The dawn of the Phanerozoic: a transitional fauna from the late Ediacaran of Southwest China

Gaorong Li[1,2], Fan Wei[1*], Wenwen Wen[1,3], Xiaodong Wang[4], Xiangtong Lei[1, 2], Ross P. Anderson[5], Yang Zhao[1,6], Frances S. Dunn[5*], Luke A. Parry[7*], Peiyun Cong[1, 5*]

1 State Key Laboratory for Vegetation Structure, Functions and Construction, Institute of Paleontology, Yunnan University; Kunming, 650500, China.

2 School of Life Science, Yunnan University; Kunming, 650500, China.

3 Yunnan Key Laboratory of Plateau Geographical Processes and Environmental Changes, Faculty of Geography, Yunnan Normal University; Kunming, 650500, China.

4 College of Arts, Yunnan University; Kunming, 650500, China.

5 Oxford University Museum of Natural History, University of Oxford; Oxford, OX1 3PW, UK.

6 Paläontologisches Institut, Universität Zürich; Zürich 8006, Switzerland.

7 Department of Earth Sciences, University of Oxford; Oxford, OX1 3AN, UK.

*Corresponding author. Email: weifan@ynu.edu.cn (F., Wei); frances.dunn@oum.ox.ac.uk (F.S. Dunn); luke.parry@seh.ox.ac.uk (L.A., Parry); cong@ynu.edu.cn (P., Cong)

Abstract: Animal diversification across the Ediacaran-Cambrian transition was a crucial event in Earth history, fundamentally altering our planet and its biosphere. However, Ediacaran fossil assemblages show limited overlap with those from the Cambrian, obscuring the critical interval when the animal phyla were diversifying. We report a new terminal Ediacaran fossil assemblage preserved as carbonaceous films from the Jiangchuan Biota, Yunnan, Southwest China. This assemblage diverges from co-eval sites, preserving Ediacaran body fossils alongside recognizable non-bilaterians and bilaterian body and trace fossils. These include diverse vermiform animals and the oldest deuterostomes (stem-group ambulacrarians). Our discovery provides insight into the radiation of Bilateria, the most diverse and disparate animal clade.

Main Text:

The terminal Ediacaran Jiangchuan Biota from Eastern Yunnan, China is known to be fossiliferous, with diverse macroalgae (*1*) (fig. S1) as well as Ediacaran-type and problematic macrofossils (e.g. *Alienum, Lobodiscus, Cycliomedusa*) (*2-4*). It occurs in the middle to upper part of Jiucheng Member of Dengying Formation, above the last occurrence of the tubular fossil *Shaanxilithes,* see Supplementary Material for the age constraints (Fig. 1A). We report new exceptionally preserved soft-bodied fossils from the type locality at Qingshuigou and a new section Shanglijiao (Fig. 1A). These fossils include over 700 specimens, encompassing macroalgae (fig. S1) and animals (Fig. 2-3), including bilaterian body fossils (Fig. 3). Animal fossils exhibit morphological and taxonomic diversity, with a high proportion of new taxa, and preserve feeding structures (Fig. 3A-E, F-G, M-P), locomotory organs (e.g. Fig. 2E-G) and guts (Fig. 3H, fig. S2A-B, F, H). They are derived from subtidal mud- and siltstones (Fig. 1)(*5*), with exceptional preservation likely facilitated by rapid burial; fossils occur at the base of event beds (Fig. 4A-D) and some taxa are demonstrably buried *in situ*. Fossils are predominantly carbonaceous films supplemented by pyritization and phosphatization (Fig. 4, fig. S3), broadly consistent with Cambrian Burgess Shale-type preservation rather than typical Ediacara-style preservation (*6*) (Fig. 1B).

Animal fossils typical of late Ediacaran assemblages are scarce in both diversity and abundance. The radialomorph *Lobodiscus* (*2*) has previously been described at Qingshuigou, and we report an additional specimen of a morphologically distinct radialomorph from Shanglijiao (Fig. 2I,J). This fossil is discoidal in shape and possesses radially arranged arms (protrusions/grooves), one of which is curved and extends to the distal margin of the specimen - the off-center position of the radiating arms may reflect an oblique burial angle. Four protrusions appear to be arranged in pairs, each consisting of two connected branches surrounding a central depression. Finer structures are present between these protrusions in one region of the specimen (Fig. 2J). The curved nature of the single complete protrusion is similar to the curvature of arms in *Tribrachidium*, whereas the possible linear structures running inbetween the protrusions are more similar to *Lobodiscus (2)*. However, our specimen does not appear to show triradial symmetry unlike *Tribrachidium* and *Lobodiscus*. It exhibits tetraradial symmetry like *Conomedusites* (*7*) but with unequal lobes.

Six specimens resemble *Haootia quadriformis,* interpreted as a cnidarian, with tetraradial symmetry and fibrous/corrugated features inferred to be muscle fibers (Fig. 2A-D) (*8, 9*). Two of these specimens are complete with additional incomplete fragments (fig. S4). As with *Haootia,* these new specimens are stalked with an inferred open goblet-shaped calyx and terminal ‘arms’, although only two arms are visible. If present, additional arms may have been obscured by burial. Although body symmetry in our specimens is unknown, considerable variation in body symmetry has been reported in early cnidarian groups, including biradial symmetry (*10*). The specimens are ~20 mm in width and 15 mm along the presumed oral-aboral axis, approximately half the size of *H. quadriformis*. Filamentous elements are arranged similarly between *H. quadriformis* and our new specimens, highlighted at the base of the calyx running parallel to the axis of the stalk and then diverging into the arms of the calyx (Fig. 2B-C). The width of the fibers (100-200 µm) and their spacing (~100-300 µm) are comparable to *H. quadriformis,* where they are ~100-600 µm and ~200-1000 µm respectively *(8)*. The base of the organism (Fig. 2D) flares terminally but shows no evidence of an enlarged holdfast (*8*) or pedicle-like structure (*9*) as in *H. quadriformis.* Our specimens likely represent a new taxon differ from *H. quadriformis* as well as the co-occurring *Mamsetia manunis*.

Other non-bilaterian animal fossils are similarly rare in abundance and diversity. One specimen (Fig. 2E-G) is consistent with the morphology of Cambrian ctenophore fossils (*11, 12*). The specimen is ~18 mm long and ~10 mm wide, within the range of Cambrian ctenophores (12-75 mm long and 6-50mm wide) (*11, 13*). The body constricts at ~12 mm from its apical end to form an oral region, comparable to the oral skirt seen in scleroctenophores and fossils like *Ctenorhabdotus* from the Cambrian Burgess Shale and Marjum formations (*12*). Candidate ctenes are preserved in discrete longitudinal rows perpendicular to the long axis, with ~7 visible longitudinal ribbon-shaped features 1 mm in width and with regular transverse bands. This arrangement is comparable to ctenes in fossil ctenophores, and the number visible suggests a total in excess of the 8 rows possessed by crown group ctenophores, but consistent with Cambrian taxa (*11, 12*). Although repeated linear features are also present in the *Haootia*-like specimens, they are carbonaceous, present across most of the body and occurr as transverse and longitudinal features with different orientations in different regions. The only other specimen with consistent linear features is the *Mackenzia*-like fossil (Fig. 2H), in which they are arranged parallel to the body axis, unlike in both *Haootia*-like and ctenophore fossils.

Two elongate and superimposed specimens exhibit a cylindrical morphology with traversing longitudinal stripes (Fig. 2H). These stripes are uniform in width with distinct convex-concave relief, likely reflecting a modular construction. This morphology is comparable with Cambrian mackenziids, although Jiangchuan specimens are smaller (~18 mm long, <3 mm wide compared to 25-200 mm long and 9-34 mm wide) (*14*). The specimens preserve a circular aperture at their apex, arguing against an algal affinity. Some flabellate algae (e.g., *Flabellophyton*) possess longitudinal striations but never exhibit convex-concave relief, nor do they adopt a cylindrical form—their morphology typically tapers from base to apex at a fixed angle (*15*).

