Dawn of complex animal food webs: A new predatory anthozoan (Cnidaria) from Cambrian
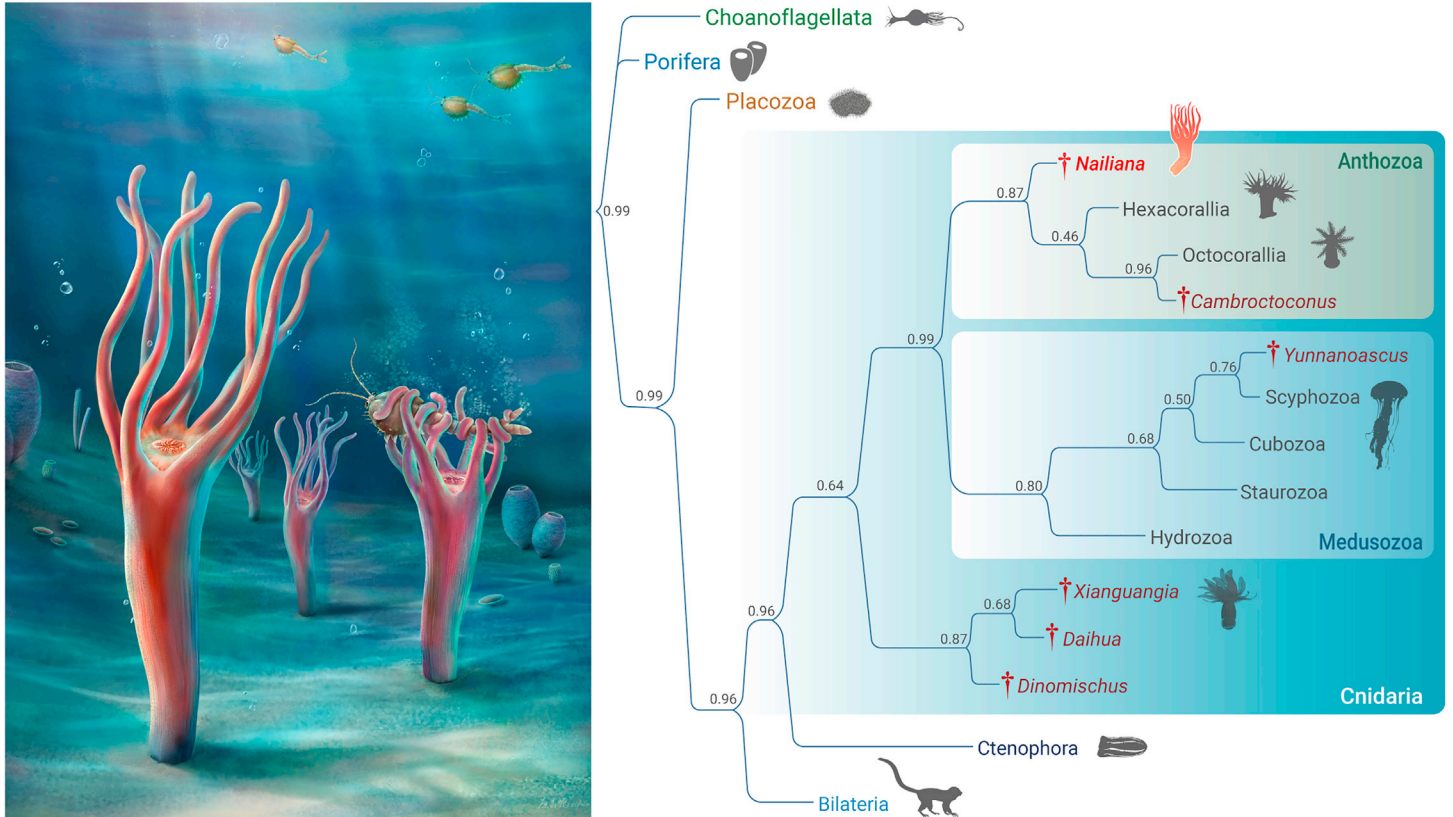
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Graphical abstract

Public summary

- Polypoid animal from early Cambrian of China is a stem-group anthozoan cnidarian

- Anthozoan ancestor inferred to be soft-bodied, solitary polyp of octoradial symmetry

- The new anthozoan provides the oldest direct evidence of macrophagous predation

- Macrophagous predation may have triggered complex food webs in early Cambrian

Dawn of complex animal food webs: A new predatory anthozoan (Cnidaria) from Cambrian

