CAMBRIAN EXPLOSION

The Qingjiang biota—A Burgess Shale–type fossil Lagerstätte from the early Cambrian of South China

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Burgess Shale–type fossil Lagerstätten provide the best evidence for deciphering the biotic patterns and magnitude of the Cambrian explosion. Here, we report a Lagerstätte from South China, the Qingjiang biota (~518 million years old), which is dominated by soft-bodied taxa from a distal shelf setting. The Qingjiang biota is distinguished by pristine carbonaceous preservation of labile organic features, a very high proportion of new taxa (~53%), and preliminary taxonomic diversity that suggests it could rival the Chengjiang and Burgess Shale biotas. Defining aspects of the Qingjiang biota include a high abundance of cnidarians, including both medusoid and polypoid forms; new taxa resembling extant kinorhynchs; and abundant larval or juvenile forms. This distinctive composition holds promise for providing insights into the evolution of Cambrian ecosystems across environmental gradients.

Our understanding of the Cambrian explosion and of the fundamental structure of the tree of animal life rests in large part on evidence from a highly enhanced fossil record, characterized by the preservation of entire assemblages of soft-bodied fossils (*1*–*3*). In the 100 years since Walcott's original discovery of the Burgess Shale, exceptionally preserved fossil assemblages have been reported from Cambrian strata of almost every paleocontinent (*4*–*9*). Nevertheless, only the early Cambrian Chengjiang biota of Yunnan Province has matched the Burgess Shale in total diversity of soft-bodied taxa and fidelity of preservation (*10*).

Here, we report the discovery of an early Cambrian Burgess Shale–type (BST) fossil Lagerstätte from the Changyang area of South China (Fig. 1), which is characterized by high taxonomic diversity, an unexpectedly large proportion of new taxa, and precise preservation of fine aspects of labile tissue anatomy (Figs. 2 to 4). Although it is approximately coeval to the Chengjiang biota (*11*), the Qingjiang biota appears to have occupied a more distal environmental setting, in which a different early Cambrian ecosystem flourished (see supplementary materials and methods).

The Qingjiang fossil locality is situated on a bank of the Danshui River, near its junction with the Qingjiang River, Hubei Province, ~1050 km northeast of Chengjiang (Fig. 1). Here, strata belonging to the middle member of the Shuijingtou Formation are composed of a succession of laminated black siltstones interrupted by two intervals of calcareous claystones, each ~2 m thick and separated by 4 m of stratigraphic section. Each claystone set consists of couplets of laminated black claystone alternating with submillimeter- to centimeter-thick, light gray colored claystones (fig. S1). Sedimentologic and taphonomic data (materials and methods) indicate that these black and gray claystone couplets are analogous to the pelagic background sediments and event-deposited claystones, respectively, of the Chengjiang Lagerstätte (*12*–*16*). As at Chengjiang (*13*), the background beds yield only depauperate assemblages of shelly fossils, whereas the event beds contain exquisite preservation of soft-bodied organisms (Figs. 2 and 3 and fig. S2).

On the basis of regional biostratigraphy, the Shuijingtou Formation is correlated to the Chiungchusuan Stage (Cambrian Series 2, Stage 3) of eastern Yunnan (*17*–*19*), which yields the Chengjiang fossils and was recently dated to ~518 million years ago (*11*). Both biotas lie within the *Wutingaspis-Eoredlichia* Assemblage Zone and share diagnostic trilobites (e.g., *Eoredlichia intermedia*) (fig. S3C) and soft-bodied taxa (materials and methods 4).

Although collection efforts have been limited to four field seasons, 101 metazoan taxa (53.2% new, 85% soft-bodied taxa), representing 18 body plans across all subkingdom-rank lineages, and eight algal forms have already been identified among 4351 specimens collected (figs. S5 and S6 and table S1). The taxonomic richness of soft-bodied taxa (table S1) approaches the top tier of BST deposits, presently occupied only by the Burgess Shale and Chengjiang biotas (*10*). Rarefaction analyses suggest that diversity may surpass that of all other BST biotas (fig. S4).

