

GEOSCIENCES

Origin of raptorial feeding in juvenile euarthropods revealed by a Cambrian radiodontan

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ABSTRACT

The rapid rise of arthropods during the Cambrian quickly established some clades, such as the euarthropod stem-group called Radiodonta, as the dominant and most diverse predators in marine ecosystems. Recent discoveries have shown that the size and dietary ecology of radiodontans are far more diverse than previously thought, but little is known about the feeding habits of juveniles. Here, we document a very small (~18-mm-long), near-complete specimen of the radiodontan *Lyrarapax unguispinus* from the early Cambrian Chengjiang Biota of China. This specimen is the smallest radiodontan individual known, representing a juvenile instar. Its adult-like morphology—especially the fully developed spinose frontal appendages and tetradial oral cone—indicates that *L. unguispinus* was a well-equipped predator at an early developmental stage, similar to modern raptorial euarthropods, such as mantises, mantis shrimps and arachnids. This evidence, coupled with the basal phylogenetic position of radiodontans, confirms that raptorial feeding habits in juvenile euarthropods appeared early in the evolutionary history of the group.

Keywords: *Lyrarapax*, Radiodonta, Arthropoda, Cambrian, predation, feeding ecology

INTRODUCTION

Many Cambrian members of the iconic euarthropod stem-group known as radiodontans (*Anomalocaris* and kin) have been viewed as giant apex predators ever since their true body plan was revealed over 30 years ago [1–3]. However, more recent findings have shown that the body size of some early Palaeozoic radiodontans can range from 4 cm to over 200 cm in length [4–6] and that the highly variable frontal appendage morphologies are suggestive of a range of feeding modes, from shell-crushing to filter-feeding [6–11]. *Lyrarapax* from the early Cambrian Chengjiang Biota of China represents the smallest radiodontan taxon, with previously reported body sizes ranging from 4 to 8 cm in length [4,5]. Until now, the frontal appendage morphology of the type species, *Lyrarapax unguispinus* was only known from a single, incomplete appendage [4,5], but the preserved details imply a predatory function. The juvenile specimen of *L. unguispinus* described here not only provides novel information on the frontal appendages and feeding mode in this taxon, but sheds new light on the morphology of the

mouth apparatus and the phylogenetic concept of the Radiodonta.

RESULTS AND DISCUSSION

General morphology

The small specimen (total body length: 18 mm) of *L. unguispinus* documented here (Figs 1–3 and Supplementary Fig. 1, available as Supplementary Data at NSR online), from the lower Cambrian (Series 2, Stage 3) Yu'an shan Member, Chiungchussu Formation of Yunnan Province in China, is relatively complete and shows features not seen in the type specimens [4,5], including a fully articulated frontal appendage (FA) and a sclerotized oral cone; see Supplementary Data at NSR online, for a detailed description and taxonomic discussion. The FA comprises 12 podomeres (P1–12): P2–6 bear complex endites of alternating sizes, but no dorsal spines; P7–11 are devoid of endites, but have stout dorsal spines; and P12 has a short, robust distal claw (Fig. 2 and Supplementary Fig. 1a, available as Supplementary Data at NSR online). Of note is the

