Preservation: The three known specimens of *Lyrarapax unguispinus* are preserved in claystone of the Yu'anshan Member, which is dominated by extremely fine-grained matrix interbedded with layers of siltstone. The claystone is subdivided into two types. One is an event grey claystone layer (yellowish after weathering), lacking algal fragments, but rich in fossils. The other is a background dark grey claystone layer (dark yellow to brown after weathering), containing abundant black algal remains[29-31]. The holotype YKLP 13304 is from the event claystone, whereas paratypes YKLP 13305 and 13306 are from the background claystone. YKLP 13304 exhibits typical Chengjiang preservation as rust-coloured flattened remains. YKLP 13305 and YKLP 13306 are both preserved as variously coloured remains (blue, rose, brown, black), of which SEM-EDX shows black as a strong carbon signal (see main account; Fig. 2g).

Preservational aspect of specimens: YKLP 13304 (Fig. 1) is preserved flat, revealing its ventral aspect based on the presence of an approximately rectangular structure in the head, which is interpreted as an oral cone (see below). YKLP 13305 (Fig. 2) is identified as a dorsal aspect not only due to the absence of a putative mouth, but particularly due to the presence of setal blades that are widely regarded as dorsal structures[7,32,33]. YKLP 13304 is preserved parallel to the bedding plane. The anterior part of YKLP 13305 is nearly parallel to the bedding plane but from about the middle part of the body, it is tilted obliquely to the bedding plane to become bent and folded. YKLP 13306 (Extended Data Fig. 3) is preserved oblique to bedding except for the head region, which is flat. In this specimen, the posterior region of the body is embedded into the matrix, obscuring morphology. The left side of the anterior body is incomplete, and the right side also bends down into the claystone.

Morphological Description: The animal is bilaterally symmetrical, with the body divided into a head region, a neck, and a trunk that terminates in a tail fan. The three known specimens suggest the length of the animal (excluding the length of the frontal appendage and the tail fan) varied from 4cm (YKLP 13304) to 8cm (YKLP 13306).

The head is equipped with a pair of preocular-preoral frontal appendages, a pair of stalked eyes, a ventral mouth and a dorsal cephalic plate. The dorsal cephalic plate has an enhanced anteroventral marginal rim (in YKLP 13304b; Fig. 1c, d, g) that is oval to subcircular in shape and is best shown in YKLP 13306 (Extended Data Fig. 3a, f), covering the most anterior part of the head. The stalked eyes are located slightly behind the frontal appendages.

Only YKLP 13304a has a frontal appendage preserved, the base of which is evidently located anterior to the mouth (Fig. 1c, d). It is incomplete in its most distal part, as indicated by a lack of podomeres that bear dorsal spines, absence of characteristic terminal spines, and having fewer podomeres than any anomalocaridid known from complete frontal appendages. It preserves six clearly identified endite-bearing podomeres, between which sutures, indicative of articulations, can be resolved. The preserved part of the frontal appendage is about 0.85 cm long, probably in life reaching about 1.2 cm (based on comparison to proportions of the frontal appendages of *Amplectobelua stephenensis*[34]), which would have been large in relation to a 4 cm body length, discounting the tail fan. Endites are located at the inner lateral side of the frontal appendage. They become smaller distally, but along the appendage the endites vary in

size, every alternating one being enlarged; the smaller endites bear two spines and the larger ones as many as four spines (Fig. 1e). The most proximal spined podomere has a remarkably stout endite, forming a spinose blade from which seven highly sclerotised spines gradually become stronger distally, all pointing towards the tip of the appendage thereby giving the whole structure a claw-like arrangement. Other endites have two to four spines directed towards this proximal endite. Frontal appendage morphology of *L. unguispinus* is, however, clearly distinguished from that of juvenile and larger frontal appendages of *Amplectobelua* (compared in Extended Data Fig. 1a-d).

All three specimens have a pair of suboval to subcircular eyes located somewhat distant from the head, each at the distal end of a long stout stalk. Together each stalk and its eye are clavate. Evidence for ommatidial organization is resolved in the eyes of YKLP 13304 (Extended Data Fig. 2)

The approximately rectangular structure opening ventrally in the head of YKLP 13304 is interpreted as an oral cone based on its similarity in size and position to the oral cone of other anomalocaridids. It comprises a concentric arrangement of wrinkled furrows, some of which show serrations along their inner margins (Fig. 1f). Laterally, and less obvious frontally, pointing inwards from its wrinkled border and extending into what is interpreted as the mouth orifice, are darker areas consisting of blurry conical outlines in which are arranged numerous darker furrows.