As in the Chengjiang biota (*7*, *13*, *19*), arthropods and sponges are the most taxonomically diverse groups in the Qingjiang biota (figs. S5 and S6) and a diversity of ecological strategies are represented (Fig. 4, fig. S11, and table S1), including infaunal (e.g., priapulids and kinorhynchs), sessile epibenthic (e.g., sponges and brachiopods), vagile epibenthic (e.g., lobopodians and hyolithids), nektobenthic (e.g., vetulicolians and arthropods), and pelagic (e.g., jellyfish, ctenophores, and arthropods) taxa. The differences between the two contemporaneous fossil assemblages (fig. S6) are surprising given that Chengjiang is the best collected early Cambrian fossil deposit in the world (*7*) and includes multiple localities with prominent differences in assemblage content (*13*, *20*, *21*). Only a small number of species ($n = 8$) are shared with Chengjiang (materials and methods), and the most abundant taxa, *Kunmingella* and *Maotianshania*, as well as the iconic *Fuxianhuia*, are absent from the Qingjiang assemblage. These patterns and the high proportion of new taxa from the Qingjiang suggest that the differences between the two biotas reflect primary differences in assemblage composition and ecological structure between the two regions rather than artifacts of taphonomic bias (materials and methods). The Qingjiang biota's distinctive aspects have the potential to substantially inform our understanding of early animal evolution.

Cnidarians are underrepresented in BST deposits, including in the Burgess Shale (*1*). The Qingjiang biota, however, is marked by high abundance and diversity of exceptionally preserved cnidarian fossils (Fig. 2, A and B, and figs. S5 and S6), which fills a major gap in knowledge of the morphology and diversity of Cambrian basal metazoans. Medusoid (Fig. 2A) and polypoid forms (Fig. 2B) are both present. Medusoid fossils are preserved with diagnostic features, including a ring of tentacles encircling the body, a convex upper exumbrella, a lower subumbrella surface, and a central mouth located at the end of a pendant-like, tubular extension (the manubrium) (Fig. 2A). Polyps are characterized by a terminal holdfast and resemble living counterparts in that they possess robust tentacles, oral and anal openings, and an oral disc (Fig. 2B). The tentacles lack cilia, which are observed in the Chengjiang fossil *Xianguangia* (*22*), indicating a different feeding strategy. The Qingjiang ctenophore, like crown group representatives, is tentaculate (Fig. 2C), undermining the argument that the ancestral ctenophore lacked tentacles and was skeletonized (*23*). It appears that the ctenophore body plan has remained essentially unchanged since the Cambrian explosion.

As is the case in all BST deposits, ecdysozoans are by far the most diverse group (Fig. 3 and figs. S5 and S6). A new lobopodian preserves an unusual structure at the anterior of the head and an atypical arrangement of lobopods bestrewn with tiny spines (Fig. 3D). Scalidophorans, including loriciferans and kinorhynchs but predominantly priapulans, are common components of BST deposits (*1*, *7*). Kinorhynchs (mud dragons) are rare in the fossil record (*24*) and previously unreported in BST deposits. The new locality has yielded 410 specimens, including three new