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Cnidarians diverged very early in animal evolution; therefore, investigations of the morphology and trophic levels of early fossil cnidarians may provide critical insights into the evolution of metazoans and the origin of modern marine food webs. However, there has been a lack of unambiguous anthozoan cnidarians from Ediacaran assemblages, and undoubted anthozoans from the Cambrian radiation of metazoans are very rare and lacking in ecological evidence. Here, we report a new polypoid cnidarian, *Nailiana elegans* gen. et sp. nov., represented by multiple solitary specimens from the early Cambrian Chengjiang biota (~520 Ma) of South China. These specimens show eight unbranched tentacles surrounding a single opening into the gastric cavity, which may have born multiple mesenteries. Thus, *N. elegans* displays a level of organization similar to that of extant cnidarians. Phylogenetic analyses place *N. elegans* in the stem lineage of Anthozoa and suggest that the ancestral anthozoan was a soft-bodied, solitary polyp showing octoradial symmetry. Moreover, one specimen of the new polyp preserves evidence of predation on an epifaunal lingulid brachiopod. This case provides the oldest direct evidence of macrophagous predation, the advent of which may have triggered the emergence of complex trophic/ecological relationships in Cambrian marine communities and spurred the explosive radiation of animal body plans.

INTRODUCTION

Cnidarians (anthozoans + medusozoans) are among the earliest diverging metazoan lineages, based on fossil and molecular evidence.[1,2] In contrast to medusozoans, which generally possess a pelagic medusoid generation, anthozoans (sea anemones, corals, soft corals, sea pens, and allies) are exclusively polypoid. Since anthozoans (hexacorallians + octocorallians) express ancestral cnidarian states,[3] gaining insights into the origin and early diversification of anthozoans may be key to understanding the evolution of metazoans. However, unequivocal records of anthozoan cnidarians from the critical interval (late Ediacaran to early Cambrian) of animal evolution are extremely rare. Thus, none of the putative Ediacaran hexacorallians[4–6] or octocorallians[7–9] has withstood further scrutiny.[10–12] Phosphatized polypoid microfossils, including *Eolympia pediculata*[13] and an undescribed form[14] from basal Cambrian deposits (~535 Ma, Fortunian) of South China, have been interpreted as having anthozoan affinities. Purported anthozoans[15–17] from the early Cambrian Chengjiang biota (~520 Ma, Age 3) have proven to be controversial. For example, *Xianguangia sinica* was originally classified as a crown sea anemone,[15] but new evidence suggests that it is a stem cnidarian with a filter-feeding habit.[18] The co-occurring, polypoid form *Archisaccophyllia kunmingensis* has been hypothesized to be either a crown actiniarian[17] or a stem phoronid.[19]

In the present article we describe a new, soft-bodied polypoid cnidarian, *Nailiana elegans* gen. et sp. nov., from the early Cambrian Chengjiang biota of South China. Multiple, radially symmetrical specimens of this taxon consist of a slender elongate body, one end of which exhibits a circular mouth region surrounded by a distinct oral disc and a single whorl of eight unbranched, prehensile tentacles. The main body column below the mouth exhibits multiple, closely spaced longitudinal grooves that may be traces of gastric mesenteries. The results of Bayesian phylogenetic analyses indicate that the new species was most likely a stem anthozoan. We also argue that *N. elegans* was a macrophagous predator, based in part on a single specimen, the tentacles of which surround a lingulid brachiopod. *In vitro* experiments demonstrating actual ingestion

of living lingulids by two species of anthozoans further strengthen the case for predation on epifaunal lingulids by *N. elegans*.

It has been hypothesized that complex modern food webs evolved in the early Cambrian oceans.[20,21] However, the structure of Cambrian trophic networks has hitherto been poorly understood, with previous reconstructions being based upon inferred feeding interactions among metazoan species[21] or upon the gut contents of putative predators.[22,23] We here argue that certain specimens of *N. elegans* preserve the oldest evidence in the known fossil record of macrophagous predation, thus providing important insights into the nature of early Cambrian food webs.

RESULTS

Phylum Cnidaria Verrill, 1865
Class Anthozoa Ehrenberg, 1834
Nailiana elegans Ou et Shu gen. et sp. nov. (Figures 1 and 2A–2F).

Etymology. The generic name honors the first author's grandmother, Nailian Fu (1912–2009), in memory of her benignity and elegance. In addition, "nailian," lotus-like in Chinese, alludes to the overall appearance of the new taxon. The gender is feminine. The specific name refers to the graceful body shape of the new taxon.

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Referred material. A total of 15 specimens (Table S1) housed in the Early Life Evolution Laboratory, China University of Geosciences, Beijing, China. Two individuals (ELEL-EJ080482-1, 2) preserved on the same slab are herein designated as the holotype and paratype specimens, respectively.

Horizon and locality. All specimens were collected from the *Eoredlichia-Wutingaspis* Biozone in the Yu'anshan Member of the Heilinpu Formation (Cambrian series 2, stage 3) in the Huaguoshan section at Erjie, Yunnan, southern China.

Diagnosis. Polypoid body entirely soft. Oral end exhibits a central mouth and circular oral disc surrounded by a whorl of eight long, unbranched, flexible tentacles. Columnar trunk highly extensible, exhibiting closely spaced, fine longitudinal grooves and stripes on the surface. Aboral end blunt or pointed.