The most numerous bilaterian fossil (185 specimens, table S1) is an elongate worm with a basal holdfast disc, terminal mouth and eversible anterior structure (Fig. 3A-E). The most complete specimen has a vermiform body ~61 mm long and 2.0-2.7 mm in diameter, with a holdfast ~15 mm in diameter (Fig. 3A). There is a spectrum of preservation from fragments of the oral end (fig. S2B-F, H), holdfasts with incomplete bodies (fig. S2G, I) and the body in association with the holdfast. Isolated holdfasts are also present and are comparable to *Cycliomedusa jiangchuanensis,* previously reported from Jiangchuan(*4*), in bearing a central carbonaceous ring structure at the junction between the body (when present) and holdfast (e.g., fig. S3I). *C. jiangchuanensis* likely represents an isolated holdfast structure. In some specimens, the body and holdfast are preserved in different layers within event beds, indicating *in situ* burial during an obrution event. The body margins are smooth and lack appendages. A dark band along the body is consistent with a gut (e.g. fig. S2A, B, F, H), but the presence and position of an anal opening is unknown. The organism could likely plasticly deform as specimens possess anterior ends at varying stages of eversion, culminating in a narrow and tongue-like (Fig. 3D, E) structure with a presumed feeding function. Elemental mapping demonstrates the anterior is enriched in carbon (fig. S3B, C). When the elongate structure is contracted, the anterior body is trumpet-shaped and blunt, becoming more bulbous when the structure is everted (Fig. 3B-E). The specimen with the longest everted structure is posteriorly incomplete, so the total extended length relative to the body cannot be determined, but in this specimen the structure is ~40 mm long, approximately 12 times the width of the body. This organism is likely a total group bilaterian: modifications of the anterior end of the digestive tract to form a pharynx are present in non-bilaterians, but in these groups, they are not eversible (*16*). The ability to evert and retract such a feeding structure would require mesodermal musculature not present outside Bilateria but the fossil lacks synapomorphies of any extant bilaterian clade. An enlarged anchoring structure in such a macroscopic, free-living and presumably macrophagous animal is unusual. Although posterior adhesion structures are present in many extant bilaterian worms, they are most common in parasites (*17*) or meiofauna (*18*), with tube building or infaunality adaptations to sessile modes of life in large-bodied extant taxa. This body plan may represent an adaptation to a sessile mode of life in anactualistic sea floor environments (*19*).

A sausage-shaped vermiform animal is reported from one specimen (part and counterpart) (Fig. 3F, G). It has a circular terminal opening (Fig. 3H), interpreted as a mouth, with a dark, slender band through the interior of the body along its length, most likely representing a gut. As in the specimens with the eversible anterior, carbon is enriched at the anterior end and in the gut (fig. S3D, E). The body of the figured specimen is strongly curved, potentially indicating body contraction after death/during burial.

Four specimens (Fig. 3M-R, fig. S5) show anatomical features compatible with stem ambulacrarian cambroernids almost only known from the Cambrian (*20*). One specimen (Fig. 3O-P) is similar to *Herpetogaster* (*21*), the earliest-diverging cambroernid (*20*). The specimen shows a coiled body with a slight invagination/constriction at one end, separating the head region from a larger trunk. The head region is flanked by simple, unbranched to minimally-branched tentacles, differing from the elaborate, branching tentacles in all Cambrian *Herpetogaster* (*21*). At least four tentacles can be distinguished using SEM backscatter (Fig. 3O, Q). In other specimens the tentacles are present, but difficult to delineate (Fig. S5G). One specimen (Fig. 3O, P) closely compares to *H. collinsi* from China (*22*), which has a slender stalk with no terminal disc. Additionally, *H. colllinsi* from China shows limited evidence of internal body regionalization – unlike specimens from the Burgess Shale and Nevada (*22, 23*). Another specimen (Fig. 3M-N) shows a thicker and shorter stalk that flares proximally (with a width of 0.2-1.0mm) before meeting the body in the middle of the trunk, like the stalk of *Phogites*, another cambroernid taxon *(21)*. However, *Phlogites* exhibits a cup-shaped body, unlike the curved body of this Jiangchuan specimen. Our Jiangchuan specimens are smaller in size than most other Cambrian *Herpetogaster* fossils, with an overall length of no more than 20 mm; the latter are usually more than 20 mm, but *Herpetogaster* from the Balang Formation in South China is consistent in size with the Jiangchuan fossils (*21, 22*).

Finally, we report elongate, tubular fossils with distinctive, regular oval-shaped holes running along their length (Fig. 3I-L). Similar features are present in the Cambrian *Margaretia dorus*, most recently interpreted as a dwelling-tube for enteropneust hemichordate worms (*24*). Our two most complete specimens are 25-30 mm long and 2-4 mm wide (Fig. 3I, J). *M. dorus* from the Burgess Shale is larger, exceeding 5 cm in length (*24*), but smaller conspecific specimens are known from other sites, e.g. specimens 50-120 mm from the Wheeler and Spence shales (*25*). The perforations in our specimens are longer (0.5-4.5 mm) than they are wide (0.3-0.7 mm) and, although smaller in size, have an aspect ratio comparable with *M. dorus* from the Burgess Shale (*24*) and other localities in North America (*25, 26*).

Macroalgae are taphonomically distinct from these specimens interpreted as animals, displaying more extensive carbonaceous preservation (Fig. 4H, fig. S1A-F) with sharper boundaries to the surrounding matrix (Fig. 4E, fig. S1A-C, G, H). Within most of ~500 macroalgal fossil specimens examined, typically discrete, tessellating, polygonal fragments of carbon indicate a relatively thick carbon film that cracked due to shrinkage (Fig. 4H), consistent with an original macromolecular composition that was more decay resistant. The preservation of macroalgae resembles that of algae from Cambrian deposits with Burgess Shale-type preservation such as *Fuxianospira* and *Sinocylindra* from the Chengjiang Biota (*27, 28*). Some specimens, we interpret as cambroernid bilaterians, do show moderately enhanced carbonaceous preservation and cracked carbon films (Fig. 4J, fig. S3F-G), likely indicative of a taphonomically resistant composition that contrasts with the other animal taxa, intermediate between that observed in macroalgae and other bilaterian fossils. Enhanced carbonaceous preservation is also seen in cambroernids from Cambrian fossil deposits (*22*). The animal fossils further exhibit morphological features that are unknown in living and fossil algae, including tapering feeding tentacles (including in the cambroernids) and an eversible feeding structure. Several morphotypes exhibit a range of aspect ratios indicating contractile, flexible bodies with tissues that are able to deform in a way that is incompatible with an algal affinity (e.g. Fig. 3A-E).

Discussion

The late Ediacaran (~575-539 Ma) records the first definitive animal fossils (*29*), heralding a radiation that transformed our planet's biosphere and biogeochemistry (*30*). Locomotion traces confirm a radiation of bilaterian animals also during this time (*19*), but body fossil evidence for Ediacaran bilaterians is meagre, with only four controversial genera, *Yilingia, Kimberella, Ikaria* and *Uncus (31-35)*. Body fossils of free-living bilaterians in the Jiangchuan Biota suggests a potentially diverse assemblage of bilaterians, including possible makers of these long-known Ediacaran trace fossils (*19*). Although bilaterian trace fossils are not found in horizons containing the new body fossils in Jiangchuan, trace fossils of comparable size are known from proximal horizons (fig. S6). Furthermore, the terminal mouth of one of our new specimens (Fig. 3H) may place it among cycloneuralian worms (*36*), which are implicated as makers of early bilaterian trace fossils (*37*).

The occurrence of total-group ambulacrarians in the Jiangchuan Biota extends the fossil record of crown-group deuterostomes into the Ediacaran, with cambroernids demonstrating the presence of stem-group ambulacrarians and the *Margaretia*-like tubes suggesting the presence of enteropneust hemichordates, implying that total-group pterobranchs had also diverged by this time. Previously, the oldest unambiguous fossil evidence for ambulacrarians were fragmentary Cambrian remains of *Sokoloviina* (*38*) interpreted as a pterobranch. Potential Ediacaran tunicates are known (*39, 40*), but remain controversial (*41*). A problematic fossil known from a different Jiangchuan locality has been tentatively compared to vetulicolians, interpreted as chordates, but this comparison is preliminary (*3, 42*).

