A *Pikaia*-like chordate from the Lower Cambrian of China

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The earliest evolution of the chordates and their relationships with other deuterostomes remains controversial[1–3]. Rejuvenation of interest in the areas of molecular phylogeny[4] and developmental genetics[5–7] has not been matched by new insights from the fossil record, which for the Lower and Middle Cambrian remains exceptionally sparse. The supposed chordate *Emmonsaspis*[8] has been shown to be a frond-like fossil[9], and phosphatic sclerites of hadimopanellids, once compared with vertebrate dermal armour[10,11], are now known to be derived from the cuticle of protostome palaeoscolecidan worms[12,13]. Other fragmentary material of supposed scales is even more dubious[14]. The best-known candidate in this thin roster remains the Burgess Shale chordate *Pikaia*[15]. Here we report a single specimen of a Lower Cambrian chordate, *Cathaymyrus diadexus*, new genus and species, that is similar to *Pikaia* but predates it by about 10 million years (Myr). Important features of this new specimen are structures interpreted as pharyngeal gill slits. The evolution of chordates was an integral part of the first stages of the Cambrian 'explosion', and steps to craniates with neural crest were probably achieved by the Middle Cambrian.

A single example (part and counterpart) of an early chordate from the Chengjiang Lagerstätte of Yunnan, China, was collected in 1995. This deposit is already celebrated for its superbly preserved soft-bodied fauna[16,17], which is similar to the Middle Cambrian Burgess Shale[18]. This animal is rare: so far only one specimen has been recognized in collections that now exceed 10,000 specimens. The specimen (Fig. 1*a*) is about 22 mm long, with a sinuous eel-like disposition. The anterior appears to show a modest expansion and contains a concave ovoid area, still partially filled with sediment. This structure presumably represents the pharynx. Closely spaced (about 16 per mm) transverse striations on the pharynx (Fig. 1*b*) are interpreted as gill slits (Fig. 2). The remainder of the body is segmented, and although faintly preserved, the arrangement of the transverse structures is consistent with that of myotomes, separated by the myocommata. Although their sigmoidal shape is clear, the quality of preservation and the possibility of superposition of either side makes a description of the precise configuration difficult. Evidence for an abrupt geniculation in some myotomes (Figures 1*a* and 2) may, however, be consistent with their having a more complex shape than the simple vee-shapes that occur in amphioxus. A rather prominent but narrow ridge runs longitudinally. This may be a product of compaction, or conceivably it represents an internal structure such as the notochord, which in amphioxus is known to be relatively resistant to decay[19]. If it is the notochord then it appears to terminate short of the head region. Parallel to this prominent ridge is a much fainter and more discontinuous structure. This could be an internal organ such as the gut. The posterior terminates in a fine tip. In this specimen there is no evidence for either fins or fin rays. Alternative explanations, notably that the structures interpreted here as gill slits are in fact fin rays similar to those in the tail of hag fish, remain possibilities, but are considered less likely.

This Chengjiang fossil has a striking resemblance to the Burgess Shale animal, *Pikaia gracilens* (Fig. 1*c*), generally accepted as a primitive chordate[15]. Similarities include overall shape, anterior pharynx, whose sediment-filled nature indicates an original spaciousness, myotomes, and possible notochord. Features equivalent to the structures interpreted as gill slits, however, have not been clearly observed in *Pikaia*, although the preservational history of the Burgess Shale is different from the Chengjiang sediments on account of the former experiencing a significantly greater degree of compaction and heating, leading to what is effectively a metamorphic rock[20]. Future discoveries from Chengjiang or nearby localities should resolve whether the similarities to *Pikaia* include a distinctive bilobed head with narrow tentacles and a series of short appendages extending from either side of the anterior region[15]. The connection, if any, of these short appendages with the presumed pharyngeal gill slits is uncertain. They are much more widely spaced than the transverse structures in the Chengjiang animal (Fig. 1*b*), and in *Pikaia* these appendages also