Description. Centimetric specimens preserved as compacted body fossils or molds in weathered argillaceous mudstone (see supplemental information for detailed information on preservation and taphonomy). Gross morphology is sea anemone like, with a crown of eight simple tentacles located at one end of the cylindrical trunk (henceforth referred to as the column) (Figures 1, 2A, and S1–S5). Elongate, distally tapering tentacles are unbranched and most likely evenly spaced, projecting from the outer edge of the column (Figure 1). Tentacles are evidently flexible (Figures 1B, 2B, and S4A) and apparently smooth, generally lacking traces of internal structures, such as an axial lumen (see, however, below), or of external features such as nematocysts (Figure S2).

Axially compressed paratype exhibits a circular central protuberance, which most likely is perforated by a mouth opening and which is bordered by a peripheral disc surrounded by eight tentacles (Figures 1D and S1). Probable gastric cavity preserved as a dark region in the upper (oral) portion of the column (e.g., Figures 2B and 2F). Middle portion of the column exhibits evidence of original flexibility in the form of smooth bending (Figures 1B, 1E, and S4D). Compared

Figure 1. Early Cambrian _Nailiana elegans_ gen. et sp. nov. (A) Two specimens preserved on the same slab and designated, respectively, as the holotype (ELEL-SJ080824-1) and paratype (ELEL-SJ080824-2). (B) Counterpart of the holotype (lateral view), showing eight slender, prehensile tentacles (numbered) and the column with fine longitudinal grooves. (C) Interpretive drawing of the holotype. (D) Close-up of the paratype (oblique oral view), showing the elevated mouth region (arrowheads), oral disc, and eight tentacles. (E) Close-up of the holotype.co, column; fg, fine longitudinal grooves; od, oral disc; te, oral tentacles. Scale bars, 5 mm in (A–C, E) and 2 mm in (D).

with the holotype (Figures 1A, 1B, and 1E), the column of other specimens commonly shows varying degrees of axial extension (Figures 2A and S3–S5), resulting in wide variation between specimens in the height/width ratio of the column and in the ratio of the column length to the tentacle length (Table S1). Specimens showing the greatest amount of axial extension also exhibit a localized constriction (Figure S3D). Surface of the column exhibits multiple, closely spaced, fine longitudinal grooves or striae (Figures 1B, 1E, S3, and S4C). The number of striae on the column varies from 6 to 12, with a spacing of 3–8 striae per millimeter. Column tapers adorally to a point (Figure S4D) or terminates in a roughly concave disc (Figures 1B and 1C). Upper portion of the column generally expanded (e.g., Figures 2B, S3, and S4) to accommodate the bulging gastric cavity.

Specimen ELEL-SJ101866 (Figures 2A–2C) shows a prominent cordiform feature surrounded by the lower portion of the tentacles and partly situated within the gastric cavity. Examination of morphological details of the cordiform feature (Figures 2C–2D) reveals that it is a partially preserved lingulid brachiopod that can be assigned to _Lingulellotreta yuanshanensis_.[24] In addition to similarity in size, several other features of the brachiopod are consistent with the anatomy of _L. yuanshanensis_ (Figure 2E). These include a pair of coiled lophophore arms, a

sub-circular lophophoral base, and a sub-triangular pseudointerarea attached to the base of the pedicle, although the preserved pedicle is shorter and slightly thinner than normal (Figures 2C and 2D). Along with the overall shape of the shell, the posterior location and rounded morphology of the lophophoral base are typical of Chengjiang lingulids,[25] and indeed the broad, elongate, sub-triangular pseudointerarea that projects from the posterior margin of the valves is diagnostic of _L. yuanshanensis_.[24] In specimen ELEL-SJ081191, an ovoid feature (Figures 2F, S4D, and S4E) impregnated by brownish iron oxides also occurs within the upper portion of the gastric cavity. In another specimen (ELEL-SJ081106), a brownish patch of coarse sediment particles, possibly remains of undigested food, occurs within the upper portion of the column and extends into a possible axial lumen in one of the tentacles (Figure S3D).

DISCUSSION
Functional morphology

The elongate flexible tentacles of _N. elegans_ lack evident suspension-feeding structures (e.g., branches, setae, or long, dense cilia) and thus were most likely adapted for detecting, grasping, and maneuvering live or dead prey to the oral opening (Figure 1D). Evident extension/contraction of the body column, coupled