The new Jiangchuan specimens close the gap between the body fossil record of protostomes (*31*) and deuterostomes for the first time and confirm that the ambulacrarian bodyplan became fixed in the Ediacaran.

Beyond bilaterians, the discovery of a ctenophore is consistent with Ediacaran occurrences of other non-bilaterian animals, including cnidarians (*8*) and sponges (*43*), and the putative placozoan-grade of some Ediacaran taxa (*44*). *Eoandromeda* has been interpreted as a ctenophore (*45*), but this has been disputed (*46*) and it has been interpreted as benthic rather than pelagic (*47*), questioning the identification of locomotory comb rows. *Attenborites janeae* may be pelagic with a radially symmetrical and globose body, but despite being a candidate ctenophore known specimens do not resolve its phylogenetic affinities (*48, 49*). The presence of a ctenophore fossil with many features of the Cambrian ctenophore body plan suggests major events in ctenophore evolution had already taken place, including colonization of the water column, by the terminal Ediacaran.

The significant differences in biotic composition and diversity among terminal Ediacaran fossil assemblages from South China (fig. S7) indicate either spatial heterogeneity in the composition of communities or taphonomic variation – a modified "Cheshire Cat" hypothesis (*50*). The Cheshire Cat hypothesis suggests that Ediacaran macrofossils only seem to go extinct before the Ediacaran-Cambrian boundary because the anactualistic environments (matgrounds (*19*)) in which they lived diminished. The new Jiangchuan animal fossils, dominated by bilaterians of apparently diverse affinities, with rarer fossils more typical of late Ediacaran deposits, could be described as a 'Cambrian-type' assemblage from the late Ediacaran. A dominantly bilaterian assemblage may not been discovered from the late Ediacaran until now due to the paucity of carbonaceous compressions from this time, hinting at a broader taphonomic bias (*51*).

References and Notes

1. F. Tang, C. Yin, P. Liu, L. Gao, W. Zhang, A new diverse macrofossil Lagerstätte from the uppermost Ediacaran of southwestern China. *Acta Geologica Sinica ‐ English Edition* **82**, 1095–1103 (2008), https://doi.org/10.1111/j.1755-6724.2008.tb00709.x.
2. M. Zhao, G. Mussini, Y. Li, F. Tang, P. Vickers-Rich, M. Li, A. Chen, A putative triradial macrofossil from the Ediacaran Jiangchuan Biota. *Iscience* **27**, (2024), https://doi.org/10.1016/j.isci.2024.108823.
3. J. Liu, A. Chen, B. Li, F. Tang, J. Zhao, K. Chen, Problematic Ediacaran sail-shaped fossils from eastern Yunnan, China. *Historical Biology*, 1–7 (2024), https://doi.org/10.1080/08912963.2024.2403588.
4. M. Zhao, Y. Zhang, F. Tang, Y. Li, M. Li, L. Zhong, L. Ren, Enigmatic discoidal macrofossils with central ring from the Ediacaran Jiangchuan biota, Southwest China. *Papers in Palaeontology* **11**, e70005 (2025), https://doi.org/10.1002/spp2.70005.
5. F. Tang, L. Gao, Z. Wang, Palaeogeography and palaeoecology of the Ediacaran (Sinian) macrofossil biota in South China. *Journal of Palaeogeography* **11**, 525–533 (2009),
6. R. R. Gaines, Burgess Shale-type preservation and its distribution in space and time. *The Paleontological Society Papers* **20**, 123–146 (2014), https://doi.org/10.1017/S1089332600002837.

7. M. F. Glaessner, The late precambrian fossils from Ediacara, South Australia. *Palaeontology* **9**, 599–628 (1966),
8. A. G. Liu, J. J. Matthews, L. R. Menon, D. McIlroy, M. D. Brasier, Haootia quadriformis n. gen., n. sp., interpreted as a muscular cnidarian impression from the Late Ediacaran period (approx. 560 Ma). *Proceedings of the Royal Society B: Biological Sciences* **281**, 20141202 (2014), https://doi.org/10.1098/rspb.2014.1202.
9. D. McIlroy, G. Pasinetti, D. Pérez-Pinedo, C. McKean, S. Dufour, J. Matthews, L. Menon, R. Nicholls, R. Taylor, The Palaeobiology of Two Crown Group Cnidarians: Haootia quadriformis and Mamsetia manunis gen. et sp. nov. from the Ediacaran of Newfoundland, Canada. *Life* **14**, 1096 (2024), https://doi.org/10.3390/life14091096.
10. Z. Song, J. Guo, J. Han, H. Van Iten, J. Peng, Y. Qiang, B. Zhang, X. Zhao, G. Li, H. Wen, Phylogenetic affinities and evolution of the Early Cambrian hexangulaconulariids. *Journal of Systematic Palaeontology* **22**, 2417668 (2024), https://doi.org/10.1017/S1477201924000104.
11. S. C. Morris, D. Collins, Middle cambrian ctenophores from the stephen formation, british columbia, canada. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **351**, 279–308 (1996), https://doi.org/10.1098/rstb.1996.0024.
12. L. Parry, R. Lerosey‐Aubril, J. C. Weaver, J. Ortega‐Hernández, Cambrian comb jellies from Utah illuminate the early evolution of nervous and sensory systems in ctenophores. *iScience* **24**, 102943 (2021), https://doi.org/10.1016/j.isci.2021.102943.
13. Q. Ou, S. Xiao, J. Han, G. Sun, F. Zhang, Z. Zhang, D. Shu, A vanished history of skeletonization in Cambrian comb jellies. *Science Advances* **1**, e1500092 (2015), https://doi.org/10.1126/science.1252673.
14. Y. Zhao, J. Vinther, Y. Li, F. Wei, X. Hou, P. Cong, An early Cambrian mackenziid reveals links to modular Ediacaran macro‐organisms. *Papers in Palaeontology* **8**, e1412 (2022), https://doi.org/10.1002/spp2.1412.
15. B. Wan, X. Yuan, Z. Chen, C. Guan, K. Pang, Q. Tang, X. Rao, Quantitative analysis of Flabellophyton from the Ediacaran Lantian Biota, South China: application of geometric morphometrics in Precambrian fossil research. *Acta Geologica Sinica‐English Edition* **87**, 905–915 (2013), https://doi.org/10.1111/1755-6724.12099.
16. R. C. Brusca, G. Giribet, W. Moore, *Invertebrates* (Oxford University Press, 2022).
17. I. D. Whittington, B. W. Cribb, T. E. Hamwood, J. A. Halliday, Host-specificity of monogenean (platyhelminth) parasites: a role for anterior adhesive areas? *International Journal for Parasitology* **30**, 305–320 (2000), https://doi.org/10.1016/S0020-7519(00)00006-0.
18. O. Giere, Biological characteristics of meiofauna. *Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments*, 87–102 (2009), https://doi.org/10.1007/978-3-662-02912-1_4.
19. M. G. Mángano, L. A. Buatois, Decoupling of body-plan diversification and ecological structuring during the Ediacaran–Cambrian transition: evolutionary and geobiological feedbacks. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140038 (2014), https://doi.org/10.1098/rspb.2014.0038.
20. Y. Li, F. S. Dunn, D. J. Murdock, J. Guo, I. A. Rahman, P. Cong, Cambrian stem-group ambulacrarians and the nature of the ancestral deuterostome. *Current Biology* **33**, 2359–2366. e2352 (2023), https://doi.org/10.1016/j.cub.2023.04.048.

