

Lower Cambrian vertebrates from south China

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The first fossil chordates are found in deposits from the Cambrian period (545–490 million years ago), but their earliest record is exceptionally sporadic and is often controversial. Accordingly, it has been difficult to construct a coherent phylogenetic synthesis for the basal chordates. Until now, the available soft-bodied remains have consisted almost entirely of cephalochordate-like animals from Burgess Shale-type faunas. Definite examples of agnathan fish do not occur until the Lower Ordovician (~475 Myr BP), with a more questionable record extending into the Cambrian. The discovery of two distinct types of agnathan from the Lower Cambrian Chengjiang fossil-Lagerstätte is, therefore, a very significant extension of their range. One form is lamprey-like, whereas the other is closer to the more primitive hagfish. These finds imply that the first agnathans may have evolved in the earliest Cambrian, with the chordates arising from more primitive deuterostomes in Ediacaran times (latest Neoproterozoic, ~555 Myr BP), if not earlier.

The 'Cambrian explosion' refers to the seemingly abrupt appearance of diverse metazoan groups, representing a number of extant phyla as well as some more problematic clades^{1,2}, during the Cambrian period. Faunas of the type found at the Burgess Shale¹ provide exceptional information on Cambrian marine communities. Recent documentation of their faunal riches has led to a series of provocative phylogenetic analyses^{3,4} which may be broadly congruent with the division of the protostomes into the Ecdysozoa and Lophotrochozoa⁵. However, the early evolution of the third triploblast superclade, the deuterostomes, is much less well understood.

In particular, the fossil record of Cambrian chordates is extremely meagre. The soft-bodied remains^{6–8} consist almost exclusively of cephalochordate-like animals, although they seem to be signifi-

cantly different from the Recent amphioxus. A unique and as yet unnamed specimen from the Burgess Shale has been compared to an ammocoete lamprey^{9,10}. Records of fish are confined to questionable scales¹¹ from the Upper Cambrian. The euconodonts, which are also chordates¹², also appear in the uppermost Cambrian, but their precise placement relative to other agnathans remains controversial^{12,13}. Transitional forms between euconodonts and paraconodonts¹⁴ imply that this group of chordates evolved during the Middle Cambrian, but nothing is yet known of the soft-part anatomy of the early representatives of this group.

Here we describe two distinct types of agnathan from the Lower Cambrian Chengjiang fossil-Lagerstätte of the Qiongzhusi Formation at Haikou¹⁵, Kunming City, Yunnan (Fig. 1). The more

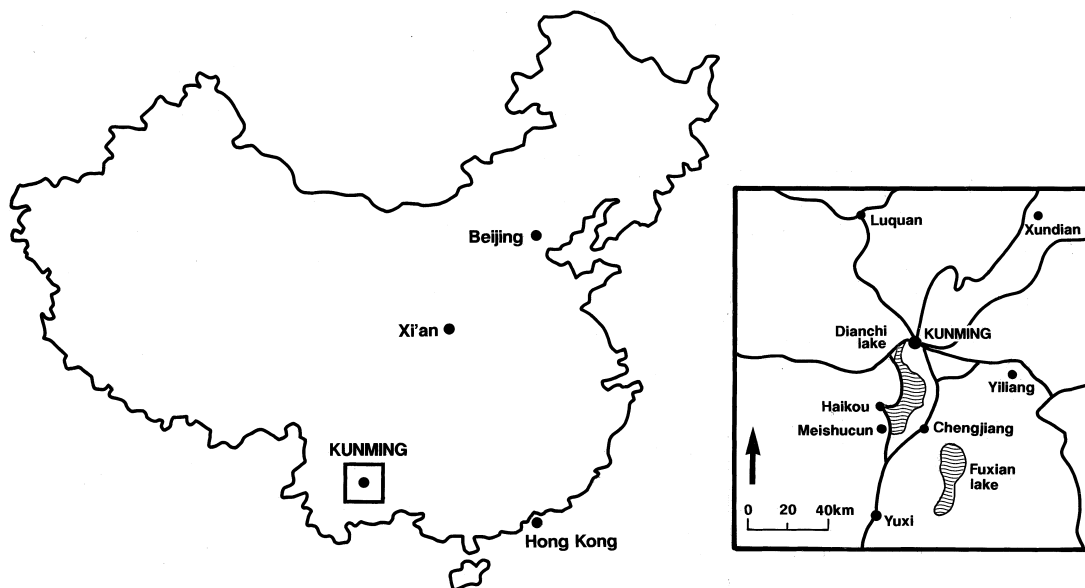


Figure 1 Map of Chengjiang area, Yunnan province and its position relative to the rest of China. The first discoveries of soft-bodied fossils were made in about 1910 near Yiliang¹, but the principal focus of activity has been near Chengjiang, especially the localities a few