Figure 2. Evidence of carnivory in *Nailiana elegans* gen. et sp. nov. (A) ELEL-SJ101866A, showing slender tentacles and an elongate column. (B) Close-up of (A), showing a single lingulid brachiopod surrounded by the basal portion of the tentacles. Roman numbers (I→IV) indicate discrete sediment laminae in descending stratigraphical order. (C and D) Anatomy of the brachiopod and interpretative drawing, showing remains of the lophophore arms, lophophore base (circular structure indicated by arrowheads) in (C), and pseudointerarea (upper margin outlined with white dots) in (C), and pedicle. Dashed lines in (D) outline inferred or extrapolated soft-part anatomy. (E) A non-ingested specimen of *Lingulellotreta yuanshanensis* (ELI L-0014A, dorsal view of ventral interior), showing anatomy similar to the specimen embedded within the polyp in (C). (F) ELEL-SJ081191A, showing possible gastric contents (outlined with white dots). co, column; fi, filaments; gc, expanded gastric cavity; la, lophophore arm; lb, lophophore base; lg, lingulid brachiopod; pd, pedicle; pi, pseudointerarea; te, tentacles; vr, visceral region. Scale bars, 5 mm in (A, B, F) and 1 mm in (C–E).

with tapering/widening of the aboral end, suggests that the column, in addition to serving for mechanical support, was adapted for vertical burrowing through a peristaltic action, which enabled the animal to anchor itself in soft substrates. Substantial extension and flexion of the column most likely were brought about by contraction of well-developed circular and longitudinal muscles in the body wall. In most specimens, the upper portion of the column is expanded to accommodate the bulging central cavity, which usually contains dark organic matter (e.g., Figures 2F and S4D). Hence, the central cavity most likely functioned as the primary site of digestion and fluid circulation, as well as a hydroskeleton, as is the case in modern anthozoan polyps.

N. elegans as a macrophagous predator

The associated lingulid, identified here on the basis of detailed anatomical evidence as *L. yuanshanensis* (Figures 2C and 2D), is neither superimposed upon nor overlain by the polyp. Rather, the presence of very thin sediment wedges between the brachiopod and the tentacles (Figures 2B, 2I–2IV in descending stratigraphical order) demonstrates that the brachiopod is topologically surrounded by the tentacles, with the pedicle

and pseudointerarea of the brachiopod located within the gastric cavity of the polyp (Figures 2C and 2D). The polyp and brachiopod could not have lived in mutualistic or commensal symbiosis, since specimens of this lingulid in the Chengjiang biota are abundant and invariably non-symbiotic. We propose therefore that the brachiopod most likely was a captured and engulfed prey item. Modern lingulid brachiopods live in a vertical burrow, with only three pseudosiphons formed by prominent setae projecting from the opening of the burrow. When disturbed, the shell and pseudosiphons are readily retracted through rapid contraction of the pedicle. Given these facts, the chances of a living lingulid being captured by tentaculate predators such as actiniarians are very slim. By contrast, early Cambrian lingulids in the Chengjiang biota were epibenthic. For example, the shell of *L. yuanshanensis* and *Lingulella chengjiangensis* was invariably tethered to the soft sediment by the distal part of a long, thin pedicle, while the distal part of the pedicle of other lingulids (including *Longtancunella chengjiangensis* and *Xianshanella haikouensis*) was attached to hard parts of a variety of other skeletal animals.[26] Therefore, the epibenthic ecology of Cambrian lingulids, including *L. yuanshanensis*
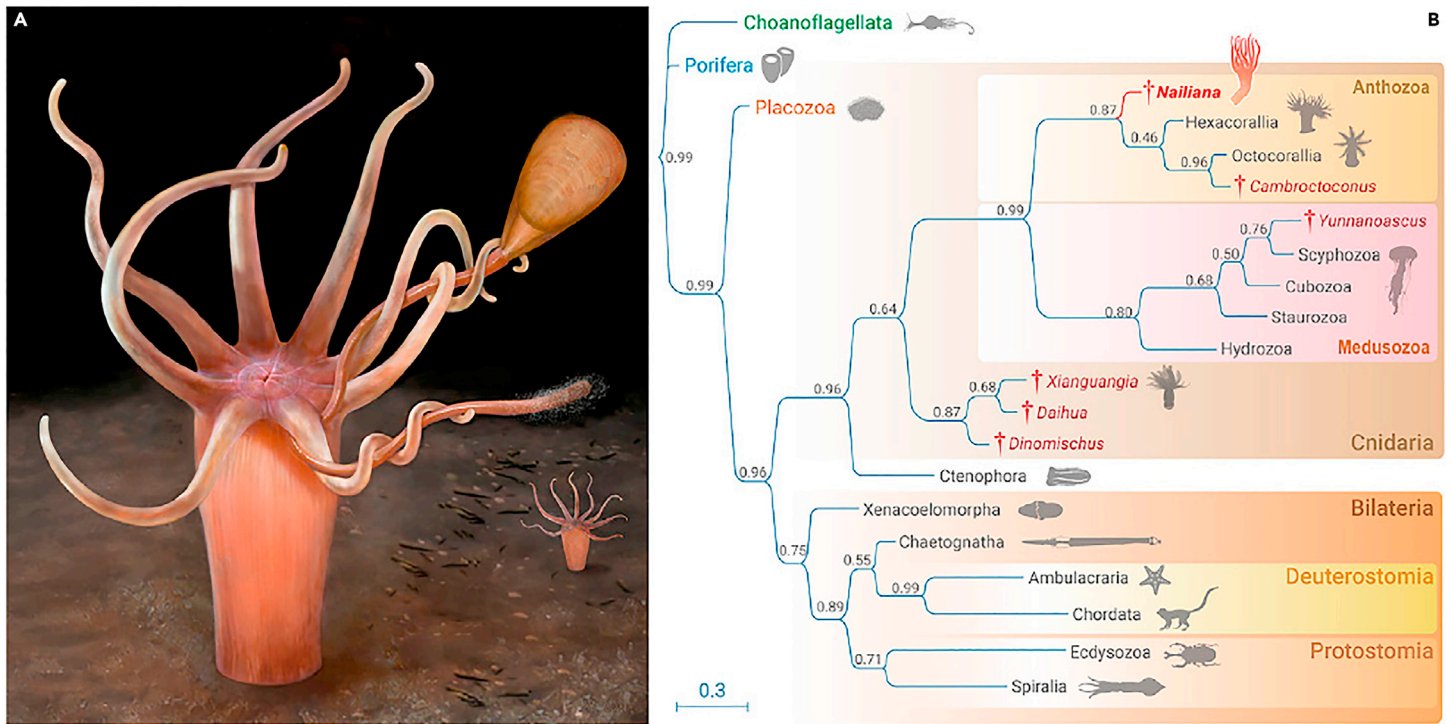
Figure 3. Interpretive reconstruction and inferred phylogenetic position of *Nailiana elegans* gen. et sp. nov. (A) Reconstruction of *N. elegans* capturing a lingulid brachiopod (artwork by Xi Liu). (B) Summary of metazoan phylogeny derived from Bayesian analyses of 126 characters and 42 taxa under Mkv + Γ model (see Figure S6 and Text S4 for details). Numbers at nodes indicate posterior probabilities. *N. elegans* is resolved as a stem-group anthozoan. Cambrian problematica *Xianguangia*, *Daihua*, and *Dinomischus* are basal among the Cnidaria. Neuralia, Bilateria, Nephrozoa, Protostomia, and Deuterostomia are monophyletic. Animal silhouettes by courtesy of PhyloPic (www.phylopic.org).