21. J. B. Caron, S. Conway Morris, D. Shu, Tentaculate fossils from the Cambrian of Canada (British Columbia) and China (Yunnan) interpreted as primitive deuterostomes. *PLoS One* **5**, e9586 (2010), https://doi.org/10.1371/journal.pone.0009586.
22. X. Yang, J. Kimmig, J. D. Schiffbauer, S. Peng, Herpetogaster collinsi from the Cambrian of China elucidates the dispersal and palaeogeographic distribution of early deuterostomes and the origin of the ambulacrarian larva. *PeerJ* **11**, e16385 (2023), https://doi.org/10.7717/peerj.16385.
23. J. Kimmig, R. C. Meyer, B. S. Lieberman, Herpetogaster from the early Cambrian of Nevada (Series 2, Stage 4) and its implications for the evolution of deuterostomes. *Geological Magazine* **156**, 172–178 (2019), https://doi.org/10.1017/S0016756818000389.
24. K. Nanglu, J.-B. Caron, S. Conway Morris, C. B. Cameron, Cambrian suspension-feeding tubicolous hemichordates. *BMC biology* **14**, 1–9 (2016), https://doi.org/10.1186/s12915-016-0271-4.
25. J. R. Foster, S. D. Sroka, T. F. Howells, H. R. Cothren, C. M. Dehler, J. W. Hagadorn, New Cambrian vermiform organisms from Burgess Shale-type deposits of the western United States. *Bull. Geosci.* **97**, (2022), https://doi.org/10.3140/bull.geosci.1858.
26. J. Kimmig, B. R. Pratt, Soft-bodied biota from the middle Cambrian (Drumian) Rockslide Formation, Mackenzie Mountains, northwestern Canada. *Journal of Paleontology* **89**, 51–71 (2015), https://doi.org/10.1017/jpa.2014.5.
27. M. Steiner, M. Zhu, Y. Zhao, B.-D. Erdtmann, Lower Cambrian Burgess Shale-type fossil associations of south China. *Palaeogeography, Palaeoclimatology, Palaeoecology* **220**, 129–152 (2005), https://doi.org/10.1016/j.palaeo.2003.06.001.
28. X. Hou, D. J. Siveter, D. J. Siveter, R. J. Aldridge, P. Cong, S. E. Gabbott, X. Ma, M. A. Purnell, M. Williams, *The Cambrian fossils of Chengjiang, China: the flowering of early animal life* (John Wiley & Sons, 2017).
29. R. Wood, A. G. Liu, F. Bowyer, P. R. Wilby, F. S. Dunn, C. G. Kenchington, J. F. H. Cuthill, E. G. Mitchell, A. Penny, Integrated records of environmental change and evolution challenge the Cambrian Explosion. *Nature ecology & evolution* **3**, 528–538 (2019), https://doi.org/10.1038/s41559-019-0821-6.
30. N. J. Butterfield, Macroevolutionary turnover through the Ediacaran transition: ecological and biogeochemical implications. *Geological Society, London, Special Publications* **326**, 55–66 (2009), https://doi.org/10.1144/sp326.3.
31. M. A. Fedonkin, B. M. Waggoner, The Late Precambrian fossil Kimberella is a mollusc-like bilaterian organism. *Nature* **388**, 868–871 (1997), https://doi.org/10.1038/42242.
32. Z. Chen, C. Zhou, X. Yuan, S. Xiao, Death march of a segmented and trilobate bilaterian elucidates early animal evolution. *Nature* **573**, 412–415 (2019), https://doi.org/10.1038/s41586-019-1522-7.
33. J. G. Gehling, B. N. Runnegar, M. L. Droser, Scratch traces of large Ediacara bilaterian animals. *Journal of Paleontology* **88**, 284–298 (2014), https://doi.org/10.1666/13-054.
34. S. D. Evans, I. V. Hughes, J. G. Gehling, M. L. Droser, Discovery of the oldest bilaterian from the Ediacaran of South Australia. *Proceedings of the National Academy of Sciences* **117**, 7845–7850 (2020), https://doi.org/10.1073/pnas.2001045117.
35. I. V. Hughes, S. D. Evans, M. L. Droser, An Ediacaran bilaterian with an ecdysozoan affinity from South Australia. *Current Biology* **34**, 5782–5788. e5781 (2024), https://doi.org/10.1016/j.cub.2024.10.030.
36. J. A. Gámez Vintaned, E. Linán, A. Yu. Zhuravlev, "A new early Cambrian lobopod-bearing animal (Murero, Spain) and the problem of the ecdysozoan early diversification"

in *Evolutionary biology–concepts, biodiversity, macroevolution and genome evolution* (Springer, 2011), pp. 193–219.

37. J. Vannier, I. Calandra, C. Gaillard, A. Żylińska, Priapulid worms: pioneer horizontal burrowers at the Precambrian-Cambrian boundary. *Geology* **38**, 711–714 (2010), https://doi.org/10.1130/G30829.1.
38. J. Maletz, The evolutionary origins of the Hemichordata (Enteropneusta & Pterobranchia) - A review based on fossil evidence and interpretations. *Bull. Geosci.*, 127–147 (2024), https://doi.org/10.3140/bull.geosci.1899.
39. A. Martyshyn, A. Uchman, New Ediacaran fossils from the Ukraine, some with a putative tunicate relationship. *PalZ* **95**, 623–639 (2021), https://doi.org/10.1007/s12542-021-00596-1.
40. G. Hahn, H. Pflug, Polypenartige Organismen aus dem Jung-Präkambrium (Nama-Gruppe) von Namibia. *Geologica et Palaeontologica*, 1–13 (1985),
41. K. Nanglu, S. R. Cole, D. F. Wright, C. Souto, Worms and gills, plates and spines: the evolutionary origins and incredible disparity of deuterostomes revealed by fossils, genes, and development. *Biological Reviews* **98**, 316–351 (2023), https://doi.org/10.1111/brv.12908.
42. G. Mussini, M. P. Smith, J. Vinther, I. A. Rahman, D. J. Murdock, D. A. Harper, F. S. Dunn, A new interpretation of Pikaia reveals the origins of the chordate body plan. *Current Biology* **34**, 2980–2989. e2982 (2024), https://doi.org/10.1016/j.cub.2024.05.026.
43. X. Wang, A. G. Liu, Z. Chen, C. Wu, Y. Liu, B. Wan, K. Pang, C. Zhou, X. Yuan, S. Xiao, A late-Ediacaran crown-group sponge animal. *Nature* **630**, 905–911 (2024), https://doi.org/10.1038/s41586-024-07520-y.
44. E. Sperling, J. Vinther, A placozoan affinity for Dickinsonia and the evolution of late Proterozoic metazoan feeding modes. *Evolution and Development* **12**, 201–209 (2010), https://doi.org/10.1111/j.1525-142X.2010.00404.x.
45. F. Tang, S. Bengtson, Y. Wang, X. Wang, C. Yin, Eoandromeda and the origin of Ctenophora. *Evolution and Development* **13**, 408–414 (2011), https://doi.org/10.1111/j.1525-142X.2011.00499.x.
46. Y. Zhao, J. Vinther, L. Parry, F. Wei, E. Green, D. Pisani, X. Hou, G. Edgecombe, P. Cong, Cambrian Sessile, Suspension Feeding Stem-Group Ctenophores and Evolution of the Comb Jelly Body Plan. *Current Biology* **29**, 1112–1125.e1112 (2019), https://doi.org/10.1016/j.cub.2019.02.036.
47. T. L. Botha, E. Sherratt, M. Droser, J. Gehling, D. García‐Bellido, Elucidating the morphology and ecology of Eoandromeda octobrachiata from the Ediacaran of South Australia. *Papers in Palaeontology* **9**, (2023), https://doi.org/10.1002/spp2.1530.
48. M. Droser, S. Evans, P. Dzaugis, E. Hughes, J. Gehling, Attenborites janeae: a new enigmatic organism from the Ediacara Member (Rawnsley Quartzite), South Australia. *Australian Journal of Earth Sciences* **67**, 915–921 (2020), https://doi.org/10.1080/08120099.2018.1495668.
49. H. K. Mccandless, M. L. Droser, Deconstructing taphonomy to reconstruct the morphology and life habit of Attenborites janeae at Nilpena Ediacara National Park. *Palaios* **39**, 411–422 (2024), https://dx.doi.org/10.2110/palo.2023.005.
50. M. Laflamme, S. A. Darroch, S. M. Tweedt, K. J. Peterson, D. H. Erwin, The end of the Ediacara biota: Extinction, biotic replacement, or Cheshire Cat? *Gondwana Research* **23**, 558–573 (2013), https://doi.org/10.1016/j.gr.2012.11.004.