kilometres north-east of Fuxian Lake, most notably Maotianshan. The vertebrate fossils described here come from close to Haikou, near Dianchi Lake.

primitive example, *Mylokunmingia* gen. nov., has well developed gill pouches with probable hemibranchs, whereas *Haikouichthys* gen. nov. has structures that we interpret as part of a branchial basket and a dorsal fin with prominent fin-radials. Shared features include complex myomeres, as well as probable paired ventral fin-folds and a pericardic cavity. These discoveries significantly predate previously published reports, but they also imply that even more primitive vertebrates had evolved before the mid-Lower Cambrian.

Phylum Chordata
Subphylum Vertebrata
Class Agnatha

Mylokunmingia Shu, Zhang & Han gen. nov.

Mylokunmingia fengjiaoa Shu, Zhang & Han sp. nov.

Etymology. The generic name refers to myllos (Greek, fish) and the capital of Yunnan. Species name from Chinese fengjiao, beautiful.

Holotype. Early Life Institute, Northwest University, Xi'an: ELI-0000201.

Stratigraphy and locality. Qiongzhusi (Chiungchussu) Formation, Yu'an-shan Member (*Eoredlichia* Zone); Lower Cambrian. Specimen collected from Haikou, Kunming City, Yunnan.

Diagnosis. Fusiform, divided into head region and trunk. Dorsal fin towards anterior, ventro-lateral fin-fold arising from trunk, probably paired. No fin-radials. Head bears series of five, possibly six, gill pouches, each with hemibranchs. Gill pouches possibly linked to extrabranchial atria. Trunk with ~25 myomeres, double V structure with ventral V directed posteriorly and dorsal V anteriorly. Internal anatomy includes alimentary canal with pharynx and intestine, notochord, and possible pericardic cavity.

Description. *Mylokunmingia* gen. nov. is fusiform, with a total length of about 28 mm and maximum height (excluding the dorsal fin) of 6 mm; this point is located about 11 mm from the anterior (Figs 2a, 3). Dermal skeleton or scales appear to have been absent. The body has two regions: a head, taken here to include both snout and complex structures interpreted as gills, and a segmented trunk.

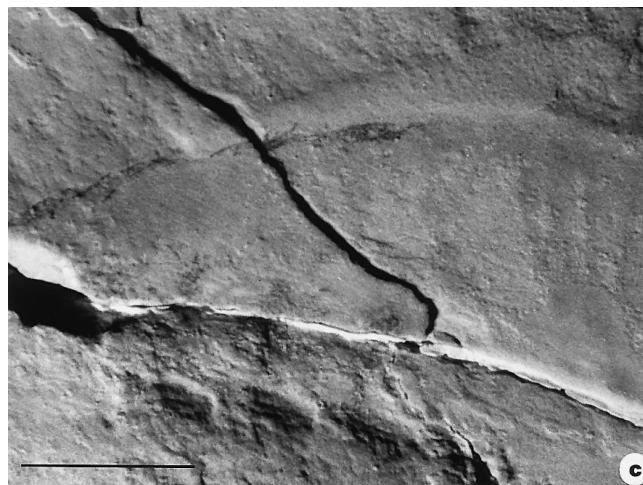
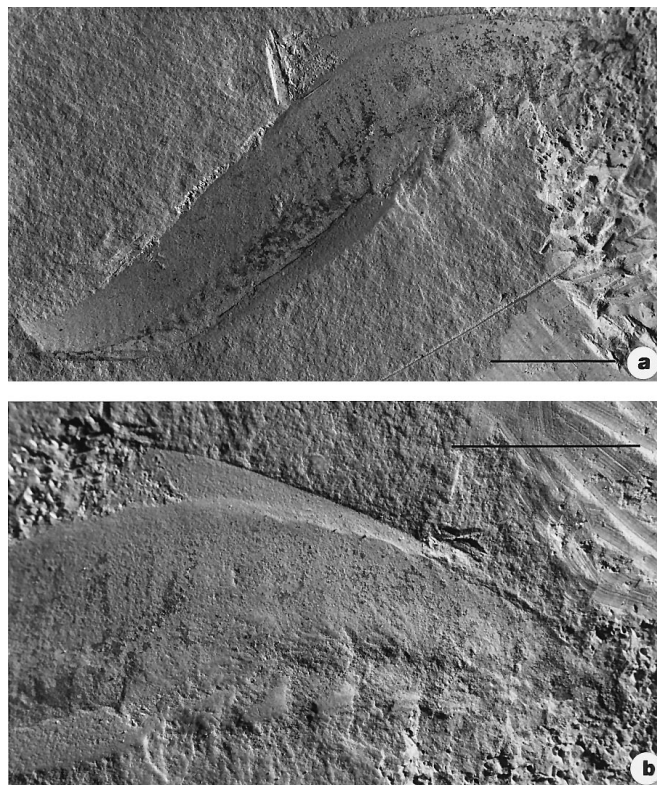