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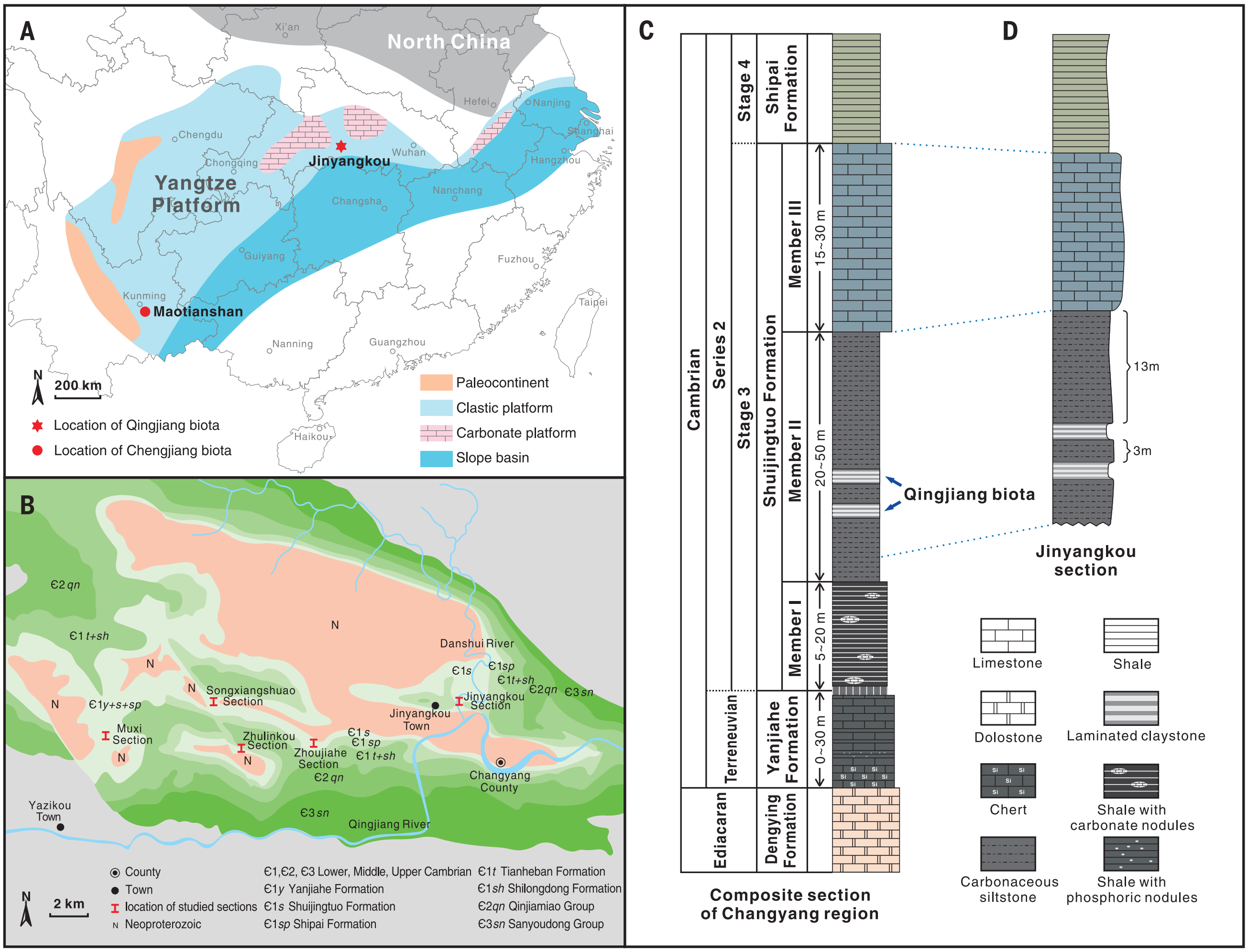

Fig. 1. Locality map and early Cambrian stratigraphy of the study area. (**A**) Lithofacies map of the Yangtze Platform during Cambrian Stage 3, with type localities of the Qingjiang and Chengjiang biotas. (**B**) Geological map of the study area, showing the distribution of Cambrian outcrops and the location of studied sections with characteristic couplets of background and event claystone beds within the middle member of the Shuijingtuo Formation. (**C**) Composite stratigraphic column for the study area. (**D**) Stratigraphic column at the Jinyangkou type locality.

macroscopic (1 to 4 cm) taxa that resemble kinorhynchs, possessing a segmented body divided into a head and a trunk, paired lateral tergal and sternal extensions, and a terminal segment with long spines (Fig. 3C). Dorsal scalids are transversely arranged on the surface of each segment and ventral ones are bilaterally positioned in longitudinal rows. However, extant kinorhynchs are meiofaunal and typically have a mouth cone (*25*), which has not yet been observed in these specimens. The putative Cambrian kinorhynch *Eokinorhynchus* (*24*) has a larger number of segments (macroannuli) than extant kinorhynchs even though it is millimeter-sized. Future description of these taxa may shed light on the evolution of the Kinorhyncha.