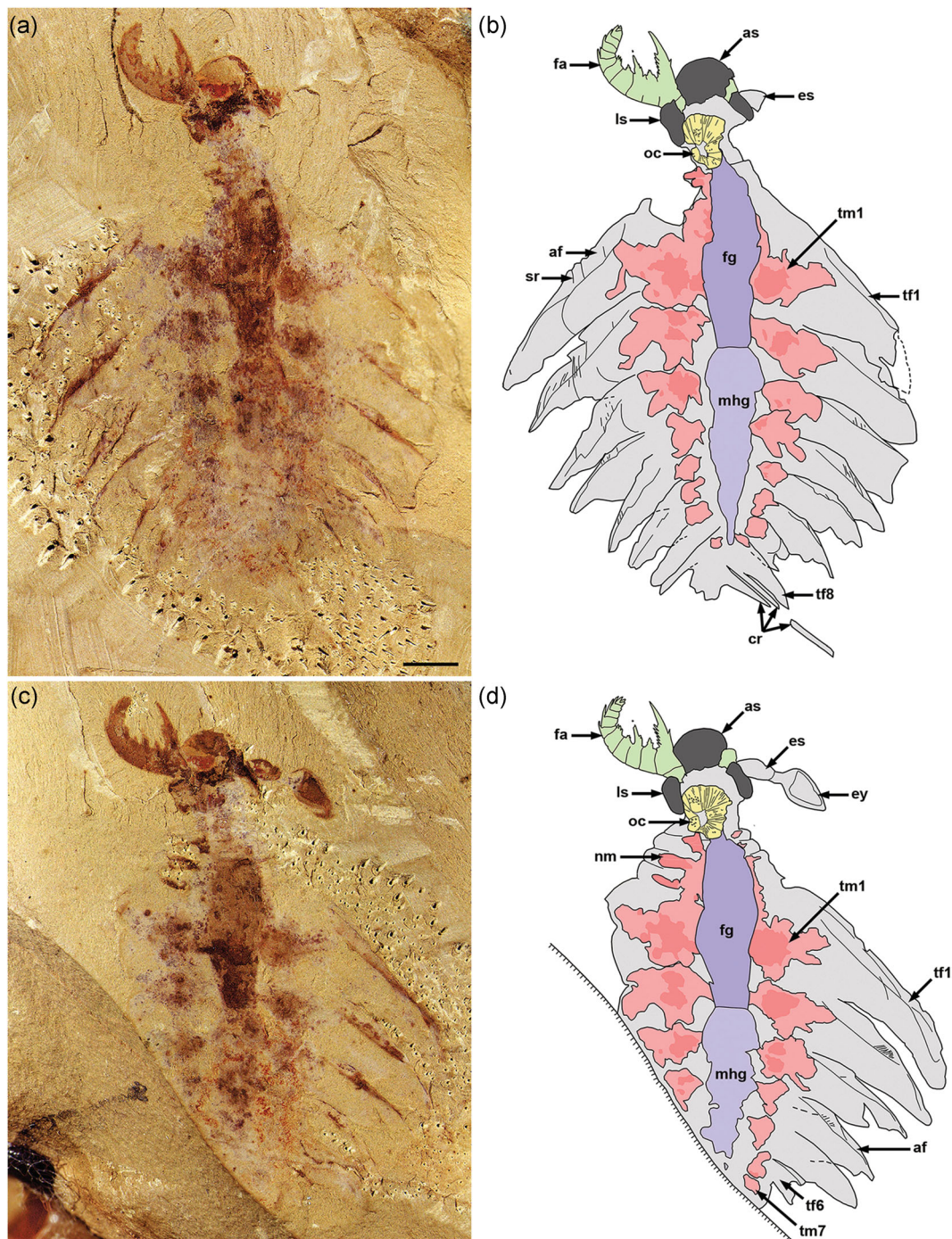


Figure 1. Juvenile specimen of *Lyrarapax unguispinus*. (a) and (b) Part of a near-complete specimen (XDMU-133) and interpretative drawing. (c) and (d) Counterpart (mirrored) and interpretative drawing. Scale bar in (a) is 2 mm and applies to all images. af, anterior flange; as, anterior sclerite; cr, caudal rami; es, eye stalk; ey, eye; fa, frontal appendage; fg, foregut; ls, lateral sclerite; mhg, undifferentiated midgut-hindgut; nm, neck muscle; oc, oral cone; sr, strengthening rays; tf, trunk flap; tm, trunk muscle. Colours: dark grey, cephalic sclerites; dark purple, foregut; green, frontal appendages; light purple, undifferentiated midgut-hindgut; pink, muscle blocks; yellow, oral cone.

hypertrophied endite on P2 that hosts at least seven anterior auxiliary spines (Fig. 2c). The oral cone consists of many circumoral plates, including four large, perpendicularly arranged plates with surficial nodes (Fig. 3a and b). This tetradial arrange-

ment of large, node-bearing plates intercalated between a series of smaller plates is very similar to the *Peytoia/Hurdia*-like oral cone recently described from the early Cambrian Guanshan Lagerstätte of China [12].