The post-cephalic region of *Lyrarapax unguispinus* includes a distinctive neck, a main trunk bearing flaps, and a terminal tail fan. The neck comprises four short segments immediately behind the head, as shown in YKLP 13304 (Fig. 1a-d), 13305 (Fig. 2a), and 13306 (Extended Data Fig. 3a). Each neck segment provides a pair of small flat extensions or flaps similar to those described from *Anomalocaris canadensis*[7]. At the junction between each flap and the neck there can be resolved a small approximately oval blue pigmented structure with a blurred outline, interpreted as the remains of muscle such as those in the much broader trunk region (YKLP 13304a, b; Fig. 1a-d). Two anteroposteriorly extended furrows are evident posterior to the neck region of YKLP 13305 (Fig. 2a, b), together forming a spindle shaped profile interpreted as the part of the midgut by comparison to *A. canadensis*[7]. The furrows are contiguous with a broad convoluted structure extending posteriorly in YKLP 13305 that may include the hindgut in its posterior part, its raised areas comprising dark flocculent aggregates suggestive of degraded gut wall muscle less cohesive than, but reminiscent of gut muscle identified in *Pambdelurion whittingtoni*[10].

The relatively narrow neck is succeeded by a broad and then tapering trunk, almost pear-shaped in profile, in which the number of segments is difficult to precisely ascertain because of the deformation in the posterior part of YKLP 13305 and 13306. In YKLP 13305 (Fig. 2a, b) and 13306 (Extended Data Fig. 3a), the first trunk segment is associated with a pair of extremely long flaps that curve backward alongside the body. In YKLP 13305 these appear almost equal in length to the entire trunk. While these paddle-like structures are unique to this taxon with regard to their segmental relationship and placement relative to the rest of the trunk, they are reminiscent of extensions described from the Devonian anomalocaridid *Schinderhannes bartelsi*, in which a pair of lateral propulsive structures originally interpreted as possibly appendicular are situated immediately behind and ventral to the eyes[35].

Pairs of approximately oval to rectangular blue-pigment structures can be clearly recognized in the main trunk of YKLP 13304 within which are darker patches, some oval, extending outwards (Fig. 1a-d). These complexes diminish in size posteriorly where there are what appear to be four pairs of smaller patches intervening between the narrower part of the trunk and the tail fan. In total, 11 pairs of dark coloured patches are present in the trunk of YKLP 13304. In YKLP 13305, corresponding patches align with body segments (Fig. 2a, b), so it is thus inferred that this taxon has at least eight and probably as many as 11 trunk segments in addition to four neck segments. Similar dark patches have been interpreted as muscle remains in *A. canadensis*[7]. In YKLP 13305 dark patches, particular on the left side of the specimen, show raised structures comprising parallel ridges (Fig. 2c, e) reminiscent of body wall muscle described from *Pambdelurion whittingtoni*[10]. In the living animal these are likely to have powered the flaps. Assuming this interpretation is correct, the decreasing size of muscle blocks from anterior to posterior in *Lyrarapax unguispinus* corresponds to the successive decrease in size of its flaps (Fig. 1a-d; Fig. 2) as might be expected of a streamlined swimmer. In YKLP 13306, the size of the flaps also decreases posteriorly (Extended Data Fig. 3a). The accentuated, almost oar-like first pairs of flaps in YKLP 13305 and YKLP 13306, as described above, support this interpretation of a fast mobile animal.

The two dorsally compacted specimens resolve filament-like structures in the main trunk, most of which are organized as bands that extend outwards from the body's longitudinal axis, but with others also arranged at various angles to this. These filaments, which are preserved in association with the dark patches in YKLP 13306, are interpreted as setal blades because of this relationship, which is comparable with that seen of *A. canadensis*[7]. They are most distinct on the anterior part of flaps in YKLP 13306 (Extended Data Fig. 3d, e), where they are arranged in parallel and oriented nearly anteroposteriorly. The more laterally oriented bands on the posterior parts of these same flaps are interpreted as muscle by comparison to musculature in YKLP 13305 (Fig. 2e).

