use change. *Science* **285,** 574–578 (1999).
22. Field, C. B. & Fung, I. Y. The not-so-big U.S. carbon sink. *Science* **285,** 544–545 (1999).
23. Oren, R. in *Plant Response to Air Pollution* (eds Iqbal, M. & Yunus, M.) 75–98 (John Wiley & Sons, Chichester, UK, 1996).
24. Kicklighter, D. W. *et al.* A first-order analysis of the potential role of CO_2 fertilization to affect global carbon budget: a comparison of four terrestrial biosphere models. *Tellus B* **51,** 343–366 (1999).
25. Vitousek, P. M. Beyond global warming: Ecology and global change. *Ecology* **75,** 1861–1876 (1994).
26. Hendrey, G. R., Ellsworth, D. S., Lewin, K. F. & Nagy, J. A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO_2. *Global Change Biol.* **5,** 293–309 (1999).
27. Tissue, D. T., Thomas, R. B. & Strain, B. R. Growth and photosynthesis of loblolly pine (*Pinus taeda*) after exposure to elevated CO_2 for 19 months in the field. *Tree Physiol.* **16,** 49–60 (1996).
28. Naidu, S. L., DeLucia, E. H. & Thomas, R. B. Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Can. J. For. Res.* **28,** 1116–1124 (1998).
29. Sokal, R. R. & Rohlf, F. J. *Biometry* (W. H Freeman and Co., San Francisco, 1969).
30. Bolin, B., Canadel, J., Moore, B., Noble, I. & Steffen, W. Effect on the biosphere of elevated atmospheric CO_2. *Science* **285,** 1851–1852 (1999).

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An Early Cambrian tunicate from China

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Like the Burgess Shales of Canada, the Chengjiang Lagerstätte from the Lower Cambrian of China is renowned for the detailed preservation as fossils of delicate, soft-bodied creatures[1–9], providing an insight into the Cambrian explosion. The fossils of possible hemichordate chordates[5–7] and vertebrates[9] have attracted particular attention. Tunicates, or urochordates, comprise the most basal chordate clade[10], and details of their evolution could be important in understanding the sequence of character acquisition that led to the emergence of chordates and vertebrates[11–18]. However, definitive fossils of tunicates from the Cambrian are scarce or debatable[4,9,19–24]. Here we report a probable tunicate *Cheungkongella ancestralis* from the Chengjiang fauna. It resembles the extant ascidian tunicate genus *Styela* whose morphology could be useful in understanding the origin of the vertebrates.

Phylum Chordata
Subphylum Urochordata
Class Ascidiacea
Cheungkongella ancestralis gen. et sp. nov.

Type species. *Cheungkongella ancestralis*.
Etymology. Genetic name is a metaphor of China and is also in honour of the Cheungkong Scholars Programme that supports this work; the specific name is a reference to its possible primitive position.
Holotype. Early Life Institute (ELI), Northwest University, Xi'an: ELI-0000195.
Stratigraphy and locality. Qiongzhusi Formation, Yu'anshan Member (*Eoredlichia* Zone); Lower Cambrian. The specimen was collected by L.C. and J.H. from the same locality and horizon as the animal *Xidazoon*[8] and agnathan vertebrate *Myllokunmingia*[9].
Diagnosis. The body is club-shaped, reminiscent of extant ascidian *Styela*, with two-fold division: an upper main body and a lower thick supporting stem attached to hard substratum (Fig. 1). The body is wholly enclosed within a structure interpreted as a secreted tunic. The stem tapers downward, and the main body is bucket-shaped in outline, bearing a large oral siphon with short tentacles on its top and a small cloacal one on the lower dorsal side. A pharynx occupies over two-thirds of the body volume.
Description. *Cheungkongella ancestralis*, new genus and species, is known from a single specimen, with a total length of about 25 mm. The whole body consists of two regions: a stout stem, which in life supported a sub-spherical main body. The stem (about 15 mm long) tapers distally, and is attached to the exterior surface of the left, free cheek of a trilobite *Eoredlichia intermedia*, an index fossil for the Lower Cambrian. The stem bears some transverse creases, consistent with an enclosing tunic, and prominent longitudinal 'ribs'. The distal section has a conspicuously coarse texture, and has several patches of agglutinated sediment including quartz grains.