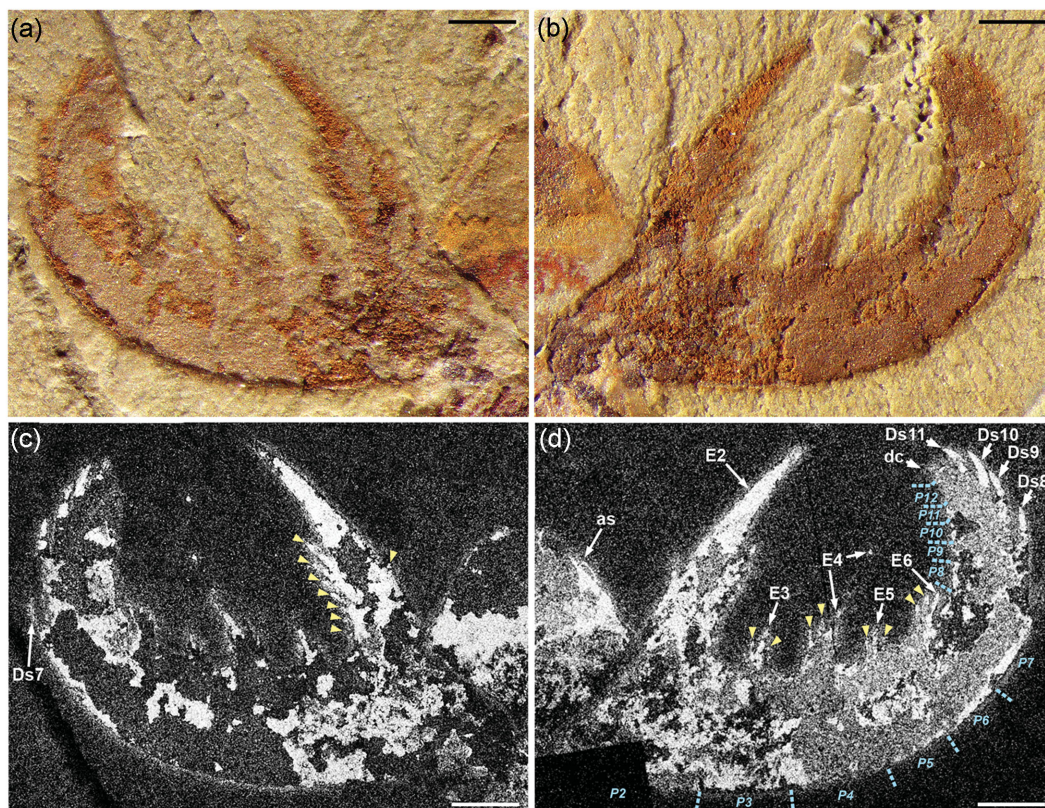


Figure 2. Frontal appendage of *Lyrarapax unguispinus*. (a) and (b) Photographs of part and counterpart. (c) and (d) Back-scattered electron micrographs of part and counterpart, showing the anterior sclerite (as), auxiliary (arrowheads) and dorsal (Ds) spines, endites (E), distal claw (dc) and podomere (P) boundaries. All scale bars: 1 mm.

Significance of the oral cone

The presence of a tetradial oral cone in *L. unguispinus* has important implications for radiodontan systematics. Previously documented specimens of *Lyrarapax* from the Chengjiang Biota do not display a plated mouth apparatus, but rather a series of concentric ridges and furrows [4,5]. Based on the occurrence of this feature in one specimen of each species (*L. unguispinus* and *L. trilobus*), a lack of circumoral plates was interpreted as a morphological characteristic of *Lyrarapax*, rather than a taphonomic artefact [5]. This prompted a revised generic diagnosis, and also challenged the original concept of the Radiodonta [3,5]. The oral cone in the new specimen of *L. unguispinus* (Fig. 3a and b) indicates that its absence in other specimens of *Lyrarapax* is indeed preservational. The displacement or lack of other external, sclerotized features (e.g. FAs) suggests that the previously illustrated *Lyrarapax* specimens represent carcasses that have suffered from some preferential decay of articulating membrane and post-mortem disturbance [13–15]; exuvia can be ruled out, as all specimens preserve internal labile tissues. Thus, an alternative interpretation of the oral structures previously de-

scribed for *L. unguispinus* (Figs 1a–d, f in [4]) and *L. trilobus* (Figs 1.3, 1.5, 2.2, 2.3 in [5]) is that they represent soft tissues—possibly the pharynx and its musculature—internally located behind the oral cone; the ‘triangular areas’ seen in the holotype (Fig. 1f in [4]) may represent impressions of, or even attachment points for, the large plates of the oral cone. Moreover, isolated radiodontan oral cones have been found in most Cambrian *Konservat-Lagerstätten* [9,12,16], demonstrating that they were often disarticulated from the body during ecdysis or after death, and later subjected to biostratinomic sorting.