51. R. P. Anderson, C. R. Woltz, N. J. Tosca, S. M. Porter, D. E. Briggs, Fossilisation processes and our reading of animal antiquity. *Trends in Ecology & Evolution* **38**, 1060–1071 (2023), https://doi.org/10.1016/j.tree.2023.05.014.
52. C. Yang, A. D. Rooney, D. J. Condon, X.-H. Li, D. V. Grazhdankin, F. T. Bowyer, C. Hu, F. A. Macdonald, M. Zhu, The tempo of Ediacaran evolution. *Science advances* **7**, eabi9643 (2021), https://doi.org/10.1126/sciadv.abi9643.
53. F. T. Bowyer, R. A. Wood, M. Yilales, Sea level controls on Ediacaran-Cambrian animal radiations. *Science Advances* **10**, eado6462 (2024), https://doi.org/10.1126/sciadv.ado6462.
54. F. Tang, X. Song, C. Yin, P. Liu, S. Awramik, Z. Wang, L. Gao, Discoveries of new Longfengshaniaceae from the uppermost Ediacaran in eastern Yunnan, South China and the significance. *Frontiers of Earth Science in China* **1**, 142–149 (2007), https://doi.org/10.1007/s11707-007-0018-1.
55. F. Tang, L. Gao, C. Yin, Y. Wang, P. Gu, Macrofossil biotas in the Late Ediacaran–Cambrian boundary interval of South China and stratotype correlation. *Geological Bulletin of China* **34**, 2150–2162 (2015), https://doi.org/10.12097/gbc.20151202.
56. M. Chen, Sinian explosion: preliminary discussion about early animal evolution. *Progress in Precambrian Research* **22**, 36–47 (1999),
57. C. Zhou, Q. Ouyang, W. Wang, B. Wan, C. Guan, Z. Chen, X. Yuan, Lithostratigraphic subdivision and correlation of the Ediacaran in China. *Journal of Stratigraphy* **45**, 211–221 (2021), https://doi.org/10.19839/j.cNKI.dCXZZ.2021.0021.
58. H. Luo, X. Wu, L. Ouyang, Z. Jiang, X. Song, New correlation opinions on the sections of Sinian–Cambrian boundary in the Yangtze platform. *Yunnan Geology* **7**, 13–27 (1988),
59. Y. Li, H. Wang, A. Liu, M. Li, Y. Liang, Y. Zhou, F. Tang, L. Ren, Sausage-like macrofossils from the Ediacaran Jiangchuan Biota in eastern Yunnan—New phylogenetic interpretation of Tawuia. *Geol. Rev* **68**, 1585–1603 (2022), https://doi.org/10.16509/j.georeview.2022.08.111.
60. C. Psarras, P. C. Donoghue, R. J. Garwood, D. V. Grazhdankin, L. A. Parry, V. I. Rogov, A. G. Liu, Three - dimensional reconstruction, taphonomic and petrological data suggest that the oldest record of bioturbation is a body fossil coquina. *Papers in Palaeontology* **9**, e1531 (2023), https://doi.org/10.1002/spp2.1531.
61. M. Zhu, J. Zhang, A. Yang, G. Li, M. Steiner, B. D. Erdtmann, Sinian-Cambrian stratigraphic framework for shallow-to deep-water environments of the Yangtze Platform: an integrated approach. *Progress in Natural Science* **13**, 951–960 (2003), https://doi.org/10.1080/10020070312331344710.
62. M. Zhu, J. Zhang, A. Yang, G. Li, F. Zhao, M. Lu, Z. Yin, L. Miao, C. Hu, "Neoproterozoic stratigraphy, depositional environments and hydrocarbon source-reservoir-seal bed assemblage in South China" in *Meso-Neoproterozoic geology and petroleum resources in China* (Springer, 2022), pp. 181–227.
63. Z. An, X. Zhao, Z. Niu, Z. Li, Q. Ye, Discovery of Shaanxilithes from the Dengying Formation in the Yangtze Gorges area, South China, and its stratigraphic significance. *China Geology* **3**, 649–651 (2020), https://doi.org/10.31035/cg2020059.
64. S. Chai, Y. Wu, H. Hua, Potential index fossils for the Terminal Stage of the Ediacaran System. *Journal of Asian Earth Sciences* **218**, 104885 (2021), https://doi.org/10.1016/j.jseaes.2021.104885.
65. K. Pang, C. Wu, Y. Sun, Q. Ouyang, X. Yuan, B. Shen, X. Lang, R. Wang, Z. Chen, C. Zhou, New Ediacara-type fossils and late Ediacaran stratigraphy from the northern Qaidam

Basin (China): Paleogeographic implications. *Geology* **49**, 1160–1164 (2021), https://doi.org/10.1130/G48842.1.

66. S. Xiao, Z. Chen, K. Pang, C. Zhou, X. Yuan, The shibantan lagerstätte: Insights into the proterozoic–phanerozoic transition. *Journal of the Geological Society* **178**, jgs2020–2135 (2021), https://doi.org/10.1144/jgs2020-135.
67. C. Yang, X.-H. Li, M. Zhu, D. J. Condon, SIMS U–Pb zircon geochronological constraints on upper Ediacaran stratigraphic correlations, South China. *Geological Magazine* **154**, 1202–1216 (2017), https://doi.org/10.1017/S0016756816001102.
68. T. Huang, D. Chen, Y. Ding, X. Zhou, G. Zhang, SIMS U-Pb zircon geochronological and carbon isotope chemostratigraphic constraints on the Ediacaran-Cambrian boundary succession in the three gorges area, south China. *Journal of Earth Science* **31**, 69–78 (2020), https://doi.org/10.1007/s12583-019-1233-x.
69. F. T. Bowyer, A. Y. Zhuravlev, R. Wood, G. A. Shields, Y. Zhou, A. Curtis, S. W. Poulton, D. J. Condon, C. Yang, M. Zhu, Calibrating the temporal and spatial dynamics of the Ediacaran-Cambrian radiation of animals. *Earth-Science Reviews* **225**, 103913 (2022), https://doi.org/10.1016/j.earscirev.2021.103913.
70. F. Ponchio, M. Corsini, R. Scopigno, RELIGHT: A compact and accurate RTI representation for the web. *Graphical Models* **105**, 101040 (2019), https://doi.org/10.1016/j.gmod.2019.101040.
71. G. Palma, M. Corsini, P. Cignoni, R. Scopigno, M. Mudge, Dynamic shading enhancement for reflectance transformation imaging. *Journal on Computing and Cultural Heritage (JOCCH)* **3**, 1–20 (2010), https://doi.org/10.1145/1841317.1841321.
72. P. Kraft, J. Bruthansová, R. Mikuláš, Feeding traces related to shells from the Prague Basin, Czech Republic (Tremadocian to early Darriwilian, Ordovician). *Palaeogeography, Palaeoclimatology, Palaeoecology* **537**, 109399 (2020), https://doi.org/10.1016/j.palaeo.2019.109399.
73. Y. Dong, B. Hui, S. Sun, J. Sun, R. Zang, B. Zhang, Q. Luo, F. Chong, K. Yu, M. Fan, The links between Neoproterozoic tectonics, paleoenvironment and Cambrian explosion in the Yangtze Block, China. *Earth-Science Reviews*, 104638 (2023), https://doi.org/10.1016/j.earscirev.2023.104638.
74. J. Liu, M. Li, F. Tang, J. Zhao, S. Song, Y. Zhou, X. Song, L. Ren, New Benthic Fossils from the Late Ediacaran Strata of Southwestern China. *Acta Geologica Sinica ‐ English Edition* **98**, 311–323 (2024), https://doi.org/10.1111/1755-6724.15153.
75. Z. Chen, C. Zhou, M. Meyer, K. Xiang, J. D. Schiffbauer, X. Yuan, S. Xiao, Trace fossil evidence for Ediacaran bilaterian animals with complex behaviors. *Precambrian Research* **224**, 690–701 (2013), https://doi.org/10.1016/j.precamres.2012.11.004.
76. F. Yang, S. Qin, W. Ding, Y. Xu, B. Shen, New Discovery of Macroscopic Algae Fossils from Shibantan Bituminous Limestone of Dengying Formation in the Yangtze Gorges Area, South China. *Acta Scientiarum Naturalium Universitatis Pekinensis* **54**, 563–572 (2018), https://doi.org/10.13209/j.0479-8023.2017.093.
77. B. Wan, Z. Chen, X. Yuan, K. Pang, Q. Tang, C. Guan, X. Wang, S. Pandey, M. L. Droser, S. Xiao, A tale of three taphonomic modes: the Ediacaran fossil Flabellophyton preserved in limestone, black shale, and sandstone. *Gondwana Research* **84**, 296–314 (2020), https://doi.org/10.1016/j.gr.2020.04.003.
78. X. Wang, K. Pang, Z. Chen, B. Wan, S. Xiao, C. Zhou, X. Yuan, The Ediacaran frondose fossil Arborea from the Shibantan limestone of South China. *Journal of Paleontology* **94**, 1034–1050 (2020), https://doi.org/10.1017/jpa.2020.43.