of roughly the same body size as the new polyp, almost certainly increased the likelihood of their being preyed upon by *N. elegans* (Figure 3A). Our *in vitro* feeding experiments on modern *Lingula anatina* and anthozoans (see supplemental information Text S3 and Videos S1-S3) further corroborate that *N. elegans* was most likely a macrophagous predator.

Phylogenetic implications

The elongate, prehensile tentacles surrounding the central mouth of *N. elegans* closely resemble the oral tentacles of extant predatory sea anemones, in particular those with a small number of tentacles arranged in a single whorl (e.g., *Halcampa* sp.[27]). Examination of available material revealed no trace of any structure indicative of an anal opening, indicating that the gut was likely blind. The fine grooves between the parallel longitudinal stripes on the column may represent imprints of gastric mesenteries similar to those of extant actiniarians. Such features, together with the bulging gastric cavity, suggest the presence of an extensively partitioned gastrovascular system homologous with that of crown-group anthozoans. The eight tentacles (and probable octoradial symmetry) of the new fossil polyp are evocative of solitary octocorallians (e.g., *Taiaroa tauhou*[28]). However, unlike the pinnate tentacles of octocorallians, those of *N. elegans* were unbranched. We notice the existence of a pinnule-less, sclerite-free species (*Acrossota amboinensis*) in extant stoloniferous cotocorals.[29] However, the phylogenetic position of this species among extant octocorals[30] suggests that its pinnules underwent secondary loss. Thus, whether unbranched tentacles represent the ancestral condition or a derived state in Octocorallia remains undetermined, although simple tentacles are presumably plesiomorphic. In short, the suite of preserved phenotypic traits displayed by *N. elegans*, coupled with evidence of predatory behavior, suggest that this fossil species is closely related to anthozoan cnidarians. However, whether its tentacles were armed with cnidae (e.g., nematocysts) remains unknown. Indeed, it seems unlikely that such subcellular features could be preserved in Chengjiang fossils, although possible nematocyst batteries preserved as a dense series of dark, transverse striae have been reported from the long, unbranched tentacles of the scyphomedusa *Yunnanoascus haikouensis*[31] (Figure 4A) from the same Lagerstätte.

