

particulates on the background concentration of CCN over the ocean could also have an effect on regional and global radiative budgets. To estimate this effect, we apply the fuel-based emission factors for particulate matter reported by Lloyds<sup>26</sup> to generate total annual particulate-matter emissions for ships (0.85 Tg yr<sup>-1</sup>). This is then globally distributed according to the method of Corbett and Fischbeck<sup>2,3</sup> to give us the emission rate of particulate matter ( $E_{x,y}$ ) for any grid cell ( $x, y$ ). We can then estimate the change in the CCN number,  $\Delta\text{CCN}_{x,y}$ , assuming steady state for the CCN concentration and using

$$\Delta\text{CCN}_{x,y} = \frac{E_{x,y}}{v_{\text{dep}}} f_m(D_p^*) N(D_p^*) \quad (1)$$

where  $v_{\text{dep}}$  is the average CCN removal velocity (wet and dry),  $f_m$  is the CCN mass fraction of the emitted particulate matter,  $N$  is the number density of CCN (number per mass larger than  $D_p^*$ ) emitted by ships, and  $D_p^*$  is minimum diameter at which these particles activate to form cloud drops. Based on the particulate-matter size-distribution measurements of Lyyranen *et al.*<sup>27</sup>, for large engines operating at full power, and assuming a  $D_p^*$  of 0.1  $\mu\text{m}$ , we estimate  $f_m$  to be 0.6 (CCN per g particulate matter emitted) and  $N$  to be  $10^{14}$  CCN per g of CCN. In addition, we assume a CCN lifetime of three days ( $v_{\text{dep}} = 0.4 \text{ cm s}^{-1}$ ). Assuming as a first-order approximation that the change in cloud droplet number is equal to  $\Delta\text{CCN}$  for the low CCN concentrations of the marine environment ( $100 \text{ cm}^{-3}$ ), the potential effect of ships on annual average cloud albedo and radiative forcing can be estimated<sup>28</sup>. To avoid problems with the nonlinear response of cloud droplet number to CCN concentration, and to keep our radiative forcing estimate conservative, we only consider ship particulate-matter emissions where continental influence is small. This is determined using our annual average model predictions for NSS-sulphate (with ships) and a threshold of 0.2 p.p.b.v. NSS-sulphate.

Using this method, we estimate the change in global radiative forcing due to cloud effects from ship particulate-matter emissions to be  $-0.11 \text{ W m}^{-2}$ . This value is 14% of the IPCC estimate for 1990 global indirect forcing from all anthropogenic sulphate<sup>29</sup>. The predicted average change in radiative forcing due to ships for the Northern Hemisphere is  $-0.16 \text{ W m}^{-2}$  and for the Southern Hemisphere is  $-0.06 \text{ W m}^{-2}$ . The direct effect of ship sulphur emissions is expected to be less dramatic<sup>28</sup>. The sensitivity of our estimate to various uncertain input parameters is shown in Table 1. As can be seen, reasonable variation in individual input parameters can affect this first-order global estimate by at least a factor of 2.

Our results suggest that the emissions of sulphur and particulate matter from the international shipping industry need to be considered in the study of marine and coastal atmospheres. Because ship emissions, as a source of background sulphur, have been neglected in the past, many observational studies of the marine atmosphere need to be re-evaluated, particularly those in the remote oceans of the Northern Hemisphere. □