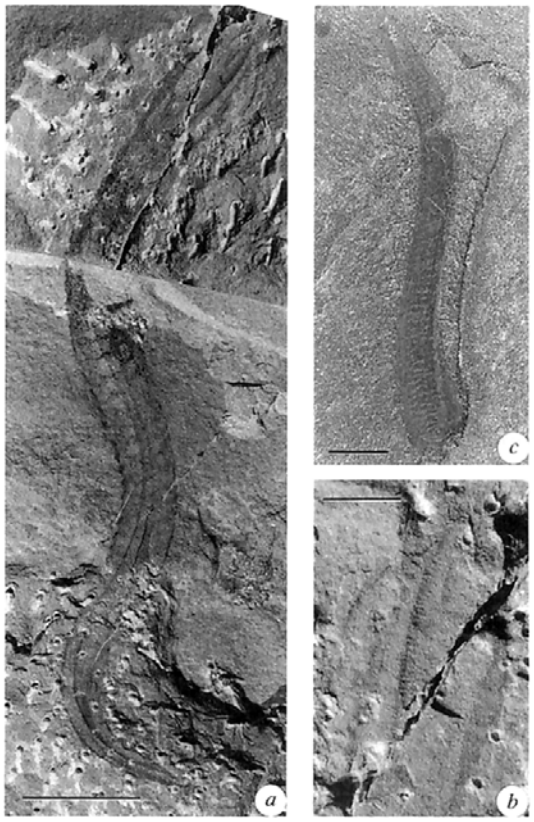

FIG. 1 The Cambrian cephalochordates *Cathaymyrus diadexus*, new species, and *Pikaia gracilens* Walcott. The specimen from the Chengjiang lies obliquely to the plane of bedding so that the anterior and posterior ends of part and counterpart, respectively, required excavation. In many specimens of *Pikaia*, including USNM 198694, parts of the body are folded beneath other regions. This is a result of the body being laterally flattened and transported in a turbulent mud-flow. *a*, *Cathaymyrus diadexus*, new species, NWU 95-1405, composite photograph of part and counterpart. Anterior region (compare with Fig. 2) has been printed with negative reversed and then mounted against the unreversed posterior region which remains, therefore, in its correct configuration. The reasons for this is that the oblique nature of the split resulted in the part consisting of the anterior half and the corresponding counterpart to the posterior half of the specimen. Only a limited region of the mid-section of the body was originally visible in part and counterpart, and mechanical excavation in either direction was necessary to expose the entire specimen. Scale bar, 3 mm. *b*, *Cathaymyrus diadexus*, new species, detail of anterior region including pharynx and gill slits. Photograph is in correct (unreversed) orientation. Scale bar, 1 mm. c, *Pikaia gracilens* Walcott, USNM 198694, notochord runs along the right-hand side. Note also the myotomes. Posterior of body is bent beneath rest of body. Scale bar, 5 mm.

extend posterior to the sediment-filled region interpreted as the pharynx. If connected, they may represent exhalant openings. Evidence for the notochord stopping well short of the anterior in *Pikaia*[15] (Fig. 1*c*), and possibly this Chengjiang animal (Figs 1*a* and 2), may be significant. In amphioxus, the notochord only extends into the rostral region later in embryology[21], even though *Brachyury* transcripts are expressed along the entire length of the notochord[7].

A detailed consideration of the place of the Cambrian taxa *Cathaymyrus* and *Pikaia* in early chordate phylogeny awaits further discoveries of the former animal and/or a detailed assessment of the hundred-plus specimens of *Pikaia* (S.C.M. and D. Collins, manuscript in preparation). Although the living cephalochordates are known only from the two genera grouped as the amphioxus animal, on present evidence it seems legitimate to include provisionally *Cathaymyrus* and *Pikaia* in this subclass as they appear to lack tissues associated with the neural crest. The amphioxus animal would retain its status as the most primitive living chordate, but known differences with the Cambrian taxa, such as anterior extent of the notochord and disposition of gill slits, would indicate its own degree of specialization. Concerning the calcichordate hypothesis, which remains very controversial[22], this discovery of a Lower Cambrian chordate emphasizes the present incongruity between interpretation of calcichordate anatomical characters (and their placement in a particular cladistic framework[3]) and the stratigraphic evidence that points to the emergence of the chordates substantially earlier in the Cambrian.