The trunk terminates as a tail fan, resolved best in YKLP 13304 (Fig. 1a, b) where the trunk is flat enough in the bedding plane to reveal, originating from the axial part of the posterior end of the body, three pairs of partly overlapping blades. The surfaces of the blades are well exposed on the left side, whereas those on the right side are more slender and lie on three different thin laminations. The apparent small size of the right side tail blades are interpreted as a result of tilting, i.e., they are inclined to bedding, because their overlap is reversed (each blade is overlain by the following one).

Discussion: The oral cone is known from a single specimen and we are cautious to ascribe taxonomic significance to its apparent differences from oral cones in other anomalocaridids. The specimen does not show any convincing evidence for overlapping radially-arranged plates, a characteristic feature of Radiodonta, though it is possible that the conical structures on each lateral side of the mouth could be remains of plates. Their extensions towards the middle of the mouth could alternatively be compared with the bilateral "jaws" of Onychophora[36]. The quadratic outline of the oral cone is mirrored by a square-shaped opening similar to better-known oral cones of *Hurdia*[37].

Paired lateral extensions from the head (cowels, Fig. 1a, c; labeled cw in c), situated dorsal to the eyestalks, are suggestive of lateral head plates (P-elements) that typify *Hurdia*[38], although in *L. unguispinus* these evidently have a more rectangular

profile and approximately align with a curved and pigmented anterior margin of a dorsal cephalic plate (Fig. 1c, g; Extended Data Fig. 3f) that is more comparable to *Anomalocaris*[7].

The frontal appendage of *Lyrarapax* especially resembles that of *Amplectobelua*[32, 34] in the presence of an enlarged endite on one proximal podomere, and this is interpreted as synapomorphic for the two genera (see "Phylogenetic position"). However, this and succeeding alternating endites are blade-like and bear multiple spines in *L. unguispinus* rather than having a single elongate spine as in the type species of *Amplectobelua*. The oar-like enlargement of the first body flap in *Lyrarapax* is not shared by *Amplectobelua* (*A. symbrachiata*: ref. 38, fig. 3A; ref. 39, fig. 267), which instead has similar sized flaps on the first few trunk segments. *Amplectobelua symbrachiata* has pronounced transverse lines ("strengthening rays") on the anterior half of its body flaps (fig. 4 in ref. 38) but these structures are not observed and are evidently lacking in *L. unguispinus*. The small *L. unguispinus* is unlikely to represent immature specimens of *A. symbrachiata* because a hypertrophied anterior body flap is not seen in the small specimen of *A. symbrachiata* noted above[38, 39], nor in other juvenile anomalocaridids. Comparison of similar sized frontal appendages (Extended Data Fig. 1) shows that the morphology of *A. symbrachiata* does not change substantially from the observed size onwards. Diagnostic differences with respect to the development of the enlarged proximal ventral spine as a blade-like endite in *L. unguispinus* versus a long spine with a pair of auxiliary spines in *A. symbrachiata* are clearly distinct.

Phylogenetic position: *Lyrarapax unguispinus* was coded in the 54-character matrix for Radiodonta of ref. 6. A character describing auxiliary spine distribution was added to distinguish *Lyrarapax* from *Amplectobelua* (character 47). Coding changes to the published matrix are as follows: character 5 ("preoral scleral plate") was re-coded as state 0 (absent) in Radiodonta because this structure has been reinterpreted as the margin of a dorsal carapace[7]; character 44 was re-coded as state 0 in *Amplectobelua stephenensis* (the ventral spines do not demonstrably alternate in length between adjacent podomeres[34]); character 48 ("legs", referring to trunk appendages) have been re-coded as absent in nematodes and priapulids; character 51 ("dorsal blades") was re-coded as state 0 (absent) in cycloneuralians and *Aysheaia* and as present in *Opabinia* (state 1) rather than as unknown; character 53 was re-coded as state 2 for *Anomalocaris canadensis* (striations on the flaps are anteroposteriorly oriented rather than transverse[7]); *Anomalocaris pennsylvanica* lacks auxiliary spines (character 37, state 0), and the possibility that this could be taphonomic[40] is weakened by their absence in better preserved material[41]; this character was re-coded and linked characters (38, 40-43) scored as inapplicable. Some characters originally left as uncertain in *A. pennsylvanica* have been documented[40, 41] and are coded with the following states (in parentheses): 24(0), 26(0), 28(0), 29(1), 30(0).