The main body (roughly 10 mm long) was probably sub-spherical in life. Wrinkling of the compressed body on the ventral side (opposite to cloacal siphon) is consistent with folding of a tough

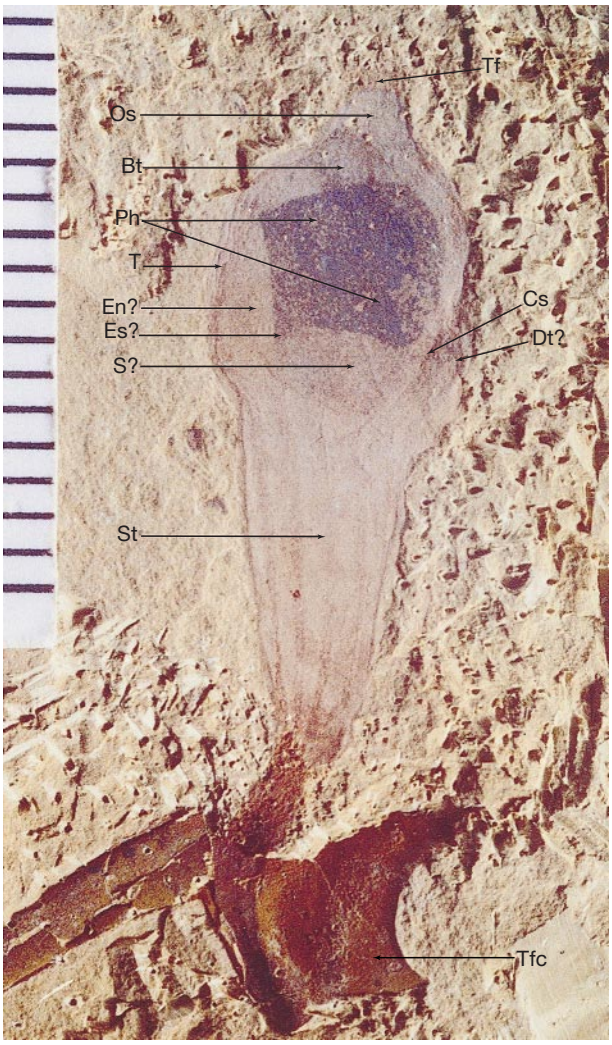

Figure 1 The Lower Cambrian urochordate *Cheungkongella ancestralis* gen. et sp. nov. from Haikou, Kunming, Yunnan. Specimen ELI-0000195, viewed from the left. Scale bar, 1 mm. Bt, buccal tentacles; Cs, cloacal siphon; Dt?, degenerating tail; Os, oral siphon; En?, presumed endostyle; Es?, possible esophagus; Ph, pharynx; S?, presumed stomach; St, stem; T, tunic; Tf, tentacle-like fringe; Tfc, trilobite free cheek.

tunic. The large funnel-like structure filled with a layer of sediment on the top is interpreted as the oral siphon, as is found in all solitary ascidians. To the lower right of the main body, presumably representing the original dorsal side, a narrow but distinct extension is interpreted as the excurrent (or cloacal) siphon, and is consistent with a rather marked change in level in this area. Lower and outside to the cloacal siphon there is an arcuate area, where there is a recongnizable recurvate dark ridge. This structure is difficult to interpret, but when compared to the last stage of metamorphosis of living ascidians[25], it could represent the remnant of a larval tail.

A prominent rectangular dark area, covered with numerous lighter dots, is located in the upper part of the body cavity. The lower ventral corner of the dark area extends downward as a 'tail-like' structure. The dark area, compared to modern ascidians, with its dextral configuration, large size and appropriate location in the body, is consistent with its identification as the pharynx. Whether the lighter dots represent gill openings remains to be confirmed.