The discovery of a sclerotized oral cone in *Lyrarapax* demonstrates that the presence of radial circumoral plates remains a consistent trait of the Radiodonta (particularly as a single coherent unit) and indeed a characteristic feature of lower stem-group euarthropods [17,18] and other ecdysozoans [19]. Also, our phylogenetic analysis of radiodontans based on an updated version of a recent dataset [6] (available as Supplementary Data at NSR online) retrieves *Lyrarapax* nested within a monophyletic Amplectobeluidae (Supplementary Fig. 2, available as Supplementary Data at

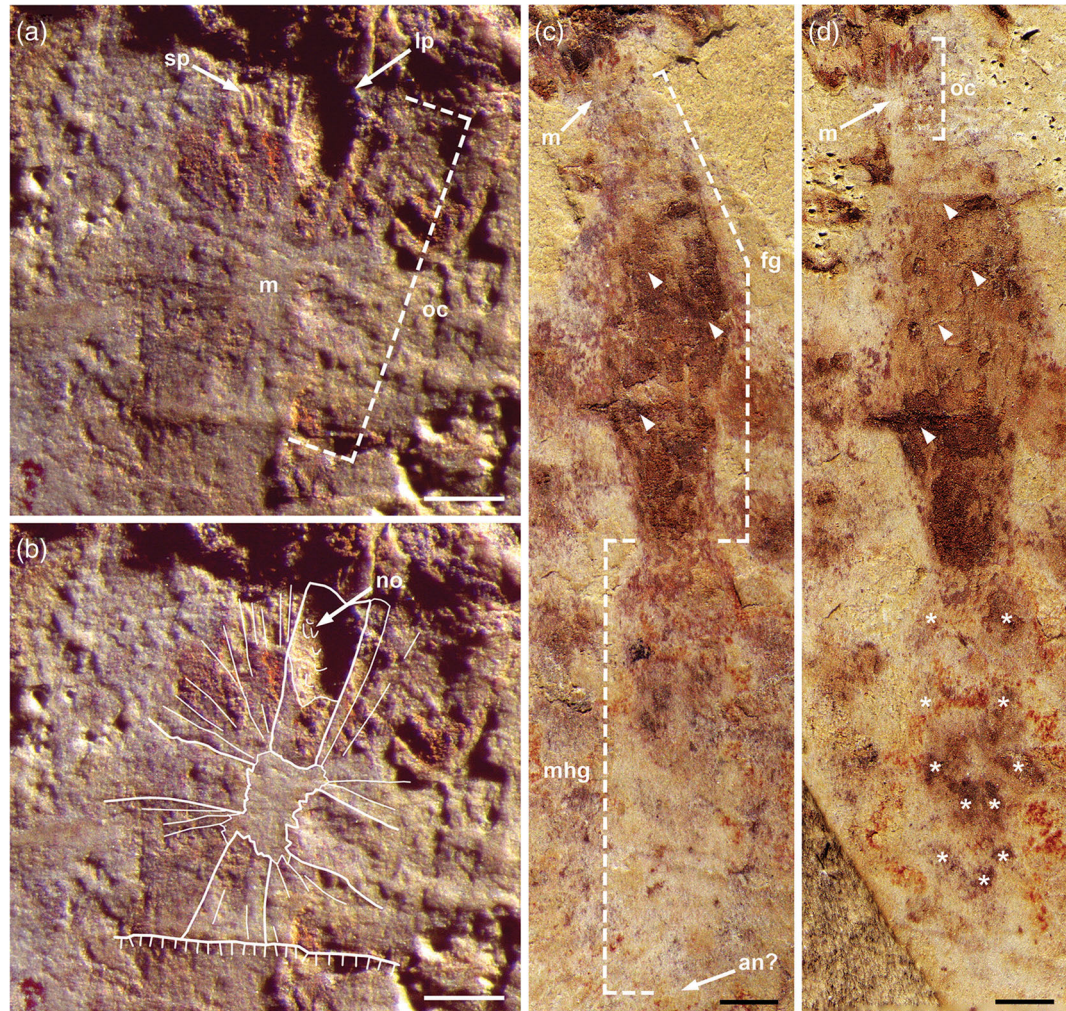


Figure 3. Mouth apparatus and gut of *Lyrarapax unguispinus*. (a) and (b) Oral cone showing tetradial arrangement of large plates. (a) Detail showing clear impressions of large and small plates. (b) Outlines of preserved plates and nodes. (c) and (d) Complete gut with impressions of segment boundaries (arrowheads) in the foregut and possible midgut digestive glands (asterisks); (c) part and (d) counterpart (mirrored). All scale bars: 1 mm. an, anus; fg, foregut; lp, large plate; m, mouth; mhg, undifferentiated midgut-hindgut; no, node; oc, oral cone; sp, small plate.