Figure 2 The Lower Cambrian agnathan vertebrate *Mylokunmingia fengjiaoa* Shu, Zhang & Han gen. et sp. nov. from Haikou, Yunnan. Specimen ELI-0000201. **a**, Entire specimen, anterior end to the right, posterior tip incomplete owing to post-mortem folding; scale bar equivalent to 5 mm. **b**, Detail of the head region of the fossil, to emphasize structures interpreted as gill pouches; scale bar equivalent to 5 mm. **c**, Anterior of counterpart, to show series of ventral structures interpreted as possible extrabranchial atria; scale bar equivalent to 3 mm.

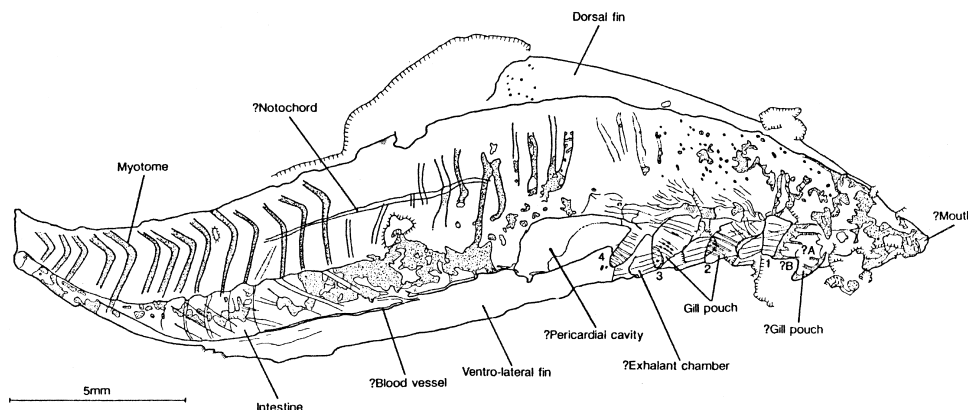


Figure 3 Camera-lucida drawing of specimen, with certain features (notably structures interpreted as extrabranchial atria) combined by reversal from the counterpart (Fig. 1c), to show interpretation. Numbers 1–4 refer to gill pouches identified with reasonable

certainty; ?A and ?B refer to more tentative identification of gill pouches, of which ?A is less certain than ?B.

