myodocopes. The long natatory setae and large basipod of the second antenna imply that it was an adept swimmer. Its apparently limited dispersal capacity [one locality, even though myodocope ostracodes of the Welsh sedimentary basin have been extensively studied (*16*, *17*)] indicates that it had a benthic rather than pelagic lifestyle. The endites on appendages 3 to 5 seem suitable for comminuting food. As in Recent myodocopids (*18*, *19*), the well-developed furca may have been used to hold and cut prey and carrion, and the processes on the labrum may have secreted enzymes to aid digestion and substances for food entanglement and bioluminescence.

C. ecplecticos proffers unequivocal evidence for the occurrence of Ostracoda in the Paleozoic. It also allows for a particular sex to be identified in an animal as old as Silurian (hemipenes occur in the Cretaceous species). Its morphological similarity to Recent myodocopids (the only notable soft part difference from living cylindroleberidids is its apparent lack of a setose comb on the fifth appendage) demonstrates evolutionary stasis within the group over 425 million years and echoes the low rates of change that are known in other crustaceans (*20*). The find also accords with molecular evidence (*14*) suggesting that cylindroleberidids originated in the Early Paleozoic.

C. ecplecticos has the only known undoubted gills in a fossil ostracode and provides the earliest direct evidence of a respiratory-cum-circulatory system in the group: The epipod on the second maxilla presumably functioned to ventilate the domiciliar cavity, and the gills with thickened edges (the site of hypobranchial and epibranchial canals in Recent cylindroleberidids) (*21*) indicate the presence of branchial circulation and, therefore, an integrated vascular circulatory system with a heart.

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Regulation of Flowering Time by Histone Acetylation in *Arabidopsis*

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The *Arabidopsis* autonomous floral-promotion pathway promotes flowering independently of the photoperiod and vernalization pathways by repressing *FLOWERING LOCUS C* (*FLC*), a MADS-box transcription factor that blocks the transition from vegetative to reproductive development. Here, we report that *FLOWERING LOCUS D* (*FLD*), one of six genes in the autonomous pathway, encodes a plant homolog of a protein found in histone deacetylase complexes in mammals. Lesions in *FLD* result in hyperacetylation of histones in *FLC* chromatin, up-regulation of *FLC* expression, and extremely delayed flowering. Thus, the autonomous pathway regulates flowering in part by histone deacetylation. However, not all autonomous-pathway mutants exhibit *FLC* hyperacetylation, indicating that multiple means exist by which this pathway represses *FLC* expression.

The developmental transition from a vegetative to a reproductive phase in *Arabidopsis* is genetically controlled by several pathways, which integrate the endogenous developmental state of the plant and environmental cues (*1*). The autonomous and the vernalization pathways independently regulate the floral transition by repressing *FLC* expression (*2*–*4*). There are six genes in the autonomous pathway: *FLD*, *FCA*, *FPA*, *FY*, *FVE*, and *LUMINIDEPENDENS* (*LD*) (*1*, *2*). *FCA* and *FPA* encode RNA binding proteins (*5*, *6*), *FY* encodes a protein involved in mRNA 3′ processing (*7*), and *LD* encodes a homeodomain-containing protein (*8*).

We have previously identified *FLD* as an autonomous-pathway gene by an analysis of *fld-1* (*9*). The *fld-1* mutant, which is in the Columbia (Col) accession, was crossed with the Landsberg *erecta* accession to create a segregating population for the map-based cloning of *FLD* (fig. S1). *FLD* consists of two exons (Fig. 1A) that encode a protein of 789 amino acid residues (*FLD* is locus At3g10390, see www.arabidopsis.org). The *fld-1* lesion is a point mutation (C to T) that converts Arg^{10} (CGA) into a premature stop codon (TGA). After the identification of *FLD*, two additional *fld* mutants (*fld-3* and *fld-4*) were obtained from the Salk Institute Genome Analysis Laboratory collection (*10*). Both alleles are the result of transferred DNA (T-DNA) insertions in the coding region (Fig. 1A), and neither expresses the full-length *FLD* mRNA (Fig. 1B).

All of the *fld* mutants flowered much later than wild-type Col in inductive long-day photoperiods (Table 1 and Fig. 2A) and flowered rapidly after exposure to a prolonged period of cold (vernalization) (Table 1), which is characteristic of autonomous-pathway mutants (*2*). The two T-DNA mutants flowered later than *fld-1* (Table 1); thus, although the *fld-1* lesion is a premature stop codon, this allele may have residual activity. *fld-3* and *fld-4* mutants flower later than any other autonomous mutant in the Col genetic background (Table 1) (*11*), and extensive aerial rosettes, which are often associated with extremely delayed flowering, are produced at the early nodes of the main inflorescence stem (Fig. 2, A and B).

Steady-state *FLC* mRNA levels are much higher in the *fld* mutants than in the parental Col line (Fig. 2D). Increased *FLC* expression is characteristic of other autonomous mutants

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