Unexpectedly, submillimeter- to millimeter-sized, delicate, larval or juvenile forms (fig. S2G), rarely seen in BST Lagerstätten, are abundant on some bedding surfaces of the Qingjiang assemblage; dozens of individuals can be recognized in a single slab. They are variable in morphology, including elongate forms with or without annulations as well as oval forms with a festooned edge. These forms have not been assigned to any taxon because their life history is not fully known. However, they may offer valuable information on development and evolution in the future.

The Qingjiang algae are abundant and diverse, and they preserve minute details including sporangia (figs. S2J, S5, and S8). Most notably, one form is dichotomously branched from a central disc into a fourfold radially symmetric thallus (Fig. 2D) unlike any living or fossil counterparts.

The Qingjiang fossils represent near-pristine examples of Burgess Shale–type preservation (*26*) that have not experienced alteration through metamorphosis, as in the Burgess Shale (*27*), or deep oxidative weathering, as at Chengjiang (*14*, *15*). Soft-bodied fossils are preserved as prominent, dark-colored, organic carbon compressions on fresh, gray claystone (figs. S7 and S8), providing the opportunity for future geochemical and taphonomic study. No authigenic mineral films or mineral replacement of selected soft tissues (e.g., pyrite, phosphate) have yet been observed. The fidelity of preservation is very high, on par with that of Chengjiang and Burgess Shale fossils (*1*, *7*, *28*). Apart from lightly sclerotized tissues, such as arthropod and worm cuticle, entirely soft-bodied animals (Fig. 2) (e.g., ctenophores and jellyfishes), labile anatomical features (eyes, gills, and guts), and juveniles are fairly common (Fig. 3 and fig. S2) and offer new phylogenetic information. Thus, the Qingjiang fossils hold promise for a refined understanding of Burgess Shale–type preservation across a wide range of body plans and tissue types.

Paleontological, sedimentological, and geochemical data (materials and methods) suggest that the circumstances surrounding the quality of fossilization of the Qingjiang biota were similar to those of other Burgess Shale–type deposits (*10*). Soft-bodied organisms of the Qingjiang biota were entrained by sediment-gravity flows and transported downslope from habitable environments to

