

A giant Ordovician anomalocaridid

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Anomalocaridids, giant lightly sclerotized invertebrate predators, occur in a number of exceptionally preserved early and middle Cambrian (542–501 million years ago) biotas and have come to symbolize the unfamiliar morphologies displayed by stem organisms in faunas of the Burgess Shale type. They are characterized by a pair of anterior, segmented appendages, a circlet of plates around the mouth, and an elongate segmented trunk lacking true tergites with a pair of flexible lateral lobes per segment^{1,2}. Disarticulated body parts, such as the anterior appendages and oral circlet, had been assigned to a range of taxonomic groups—but the discovery of complete specimens from the middle Cambrian Burgess Shale showed that these disparate elements all belong to a single kind of animal³. Phylogenetic analyses support a position of anomalocaridids in the arthropod stem, as a sister group to the euarthropods^{4–6}. The anomalocaridids were the largest animals in Cambrian communities. The youngest unequivocal examples occur in the middle Cambrian Marjum Formation of Utah⁷ but an arthropod retaining some anomalocaridid characteristics is present in the Devonian of Germany⁵. Here we report the post-Cambrian occurrence of anomalocaridids, from the Early Ordovician (488–472 million years ago) Fezouata Biota⁸ in southeastern Morocco, including specimens larger than any in Cambrian biotas. These giant animals were an important element of some marine communities for about 30 million years longer than previously realized. The Moroccan specimens confirm the presence of a dorsal array of flexible blades attached to a transverse rachis on the trunk segments; these blades probably functioned as gills.

Anomalocaridids were first described from the middle Cambrian of Mount Stephen in British Columbia, Canada⁹. The specimens, which consisted of isolated raptorial appendages, were interpreted as the body of a shrimp⁹. A different raptorial appendage from the middle Cambrian Burgess Shale was subsequently misinterpreted by Walcott as that of the arthropod *Sidneyia*^{3,10}. Walcott interpreted the oral circlet as a medusoid and also described an incomplete specimen of the body as a holothurian¹¹. The carapace elements of the anomalocaridid *Hurdia* also were misidentified originally—as two different arthropods^{6,12,13}. The first reconstruction of an anomalocaridid based on complete specimens dates from the 1980s^{2,3}. As a result of discoveries from other Cambrian localities worldwide, it was largely accepted by the mid-1990s that anomalocaridids are arthropods¹. Some authors, however, continued to argue for non-arthropodan affinities¹⁴ and the exact systematic placement of the group remained uncertain. Although inclusion of anomalocaridids in the arthropod crown has been favoured by some¹⁵, they are generally regarded as belonging in the euarthropod stem^{4–6,16}.

Anomalocaridids are known from early and middle Cambrian sites in Canada, the United States, Poland, Russia, China, Australia and, possibly, Greenland and the Czech Republic^{6,7,16–20}. The oldest known example is *Cassubia infercambriensis* from the early Cambrian of Poland¹⁶, while the youngest are from the middle Cambrian of the United States⁷; a single specimen from the late Cambrian of the Holy Cross Mountains in Poland may represent an oral circlet²¹. It has been suggested that the Early Ordovician *Pseudoangustidontus duplospineus* might represent an anomalocaridid spine²² or a complete grasping

appendage²⁰. Its morphology, however, differs from an anomalocaridid spine²⁰, and its unsegmented, sclerotized nature is inconsistent with an anterior appendage²². *Schinderhannes bartelsi* from the Lower Devonian Hunsrück Slate retains some anomalocaridid characters, including a circular mouth and anterior raptorial appendages, but clearly lies crownward as a sister taxon to the euarthropods⁵.

The Fezouata Biota preserves a fully marine Burgess Shale fauna in combination with more advanced taxa^{8,23}. The anomalocaridid specimens are associated with a diverse fauna⁸ and were recovered from five excavations north of Zagora, in southeastern Morocco. Excavations 1 and 2 are approximately coeval, and sit just below the boundary between the Lower and Upper Fezouata Formations; they are latest Tremadocian in age. The remaining excavations are slightly younger, but all three occupy approximately the same stratigraphic level: they sit at the base of the Upper Fezouata Formation, dating them to the earliest Floian (Supplementary Fig. 1).