NSR online). The tetradial arrangement appears to be plesiomorphic for Radiodonta, and the presence of node-bearing plates is a synapomorphy of Anomalocarididae + Amplectobeluidae [12,20].

Raptorial feeding in adult and juvenile radiodontans

Of the diverse radiodontan FA morphologies [5,6,8,10], those of amplectobeluids appear the best suited for grasping and manipulating prey, characterized by a proximal hypertrophied endite and a series of robust dorsal spines distally [4,5,8,20–22] (Supplementary Fig. 3, available as Supplementary Data at NSR online). Lack of an articulation joint at the base of the hypertrophied endite indicates that it may have functioned as the rigid part of a ‘claw’, with the more flexible portion

of the FA represented by the distal podomeres, thus permitting pincer-like capture of prey [2,8]. The stout, curved dorsal spines on the distal podomeres, when curled inwards, would have aided in securing the prey [8]. Also, the combination of a ‘dorsal kink’ in the proximal portion of the FAs (Fig. 4b and Supplementary Fig. 3, available as Supplementary Data at NSR online) and reduced head sclerites may have afforded the raptorial appendages a greater range of motion and degree of flexibility for striking and seizing prey [23]. As described above, the FA of *L. unguispinus* shows a pronounced morphological and therefore functional differentiation along its proximo–distal axis. The proximal podomeres are armed with complex endites, the smaller of which would have converged towards the serrated margin of the hypertrophied spine during flexion (Fig. 2 and Supplementary Fig. 1a, available as Supplementary

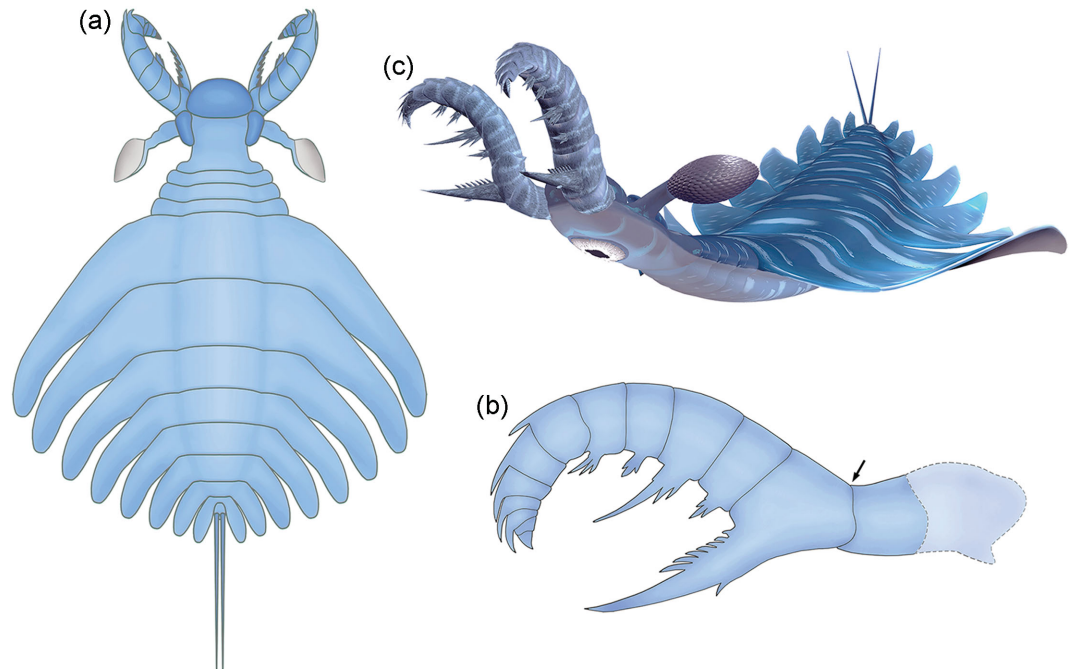


Figure 4. Reconstructions of *Lyrarapax unguispinus*. (a) Complete body in dorsal view. (b) Frontal appendage in lateral view, showing the spinosity pattern along the proximo–distal axis and dorsal kink (arrow). A more proximal, long podomere is suggested based on the morphology of *Amplectobelua symbrachiata*. (c) Artistic representation of the animal.