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1. Charlson, R. J., Lovelock, J. E., Andreae, M. O. & Warren, S. G. Oceanic phytoplankton, atmospheric sulphur, cloud albedo, and climate. *Nature* **336**, 655–661 (1987).
2. Corbett, J. J. & Fischbeck, P. S. Emissions from ships. *Science* **278**, 823–824 (1997).
3. Corbett, J. J., Fischbeck, P. S. & Pandis, S. N. Global nitrogen and sulfur emissions inventories for oceangoing ships. *J. Geophys. Res.* **104**, 3457–3470 (1999).
4. Benkovitz, C. M. *et al.* Global gridded inventories of anthropogenic emissions of sulfur and nitrogen. *J. Geophys. Res.* **101**, 29239–29253 (1996).
5. Kasibhatla, P., Chameides, W. L. & St John, J. A three-dimensional global model investigation of seasonal variations in the atmospheric burden of anthropogenic sulfate aerosols. *J. Geophys. Res.* **102**, 3737–3759 (1997).
6. Pham, M., Muller, J.-F., Brasseur, G. P., Granier, C. & Mégie, G. A three-dimensional study of the tropospheric sulfur cycle. *J. Geophys. Res.* **100**, 26061–26092 (1995).
7. Benkovitz, C. M. *et al.* Sulfate over the North Atlantic and adjacent continental regions: evaluation for October and November 1986 using a three-dimensional model driven by observation-derived meteorology. *J. Geophys. Res.* **99**, 20725–20756 (1994).
8. Capaldo, K. & Pandis, S. Dimethylsulfide chemistry in the remote marine atmosphere: Evaluation and sensitivity analysis of available mechanisms. *J. Geophys. Res.* **102**, 23251–23267 (1997).
9. Davison, B. & Hewitt, C. N. Elucidation of the troposphere reactions of biogenic sulfur species from a field measurement campaign in NW Scotland. *Chemosphere* **28**, 543–557 (1994).

10. Davison, B. *et al.* Dimethyl sulfide, methane sulfonic acid and physicochemical aerosol properties in Atlantic air from the United Kingdom in Halley Bay. *J. Geophys. Res.* **101**, 22855–22867 (1996).
11. De Bruyn, W. J., Bates, T. S., Caine, J. M. & Saltzman, E. S. Shipboard measurements of dimethylsulfide and SO<sub>2</sub> southwest of Tasmania during the first Aerosol Characterization Experiment (ACE 1). *J. Geophys. Res.* **103**, 16703–16711 (1998).
12. Ferek, R. J. *et al.* Dimethyl sulfide in the Arctic atmosphere. *J. Geophys. Res.* **100**, 26093–26104 (1995).
13. Pio, C. A., Cerqueira, M. A., Castro, L. M. & Salgueiro, M. L. Sulphur and nitrogen compounds in variable marine/continental air masses at the southwest European coast. *Atmos. Environ.* **30**, 3115–3127 (1996).
14. Talbot, R. W. *et al.* Chemical characteristics of continental outflow from Asia to the troposphere over the western Pacific Ocean during February–March 1994: Results from PEM-West B. *J. Geophys. Res.* **102**, 28255–28274 (1997).
15. Thornton, D. C. & Bandy, A. R. Sulfur dioxide and dimethyl sulfide in the central Pacific troposphere. *J. Atmos. Chem.* **17**, 1–13 (1993).
16. Bandy, A. R., Scott, D. L., Blomquist, B. W., Chen, S. M. & Thornton, D. C. Low yields of SO<sub>2</sub> from dimethyl sulfide oxidation in the marine boundary layer. *Geophys. Res. Lett.* **19**, 1125–1127 (1992).
17. Hertel, O., Christensen, J. & Hov, O. Modelling of the end products of the chemical decomposition of DMS in the marine boundary layer. *Atmos. Environ.* **28**, 2431–2449 (1994).
18. Saltelli, A. & Hjorth, J. Uncertainty and sensitivity analyses of OH-initiated dimethyl sulphide (DMS) oxidation kinetics. *J. Atmos. Chem.* **21**, 187–221 (1995).
19. Suhre, K. *et al.* Physico-chemical modeling of the first Aerosol Characterization Experiment (ACE 1) Lagrangian B1: A moving column approach. *J. Geophys. Res.* **103**, 16433–16455 (1998).
20. Carlton, J. S., Wright, A. A. & Coker, R. J. *Marine Exhaust Emissions—A Regional Survey of the English Channel* (Marine Management (Holdings) Ltd, London, 1994).
21. Port of Los Angeles, Port of Long Beach, Dames & Moore, Morrison and Foerster *Control of Ship Emission in the South Coast Air Basin: Assessment of the Proposed Federal Implementation Plan Ship Fee Emission Fee Program* (Port of Los Angeles, Los Angeles, California, 1994).
22. *Nonroad Engine and Vehicle Emission Study* (US Environmental Protection Agency, Washington DC, 1991).
23. Radke, L. F., Coakley, J. A. Jr & King, M. D. Direct and remote sensing observations of the effects of ships on clouds. *Science* **246**, 1146–1149 (1989).
24. King, M. D., Radke, L. F. & Hobbs, P. V. Optical properties of marine stratocumulus clouds modified by ships. *J. Geophys. Res.* **98**, 2729–2739 (1993).
25. Ferek, R. J., Hegg, D. A., Hobbs, P. V., Durkee, P. & Nielsen, K. Measurements of ship-induced tracks in clouds off the Washington coast. *J. Geophys. Res.* **103**, 23199–23206 (1998).
26. Carlton, J. S. *et al.* *Marine Exhaust Emissions Research Programme* (Lloyd's Register Engineering Services, London, 1995).
27. Lyyranen, J., Jokiniemi, J., Kauppinen, E., Joutsensaari, J. & Auvinen, A. Particle formation in medium speed diesel engines operating with heavy fuel oils. *J. Aerosol Sci.* **29**, S1003–S1004 (1998).
28. Seinfeld, J. H. & Pandis, S. N. *Atmospheric Chemistry and Physics: From Air Pollution to Climate Change* (Wiley & Sons, New York, 1998).
29. IPCC *Radiative Forcing of Climate Change. The 1994 Report of the Scientific Assessment Working Group of the Intergovernmental Panel on Climate Change (IPCC)* (Cambridge Univ. Press, 1995).