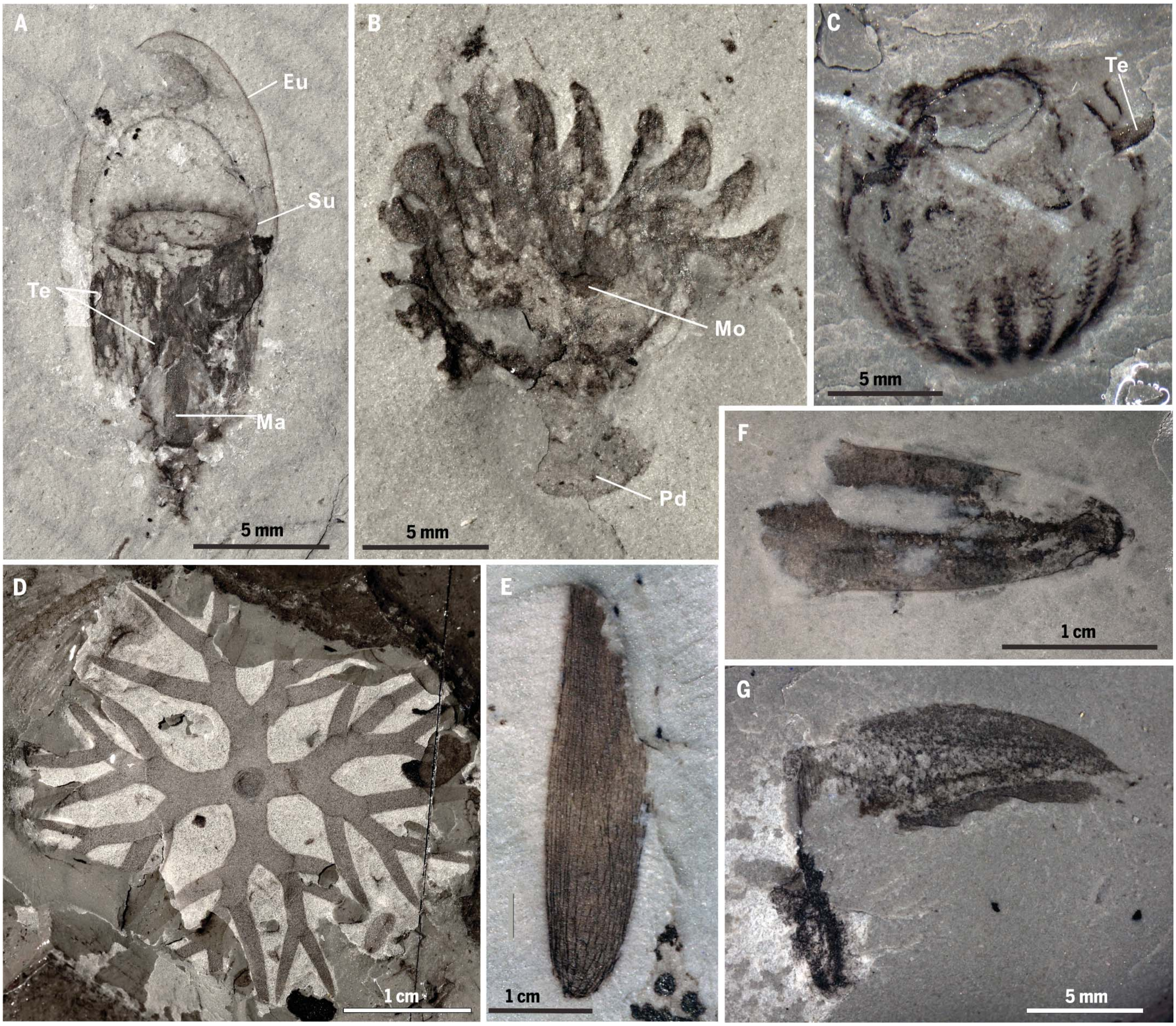

Fig. 2. New soft-bodied taxa from the Qingjiang biota. (**A**) Medusoid cnidarian, showing radially symmetrical body plan, exumbrellar/subumbrellar surfaces (Eu/Su), manubrium (Ma), and tentacles (Te). (**B**) Polypoid cnidarian, showing oral disc and mouth (Mo), tentacles, column, and pedal disc (Pd). (**C**) Ctenophore, showing that comb rows and oral-aboral body axis have a biradial symmetry resulting from sheathed tentacles. (**D**) Branched alga, showing quadripartite thallus. (**E**) Sponge *Leptomitella* sp. (**F**) New chordate. (**G**) *Yunnanozoon* sp.

nearby anoxic settings that lay below storm wave base (fig. S11), and rapidly buried, without subsequent disturbance by bioturbation (fig. S1). During early diagenesis, both calcite and pyrite precipitated within the sediments but did not result in mineral replacement of soft-tissue morphology.

The pronounced differences (fig. S6) in the composition of the Qingjiang biota relative to the contemporaneous Chengjiang biota suggest that the rich assemblages developed in response to different paleoenvironmental conditions. It is clear from regional facies relationships that the Qingjiang biota was preserved in a somewhat more distal setting than the Chengjiang biota (*4*, *12*), yet both appear to represent outer shelf settings (materials and methods *6*). The comparison of the two biotas offers a rare opportunity to understand how early metazoan communities developed in response to environmental parameters. Moreover, the differences in composition between the biotas suggest great potential for continued discovery of new taxa with further excavation at Qingjiang and elsewhere in the region.

The Shuijingtuo Formation is widespread in the Cambrian of the Yangtze Platform (*29*), and the characteristic claystones that yield the Qingjiang biota can be found at a number of localities in the Changyang region (Fig. 1). This suggests that the potential of the Shuijingtuo Formation to yield exceptional biotas across a spectrum of ecological, environmental, and taphonomic gradients remains to be explored. The particularly large proportion of new taxa in the Qingjiang biota (fig. S5), which lies in close temporal proximity to the extensively sampled Chengjiang biota, suggests that the present understanding of the diversity and disparity of metazoan ecosystems in the immediate aftermath of the Cambrian explosion is far from complete (*30*) and will be greatly informed by future discoveries.