Data at NSR online). This likely resulted in crushing or slicing of prey before ingestion; the similar FAs of *Amplectobelua stephenensis* may have had a comparable function [8]. In contrast, the endites of *A. symbrachiata* are more simple and slender and, while the FA of this species would have undoubtedly been used to grab prey, mastication was likely performed separately by gnathobase-like structures [20]. Amplectobeluid FAs may have been able to apply considerable force, as evidenced by the darker pigmentation of their spines in Chengjiang specimens (e.g. Supplementary Fig. 3a, available as Supplementary Data at NSR online; Figs 3.2, 3.4 in [5]; Fig. 1A in [20]). This darker colouration is often indicative of a local thickening of the cuticle, as recently demonstrated for the gnathobases of the Cambrian durophagous euarthropod *Sidneyia inexpectans* [24]. However, forceful capture may have caused occasional damage, as seen in *A. symbrachiata* FAs where the more delicate (non-hypertrophied) endites have broken off in some cases [20,21].

This raptorial feeding mode in *Lyrarapax* and *Amplectobelua* seems to extend to juveniles as well. Immature specimens of *L. unguispinus* (Figs 1 and 2) and *A. symbrachiata* (Fig. 3A in [2]; Fig. 12S in [25]; extended data Fig. 1b–d in [4]) show that the FAs have distinct adult-like morphologies. Also, the presence of large eyes, well-developed body flaps and an enlarged gut in juveniles [2,25] (Figs 1, 3c, 3d and

Supplementary Fig. 1c–e, available as Supplementary Data at NSR online) suggests that *Lyrarapax* and *Amplectobelua* were already highly mobile visual predators during the early stages of post-embryonic development. It is possible that similar predatory modes occur among juveniles of some other radiodontans, such as *Anomalocaris*, given the comparable set of traits in adults [17,26,27], but this can only be confirmed by studying juvenile specimens.

Despite the lack of suitable modern analogues for reaffirming the proposed functional morphology and feeding ecology of radiodontans [28], there exist several predatory euarthropod groups that hunt using enlarged, spinose raptorial appendages. These include terrestrial clades such as the amblypygids (whip spiders) [29,30], uropygids (whip scorpions) [30] and mantodeans (mantises) [31], as well as the marine stomatopod crustaceans (mantis shrimps) [32–35] (Supplementary Figs 4 and 5, available as Supplementary Data at NSR online). Interestingly, the highly specialized morphology of grasping appendages develops very early during the ontogeny of these taxa.

Perhaps the most striking resemblance to radiodontan FAs are the pedipalps of uropygids [30] (Supplementary Fig. 5, available as Supplementary Data at NSR online), which provide one of the best modern analogues for understanding the functional morphology of the FAs of *Lyrarapax* throughout ontogeny. Both adult and juvenile uropygids use

their large, curved raptorial pedipalps to catch and hold prey, with the various stout spines on the tarsus, tibia and patella acting like prehensile pincers, while the opposing gnathobases on the proximal trochanters crush and masticate the victim [30]. The robust construction of the pedipalps affords urypygids a varied diet [30,36], but juveniles seem to avoid prey with hard exoskeletons [30]. This may have also been the case in *Lyrarapax* and *Amplectobelua*, although the reinforced spines in immature FAs may have allowed juveniles to manipulate hard (possibly even biomineralized) food items. So, while the FAs of amplectobeluid radiodontans may have functioned in a similar way to the pedipalps of urypygids, consumption of the prey was clearly different. Uropygids use their chelicerae to tear tissue from the prey before passing it to the preoral cavity, where it is liquefied by digestive fluids [30]. For radiodontans, there is still debate as to whether the oral cone performed an additional masticatory role or was used to ingest food via suction [16,28]; also, *A. symbrachiata* would have used its gnathobase-like structures to initially process food before passing it to the mouth opening [20]. However, given the variable morphologies of the oral cone (as corroborated by FAs), it is likely that the assorted radiodontan species used this structure in different ways [12,16].