The Fezouata anomalocaridids occur in two distinct preservational styles. Smaller specimens, like the majority of Fezouata fossils^{8,23}, are flattened in the mudstones and preserved in pyrite weathered to iron oxides. Larger specimens occur in massive concretions, dominated by authigenic silica, in close proximity to each other within the mudstones. The composition of the fossils indicates weathered pyrite, but a significant proportion of manganese is present. Concretion formation was probably the result of the rapid decay of a large amount of organic material (large trilobites are also preserved in this way²⁴). The concretions provided a degree of protection from compaction, so that the trunk retains some convexity and the lateral lobes project at a high angle.

The large anomalocaridid specimens were collected at Excavation 1. They comprise articulated bodies but they lack most or all of the head region. The most complete specimen (Fig. 1a–c, Supplementary Fig. 2) preserves the posterior margin of the head and a trunk of 11 segments; there is no evidence of tergites. The maximum preserved length and width (excluding lateral lobes) of this fossil (Fig. 1a) are respectively ~915 mm and ~295 mm. Specimens YPM 226438 and YPM 226439 (Supplementary Fig. 3a, b) are less complete, but their trunks attain a comparable width, indicating that they were of similar size. The segments are approximately equal in length except for the posteriormost 3 or 4, which become progressively shorter where the trunk tapers to a blunt end. They are covered by long, flexible blade-like structures, more than 100 in the widest segments, oriented parallel or slightly oblique to the axis of the trunk (Fig. 1a, b, Supplementary Figs 2, 3a). They are interpreted as covering the dorsal surface of the segments, based on the position of similar structures in *Laggania*^{14,25,26}. Their attitude may be straight to gently curved or even sinuous; they run parallel to each other with limited overlap, except where they are folded and distorted in the incomplete terminal body segment of YPM 226437 (Supplementary Fig. 2c, d). There is no evidence that the blades continue laterally across the small triangular, flexible lobes that project from the ventro-lateral margin of the trunk (Fig. 1a–c; Supplementary Figs 2a, b, 3a, b); their exact relationship to the base of the lobes is unclear. Only the most proximal part of the lobes is clearly preserved; narrow closely spaced rays run parallel to the axis (Fig. 1c, Supplementary Fig. 3b).

