33. Although these data are available since 1851, only the data for the years since 1944, when routine aircraft reconnaissance of Atlantic tropical cyclones began, are considered very reliable. The greatest reliability starts around the mid-1960s when operational satellite detection of Atlantic tropical cyclones began (*50*). Before satellite coverage, a portion of the lifetimes of many systems had probably been missed.
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A Phosphatocopid Crustacean with Appendages from the Lower Cambrian

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Here we describe a phosphatocopid arthropod with preserved soft anatomy from Lower Cambrian rocks of Shropshire, England, which provides evidence for the occurrence of Crustacea, including Eucrustacea, in the Early Cambrian. The find identifies an important, stratigraphically early source of well-preserved fossils (Konservat-Lagerstätte).

Most metazoan groups first appear in the fossil record during the Cambrian Period, but the nature and validity of the so-called "Cambrian Explosion" are unresolved. Some propose that cladogenic events gave rise to the metazoans in the Proterozoic [e.g., (*1*, *2*)]. Others conclude that the Cambrian explosion is real (*3*). Still others maintain that in most cases the appearance of modern body plans ('crown groups'), including those of extant arthropod classes, was later than the early Cambrian (*4*) and favor a model of progressive diversification through the end of the Proterozoic to beyond the Cambrian.

Our material is from the Protolenus Limestone (*5*), which is correlated to the Toyonian Stage of Siberia (*6*) and is of Branchian age in terms of the Newfoundland standard for the Avalonian microplate [circa 511 million years ago (Ma); base of Cambrian circa 543 Ma] (*7*). The specimens are an example of "Orsten"-type preservation [e.g., (*8*)]; they are phosphatized and were recovered with acetic acid techniques. Phosphatocopids are a clade (*9*) of about 60 species of globally widespread, Lower to Upper Cambrian bivalved arthropods [see (*10*, *11*)] that are mostly known from their purportedly primary phosphatic (*12*, *13*) carapaces. Rare phosphatocopid specimens with preserved soft part anatomy (which has been secondarily phosphatized) are known chiefly from Upper Cambrian concretionary Orsten limestones of Sweden (*12*, *13*). They have also been reported from the Middle Cambrian (*14*) (isolated limbs only) and the Lower Cambrian (*15*) (two specimens, showing only the labrum and sternum).

The specimens are classified as Arthropoda, Crustacea, Phosphatocopida sp.

Material. The specimens are two carapaces, both bearing soft part anatomy [Oxford University Museum of Natural History (OUM)]. OUM A.2209 shows a labrum, sternum, and the remains of the left second, third, and fourth appendages and possibly the left first appendage; its right-side appendages are mostly obscured by matrix. OUM A.2209 bears a labrum and sternum.

Locality and stratigraphy. The fossils came from a temporary trench excavation (made by D.J.S. and M.W.), near Comley hamlet, Shropshire [Protolenus Limestone (Protolenid-Strenuellid Biozone), Lower Comley Limestones, Comley "Series"].

Description. The subspherical shaped carapace consists of two halves ("valves") of equal size (Fig. 1, A through C); it has no hinge line or interdorsum and has a permanent gape of about 80°; its dorsal margin is 340 μm (OUM A.2209) to 330 μm (OUM A.2209) long. The doublure is well developed and is confluent with the inner lamella cuticle lining each valve.

The only visible structure that is possibly part of an antennula is a slender setulate seta on the left side of the labrum, projecting almost vertically, just below the endopod of the left second antenna (Fig. 1C). The second antenna (Figs. 1, A and D, and 2) consists of a coxa but with a gnathobasic endite carrying two or possibly three spines, a basis whose endite has two main spines flanked by four smaller spines, and an endopod consisting of three podomeres, in which the proximal podomere bears one long

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central and three smaller spines, the second podomere has a single slender spine, and the distal podomere has a small medial spine and is extended into a spine distally. The exopod is of multiannulate form, with at least eight annuli visible (Upper Cambrian phosphatocopids have up to 14 annuli), each bearing one seta mediodistally (proximal parts of four setae visible).