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## A pipiscid-like fossil from the Lower Cambrian of south China

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Exceptional fossil preservation is critical to our understanding of early metazoan evolution. A key source of information is the Burgess Shale-type faunas<sup>1–5</sup>. Fossils from these deposits provide important insights into metazoan phylogeny, notably that of stem-group protostomes<sup>2,3,6</sup>, and related topics such as trophic specialization<sup>7</sup>. Metazoan relationships are also being significantly reappraised in terms of molecular-based phylogenies<sup>8,9</sup>, but integration of these data with palaeontological systematics is not straightforward<sup>10,11</sup>. Moreover, molecular phylogenies are silent concerning the anatomies of stem-groups and the functional transitions that underpin the origin of different body plans<sup>2,6</sup>. Some hitherto enigmatic fossils possess unique character-state combinations that, although they can be shoe-horned into extinct phyla<sup>12</sup>, may be more profitably interpreted as defining major stem-groups<sup>2,3</sup>. Here we describe a possible pipiscid, a metazoan previously known only from the Upper Carboniferous<sup>13,14</sup>, from the Lower Cambrian of south China. Pipiscids

are currently interpreted as being agnathan chordates<sup>13–15</sup>, but this discovery from the Chengjiang fossil-Lagerstätte indicates that the assignment of pipiscids to the Agnatha deserves to be reconsidered.

Phylum Uncertain

*Xidazoon* Shu, Conway Morris & Zhang gen. nov.