Two interesting structures are located above and below the oral siphon. The area between the siphon and the pharynx is preserved in dark grey. Observation shows a longitudinal alignment of structures suggestive of buccal tentacles. Above the oral siphon, another set of short tentacle-like filaments is recognizable. They are superficially similar to siphonal fringe or oral lobes of some extant ascidians, but are also reminiscent of the tentacles of extant lophophorate phoronids and the Lower Cambrian lophophorate *Cambrotentacus*[4]. We suggest that this Cambrian tunicate was a suspension feeder, with water entering the oral siphon and being expelled through the cloacal siphon after filtration.

The main body and upper two-thirds of the supporting stem lie laterally on the same bedding plane, but the lower third of the stem is bent steeply into the sediment and attached to a free cheek of a trilobite. This arrangement could indicate burial of the tunicate *in situ*. The presence of agglutinated quartz grains, substantially coarser than the surrounding matrix, on the lower stem suggests, however, that the animal inhabited a higher-energy, sandy sea floor and was transported to its point of burial. During deposition the heavier trilobite sclerite sank first, so tethering the tunicate in the rapidly accumulating sediment. The three-dimensional preservation and remains of the delicate tentacles are indicative of its suffering little decomposition.

Urochordata are believed to represent the most basal chordate branch within Chordata[11,26]; however, whether the ancestral chordates were free-swimming or sessile has been a long-standing question[18,26,27]. Traditional hypotheses hold that vertebrates evolved by paedomorphosis from a urochordate-like larval stage, and that the ancestor of chordates would have resembled a sessile lophophorate[12,13,27]. Recent models, supported by molecular data, posit a free-swimming ancestry of chordates, including urochordates[28–30].

Fossils may preserve combinations of characters not seen in extant groups, and so are crucial for testing schemes of how characters were acquired in the origin of new body plans. The interpretation of the present specimen, as possessing oral tentacles comparable to those seen in lophophorates, is consistent with traditional views—if not modern, molecule-based hypotheses—but a single example is far from being conclusive. Further palaeontological and molecular work is needed to investigate the problem. □