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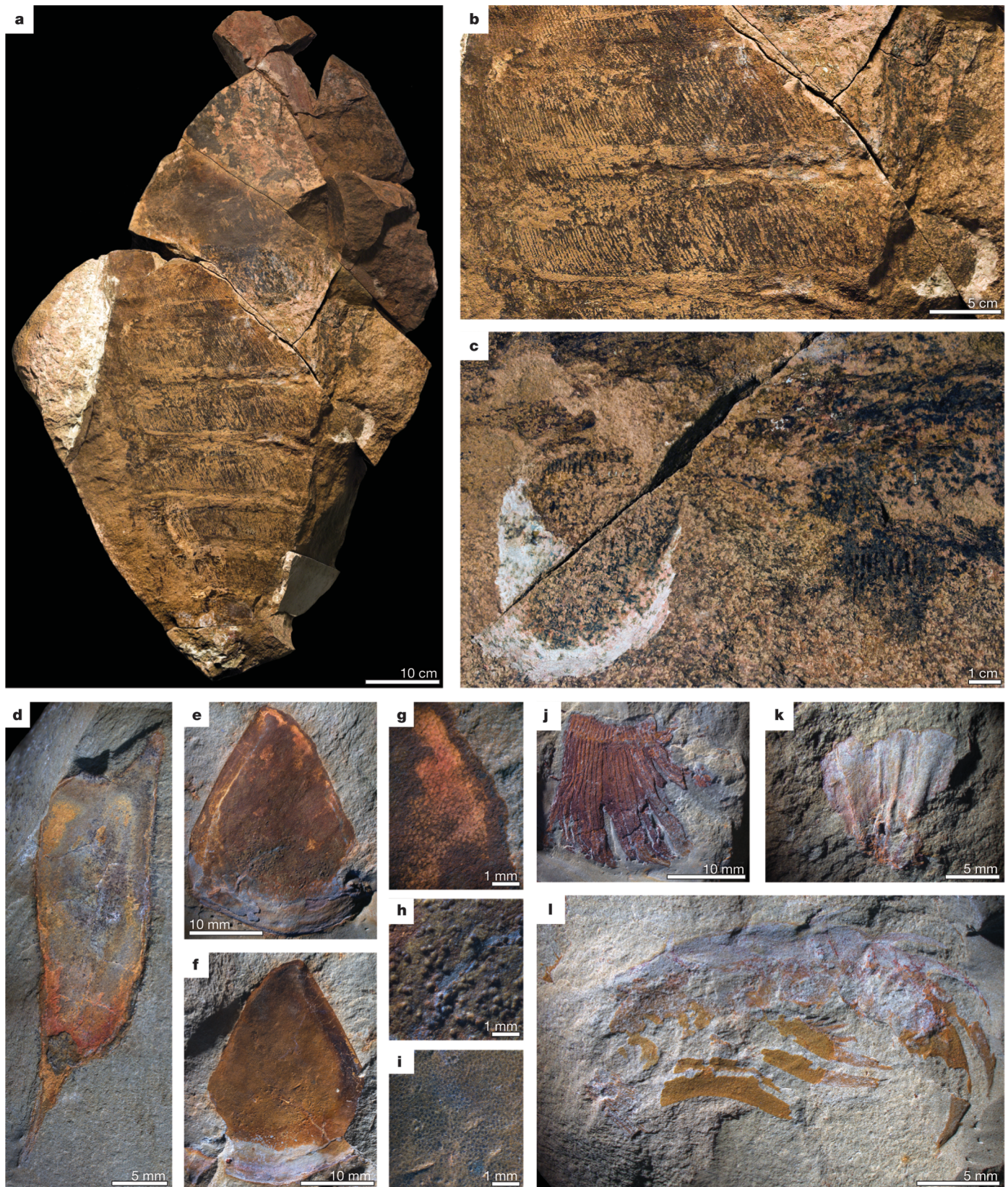


Figure 1 | Anomalocaridid specimens from the Lower Ordovician Fezouata formations. Drawings by *camera lucida* of the specimens are provided in Supplementary Fig. 4. **a–c**, Giant, near-complete specimen preserved in a concretion, dorsal side exposed, Excavation 1 (YPM 226437). **a**, Entire specimen. **b**, Segments 5 and 6 showing blades. **c**, Right lobes 5 and 6 showing rays. **d**, Left lateral 'P-element' of carapace, part, Excavation 2 (YPM 227518). **e–i**, Central 'H-element' of carapace, Excavation 2 (YPM 227517). **e**, Part

showing evidence of a healed injury, posterior right. **f**, Counterpart.

g, Reticulate structure on the anterior right of the part. **h**, Coarse tubercles on the mid-posterior of the part. **i**, Fine tubercles on the counterpart. **j**, Fragment of gill, part, Excavation 2 (YPM 227934). **k**, Incomplete oral circler, part, Excavation 3 (YPM 227643). **l**, Great appendage, part, Excavation 5 (YPM 227644).

Smaller individuals were represented in the Fezouata Formation at other excavations (Supplementary Fig. 1). Excavation 2 yielded an elongate valve-like sclerite (41 mm long including spines), with a robust triangular projection at one end and a long slender pointed projection at the other (Fig. 1d, Supplementary Fig. 4c). A sub-triangular sclerite (Fig. 1e–i, Supplementary Fig. 4b, c), 32 mm long, was found at the same excavation. It preserves a reticulate structure on the part (Fig. 1e, g) but not on the counterpart (Fig. 1f): this may be an internal feature of the cuticle revealed by exfoliation. Coarse tubercles are scattered in the posterior half (Fig. 1e, h) and fine tubercles are closely spaced elsewhere (Fig. 1i).