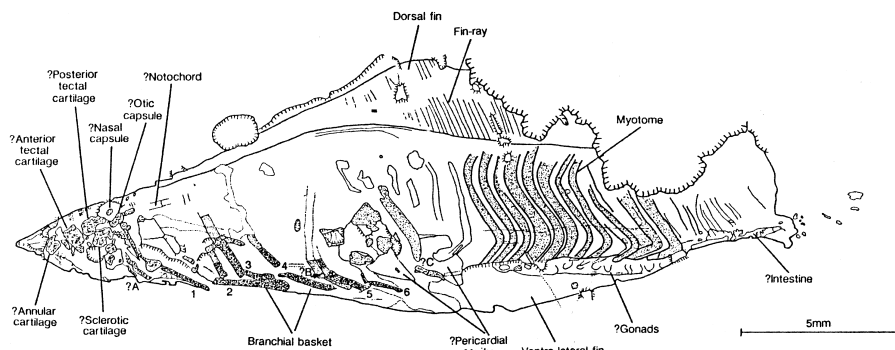
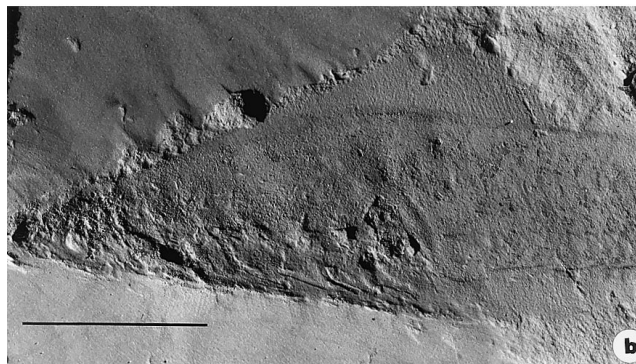


Figure 4 The Lower Cambrian agnathan vertebrate *Haikouichthys ercaicunensis* Luo, Hu & Shu gen. et sp. nov. from Haikou, Yunnan. Specimen HZ-f-12-127. **a**, Entire specimen, anterior to the left; more posterior region appears to fade out into sediment, possibly representing decay of body; attempts to excavate this area were not successful. Scale bar equivalent to 5 mm. **b**, Detail of anterior to show putative gill bars, possible elements of cranial endoskeleton, and pericardic area; scale bar equivalent to 5 mm. **c**, Camera-

lucida drawing of specimen to show interpretation. Numbers 1–6 indicate units of the branchial basket that are identified with some confidence; ?A–?C refer to less secure identifications. Two possible areas representing the pericardic cavity are indicated. To the anterior of ?C a triangular area with patches of diagenetic mineralization is one possibility; a fainter region to the posterior is the alternative location.

A sail-like dorsal fin arises fairly close to the anterior tip and increases to a maximum observed height of 1.5 mm. Its more posterior development is uncertain. On the ventro-lateral side, and more to the posterior, there is a prominent fin-fold which in the fossil is inclined at an angle to the rest of the trunk. This deflection may indicate that originally the fin-fold was paired, with the corresponding structure concealed at a deeper level within the sediment. Neither the dorsal nor the exposed ventral fin-fold display fin-radials.

The details of the head are complex (Fig. 2b, c). Most conspicuous is a series of relatively large, posteriorly inclined structures with transverse lineations. We interpret these as gill pouches with hemibranchs. Some of the latter have a beaded appearance, possibly indicating original folding or crenulation. Four pouches are clearly visible, the posteriormost being reduced in size. Anteriorly a fifth pouch is identified with some confidence, and more tentatively a sixth. Ventral to these pouches, and more clearly preserved on the counterpart (Fig. 2c), are convex (in the part) units, each with two or three longitudinal ridges. The position of these structures relative to the gill pouches is consistent with their representing extrabranchial atria (Fig. 3). The posteriormost pouch, however, appears to have lacked a well developed atrium. No branchial basket or other skeletal units have been identified in association with the gills. Other regions of the head show scattered patches of darker tissue. Apart from some segmental structures, close to the boundary with the trunk, these patches show no coherent pattern such as might represent parts of an endoskeleton. The mouth was presumably located at the anterior end and, although there is perhaps the suggestion of an annular ring (Fig. 2a, c), precise details are difficult to discern. An approximately oval area posterior to the gills may represent the pericardic cavity.

The trunk bears prominent sigmoidal segments (Figs 2a, 3), interpreted as myocommata, which in life separated about 25 myomeres. In lateral view the dorsal V points anteriorly and the ventral one posteriorly. Accordingly, on the dorsum the myomeres of either side would have converged posteriorly, and along the venter in an anterior direction. Towards the ventral margin of the trunk a dark area with positive relief presumably represents a sediment-filled intestine. The gut can be traced, more clearly in the counterpart, to the incomplete posterior termination. It is uncertain, therefore, whether *Myllokunmingia* possessed a post-anal tail. In the mid-region of the trunk there is a fairly prominent strand (Figs 2a, 3), which probably represents the incomplete remains of the notochord. At the trunk–fin-fold boundary there are very narrow dark lines, which show at least one bifurcation. These may be blood vessels.