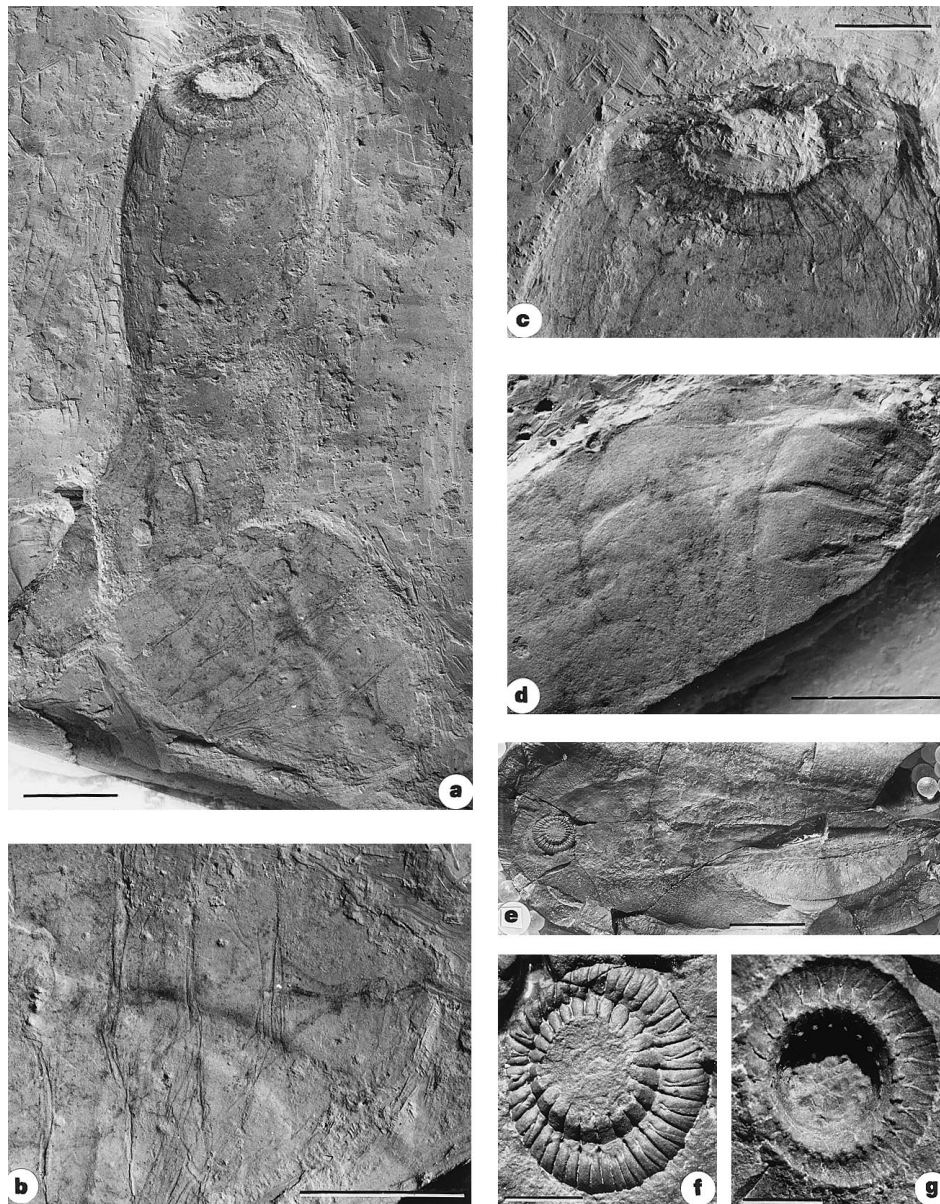
*Xidazoon stephanus* Shu, Conway Morris & Zhang sp. nov.

**Etymology.** Genus name an abbreviation of Chinese name for Northwest University at Xi'an. Species name *stephanos* (Greek) for crown.

**Holotype.** Early Life Institute, Northwest University, Xi'an. ELI-0000194.

**Stratigraphy and locality.** Qiongzhusi (Chiungchussu) Formation, Yu'an shan member (*Eoredlichia* Zone); Lower Cambrian. Specimen collected from Haikou, Kunming, located about 50 km west of Chengjiang.

**Diagnosis.** Body with two-fold division, reminiscent of *Banffia* but anterior section more inflated and possessing prominent mouth circler. Anterior section with faint transverse divisions towards front, otherwise smooth. Mouth defined by circler of about 25 plates, divided into inner and outer regions, otherwise unarmed. Circler similar to plated mouth of *Pipiscius*, although in the latter taxon the plates are more cuticularized and inner circler folded into pharynx. Posterior section tapering towards front and back, segmented with cuticularized region of about six segments succeeded anteriorly by about three less well-defined segments. Posterior section similar to arthropodan metamerites, but lacking evidence of appendages. Cuticular segments also reminiscent of posterior region in *Yunnanozoon*, but in latter taxon segments are ventrally incomplete. Short terminal spines at posterior tip. Alimentary canal with terminal openings, anterior region possibly expanded and rectum with ?dilator muscles.