Excavation 2 also yielded a relatively broad jointed rachis about 15 mm long, to which long, flat, blunt-tipped, overlapping flexible blades are attached, one on each podomere (Fig. 1j, Supplementary Fig. 4d). These structures are similar to those on the segments of the largest specimens (Fig. 1a, b; Supplementary Figs 2, 3a). Two less well-preserved fragments of similar morphology were also recovered from the slightly younger Excavation 4.

An incomplete oral circling consisting of one major and two minor plates (Fig. 1k, Supplementary Fig. 4e) was found at Excavation 3. The major plate (preserved length ~13 mm) shows two narrow radial strengthening ridges; only one wider ridge is present on the minor plates. The teeth were broken away as the shale was split to reveal the fossil. Extrapolation suggests a diameter of the complete circling of slightly more than 30 mm.

Two specimens of a great appendage were also recovered. The number of podomeres and the morphology of the spines indicates that they belong to an anomalocaridid. The larger specimen from Excavation 5 (preserved length ~34 mm along the curve) is incomplete at both ends, but preserves evidence of 9 podomeres (Fig. 1l, Supplementary Fig. 4f). A distal spine on the dorsal side is small and more dorsally directed on the more proximal podomeres; these spines become more robust and near parallel to the appendage on successively distal podomeres. A very robust, slightly recurving, long spine projects ventrally from the mid-length of the more proximal podomeres but may have been absent from the distalmost four. This ventral spine terminates in a curved point, and bears five or six secondary spines along its proximal length. A fine bundle of spines or setae is associated with the proximal part of this larger specimen but it is not known whether this is simply a chance association. A smaller specimen from Excavation 3 (preserved length ~16 mm along the curve) comprises 10 or 11 podomeres (Supplementary Fig. 3c, d); ventral spines appear to be present only on the median 4 podomeres.

In summary, the large articulated bodies all derive from Excavation 1, whereas the small carapace elements were found at an adjacent site of similar age (Excavation 2) together with a fragment of rachis with blades. Blade-like structures were collected from the younger Excavation 4 whereas the similar aged Excavations 3 and 5 yielded raptorial appendages, associated with a partial oral circling at Excavation 3. It is unclear whether the Moroccan specimens represent more than one type of anomalocaridid: a formal description awaits the discovery of more material.

The blade-like structures on the surface of the segments and in the fragmentary specimens are similar to those in *Hurdia* and *Laggania*⁶, and may be comparable to the blades in *Opabinia*²⁷. A transverse arrangement of blades across the trunk similar to that in the large Moroccan specimens has been described and reconstructed on the dorsal surface of *Laggania*^{14,25,26}. The attachment of the blades to a rachis is similar to the arrangement in *Hurdia*, and the transverse mineralized structures in *Laggania* may be homologous. The lateral lobes show rays, as observed in *Laggania*. The carapace elements are strikingly similar to the central 'H-element' and lateral 'P-element' that make up the tripartite *Hurdia* headshield⁶. Although they differ in outline from those typical of *Hurdia victoria* from the Burgess Shale, the H-element preserves an internal reticulate structure similar to that in *Hurdia* sclerites⁶. The great appendages resemble morph B in *Hurdia*⁶ although they differ in detail.

The specimens from Excavation 1 represent the largest articulated anomalocaridid specimens known, and even though the size of the head is unknown, it is likely that the largest Moroccan individual was significantly larger than its Burgess Shale counterparts³. These anomalocaridids are rivalled in size among arthropods only by pterygotid eurypterids²⁸ and the terrestrial arthropleurids²⁹ (although extrapolation based on remains of the oral circling from the early Cambrian Chengjiang biota of China¹ has been used to infer an even larger anomalocaridid, these estimates are uncertain¹⁴). They dwarf the other organisms known from the Fezouata Biota: the largest trilobites are nileids, asaphids and dikelokephalinids, which reach a maximum of ~30 cm (ref. 24), less than 30% of the length of the anomalocaridids.