79. L. Zhang, S. Chang, C. Chen, X. Wang, Q. Feng, M. Steiner, B. Yang, R. Mason, Z. She, J. Yan, Cloudina aggregates from the uppermost Dengying Formation, Three Gorges area, South China, and stratigraphical implications. *Precambrian Research* **370**, 106552 (2022), https://doi.org/10.1016/j.precamres.2021.106552.

80. H. Hua, Y. Cai, X. Min, S. Chai, Q. Dai, Z. Cui, Ecological diversity in the terminal Ediacaran Gaojiashan biota. *Earth Science Frontiers* **27**, 28 (2020), https://doi.org/10.13745/j.esf.sf.2020.6.2.

81. Y. Cai, J. D. Schiffbauer, H. Hua, S. Xiao, Morphology and paleoecology of the late Ediacaran tubular fossil Conotubus hemiannulatus from the Gaojiashan Lagerstätte of southern Shaanxi Province, South China. *Precambrian Research* **191**, 46–57 (2011), https://doi.org/10.1016/j.precamres.2011.09.002.

82. Y. Cai, S. Xiao, H. Hua, X. Yuan, New material of the biomineralizing tubular fossil Sinotubulites from the late Ediacaran Dengying Formation, South China. *Precambrian Research* **261**, 12–24 (2015), https://doi.org/10.1016/j.precamres.2015.02.002.

83. Y. Cai, I. Cortijo, J. D. Schiffbauer, H. Hua, Taxonomy of the late Ediacaran index fossil Cloudina and a new similar taxon from South China. *Precambrian Research* **298**, 146–156 (2017), https://doi.org/10.1016/j.precamres.2017.05.016.

84. X. Min, H. Hua, L. Liu, B. Sun, Z. Cui, T. Jiang, Phosphatized Epiphyton from the terminal Neoproterozoic and its significance. *Precambrian Research* **331**, 105358 (2019), https://doi.org/10.1016/j.precamres.2019.105358.

85. X. Min, H. Hua, L. Liu, B. Sun, Z. Cui, Q. Dai, A diverse calcified cyanobacteria assemblage in the latest Ediacaran. *Precambrian Research* **342**, 105669 (2020), https://doi.org/10.1016/j.precamres.2020.105669.

86. J. Hou, X. Wang, Z. Hou, J. Ramezani, Q. Tang, S. Shen, The terminal Ediacaran Tongshan Lagerstätte from South China. *Nature Communications* **16**, 10161 (2025), https://doi.org/10.1038/s41467-025-65176-2.

Acknowledgments: Thanks are given to Prof. F. Tang for showing us the Qingshuigou Section in 2017, which initiated this study. We thank A. Liu for providing specimen images, X. Yuan for his insightful comments on the fossil material and G. Wang for suggestion on stratigraphic correlations. We also thank J. Guo, M. Luo, C. Feng, X. Wang and S. Zhang for their help with fieldwork, which was supported by the Department of Natural Resources of Yunnan Province. We would also like to thank three anonymous reviewers who provided detailed and constructive comments which significantly improved our manuscript.

Funding:

National Natural Science Foundation of China 42062001, 42072019,

Joint funding from YNU-Yunnan Government 202201BF070001-016,

Yunnan Science & Technology Champion Project, 202305AB350006

Royal Society University Research Fellowship URF\R1\221220 and RF\ERE\221057 (RPA)

Natural Environment Research Council Fellowship NE/W00786X/1 (FSD)

Natural Environment Research Council Fellowship NE/W007878/1 (LAP)

Yunling Scholarship (PC)

Author contributions:

Conceptualization: GL, FW, PC
Methodology: GL, FW, WW, LAP, FSD, RPA, PC
Investigation: GL, FW, WW, XW, LAP, FSD, RPA, XL, YZ, PC
Visualization: GL, XW, LAP, FSD
Funding acquisition: FW, PC
Project administration: FW, PC
Supervision: FW, PC, LAP, FSD, RPA
Writing-original draft: GL, FW, FSD, LAP, RPA, PC
Writing – review & editing: GL, FW, FSD, LAP, RPA, PC

Competing interests: Authors declare that they have no competing interests.

Data and materials availability: All data are provided in the main text and supplementary materials. All fossils are deposited in Yunnan University as part of collections of Yunnan Geology, Invertebrate Paleontology (YNGIP), and all related images can be accessed by contacting Peiyun Cong (cong@ynu.edu.cn). The illustrated fossils in this study are deposited with accession numbers YNGIP 90301-YNGIP90335.

Supplementary Materials

Materials and Methods
Macroalgae and Animal co-occurrence
Trace fossils
Figs. S1 to S7
Table S1

Figure captions:

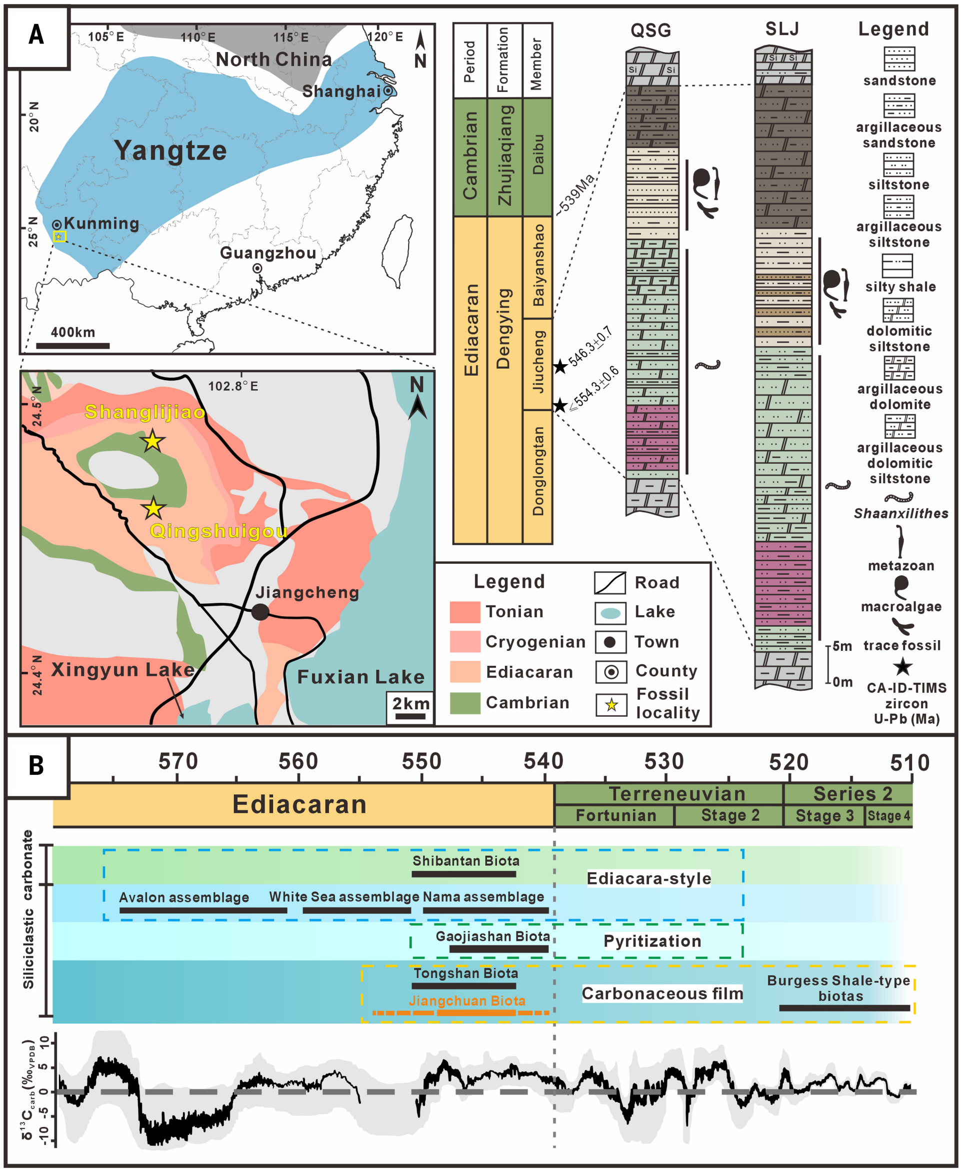

Fig. 1. Geological map and stratigraphic column of the Jiangchuan Biota. (**A**) Locations of fossil sites and geological context of the Fuxian Lake area (left), and stratigraphic column of the Ediacaran Jiucheng Member of the Dengying Formation, showing the distribution of macroalgae, metazoans, *Shaanxilithes* and trace fossils (right). The column includes U-Pb zircon ages from (*52*).(**B**) Preservation mode of the Jiangchuan biota in comparison to other late Ediacaran fossil assemblages from South China, plotted against geological time and the global carbon isotope record from (*53*).

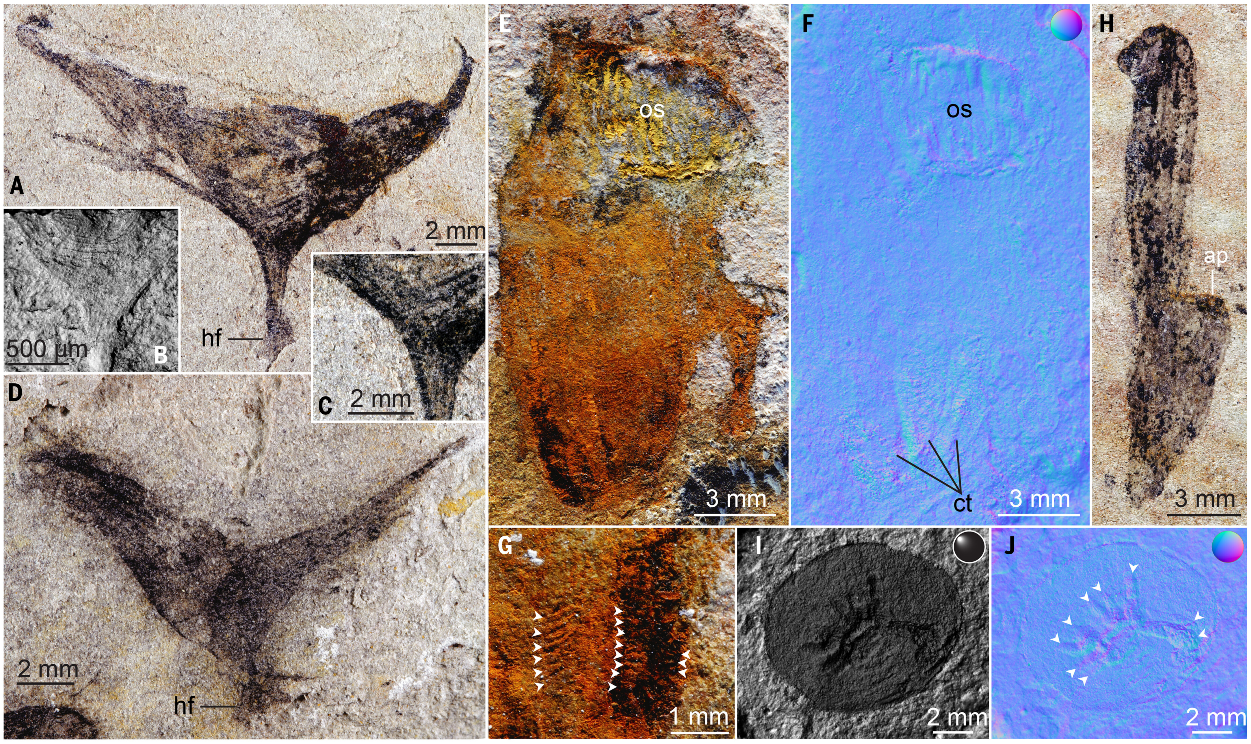

Fig. 2. Non-bilaterian animals from the Jiangchuan Biota. (A-D) Specimens of *Haootia*-like organism and *Haootia quadriformis* from Newfoundland. (A) YNGIP 90301 and (D) YNGIP 90302 are from the Jiangchuan Biota with (C) showing the filamentous construction of the base of the specimen in (A). (B) The base of the specimen of the paratype of *Haootia quadriformis* from the Fermeuse Formation of Newfoundland, Canada. Its filamentous construction is similar to the anatomy of YNGIP 90301. **(E-G)** YNGIP 90303, a putative ctenophore. (E) Part illuminated directly from above. (F) RTI image using normal visualization. (G) Detail image of ctenes, with individual combs highlighted with white arrowheads. **(H)** Specimen YNGIP 90304 comparable to *Mackenzia* known from the Chengjiang Biota. **(I-J)** YNGIP 90305, a radialomorph, using normals visualization from an RTI dataset, arrows indicate the positions of the radial protrusions (J). Abbreviations: ap – aperture, ct – ctenes, hf – holdfast, os – oral skirt.