Recently, doubt[23] has been thrown on the thesis that the Lower Cambrian fossil *Yunnanozoon lividum*, also from Chengjiang, is a chordate[24,25]. For example, the supposed notochord appears to have gut contents. In addition, the putative myotomes have no indication of the 'cone-in-cone' musculature seen in chordates (or its sigmoidal surface expression that is clearly expressed in *Cathaymyrus* and *Pikaia*), but transpire to be cuticularized segments with clear evidence of post-mortem wrinkling. The specimen described here also gives no support to the earlier interpretation of *Yunnanozoon* as a chordate[24–26]. An affinity of this taxon with the hemichordates[23] fits the present evidence best, but even this hypothesis may require some further consideration. Why, for example, are the structures interpreted as gill slits so widely spaced in comparison with the balanoglossid acorn-worms, amphioxus, and this Chengjiang chordate?

The Chengjiang biota is generally regarded as late Atdabanian, although some correlations indicate a Botomian-equivalent age[27]. Thus, perhaps 10 Myr separate this assemblage from the time of deposition of the Burgess Shale. Burgess Shale-type faunas, however, show a pronounced conservatism[18] and the evolutionary steps to the craniates with neural crest tissue were probably well underway during this geological interval. This is because of the recognition of the conodonts as vertebrates[28,29], and the evidence that the paraconodonts, which appeared in the Middle Cambrian, are the direct evolutionary predecessors of conodonts[30]. It also remains to be seen what fossil evidence may become available concerning both the hemichordate/echinoderm–chordate transition and, more importantly perhaps, the deuterostome–protostome divergence.

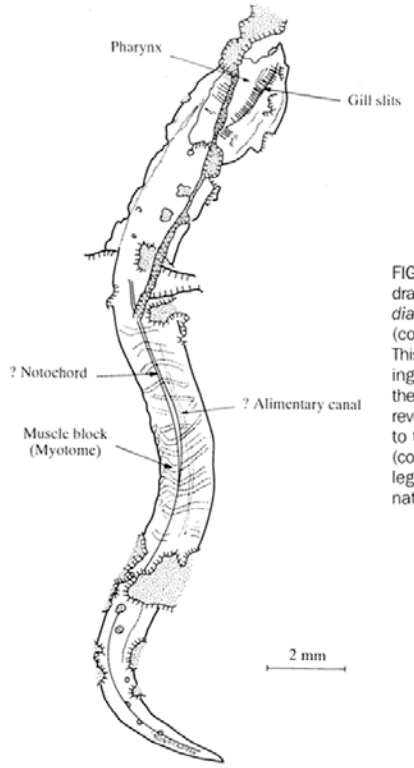

FIG. 2 Camera lucida drawing of *Cathaymyrus diadexus*, new species (compare with Fig. 1*a*). This interpretative drawing is a composite, with the anterior section (part) reversed and connected to the posterior section (counterpart). See Fig. 1 legend for a full explanation.

Phylum Chordata
Class Cephalochordata
Cathaymyrus diadexus gen. et sp. nov.

Diagnosis. Angulliform cephalochordate with anterior, possibly expanded, containing large pharynx and associated closely spaced gill slits. Trunk with myomeres, tapering to fine point.

Type (and only known) species. *Cathaymyrus diadexus*.

Etymology. *Myrus* (Latin) refers to the fossil's eel-like shape, *Cathay* to its provenance in China. Greek *diadexus*, presaging good luck, in anticipation of future discoveries.

Holotype. Department of Geology, Northwest University, Xi'an: NWU 95-1405.

Stratigraphy and locality. Qiongzhusi (Chiungchussu) Formation, Yu'anshan Member (*Eoredlichia* Zone); Lower Cambrian. Specimen collected from the Ma'anshan section, a new productive locality of the Chengjiang Lagerstätte, situated 3 km north of the classic Maotianshan section. □

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