Haikouichthys Luo, Hu & Shu gen. nov.

Haikouichthys ercaicunensis Luo, Hu & Shu sp. nov.

Etymology. After a locality at Haikou, near Kunming City, and the Greek ichthys. The specific name refers to Ercaicun, a small village close to where the specimen was found.

Holotype. Yunnan Institute of Geological Sciences, Kunming: HZ-f-12-127.

Stratigraphy and locality. As for *Myllokunmingia fengjiaoa*.

Diagnosis. Fusiform, more slender than *Myllokunmingia*, divided into head region and trunk. Prominent dorsal fin towards anterior, with fin-radials. Ventro-lateral fin-fold arising from trunk, probably paired. Head bears at least six, possibly up to nine, gill arches. Trunk with myomeres, double V as in *Myllokunmingia*. Internal anatomy includes cranial cartilages, pericardic cavity, intestine and metameric ?gonads, the last being arranged along the ventral trunk.

Description. *Haikouichthys* has a known length of about 25 mm

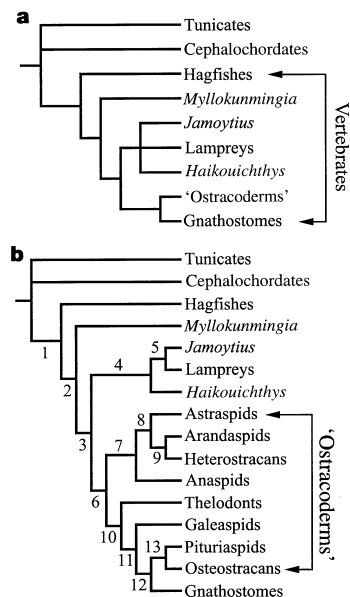


Figure 5 Phylogenetic analysis of early vertebrates, to include *Myllokunmingia* gen. nov. and *Haikouichthys* gen. nov. **a**, Strict consensus tree of the six most parsimonious trees. **b**, One of the six most parsimonious trees; the other five should show minimal differences. Data set based on refs 20 and 21. Supporting characters for each node are given in Supplementary Information.

(Fig. 4a, c). An important question is its orientation. The dorsal side is recognized on the basis of a prominent fin with fin-radials (Fig. 4b). They are inclined towards the preserved end at about 20° to the vertical. In nearly all fish, such an inclination would unequivocally indicate that the posterior end is preserved. There are, however, some rare exceptions to this rule in extant agnathans. In the second dorsal fin of lamprey the fin rays are orientated forwards in the male during the mating period¹⁶. In the hagfish, the rays at the front of the caudal fin may be vertical or even be inclined forwards¹⁷. Moreover, identification of this fossil as the posterior end would be difficult to reconcile with the complex structures, identified with varying degrees of confidence, as part of the branchial basket, cranial cartilages and a pericardic area. To our knowledge, no other living or extinct agnathan has remotely similar structures towards the posterior. The anomalous orientation of these fin-radials, therefore, is assumed to be either comparable to the similar case in the lamprey or alternatively (and less plausibly) due to post-mortem distortion.

In several respects *Haikouichthys* is similar to *Myllokunmingia*. The overall shapes are comparable, although the former is slightly more slender. The presumed head region and trunk are clearly distinguished. In the trunk the myomeres of *Haikouichthys* (Fig. 4a, c) have the same configuration as those of *Myllokunmingia*. The strongly expressed nature of the posteriorly inclined Vs may result from slightly oblique burial. The dorsal fin is more prominent than in *Myllokunmingia*, and differs in possessing closely spaced fin-radials (~7 per mm; Fig. 4b). The rather abrupt scarp between the trunk and ventro-lateral insertion of the fin-fold strongly indicates that originally the fin-folds were paired.