**Figure 1** The Cambrian fossil *Xidazoon stephanus*, new species and Carboniferous ?agnathan *Pipiscius zangerli*. **a**, Entire specimen and (to lower left) incomplete individual of *Xidazoon* (compare to Fig. 2); **b**, detail of posterior section showing segmental divisions, gut trace, ?dilator muscles and posterior spines (right-hand side); **c**, detail of feeding apparatus of complete specimen; **d**, detail

of anterior and incomplete feeding apparatus of second specimen. **e**, Entire specimen of holotype of *Pipiscius*, part (PF 8345); **f**, detail of feeding apparatus of part; **g**, detail of feeding apparatus of counterpart. Scale bars: 10 mm (**a**, **b**, **e**), 5 mm (**c**, **d**) and 2 mm (**f**, **g**).



**Description.** *Xidazoon stephanus*, new genus and species, is known from two, or possibly three, specimens on a single slab (Figs 1a, 2). The most complete specimen is about 8.5 cm long and a second individual shows details of the anterior (Fig. 1d). The body comprises two main regions. The anterior section is moderately inflated, and the prominent circllet of the presumed anterior is interpreted as a feeding apparatus surrounding a voluminous mouth (Fig. 1c). The apparatus itself consists of plate-like structures, transversely folded to define inner and outer circllets. The edges of the inner circllet of plates are ridged (Fig. 1c), but they do not bear teeth or other extensions. In the second specimen (Fig. 1d) the plates appear to be separated anteriorly by narrower recessed areas. These may represent flexible inter-plate membranes. The anterior of the second specimen is incomplete, and that of the first is too crushed to give more than an estimate of the total number of plates. The better-preserved half-circumference displays about 13 plates, and an allocation of typical plate width around the circumference (~45 mm) gives a total of about 25. The mouth is gaping, but apart from the circllet of plates lacks evidence of jaws or other associated structures. Behind the feeding apparatus the anterior region bears faint, widely separated transverse divisions that may be segmental.

The posterior section tapers in either direction from an expanded central zone. It consists of about six well-defined segments (Figs 1b, 2), and in the anterior direction there is a series of more faint transverse annulations. The surface appears to have been lightly cuticularized. The segment boundaries vary from tightly adpressed to separated, indicating originally relatively wide and flexible inter-segmental membranes. At the posterior tip there are two or three spinose projections (Figs 1b, 2).

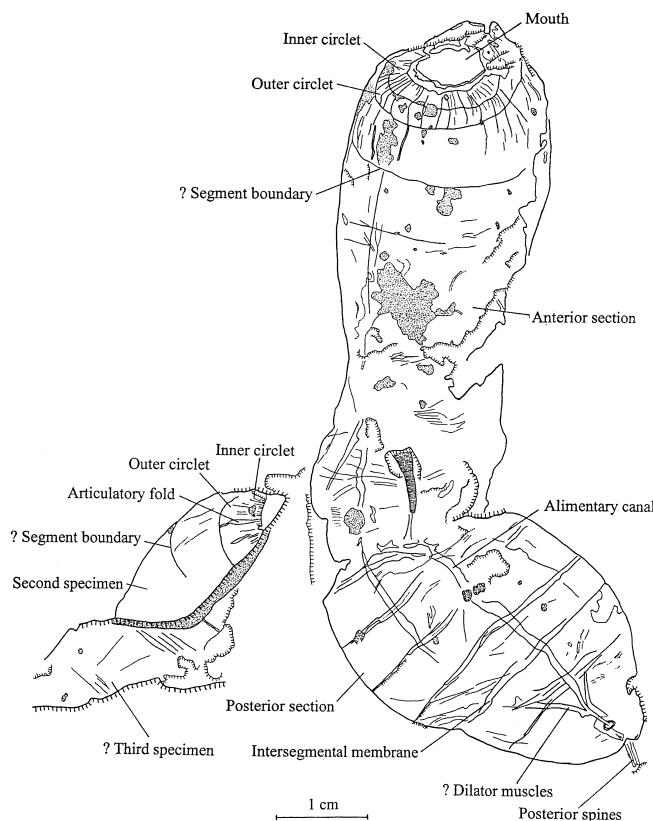
Little is known of the internal anatomy. A gut trace is present in the mid and posterior sections, and near the terminal anus diverging strands may represent dilator muscles (Figs 1a, b, 2). Towards the anterior of the visible gut trace it appears to expand, and in the anterior section it may have been voluminous.