The results of our phylogenetic analyses, conducted using Bayesian inference on a data matrix consisting of 126 characters and 42 eukaryotic taxa

(Text S4 and Table S2), indicate that *N. elegans* was a stem-group anthozoan (Figures 3B and S6; posterior probability = 87%). This conclusion implies that the most recent common ancestor of *N. elegans* and crown-group anthozoans was a benthic (sedentary but mobile), solitary, predatory polyp lacking a sclerotized or mineralized exoskeleton. Given that anthozoans are basal among the Cnidaria,[1,3] this hypothesis is consistent with the results of recent phylogenomic analyses, which imply that the ancestral cnidarian was a solitary, nonsymbiotic polyp.[1] In addition, the plesiomorphic polypoid body form and predatory habit of *N. elegans* have since been retained in crown anthozoans. The body symmetry of total-group anthozoans remains conjectural. *N. elegans* likely possessed octoradial symmetry, as suggested by the radial arrangement of the eight tentacles (Figure 1) and by the absence of any features indicative of bilateral/biradial symmetry. Octoradial symmetry may have evolved independently in *N. elegans* and octocorallians; however, it is more parsimonious to assume that the most recent common ancestor of *N. elegans* and crown anthozoans was an octoradiate polyp and that such symmetry has persisted in modern octocorallians. Although this inference seems consistent with the interpretation that the mid-Cambrian octoradial polyp *Cambroctoconus* was a stem cnidarian,[32] the results of our phylogenetic analyses suggest instead that more likely it was just a stem octocoral (Figure 3B). Finally, our findings suggest that the ancestral anthozoan was a solitary, soft-bodied organism, although of course some of its hexacorallian and octocorallian descendants evolved coloniality and mineralized skeletons or sclerites.

Recently, *Xianguangia sinica*, *Daihua sanqiong*, and *Dinomischus venustus* from the Chengjiang biota were placed in the ctenophore stem lineage, which would suggest that ctenophores stemmed from sessile, sea anemone-like ancestors.[33] This hypothesis is based foremost on the resemblance of the tentacles of these three species to the ctene rows of ctenophores. However, the architecture of their tentacles, which were well adapted for microphagous filter feeding in these three taxa, is fundamentally distinct from the unique structure of ctene rows in ctenophores that are octaradially arranged on the body surface for locomotion. The axial series of dark, transverse paired striae on their tentacles were interpreted as cushion plates,[33] which are unique to ctenophores and used exclusively for supporting ciliary combs (ctenes). However, this argument is untenable because the cushion plate is a rectangular tuft of epithelial polster cells specialized for the development of locomotory cilia (i.e., formation of a ciliary
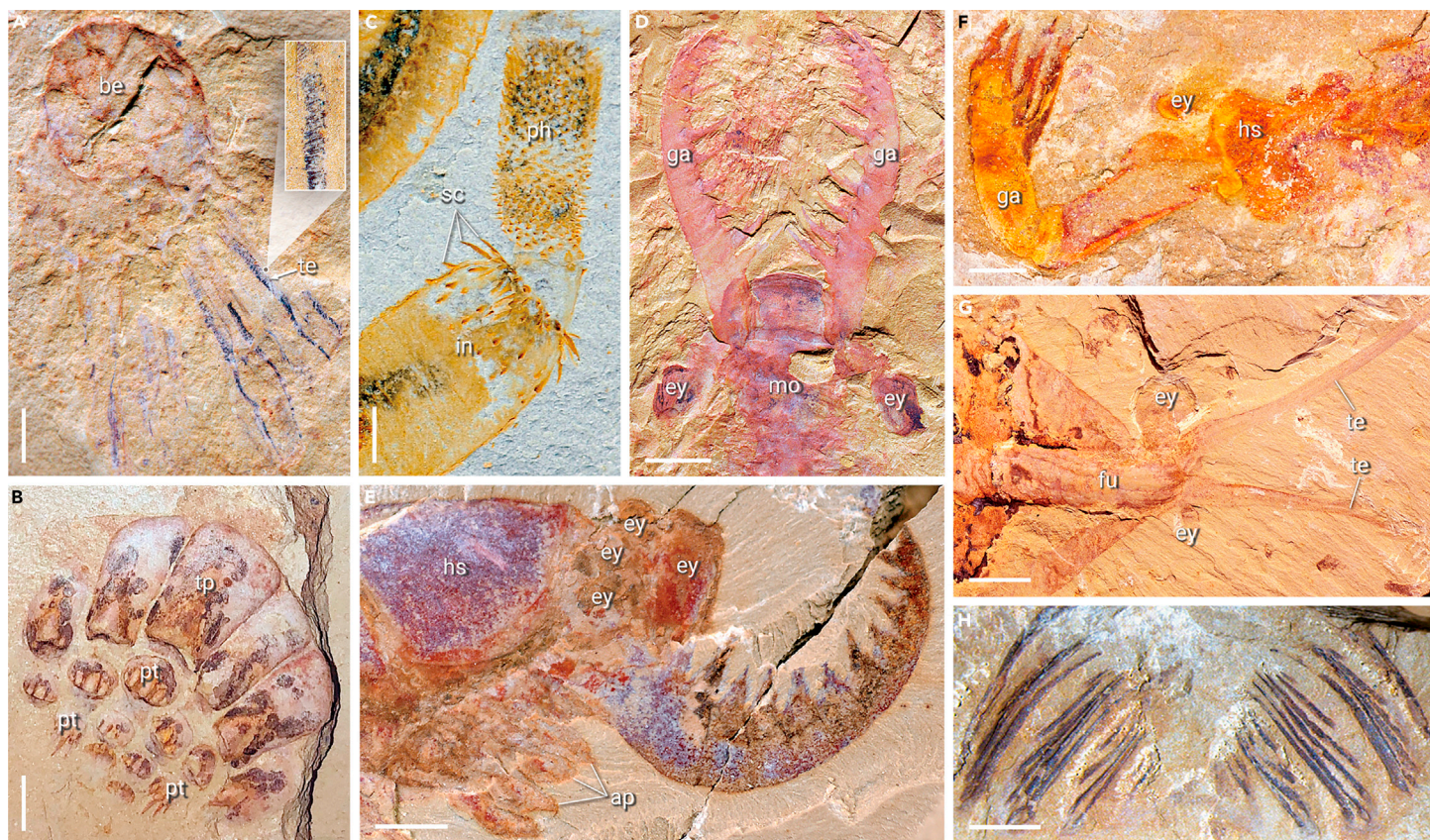
Figure 4. Representative weaponry of early Cambrian predators from the Chengjiang biota (A) *Yunnanoascus haikouensis* (YDKS-35), a medusa showing slender tentacles with nematocyst batteries (see inset for details). (B) *Omnidens amplus* (ELEL-SJ100436), probably mouthparts of a *Pambdelurion*-like lobopodian. (C) Priapulid *Cricocosmia jinningensis* (YKLP 13226), showing everted pharynx with teeth and introvert with scalids. (D) Arthropod *Anomalocaris* sp. (ELRC 20001), showing stalked eyes and spinous great appendages. (E) Arthropod *Kylinxia zhangi* (YLSNHM 01124), showing eyes and spinous claws. (F) Arthropod *Fortiforceps foliosa* (NIGP 169954), showing raptorial frontal appendages. (G) Mollusc *Petalilium latus* (NIGP 158642), showing large eyes and predatory tentacles. (H) Chaetognath *Ankalodous sericus* (ELI-JS-16-001), showing grasping spines. ap, appendages; be, bell; ey, eye; fu, funnel; ga, great appendage; hs, head shield; in, introvet; mo, mouth; ph, pharynx; pt, pharyngeal teeth; sc, scalids; te, tentacle; tp, triangular plate. Scale bars, 1 mm in (C, F), 2 mm in (A, E, H), and 5 mm in (B, D, G). Permission for use of images was granted by X.Y. Ma (C) and F.C. Zhao (D–G).