REFERENCES AND NOTES

1. D. E. G. Briggs, D. H. Erwin, F. J. Collier, *The Fossils of the Burgess Shale* (Smithsonian Institution Press, 1994).
2. X. L. Zhang, *Natl. Sci. Rev.* **1**, 488–489 (2014).
3. A. C. Daley, J. B. Antcliffe, H. B. Drage, S. Pates, *Proc. Natl. Acad. Sci. U.S.A.* **115**, 5323–5331 (2018).

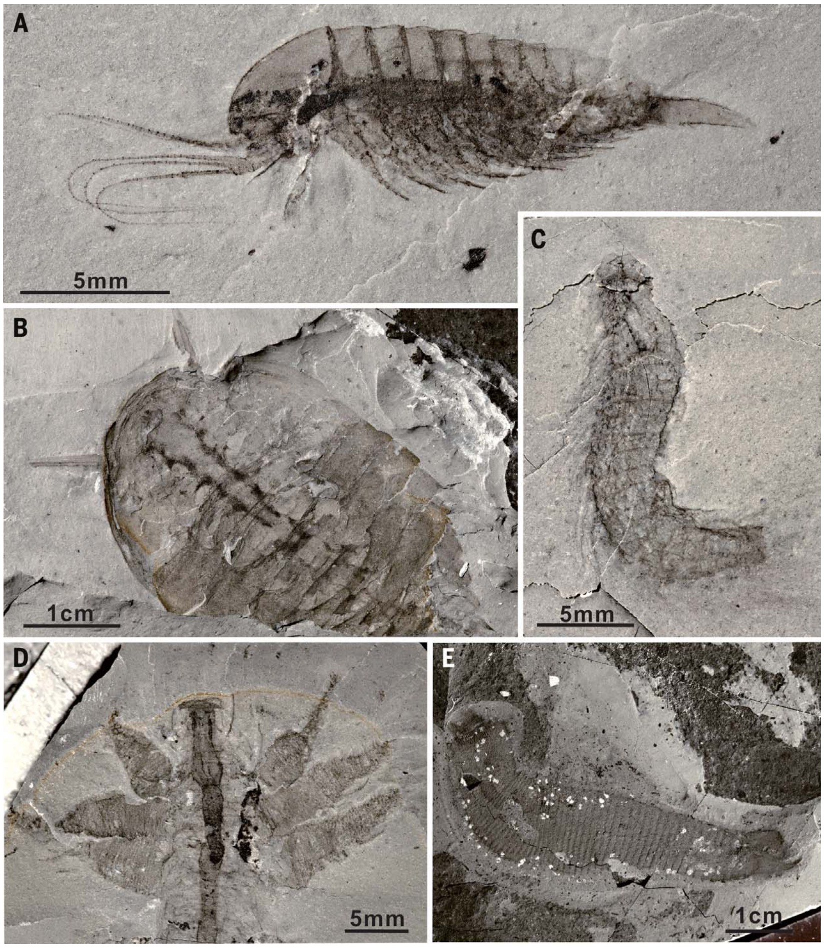

Fig. 3. Ecdysozoans of the Qingjiang biota. (**A**) *Leanchoilia* sp., showing fine anatomical details, including those of the great appendages. (**B**) New megacherian preserved with internal soft tissues. (**C**) A possible kinorhynch scalidophoran, with segmented body armored by scalids. (**D**) Lobopodian. (**E**) Priapulid worm.

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Fig. 4. Artist's rendering of the Qingjiang biota showing characteristic early Cambrian taxa from the Lagerstätte.