The mandible (Figs. 1, A, B, E, and G, and

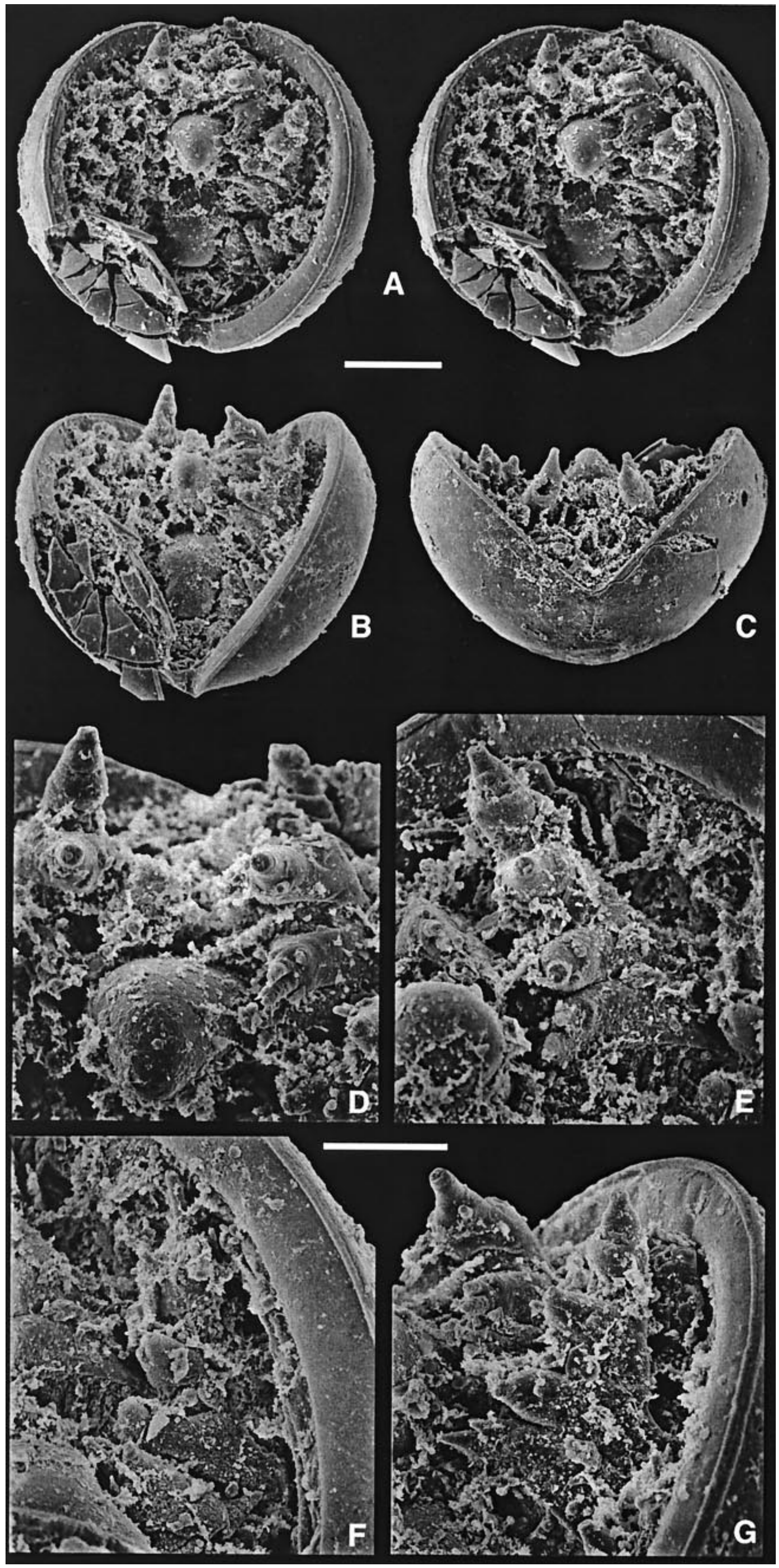

Fig. 1. Phosphatocopida sp., Lower Cambrian, Shropshire. All figures are of OUM A.2209. (**A**) Ventral view, stereo pair. (**B**) Posteroventral view. (**C**) Anterior view. (**D**) Ventral view of labrum, endopod (coxa, basis, and proximal podomere; podomeres 2 and 3 missing) and distal part of exopod of left second antenna, and endopod of right second antenna [see also (*29*)]. (**E**) Left mandible (coxa, basis, and endopod), medial view [see also (*29*)]. (**F**) Left first maxilla (proximal endite, basis, and endopod), posterior view [see also (*29*)]. (**G**) Left mandible (coxa, basis, and endopod) and part of left second antenna, posterior view [see also (*29*)]. (A) to (C) are to same scale (scale bar, 100 μm); (D) to (G) are to same scale (scale bar, 50 μm).

2) also has a coxa with a slightly oblique gnathobasic endite with a stout medial and five smaller spines, a basis whose endite bears one medial spine flanked by five smaller spines, and an endopod consisting of three podomeres, in which the proximal podomere has a single medial spine and four smaller spines, the second podomere has two tiny spines, and the distal podomere has a small medial spine and is extended into a spine distally. Visible parts of the exopod consist of three incomplete setae, sited adjacent to the inner lamella just anterior to the endopod of the mandible. The exopod is possibly as long as that of the second antenna and with a similar number of annuli.

The first maxilla (Figs. 1, A and F, and 2) consists of a basis whose endite bears one medial spine flanked by four smaller spines and a proximal endite as a lobate protrusion medioproximal to the basis with one large medial spine and four smaller spines. Its endopod consists of three podomeres; the proximal podomere has an enditic protrusion extended into a spine and is flanked by one or two smaller spines, the second podomere (mostly obscured by matrix) bears at least one spine, and the third podomere (mostly covered by matrix) is small and distally extended into a long stout spine. The exopod is not seen.