The variety of radiodontan feeding structures clearly points to these stem-group euarthropods having played key, often high-tier, trophic roles within early Palaeozoic food webs, including the consumption of zooplankton, as well as nektonic and benthic fauna [6,8,10–12,16,20,37,38]. While certain taxa such as *Anomalocaris* [27] can still be considered giant apex predators of their time and capable of consuming large prey, the juveniles of some radiodontans like *Lyrarapax* (Fig. 4 and Supplementary Fig. 6, available as Supplementary Data at NSR online) demonstrate that predation in the water column was occurring on a variety of scales during the Cambrian [10,37,39–41]. On the smaller scale of prey, taxa such as *Tamisiocaris* were likely microphagous suspension feeders of plankton (≥ 0.5 mm in size) [10], whereas juvenile amplectobeluids were probably capable of feeding on very small (<5-mm) benthic and nektonic prey items, possibly including sclerotized taxa or biomineralized forms such as trilobites, molluscs and brachiopods. The consistent raptorial feeding habits of both juvenile and adult *Lyrarapax* contrast with the example of another early Cambrian euarthropod: the megacheiran *Leanchoilia illecebrosa*, where it is thought that juveniles and adults occupied separate ecological niches due to differing appendage morphologies [42]. Hence, the predatory lifestyles of certain radiodontan offspring adds further tier-

ing complexity to Cambrian marine food webs, and would have likely placed extra selective pressures on animal communities, particularly small benthic and nektonic prey [28,37]. Intense predation occurring on all scales during the early phase of animal evolution was undoubtedly a critical driver behind the morphological and ecological innovations arising throughout the Cambrian [28].

SUPPLEMENTARY DATA

Supplementary data are available at NSR online.

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REFERENCES

- Whittington HB and Briggs DEG. The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia. *Phil Trans R Soc Lond B* 1985; **309**: 569–609.
- Chen J, Ramsköld L and Zhou G. Evidence for monophyly and arthropod affinity of giant Cambrian predators. *Science* 1994; **264**: 1304–8.
- Collins D. The 'evolution' of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov) and order Radiodonta (nov). *J Paleontol* 1996; **70**: 280–93.
- Cong P, Ma X and Hou X *et al.* Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature* 2014; **513**: 538–42.
- Cong P, Daley AC and Edgecombe GD *et al.* Morphology of the radiodontan *Lyrarapax* from the early Cambrian Chengjiang biota. *J Paleontol* 2016; **90**: 663–71.