Several structures are visible in the anterior (Fig. 4b, c). Towards the ventral side there is a series of rod-like units, each of which consists of two components: one rod is inclined posteriorly whereas the other is more or less parallel to the ventral margin. Six sets of these units are readily discernible, two more are questionable, and a final set is only tentatively identified (Fig. 4b, c). The total number of sets, therefore, may have been as high as nine. We interpret these rods as part of a branchial basket. No associated gills or filaments are visible. Nearer to the anterior there is a complex series of miner-

alized masses. A preliminary attempt has been made to reconcile some of these areas with both units within the cranial cartilage of the lamprey¹⁸ and the eye. Adjacent to this area, a very short length of the notochord may also be visible. Close to the head–trunk boundary there is an approximately triangular area with mineralized patches. This may represent either the pericardic cavity or cavity. This, however, assumes that the structures immediately to the posterior are not part of the branchial basket. If these are branchial structures then to the posterior a rather faint pale area, consisting of two regions, is an alternative site for the pericardic cavity. Along the ventral side of the trunk there is a metameric (~13) series of roughly circular structures. These may be the remains of the gonads, although a possible alternative is slime-glands comparable to those of the hagfish¹⁸. A faint trace within the trunk may denote the intestine, and more posteriorly a dark strand may represent its continuation.

Preservation and ecology

The co-occurring fauna includes the trilobites *Eoredlichia* and *Yunnanoccephalus*, as well as exceptionally preserved fossils such as the arthropods *Naraoia* and *Waptia*. Each fossil is preserved in lateral view (Figs 2a, 4a). *Myllokunmingia* gen. nov. is almost complete. One consequence of burial is that the tail has been bent steeply into the sediment, so that the posteriormost section is not visible. This configuration, and what appears to be sediment in the pharynx, suggest that the animal was buried alive. *Haikouichthys* gen. nov. lies parallel to the bedding. The presumed posterior is absent (Fig. 4a, c), possibly owing to decay. There has been growth of sulphide minerals, especially in the head region. The extreme rarity (<0.025%) of chordates in the Chengjiang assemblages⁶ may be because they were active swimmers and could avoid being engulfed by benthic sediment flows that are believed to have been the principal method of burial¹⁹.

Phylogeny

To examine the phylogenetic positions of *Myllokunmingia* and *Haikouichthys* we compiled a data set with 16 taxa (14 vertebrates and two outgroups (tunicate, cephalochordates)) and 116 characters (see Supplementary Information). Most of the characters we used were adopted from existing matrices^{20,21}. Our analysis places both Chengjiang taxa firmly in the agnathans, with both more closely related to lampreys than to hagfishes (Fig. 5). The cladogram is fairly robust when a more cautious attitude is adopted for a number of character states that depend either on specific identifications (such as pericardic cavity) or an absence (for example, arcualia) that might in fact be preservational. Given these provisos, then, in detail *Haikouichthys* forms a monophyletic group with *Jamoytius* and lampreys, but the inter-relationships among them are unresolved. *Myllokunmingia*, however, is evidently more primitive and is basal to the clade comprising both the lamprey–*Jamoytius*–*Haikouichthys* and the ‘ostracoderms’–gnathostomes branches. The inclusion of the two Chinese fossils in this cladistic analysis is a significant extension of our knowledge of extinct agnathans. It does not, however, substantially change the internal configuration of existing cladograms in early vertebrates^{18,20–22}.

The phylogenetic implications of this discovery are significant. These agnathan vertebrates predate previous records^{11,23} by at least 20 and possibly 50 Myr (see refs 24 and 25 for Cambrian and early Ordovician radiometric time scales). The differences between *Haikouichthys* and *Myllokunmingia* indicate that, by Chengjiang times, there may already have been a diversity of forms. Neither animal shows evidence for unequivocal biomineralization, and this corroborates the hypothesis that the evolution of bone tissue was a relatively late development in the vertebrate lineage^{18,20}, although the euconodont¹², and possibly paraconodont¹⁴, record indicates that chordate biomineralization was achieved in the Cambrian. In both fossils there is evidence that the ventral fin may have been

paired. The theory of lateral fin folds²⁶ has had considerable significance²¹, but of the fossil agnathans only the anaspids¹⁸ and *Jamoytius*²⁷ have such paired fin-folds. The possible occurrence of this condition in these Lower Cambrian agnathans indicates, however, that fin-folds may be a primitive feature within the vertebrates. The occurrence of close-set dorsal fin-radials in *Haikouichthys*, on the other hand, may be a relatively advanced feature.