Like other anomalocaridids, the Moroccan examples are assumed to have been swimming predators. The great appendages seem to be adapted to entrap prey and to help to transfer it to the mouth. No biomineralized organisms with injuries compatible with the anomalocaridid oral circling have been recovered from the Fezouata formations, but it is likely that the Moroccan anomalocaridids, like their Cambrian predecessors, fed mostly on unmineralized organisms³. The size and associated food requirements of the largest Fezouata individuals might imply low population densities. The association of at least five individuals in close proximity at Excavation 1 may indicate an abundant food source, or congregation for some other purpose, such as moulting or mating.

The most striking feature of the Moroccan specimens, apart from their size, are the series of dorsal blades. These specimens provide the most compelling evidence yet that such structures traversed the entire trunk of some anomalocaridid taxa^{19,25,26}. They do not resemble scales²⁵ and their interpretation as gills is more plausible, even if their unprotected position is anomalous. There is no sign of any separation of the left and right halves as in *Hurdia*⁶. While the blades may originate as exites⁶, the rachis to which they connect appears to be attached across the dorsal width of the trunk in the middle of the intersegment areas in a manner unknown in euarthropods; it is unclear whether the rachis also attached to the base of the lobes. If the function of the blades was respiratory, they may reflect low oxygen conditions or the high oxygen requirement of a large active swimmer; their dorsal position would have assured continued oxygenation when in close proximity to anoxic bottom conditions.

The Fezouata discoveries extend the range of unequivocal anomalocaridids by about 30 million years ago, from the middle Cambrian to the Early Ordovician, and provide the only temporal link between the Cambrian occurrences and the Early Devonian great appendage arthropod *Schinderhannes*, which retains some anomalocaridid characters⁵. The Moroccan occurrences show that anomalocaridids were the largest organisms in some ecosystems even in the Ordovician, and were presumably at the top of the food chain. With the exception of the singular Polish and possible Czech occurrences, which are from intermediate and polar palaeolatitudes respectively, all Cambrian anomalocaridid localities are situated in the palaeotropics. The Fezouata formations, in contrast, were deposited at a high polar southern palaeolatitude, confirming a global distribution of anomalocaridids, at least latitudinally, during the early Palaeozoic, as observed for many other taxa of Burgess Shale type⁸. The demise of anomalocaridids may have been associated with the diversification of large predatory eurypterids and stem cephalopods during the Great Ordovician Biodiversification Event³⁰.

METHODS SUMMARY

All figured specimens are housed in the collections of the Yale Peabody Museum of Natural History. Locality details are kept at the Museum, and can be provided on request. Small specimens were prepared with scalpels and fine needles under high magnification using Leica MZ6 and MZ16 stereomicroscopes and, when necessary, repaired using cyanoacrylate glue. The large specimens were prepared with the aid of fine chisels and electric engravers, and assembled using cyanoacrylate glue and epoxy. Interpretative drawings were made with a *camera lucida* attached to a Leica MZ6 stereomicroscope. Photographs of the large specimens were made with a

Canon EOS 300D digital reflex camera with a Sigma EX 50 mm f2.8 DG macro lens stopped down to f5 for maximum sharpness, while smaller specimens were imaged using a Leica MZ16 stereomicroscope with Leica DFC 425 digital camera. All photographs were taken with crossed polarizers, and, in addition, the specimen in Supplementary Fig. 3c was photographed under ethanol. Digital photographs were processed in Adobe Photoshop CS2 and CS3. To maximize depth of field, between 10 and 30 images were stacked using CombineZP and Helicon Focus Pro software. Figures 1a, b, d, e, f, j, l and Supplementary Figs 2a, c, and 3a are composite images, stitched together using Adobe Photoshop CS3 and Microsoft ICE. Elemental composition was analysed in a Philips XL 30 environmental scanning electron microscope (ESEM) equipped with an energy dispersive X-ray analyser (EDX).

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