6. Van Roy P, Daley AC and Briggs DEG. Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps. *Nature* 2015; **522**: 77–80.
7. Nedin C. *Anomalocaris* predation on nonmineralized and mineralized trilobites. *Geol* 1999; **27**: 987–90.
8. Daley AC and Budd GE. New anomalocaridid appendages from the Burgess Shale, Canada. *Palaeontology* 2010; **53**: 721–38.
9. Daley AC, Paterson JR and Edgecombe GD *et al.* New anatomical information on *Anomalocaris* from the Cambrian Emu Bay Shale of South Australia and a reassessment of its inferred predatory habits. *Palaeontology* 2013; **56**: 971–90.
10. Vinther J, Stein M and Longrich NR *et al.* A suspension-feeding anomalocarid from the Early Cambrian. *Nature* 2014; **507**: 496–9.
11. Pates S and Daley AC. *Caryosyntrips*: a radiodontan from the Cambrian of Spain, USA and Canada. *Papers in Palaeo* 2017; **3**: 461–70.
12. Zeng H, Zhao F and Yin Z *et al.* A new radiodontan oral cone with a unique combination of anatomical features from the early Cambrian Guanshan Lagerstätte, eastern Yunnan, South China. *J Paleontol* 2018; **92**: 40–8.
13. Briggs DEG. The role of decay and mineralization in the preservation of soft-bodied fossils. *Annu Rev Earth Planet Sci* 2003; **31**: 275–301.
14. Butler AD, Cunningham JA and Budd GE *et al.* Experimental taphonomy of *Artemia* reveals the role of endogenous microbes in mediating decay and fossilization. *Proc R Soc B* 2015; **282**: 20150476.
15. Klompmaker AA, Portell RW and Frick MG. Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. *Palaeontology* 2017; **60**: 773–94.
16. Daley AC and Bergström J. The oral cone of *Anomalocaris* is not a classic ‘peytoia’. *Naturwissenschaften* 2012; **99**: 501–4.
17. Vannier J, Liu J and Leroosey-Aubril R *et al.* Sophisticated digestive systems in early arthropods. *Nat Commun* 2014; **5**: 3641.
18. Vinther J, Porras L and Young FJ *et al.* The mouth apparatus of the Cambrian gilled lobopodian *Pambdelurion whittingtoni*. *Palaeontology* 2016; **59**: 841–9.
19. Smith MR and Caron J-B. *Hallucigenia*’s head and the pharyngeal armature of early ecdysozoans. *Nature* 2015; **523**: 75–8.
20. Cong P, Daley AC and Edgecombe GD *et al.* The functional head of the Cambrian radiodontan (stem-group Euarthropoda) *Amplectobelua symbrachiata*. *BMC Evol Biol* 2017; **17**: 208.
21. Hou X, Bergström J and Ahlberg P. *Anomalocaris* and other large animals in the Lower Cambrian Chengjiang fauna of southwest China. *GFF* 1995; **117**: 163–83.
22. Wang Y, Huang D and Hu S. New anomalocaridid frontal appendages from the Guanshan biota, eastern Yunnan. *Chin Sci Bull* 2013; **58**: 3937–42.
23. Zeng H, Zhao F and Yin Z. Morphology of diverse radiodontan head sclerites from the early Cambrian Chengjiang Lagerstätte, south-west China. *J Sys Palaeo* 2017; **16**: 1–37.
24. Bicknell RDC, Paterson JR and Caron J-B *et al.* The gnathobasic spine microstructure of recent and Silurian chelicerates and the Cambrian arthropodan *Sidneyia*: functional and evolutionary implications. *Arthropod Struct Dev* 2018; **47**: 12–24.
25. Chen J and Zhou G. Biology of the Chengjiang fauna. *Bull Nation Mus Natur Sci* 1997; **10**: 11–105.
26. Paterson JR, García-Bellido DC and Lee MSY *et al.* Acute vision in the giant Cambrian predator *Anomalocaris* and the origin of compound eyes. *Nature* 2011; **480**: 237–40.
27. Daley AC and Edgecombe GD. Morphology of *Anomalocaris canadensis* from the Burgess Shale. *J Paleontol* 2014; **88**: 68–91.
28. Bicknell RDC and Paterson JR. Reappraising the early evidence of durophagy and drilling predation in the fossil record: implications for escalation and the Cambrian Explosion. *Biol Rev* 2018; **93**: 754–84.
29. Weygoldt P. *Whip spiders (Chelicerata: Amblypygi) – Their Biology, Morphology and Systematics*. Stenstrup: Apollo Books, 2000.
30. Beccaloni J. *Arachnids*. Collingwood: CSIRO Publishing, 2009.
31. Grimaldi D and Engel MS. *Evolution of the Insects*. Cambridge: Cambridge University Press, 2005.
32. Haug JT, Waloszek D and Maas A *et al.* Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. *Palaeontology* 2012; **55**: 369–99.
33. Ah Yong ST, Haug JT and Haug C. Stomatopoda. In: Martin JW, Olesen J and Høeg JT (eds). *Atlas of Crustacean Larvae*. Baltimore: Johns Hopkins University Press, 2014, 185–9.
34. Eastman LB and Thiel M. Foraging behavior of crustacean predators and scavengers. In: Thiel M and Watling L (eds). *The Natural History of the Crustacea, Vol. 2: Lifestyles and Feeding Biology*. Oxford: Oxford University Press, 2015, 535–56.
35. Haug C, Ah Yong ST and Wiethase JH *et al.* Extreme morphologies of mantis shrimp larvae. *Nauplius* 2016; **24**: e2016020.
36. Gallant J and Hochberg R. Elemental characterization of the exoskeleton in the whipscorpions *Mastigoproctus giganteus* and *Typopeltis dalyi* (Arachnida: Thelyphonida). *Invertebr Biol* 2017; **136**: 345–59.
37. Perrier V, Williams M and Siveter DJ. The fossil record and palaeoenvironmental significance of marine arthropod zooplankton. *Earth Sci Rev* 2015; **146**: 146–62.
38. Pates S, Daley AC and Lieberman BS. Hurdiid radiodontans from the middle Cambrian (Series 3) of Utah. *J Paleontol* 2018; **92**: 99–113.
39. Vannier J and Chen J. Early Cambrian food chain: new evidence from fossil aggregates in the Maotianshan Shale biota, SW China. *Palaos* 2005; **20**: 3–26.
40. Hu S, Steiner M and Zhu M *et al.* Diverse pelagic predators from the Chengjiang Lagerstätte and the establishment of modern-style pelagic ecosystems in the early Cambrian. *Palaeogeogr Palaeoclimatol Palaeoecol* 2007; **254**: 307–16.
41. Vannier J, García-Bellido DC and Hu S *et al.* Arthropod visual predators in the early pelagic ecosystem: evidence from the Burgess Shale and Chengjiang biotas. *Proc R Soc B* 2009; **276**: 2567–74.
42. Liu Y, Haug JT and Haug C *et al.* A 520 million-year-old chelicerate larva. *Nat Commun* 2014; **5**: 4440.