Wider implications

The record of Cambrian chordates is very sporadic, and also controversial. Fossils generally accepted to be of a grade comparable to the cephalochordates include the Lower Cambrian *Cathaymyrus*⁶ and Middle Cambrian *Pikaia*⁷. The former genus has been synonymized with the co-eval *Yunnanozoon*²⁸, but this is very doubtful. Moreover, the status of *Yunnanozoon* as a chordate²⁹ is also questionable³⁰, and it may be related to *Xidazoon*³¹ and other stem-group deuterostomes.

The discovery of these Lower Cambrian vertebrates has implications for the likely timing of chordate evolution. The occurrence of *Myllokunmingia* and *Haikouichthys* in the Chengjiang Lagerstätte shows that even more primitive hagfish-like vertebrates had almost certainly evolved by the beginning of the Atdabanian Stage of the Lower Cambrian. Such a find may help to elucidate the transition between the cephalochordates and the first vertebrates. The derivation of the first vertebrates from the cephalochordates must have entailed a major reorganization of the body, especially by the first effective expression of neural-crest tissue³². Key functional steps were the elaboration of the nervous system and active pharyngeal ventilation. However, the range of anatomies seen in the Cambrian cephalochordates^{6,7,9,10} indicates that our documentation of this pre-vertebrate evolutionary plexus is far from complete. It is possible that *Pikaia*, until now the cynosure of Cambrian chordates^{7,8}, is peripheral to the lineage leading to the vertebrates. It has several peculiarities. The head consists of two lobes, each of which bears a prominent, slender tentacle, the mycommata have the reverse configuration of that seen in *Myllokunmingia* and *Haikouichthys*, and the notochord stops well short of the anterior.

The major steps in the early evolution of chordates may well have occurred in the late Neoproterozoic. So far, however, no suitable fossil candidates have been identified amongst the Ediacaran assemblages, although preservation in siltstones and sandstones is less conducive to survival of delicate soft-bodied taxa. Our discovery, however, gives no reason to suppose that the origin of vertebrates was hundreds of millions of years earlier³³, and the reliability of the methods used to reach such a conclusion has been questioned elsewhere^{2,34}. □

Methods

Phylogenetic analysis

The analysis was performed using the software package PAUP 3.1 with a data set of 16 taxa and 116 characters (see Supplementary Information). The analysis was rooted on tunicates. All characters were weighted equally. Characters 62, 63 and 95 were ordered. Most parsimonious trees were identified using the branch and bound search algorithm, stepwise addition. The most parsimonious tree has: tree length, 196; consistency index, 0.628; retention index, 0.700.

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1. Conway Morris, S. *The Crucible of Creation: The Burgess Shale and the Rise of Animals* (Cambridge Univ. Press, Cambridge, 1998).
2. Valentine, J. W., Jablonski, D. & Erwin, D. H. Fossils, molecules and embryos: new perspectives on the Cambrian explosion. *Development* **126**, 851–859 (1999).