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1. Shu, D.-G., Geyer, G., Chen, L. & Zhang, X.-L. Redlichiacean trilobites with preserved soft-parts from the Lower Cambrian Chengjiang fauna. *Beringaria Spec. Iss.* **2,** 203–241 (1995).
2. Shu, D.-G., Zhang, X. & Geyer, G. Anatomy and systematic affinities of Lower Cambrian bivalved arthropod *Isoxys auritus*. *Alchringa* **19,** 333–342 (1995).
3. Hou, X. & Bergstrom, J. Arthropods of the Lower Cambrian Chengjiang fauna, southwest China. *Fossils Strata* **45,** 1–115 (1997).
4. Zhang, X.-L., Shu, D.-G., Li, Y. & Han, J. New sites of Chengjiang fossils: crucial windows on the Cambrian explosion. *J. Geol. Soc. Lond.* **158,** 211–218 (2001).
5. Chen, J.-Y., Dzik, J, Edgecombe, G. D., Ramskoeld, L. & Zhou, G.-Q. A possible early Cambrian chordate. *Nature* **377,** 720–722 (1995).
6. Shu, D.-G. & Zhang, X.-L. Reinterpretation of *Yunnanozoon* as the earliest known hemichordate. *Nature* **380,** 428–430 (1996).
7. Shu, D.-G., Conway Morris, S. & Zhang, X.-L. A *Pikaia*-like chordate from the Lower Cambrian of China. *Nature* **384,** 156–157 (1996).
8. Shu, D. *et al.* A pipiscid-like fossil from the Lower Cambrian of South China. *Nature* **400,** 746–749 (1999).
9. Shu, D. *et al.* Lower Cambrian vertebrates from South China. *Nature* **402,** 42–46 (1999).
10. Cameron, C. B., Garey, J. R. & Swalla, B. J. Evolution of the chordate body plan: new insights from phylogenetic analyses of deuterostome phyla. *Proc. Natl Acad. Sci. USA* **97,** 4469–4474 (2000).
11. Garstang, W. The morphology of the Tunicata and its bearing on the phylogeny of the Chordata. *J. Microscop. Soc.* **72,** 51–87 (1928).
12. Romer, A. S. *The Vertebrate Story* (Univ. Chicago Press, 1971).
13. Gee, H. *Before the Backbone: Views on the Origins of Vertebrates* (Chapman and Hall, London, 1996).
14. Ogasawara, M., Di Lauro, R. & Satoh, N. Ascidian homologs of mammalian thyroid transcription Factor-1 gene expressed in the endostyle. *Zool. Sci.* **16,** 559–565 (1999).
15. De Gregorio, A. & Levine, M. Ascidian embryogenesis and the origins of the chordate body plan. *Curr. Opin. Genet. Dev.* **8,** 457–463 (1998).
16. Swalla, B. J. *et al.* Urochordates are monophyletic within the deuterostomes. *System. Biol.* **49,** 52–64 (2000).
17. Nielsen, C. *Animal Evolution: Interrelationships of Living Phyla* (Oxford Univ. Press, Oxford, 1997).
18. Conway Morris, S. in *Atlas of the Burgess Shale* (ed. Conway Morris, S.) 26 (Palaeontological Association, London, 1982).
19. Briggs, D. E. G. *et al. The Fossils of the Burgess Shale* (Smithsonian, Washington, 1994).
20. Satoh, N. *Developmental Biology of Ascidians* (Cambridge Univ. Press, New York, 1994).
21. Mueller, K. J. Palaeobotryllus from the Upper Cambrian of Nevada—a possible ascidian. *Lethaia* **10,** 107–118 (1977).
22. Lehnert, O., Miller, J. F. & Cochrane, K. Alaeobotryllus and friends: Cambro-Ordovician record of probable ascidian tunicates. *Acta Univ. Carol. Geol.* **43,** 447–450 (1999).
23. Lohmann, H. Oesia disjuncta Walcott, eine Appendicularie aus dem Kambrium. *Mitt. Zool. Mus. Hamburg* **38,** 69–75 (1922).
24. Zhang, A. Fossil appendicularians in the early Cambrian. *Scient. Sinica B* **30,** 888–896 (1987).
25. Meglitsch, P. A. & Schram, F. P. *Invertebrate Zoology* 3rd edn, 576–587 (Oxford Univ. Press, 1991).
26. Wada, H. & Satoh, N. Details of the evolutionary history from invertebrates to vertebrates, as deduced from the sequences of 18S rDNA. *Proc. Natl Acad. Sci. USA* **91,** 1801–1804 (1994).
27. Berrill, N. J. *The Origin of Vertebrates* (Oxford Univ. Press, Oxford, 1955)
28. Carter, G. S. Chordate Phylogeny. *Syst. Zool.* **6,** 187–192 (1957).
29. Jollie, M. What are the 'Calcichordata'? and the larger question of the origin of chordates. *Zool. J. Linn. Soc.* **75,** 167–188 (1982).
30. Wada, H. Evolutionary history of free-swimming and sessile lifestyles in urochordates as deduced from 18S rDNA molecular phylogeny. *Mol. Biol. Evol.* **15,** 1189–1194 (1998).

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Orientation-selective adaptation and tilt after-effect from invisible patterns

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Exposure to visual patterns of high contrast (for example, gratings formed by alternating white and black bars) creates after-effects in perception. We become temporarily insensitive to faint test patterns that resemble the pre-exposed pattern (such as gratings of the same orientation), and we require more contrast to detect them[1]. Moreover, if the test pattern is slightly tilted relative to the pre-exposed one, this tilt may be perceptually exaggerated: we experience a tilt after-effect[2,3]. Here we show that these visual after-effects occur even if the pre-exposed grating is too fine to be perceptually resolved. After looking at a very fine grating, so high