Coding for *L. unguispinus* treats the endites on the frontal appendage as homologous with ventral spines (characters 31-47), as justified by their position, their alternation in size on successive podomeres (character 44, state 1), and correspondence of the proximal endite to the "hypertrophied pincer spine" (character 36) of *Amplectobelua*, which is clearly an enlarged ventral spine[6]. Accordingly, smaller spines on the endites are likely homologous with auxiliary spines (character 37) on ventral spines. Based on their arrangement on the anterior edge of the proximal endite, the auxiliary spines are coded as

pectinate (character 38, state 1). The modified matrix in Nexus format is a Supplementary File.

As in ref. 6, characters 3, 6, 39 and 40 were coded as ordered. Analysis of the matrix with a heuristic search under equal character weights in TNT[42] produced 108 shortest cladograms of 96 steps (Consistency Index 0.667; Retention Index 0.867). Their strict consensus preserves the monophyly of the Anomalocaridae + Amplectobeluidae clade reported in ref. 6, but with largely ambiguous relationships between species of *Anomalocaris* and with *L. unguispinus* grouping with *Amplectobelua symbrachiata* and *A. stephenensis* (Extended Data Fig. 4). Membership of *Lyrarapax* in Amplectobeluidae is based on two unique unreversed synapomorphies of the frontal appendage: a single proximal ventral spine directed forwards to oppose the tip of the appendage and form a claw (character 35) and a hypertrophied pincer spine (character 36). A subset of 54 cladograms is found with implied character weights and is stable under varying concavity constants ($k=2, 3, 4, 5, 6$); in these *L. unguispinus* is sister group of *A. symbrachiata* + *A. stephenensis*.

Further references

29. Zhu, M., Zhang, J. & Li, G. Sedimentary environments of the Early Cambrian Chengjiang Biota: Sedimentology of the Yu'anshan Formation in Chengjiang County, Eastern Yunnan. *Acta Paleontol. Sin.* **40,** 80–105 (2001).

30. Zhao, F., Caron, J. B., Hu, S. & Zhu, M. Quantitative analysis of taphofacies and paleocommunities in the early Cambrian Chengjiang Lagerstätte. *Palaios* **24,** 826–839 (2009).

31. Gaines, R. R., Hammarlund, E. U., Hou, X., Qi, C., Gabbott, S. E., Zhao, Y. L., Peng, J. & Canfield, D. E. Mechanism for Burgess Shale-type preservation. *PNAS* **109,** 5180–5184 (2012).

32. Hou, X. G., Bergström, J. & Ahlberg, P. *Anomalocaris* and other large animals in the lower Cambrian Chengjiang fauna of Southwest China. *GFF* **117**, 163–183 (1995).

33. Van Roy, P. & Briggs, D. E. G. A giant Ordovician anomalocaridid. *Nature* **473**, 510–513 (2011).

34. Daley A. C. & Budd, G. E. New anomalocaridid appendages from the Burgess Shale, Canada. *Palaeontology* **53**, 721–738 (2010).

35. Kühl, G., Briggs, D. E. G. & Rust, J. A great-appendage arthropod with a radial mouth from the Lower Devonian Hunsrück Slate, Germany. *Science* **323**, 771–773 (2009).

36. Oliveira, I. & Mayer, G. Apodemes associated with limbs support serial homology of claws and jaws in Onychophora (velvet worms). *J. Morphol.* **274**, 1180–1190 (2013).

37. Daley, A. C., Budd, G. E. & Caron, J-B. Morphology and systematics of the anomalocaridid arthropod *Hurdia* from the Middle Cambrian of British Columbia and Utah. *J. Syst. Pal.* **11**, 743–787 (2013).

38. Chen, J. Y, Ramsköld, L. & Zhou, G. Q. Evidence for monophyly and arthropod affinity of Cambrian giant predators. *Science* **264**, 1304–1308 (1994).

39. Chen, J. Y., Zhou, G. Q., Zhu, M. Y. & Yeh, K. Y. *The Chengjiang Biota: A Unique Window of the Cambrian Explosion* (National Museum of Natural Science, Taichung, 1997).

40. Briggs, D. E. G. *Anomalocaris*, the largest Cambrian arthropod. *Palaeontology* **22**, 631–664 (1979).

41. Lieberman, B. S. A new soft-bodied fauna: the Pioche Formation of Nevada, *J. Paleontol.* **77**, 674–690 (2003).

42. Goloboff, P. A., Farris, J. S. & Nixon, K. C. TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 774–786 (2008).