The labrum (Fig. 1, A and D) is prominent and triangular-shaped. The area of the presumed atrium oris and mouth (Fig. 1, A and B) is mostly obscured by matrix. The sternum (Fig. 1, A and B) is long, anteriorly is as wide as the base of the labrum, and widens at the site of the paragnaths at about midlength. The area between the posterior margin of the sternum and the edge of the posterior part of the doublure (i.e., the supposed site of the trunk) is mostly obscured by matrix (Fig. 1, A and B).

Developmental stage. The overall size and morphology of these specimens, especially the presence of only four limbs, suggest that these specimens represent an early, if not the first, instar. They are closely comparable to the earliest instars known from Upper Cambrian Orsten phosphatocopids (*16*).

Evolutionary significance. The appendage morphology of the Shropshire material provides evidence for the occurrence of phosphatocopids and thereby Crustacea, including Eucrustacea [in the sense of (*9*)] in the Early Cambrian. Crustacea are not known, for example, from the Chengjiang (*17*) or Sirius Passet [e.g., (*18*)] Early Cambrian Lagerstätten. On the tenuous basis of shell morphology alone, phosphatocopids have traditionally been regarded as ostracod crustaceans [e.g., (*10*, *12*, *13*, *15*, *19*, *20*)], but evidence from their soft part anatomy resolves phosphatocopids as the sister group to the Eucrustacea [equivalent to Crustacea sensu stricto, i.e., crown group Crustacea (*9*, *21*, *22*)]. That in the Shropshire phosphatocopid both the second antenna and mandible each bear a limb stem consisting of a separate basis and coxa is an additional synapomorphy; species of both groups also have a labrum with glandular openings and sensilla posteriorly, an atrium oris, and a sternum with paragnaths (i.e., a complete set of features pertinent to the anterior cephalic feeding system). That phosphatocopids occur in the Early Cambrian implies that Eucrustacea are present coevally. The Shropshire species has tripartite endopods, thus enhancing the ground pattern character set (*9*) of the Phosphatocopida (autapomorphy, and plesiomorphic within the group).

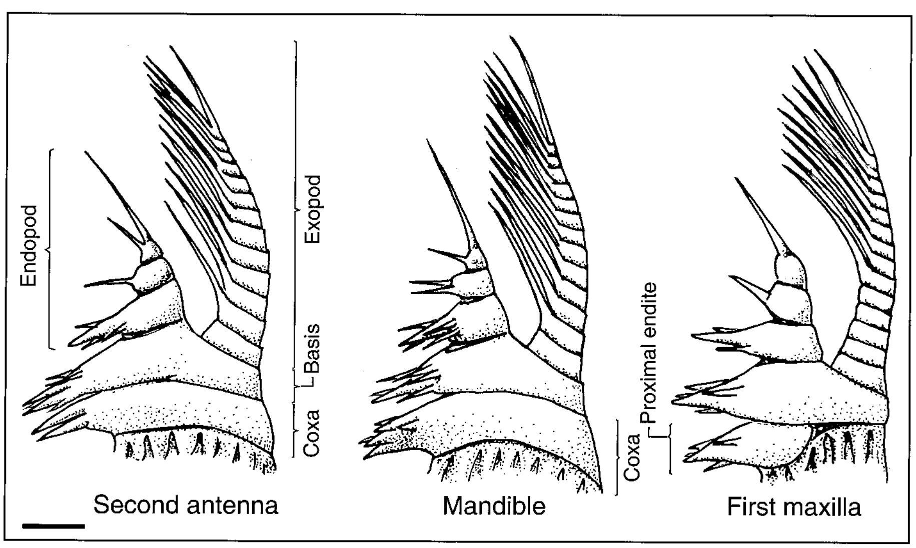

Fig. 2. Reconstructions in posterior view of the second antenna, mandible, and first maxilla of Phosphatocopida sp., Lower Cambrian, Shropshire. The length of the spines in general, the exopod of the mandible, and the exopod of the first maxilla are based on what is known from early instars of Upper Cambrian phosphatocopids (*16*), especially *Hesslandona unisulcata* (*13*). Scale bar, 50 μm.

The earliest occurrences of Orsten-type, three-dimensional preservation comprise algae, eggs, embryos, and early ontogenetic stages (of worms, Cnidaria, and problematica) from the Lower Cambrian of China and Siberia (*23–25*) and Neoproterozoic of China (*26–28*). The find from Shropshire, recovered from one of only four limestone samples, identifies an important, early stratigraphical source of metazoan fossils with preserved soft parts. That such relatively advanced arthropods as crustaceans, including eucrustaceans, occur by the Early Cambrian lends support to the hypothesis (*1*, *2*, *26*, *9*) of a late Precambrian history for the Metazoa.

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