**Preservation.** The style and quality of preservation is similar to other Chengjiang taxa, such as *Yunnanozoon*<sup>16–19</sup>. Thus, the extent of decay appears to be limited. Features, notably the circllet of plates and the posterior segmentation, seem to be original rather than post-mortem artefacts.

**Ecology.** The ecology of *Xidazoon* is problematic. It was presumably benthic, with the anterior circllet periodically contracting to ingest detritus. The inflated nature of the anterior section in the most complete specimen might be because of sediment ingestion. An alternative possibility is that the anterior organ acted as a sucker for lodgement on prey or hard substrates.

**Discussion.** Comparisons between *Xidazoon* and various extant metazoan groups, such as the sipunculans and the much smaller cyclophorans, are not convincing. Similarly, among the diverse Burgess Shale-type assemblages, no exact counterpart to *Xidazoon* has been recognized. There are some similarities to the otherwise enigmatic *Banffia confusa*<sup>5</sup>, which consists of a segmented unit, apparently posterior to an elongate and smooth section, but this taxon lacks evidence for the prominent feeding apparatus of *Xidazoon*. The better-known anomalocaridids<sup>20</sup> have a prominent circular feeding apparatus and a bipartite body with segmented posterior section. There are, however, many differences. The feeding apparatus occurs in a variety of forms<sup>3,5,20</sup>, but none is particularly similar to *Xidazoon*. Other characteristic features of the anomalocaridids, notably the anterior giant appendages and lateral lobes, have no parallel in this new fossil.

The anterior circllet of *Xidazoon* is, however, similar to the otherwise unique feeding apparatus of the putative agnathan *Pipiscius zangerli* (Fig. 1e), a rare species from the 300-Myr-old Mazon Creek fossil-Lagerstätte (Upper Carboniferous) of Illinois. The original description<sup>13</sup> is convoluted, but in essence the feeding apparatus is composed of two circles of sclerotized plates. The inner series ('collar lamellae' of ref. 13) total 23, a number with no apparent parallel in other metazoan organ systems. The outer circllet is also cited<sup>13</sup> as consisting of 23 plates. There is, however, a hitherto



**Figure 2** Camera-lucida drawing of slab containing the two (or possibly three) specimens of the Cambrian fossil *Xidazoon stephanus*, new species.

unrecognized duplication on the leading anterior plate, so that the total number of plates is effectively 24. This duplication defines a line of bilateral symmetry in the apparatus. The plates are separated by narrow clefts ('vanes' of ref. 13) that presumably accommodated shape changes associated with feeding. The principal similarities between the anterior apparatus of *Pipiscius* and *Xidazoon* are the double nature of the circler with direct continuity between the inner and outer plates, the similar number of plates and evidence for articular zones (Fig. 1d) that seem to be comparable to the 'vanes' (Fig. 1f). The apparatus, however, are not identical. In *Pipiscius* the outer plates have a more complex structure, housing triangular insets. These latter units may have accommodated movement of the apparatus, possibly necessitated by a more pronounced sclerotization. Deep pits associated with the 'vanes', and possibly employed for muscle insertions<sup>13</sup>, are not evident in *Xidazoon*. Finally, the inner circle ('collar') of *Pipiscius* is directed inwards, whereas in *Xidazoon* it appears to be more rim-like.

Concerning the possible connection between *Xidazoon* and *Pipiscius*, there seems to be three alternative evolutionary scenarios. First, the annular feeding apparatus is simply an example of convergence. Among the many suctorial and other biological attachment structures similarities can be shown, for example, with the attachment organ of the ectoparasitic ciliate *Trichodina pediculus*<sup>21</sup> and the arm suckers of the octopus<sup>22</sup>, although no phylogenetic connection with *Xidazoon* can be seriously entertained. Notwithstanding the bi-annular arrangement of about 25 plates, the few similarities that otherwise exist between *Xidazoon* and *Pipiscius* make convergence a reasonable option. Second, *Xidazoon* and *Pipiscius* are related, but the assignment of the latter taxon to the agnathans<sup>13,14</sup> is erroneous: together they would represent a new major Palaeozoic clade of as yet unknown affinities. In this sense it would be comparable to such enigmatic groups as the typhloesids<sup>23</sup> and tullimonstrids<sup>24</sup>.