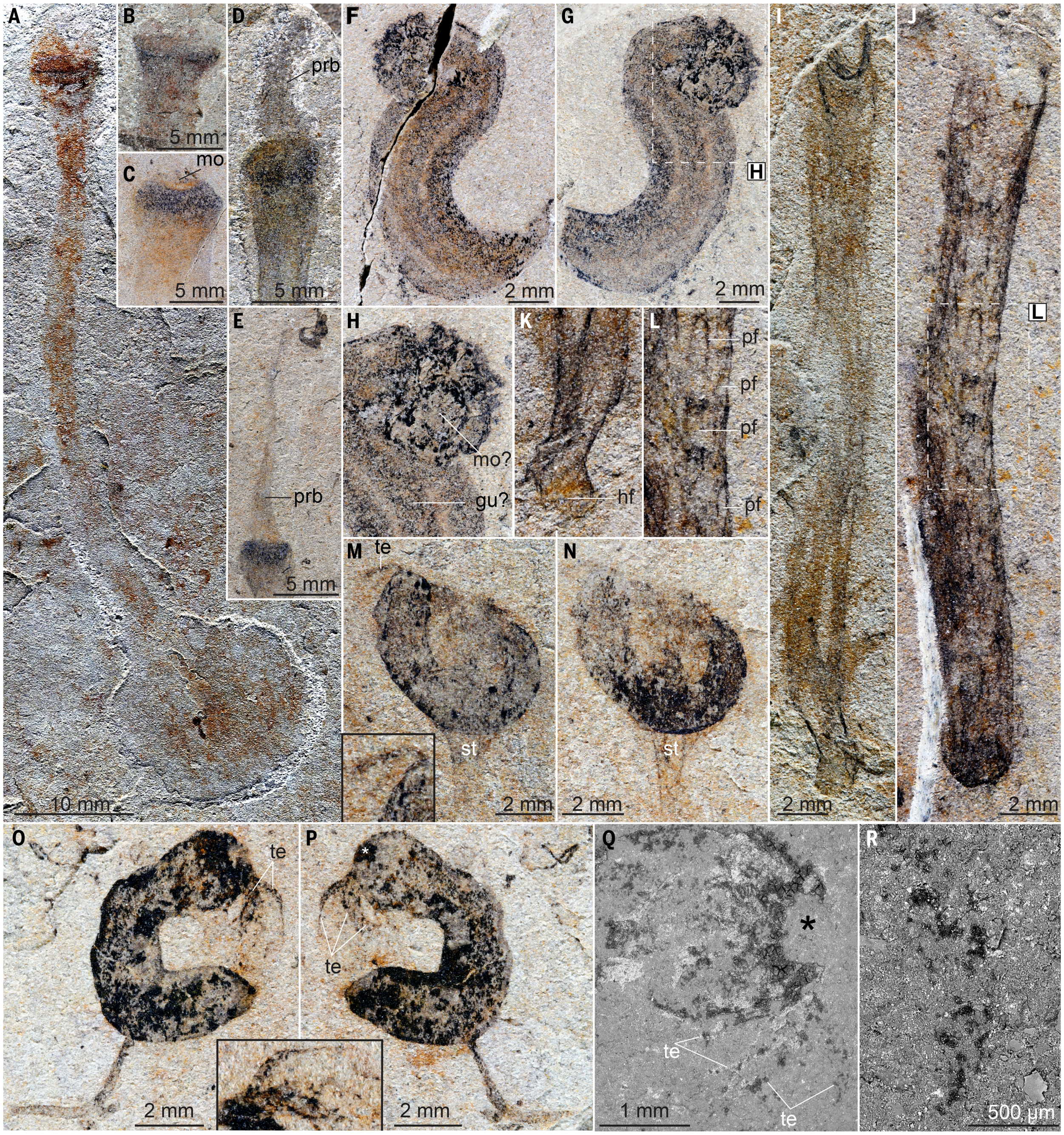

Fig. 3. Bilaterian fossils from the Jiangchuan Biota. (A-E) Sessile, vermiform animal with attachment disc. Oral projection visible in (A) YNGIP 90306, (C) YNGIP 90308 and (E) YNGIP 90310 everted from the body to different degrees. (B) YNGIP 90307 shows a fully contracted oral region, (C) shows the initial stages of eversion, (D) YNGIP 90309 shows partial eversion and (E) YNGIP 90310 shows full eversion. **(F-H)** Part and counterpart of YNGIP 90311, a sausage-shaped vermiform animal with terminal mouth. (H) Close-up of the white box in (G), showing the possible mouth and gut. **(I-L)** YNGIP90312 (I) and YNGIP90313 (J), *Margaretia*-like animal now known as a dwelling-tube for enteropneust hemichordate worm. **(I)** and **(J)** show complete specimens. (K) represents the holdfast preserved in the counterpart of (I). (L) shows the close-up of the white box in (J), exhibiting perforations. (**M-R)** YNGIP90314 (M-N) and YNGIP90315 (O-P), deuterostome animals similar to the cambroernid *Herpetogaster*. (M-N) shows an animal with a similar stalk region to the cambroernid *Phogites*. (O-P) shows an animal very similar in morphology to *Herpetogaster*. **(Q-R)** Backscattered electron image of the head (Q) and tentacles (R) of (O) under SEM**.** Note that the asterisk (*) in Q highlights a region where the carbon film is absent

but retained in the counterpart (see panel **P**). Abbreviations: gu **-** gut hf – holdfast, mo – mouth, pf – perforations, prb – proboscis, te – tentacles.

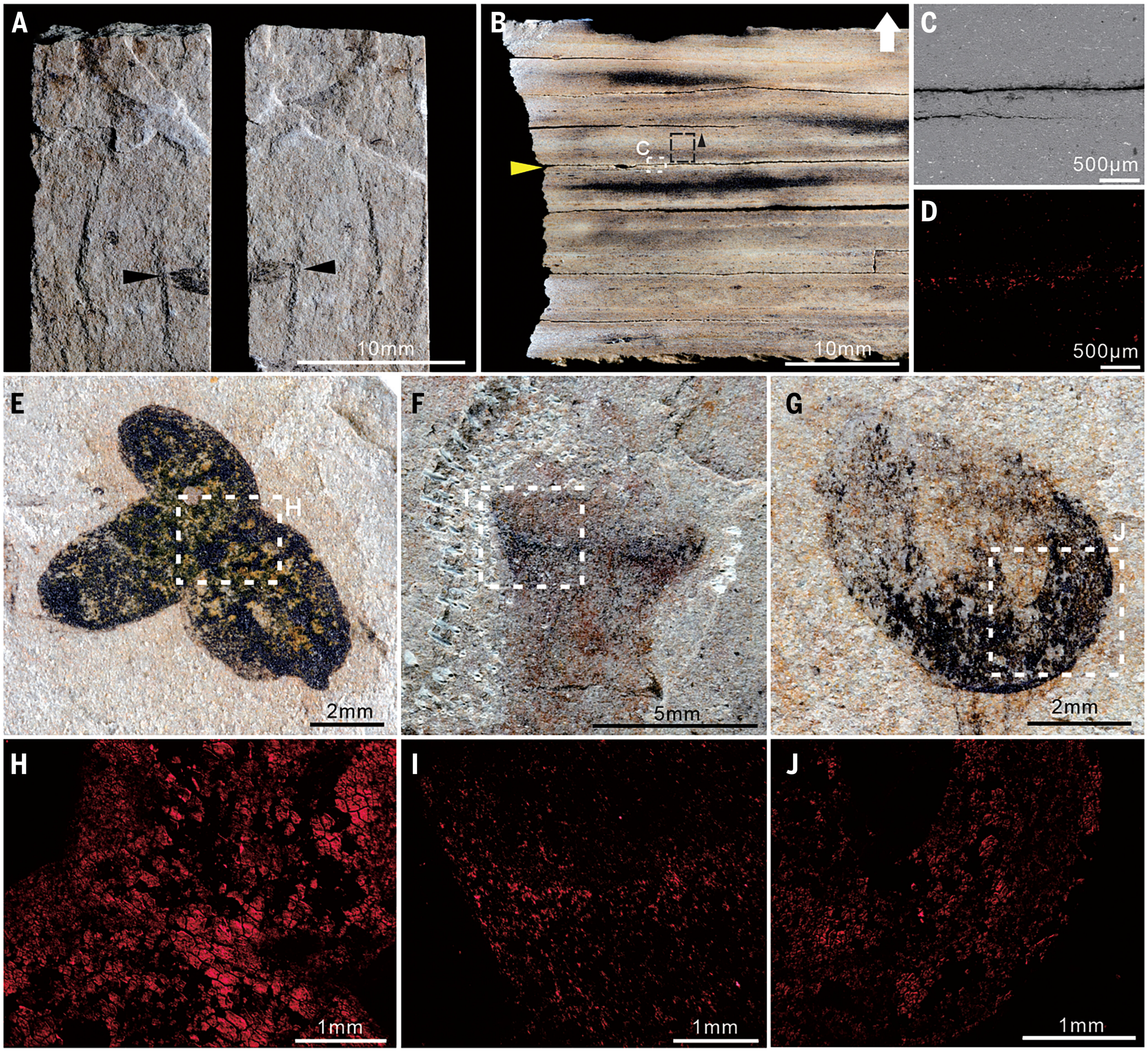

Fig. 4. Taphonomy of the Jiangchuan Biota. (A) Macroalgal fragment fossils preserved along bedding (indicated by black arrows), where specimens represent counterparts of the same fossil. **(B)** Polished slab on the lateral view of the macroalgal specimen (A) (the side pointed by black arrow), where the white arrow denotes top, yellow triangle shows the fossil-bearing horizon, white box indicates the fossil (A) and black box highlights graded bedding with black triangle indicating fining upward direction. **(C)** Backscattered electron image of the region outlined by the white box (B). **(D)** Energy dispersive X-ray spectroscopy map of carbon (C). **(E-G)** Macroalgae *Tawuia* YNGIP90316 (E), sessile vermiform animal fossil YNGIP90307 (F) and Cambroernids YNGIP90314 (G). **(H-J)** Carbon maps of the regions outlined by white boxes in (E-G).