4. X. L. Zhang, W. Liu, Y. L. Zhao, *Gondwana Res.* **14**, 255–262 (2008).
5. J. Yang, J. Ortega-Hernández, N. J. Butterfield, X. G. Zhang, *Nature* **494**, 468–471 (2013).
6. H. Zeng, F. C. Zhao, Z. J. Yin, G. X. Li, M. Y. Zhu, *Chin. Sci. Bull.* **59**, 3169–3175 (2014).
7. X.-G. Hou *et al.*, *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life* (Wiley Blackwell, ed. 2, 2017).
8. J. R. Paterson *et al.*, *J. Geol. Soc. London* **173**, 1–11 (2016).
9. J. S. Peel, J. R. Ineson, *Palaeontographica Canadiana* **31**, 109–118 (2011).
10. R. R. Gaines, in *Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization*, M. Laflamme, J. D. Schiffbauer, S. A. F. Darroch, Eds. (Paleontol. Soc. Papers, 2014), vol. 20, pp. 123–146.
11. C. Yang, X. H. Li, M. Y. Zhu, D. J. Condon, J. Y. Chen, *J. Geol. Soc. London* **175**, 659–666 (2018).
12. M.Y. Zhu, J. M. Zhang, G. X. Li, *Acta Paleont. Sinica* **40**, 80–105 (2001).
13. F. C. Zhao, J. B. Caron, S. X. Hu, M. Y. Zhu, *Palaios* **24**, 826–839 (2009).
14. R. R. Gaines *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 5180–5184 (2012).
15. A. Forchielli, M. Steiner, J. Kasbohm, S. X. Hu, H. Keupp, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **398**, 59–85 (2014).
16. E. U. Hammarlund *et al.*, *Earth Planet. Sci. Lett.* **475**, 160–168 (2017).
17. S. S. Zhang, in *Sinian to Permian Palaeontology and Stratigraphy of Eastern Three-Gorge Area*, Stratigraphical Research Group of Hubei Geological Bureau, Eds. (Geol. Press China, 1978), chap. 2, pp. 25–43.
18. S. C. Peng, L. E. Babcock, R. A. Cooper, in *The Geologic Time Scale*, F. M. Gradstein, J. G. Ogg, M. D. Schmitz, G. M. Ogg, Eds. (Elsevier 2012), vol. 2, pp. 437–488.
19. X. L. Zhang *et al.*, *Earth Sci. Rev.* **172**, 124–139 (2017).
20. F. C. Zhao *et al.*, *Paleobiology* **40**, 50–69 (2014).
21. X. L. Zhang, D. G. Shu, Y. Li, J. Han, *J. Geol. Soc. London* **158**, 211–218 (2001).
22. Q. Ou *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **114**, 8835–8840 (2017).
23. Q. Ou *et al.*, *Sci. Adv.* **1**, e1500092 (2015).
24. H. Zhang *et al.*, *Sci. Rep.* **5**, 16521 (2015).
25. M. V. Sørensen, F. Pardos, *Meiofauna Marina* **16**, 21–73 (2008).
26. R. R. Gaines, D. E. G. Briggs, Y. L. Zhao, *Geology* **36**, 755–758 (2008).
27. N. J. Butterfield, U. Balthasar, L. A. Wilson, *Palaeontology* **50**, 537–543 (2007).
28. J. B. Caron, R. R. Gaines, C. Aria, M. G. Mángano, M. Streng, *Nat. Commun.* **5**, 3210 (2014).
29. X. S. Wu, G. X. Liu, G. X. Chen, B. X. Sheng, Y. M. Wang, in *Lithostratigraphy of Hubei Province*, G. X. Chen, J. W. Jin, Eds. (Multiple Classification and Correlation of the Stratigraphy of China Series 42, China Univ. Geosci. Press, 1996), chap. 3, pp. 59–139.
30. X. L. Zhang, D. G. Shu, *Sci. China Earth Sci.* **57**, 930–942 (2014).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/363/6433/1338/suppl/DC1
Materials and Methods
Figs. S1 to S11
Table S1
References (*31*–*42*)

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A treasure trove of Cambrian secrets

Animal life exploded in diversity and form during the Cambrian period about 500 million years ago. Fu *et al.* describe an early Cambrian fossil site in China that contains a variety of specimens, more than half of which are previously undescribed (see the Perspective by Daley). The site rivals previously described Cambrian sites, such as the Burgess Shale, and should help to elucidate biological innovation and diversification during this period.

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