ctene). Hence, cushion plates cannot occur independently of ciliary ctenes, and ctene rows as a propulsive apparatus should not be present on the tentacle surface of a sessile animal. We believe that the purported "cushion plates" are better interpreted as organic remains of internal canals for transporting nutrients from the tentacle lumen to the pinnules. The other major argument for the stem cteno-phore hypothesis is the purported existence of macrocilia,[33] which are unique to ctenophores. However, the extraordinary thickness of the suspension-feeding "macrocilia" could have resulted from secondary thickening during diagenesis, i.e., the cilia were replaced and coated by microscopic aluminosilicates and pyrite during decay. Moreover, there are substantial evolutionary gaps between a sessile polyp and a free-swimming comb jelly. These gaps entail major anatom-ical transformations, including (1) relocation of the ciliary apparatus from the ten-tacles to the body surface to form the ctene rows, which would require fixation and fusion of the tentacles to/with the body surface, loss of ciliated pinnules (i.e., the filter-feeding apparatus), and development of ctene rows on the tentacles; (2) revolution of the alimentary system from a radially partitioned, blind gut into a non-partitioned through gut, which would require perforation of the gastrovas-cular cavity at the aboral end via the anal pores; (3) derivation of an elaborated canal system from the through gut; and (4) innovation of an apical sense organ at the aboral end to regulate the rhythm of the comb rows. Furthermore, the pres-ence of mesenteries, one of the key defining autapomorphies of cnidarians,[1–3] in all three fossil taxa suggests that they are more likely to have been affiliated with cnidarians than with ctenophores. Although phylogenetic analyses based on fos-sil data have suggested a monophyletic "Coelenterata,"[18,33] most phylogenomic studies favor Cnidaria as sister to Bilateria.[1,2] Hence, mesenteries are unlikely pre-sent in stem ctenophores. Our analyses resolve the Cambrian problematica *Xianguangia*, *Daihua*, and *Dinomischus* as a monophyletic basal group within Cnidaria (Figure 3B), further supporting the existence of a suspension-feeding stem group in this phylum.