3. Conway Morris, S. & Peel, J. S. Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. *Phil. Trans. R. Soc. Lond. B* **347**, 305–358 (1995).
4. Budd, G. E. in *Arthropod Relationships* (eds Fortey, R. A. & Thomas, R. H.) *Syst. Ass. Spec. Vol. 55*, 125–138 (1997).
5. de Rosa, R. *et al.* Hox genes in brachiopods and priapulids and protostome evolution. *Nature* **399**, 772–776 (1999).
6. Shu, D.-G., Conway Morris, S. & Zhang, X.-L. A *Pikaia*-like chordate from the Lower Cambrian of China. *Nature* **384**, 156–157 (1996).
7. Conway Morris, S. in *Atlas of the Burgess Shale* (ed. Conway Morris, S.) 26 (Palaeontological Association, London, 1982).
8. Briggs, D. E. G., Erwin, D. H. & Collier, F. J. *The Fossils of the Burgess Shale* (Smithsonian, Washington, 1994).
9. Simonetta, A. M. & Insom, E. New animals from the Burgess Shale (Middle Cambrian) and their possible significance for understanding of the Bilateria. *Boll. Zool.* **60**, 97–107 (1993).
10. Insom, E., Pucci, A. & Simonetta, A. M. Cambrian Protochordata, their origin and significance. *Boll. Zool.* **62**, 243–252 (1995).
11. Young, G. C., Karatajute-Talimaa, V. N. & Smith, M. M. A possible Late Cambrian vertebrate from Australia. *Nature* **383**, 810–812 (1996).
12. Donoghue, P. C. J., Purnell, M. A. & Aldridge, R. J. Conodont anatomy, chordate phylogeny and vertebrate classification. *Lethaia* **31**, 211–219 (1998).
13. Pridmore, P. A., Barwick, R. E. & Nicoll, R. S. Soft anatomy and the affinities of conodonts. *Lethaia* **29**, 317–328 (1997).
14. Szaniawski, H. & Bengtson, S. Origin of euconodont elements. *J. Paleontol.* **67**, 640–654 (1993).
15. Luo, H. *et al.* New occurrence of the early Cambrian Chengjiang fauna from Haikou, Kunming, Yunnan province. *Acta. Geol. Sin.* **71**, 97–104 (1997).
16. Marinelli, W. & Strenger, A. *Vergleichende Anatomie und Morphologie der Wirbeltiere, 1. Lampetra fluviatilis (L.)* (Franz Deuticke, Vienna, 1954).
17. Marinelli, W. & Strenger, A. *Vergleichende Anatomie und Morphologie der Wirbeltiere, 2. Myxine glutinosa (L.)* (Franz Deuticke, Vienna, 1956).
18. Janvier, P. *Early Vertebrates* (Oxford Univ. Press, Oxford, 1996).
19. Chen, J.-Y. & Zhou, G.-Q. Biology of the Chengjiang fauna. *Bull. Natl Mus. Nat. Sci. Taiwan* **10**, 11–105 (1997).
20. Forey, P. L. Agnathans recent and fossil, and the origin of jawed vertebrates. *Rev. Fish Biol. Fisheries* **5**, 267–303 (1995).
21. Janvier, P. The dawn of the vertebrates: character versus common ascent in the rise of current vertebrate phylogenies. *Palaeontology* **39**, 259–287 (1996).
22. Forey, P. L. & Janvier, P. Evolution of the early vertebrates. *Am. Sci.* **82**, 554–565 (1994).
23. Young, G. C. Ordovician microvertebrate remains from the Amadeus Basin, central Australia. *J. Vert. Paleont.* **17**, 1–25 (1997).
24. Landing, E. *et al.* Duration of the Early Cambrian: U-Pb ages of volcanic ashes from Avalon and Gondwana. *Can. J. Earth Sci.* **35**, 329–338 (1998).
25. Landing, E. *et al.* U-Pb zircon date from Avalonian Cape Breton Island and geochronologic calibration of the Early Ordovician. *Can. J. Earth Sci.* **34**, 724–730 (1997).
26. Goodrich, E. S. Notes on the development, structure, and origin of the median and paired fins of fish. *Q. J. Microsc. Sci.* **50**, 333–376 (1906).
27. Ritchie, A. New evidence on *Jamoytius kerwoodi*, an important ostracoderm from the Silurian of Lanarkshire. *Palaeontology* **11**, 21–39 (1968).
28. Chen, J.-Y. & Li, C. Early Cambrian chordate from Chengjiang, China. *Bull. Natl Mus. Nat. Sci. Taiwan* **10**, 257–273 (1997).
29. Chen, J.-Y. *et al.* A possible early Cambrian chordate. *Nature* **377**, 720–722 (1995).
30. Shu, D.-G., Zhang, X. & Chen, L. Reinterpretation of *Yunnanozoon* as the earliest known hemichordate. *Nature* **380**, 428–430 (1996).
31. Shu, D. *et al.* A pipiscid-like fossil from the Lower Cambrian of South China. *Nature* **400**, 746–749 (1999).
32. Gans, C. & Northcutt, R. G. Neural crest and the origin of vertebrates: A new head. *Science* **220**, 268–274 (1983).
33. Bromham, L. *et al.* Testing the Cambrian explosion hypothesis by using a molecular dating technique. *Proc. Natl Acad. Sci. USA* **95**, 12386–12389 (1998).
34. Ayala, F. J., Rzhetsky, A. & Ayala, F. J. Origin of the metazoan phyla: Molecular clocks confirm paleontological estimates. *Proc. Natl Acad. Sci. USA* **95**, 606–611 (1998).

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