In summary, early Cambrian epibenthic lingulids and primitive anthozoans, such as *Nailiana*, inhabited the same shallow-sea-bottom environment (although some modern anthozoan descendants have migrated to the deep seafloor[34]); their record of mutual interaction provides a unique snap-shot of the early evolution and subsequent retention of efficient predation us-ing flexible tentacles in epibenthic anthozoan cnidarians. Given that the Chengjiang medusozoan *Yunnanoascus* possessed nematocyst batteries,[31] and given also that stem cnidarian *Xianguangia* bore feather-like tentacles,[18] it follows that both the ancient (suspension) and the derived (predatory) feeding modes co-existed, and that both basic body forms (polypoid and medusoid) of modern cnidarians originated at least as far back as the early Cambrian.

Origin and expansion of macrophagous predation

Predation appeared early in eukaryote evolution.[35] Biomineralized skele-tons of protists dated to at least 700 Ma (e.g., *Characodictyon*) are thought to have evolved in response to microphagous predation.[36] Still, the subse-quent Ediacaran Period (635–542 Ma) was a relatively "peaceful" interval during which complex soft-bodied organisms, including the earliest meta-zoans,[37] engaged in direct absorption of dissolved nutrients (osmotrophy),[38] filtration of solid organic matter,[39] or grazing on microbial mats.[40] Fossil as-semblages of the latest Ediacaran age record a considerable reduction in the diversity of soft-bodied frondose forms (which were replaced by abundant endo-epibenthic trace makers) and the concomitant emergence of both organic and mineralized skeletons.[41] As a relatively complex and metaboli-cally expensive feeding strategy, macrophagous predation is thought to have emerged later than all/most other modes of nutrition, such as osmotro-phy, suspension/filter feeding, saprophagy, and herbivory. Facilitated in part by increasing levels of dissolved oxygen in the oceans worldwide, a rapid

diversification of bilaterians with mineralized skeletons took place during the earliest Cambrian,[42] and it is widely believed that the evolution of such skeletons was triggered by macrophagous predation.[35,43] Although probable boreholes in calcareous skeletons of *Cloudina* from the latest Ediacaran (∼550 Ma) have been widely regarded as the oldest known indicators of macrophagous predation,[44] the identity of the predator remains unknown, and the phylogenetic affinity of *Cloudina* is problematic.[45] Early Cambrian (Fortunian Age, ∼542–530 Ma) scalidophorans[46] and protoconodonts presumably representing isolated teeth and grasping spines of chaetognaths[47] also provide indirect evidence of early macrophagous predation. Thus, the lingulid-bearing specimen of *N. elegans* documented here from the early Cambrian (∼520 Ma) may constitute the oldest direct evidence of macrophagous predation in the fossil record.

Finally, the general prerequisites for macrophagous predation include not only an increase in body size but also the evolution of a suite of anatomical structures (e.g., maneuverable tentacles and an efficient gastric cavity in the case of early cnidarians) collectively adapted/preadapted for capture, ingestion, and digestion of prey items. Increased efficiency of predation may have been fueled by innovations in weaponry, including the venomous cnidae of cnidarians,[31] the eversible tooth-lined pharynx of priapulids,[48] the grasping spines of chaetognaths,[49] the raptorial appendages,[50] armored mouthparts,[51] and venom glands of arthropods[52] (Figure 4). The tentacles of *N. elegans* gen. et sp. nov., like those of the coeval medusa *Y. haikouensis*,[31] probably were armed with nematocysts. To avoid predation, early prey animals evolved a variety of defensive morphologies, physiologies, and locomotive abilities, and they also colonized/engineered novel ecological niches in diverse (pelagic, nectobenthic, epifaunal, and infaunal) habitats. Together, these events initiated positive feedback loops that increased biodiversity.[53] Thus, the advent of macrophagous predation in the terminal Neoproterozoic triggered the subsequent Cambrian "arms race" among early animals. Within a geologically brief interval of ∼30 Ma, early Cambrian marine communities established complex trophic networks that were strikingly similar to modern food webs.[21,22] The concomitant Cambrian radiation of metazoan body plans (e.g., the recently reported bryozoans from the early Cambrian South China[54]) has been attributed to a combination of intrinsic genetic/developmental innovations and extrinsic causes, such as oxygenation of shallow-water habitats.[43,55] This early diversification of metazoans may have been accelerated by the emergence of, and the escalating selective force imposed by, macrophagous predation, which contributed to the rapid radiation of nearly all major branches of the "Tree of Animals" by the time of the iconic Chengjiang biota.[56]

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AUTHOR CONTRIBUTIONS

Q.O. and D.S. designed the research. Q.O. wrote the paper, with input from J.H., G.M., H.V.I., and D.S. Q.O., J.H., Z.Z., M.C., and R.W. collected and prepared the fossil specimens. Q.O. produced the figures, designed the ecological reconstruction, and conducted the phylogenetic analyses. Q.O. and X.Y. collected the specimens of modern lingulid brachiopods. J.H., J.S., and X.Y. conducted the *in vitro* experiments. All authors analyzed and interpreted the data, discussed the conclusions, and approved the final manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

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