The third proposal is that *Xidazoon* is a precursor to the agnathans, including *Pipiscius*. This presupposes the homology of the circular feeding apparatus in the two taxa, and that certain features (such as fin-rays and possible myotomes) of *Pipiscius* are indicative of a chordate relationship. In this scenario *Xidazoon* would potentially provide new insights into the organization of stem-group deuterostomes. A link may also exist with the coeval *Yunnanozoon*<sup>16–19</sup>. This Chengjiang taxon displays putative gill slits, and the cuticular segmentation has some similarities with *Xidazoon*. One reconstruction<sup>18</sup> of *Yunnanozoon* also depicts a circum-oral set of plates. The bipartite nature of *Xidazoon* is more strongly developed than in *Yunnanozoon*, but the almost arthropod-like segmented posterior section could provide an intriguing phylogenetic link with the protostomes<sup>25</sup>. Continuing investigations of Lower Cambrian fossil-Lagerstätten may yield relatives of *Xidazoon* that will help to resolve the controversial status of these fossils in the context of metazoan phylogeny. □

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1. Conway Morris, S. *The Crucible of Creation: The Burgess Shale and the Rise of Animals* (Oxford Univ. Press, Oxford, 1998).
2. 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).
3. Budd, G. E. in *Arthropod Relationships* (eds Fortey, R. A. & Thomas, R. H.) *Syst. Ass. Spec. Vol.* **55**, 125–138 (1997).
4. Chen, J.-Y. et al. *The Chengjiang Biota* (National Museum of Natural Science, Taiwan, c. 1996).
5. Chen, J.-Y. & Zhou, G.-Q. Biology of the Chengjiang fauna. *Bull. Natl Mus. Nat. Sci. Taiwan* **10**, 11–105 (1997).
6. Budd, G. E. The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group. *Lethaia* **29**, 1–14 (1996).
7. Butterfield, N. J. Burgess Shale-type fossils from a Lower Cambrian shallow-shelf sequence in northwestern Canada. *Nature* **369**, 477–479 (1994).
8. de Rosa, R. et al. Hox genes in brachiopods and priapulids and protostome evolution. *Nature* **399**, 772–776 (1999).
9. Ruiz-Trillo, I. et al. Acoel flatworms: Earliest extant bilaterian metazoans, not members of platyhelminthes. *Science* **283**, 1919–1923 (1999).
10. Conway Morris, S. Why molecular biology needs palaeontology. *Development* (Suppl.) **1994**, 1–13 (1994).
11. Conway Morris, S. Metazoan phylogenies: falling into place or falling to pieces? A palaeontological perspective. *Curr. Op. Genet. Dev.* **8**, 662–667 (1998).

12. Gould, S. J. *Wonderful Life: The Burgess Shale and the Nature of History* (Norton, New York, 1989).
13. Bardack, D. & Richardson, E. S. New agnathous fishes from the Pennsylvanian of Illinois. *Fieldiana Geol.* **33**, 489–510 (1977).
14. Bardack, D. in *Richardson's Guide to the Fossil Fauna of Mazon Creek* (eds Shabica, C. W. & Hay, A. A.) 226–243 (Northeastern Illinois Univ. Press, Chicago, 1997).
15. Janvier, P. *Early Vertebrates* (Clarendon, Oxford, 1996).
16. Chen, J.-Y. et al. A possible early Cambrian chordate. *Nature* **377**, 720–722 (1995).
17. Chen, J.-Y. & Li, C.-W. Early Cambrian chordate from Chengjiang, China. *Bull. Natl Mus. Nat. Sci. Taiwan* **10**, 257–273 (1997).
18. Dzik, J. *Yunnanozoon* and the ancestry of chordates. *Acta Palaeont. Pol.* **40**, 341–360 (1995).
19. Shu, D., Zhang, X.-L. & Chen, L. Reinterpretation of *Yunnanozoon* as the earliest known hemichordate. *Nature* **380**, 428–430 (1996).
20. Collins, D. The "evolution" of *Anomalocaris* and its classification in the arthropod class Dinocarida (nov.) and order Radiodonta (nov.). *J. Paleont.* **70**, 280–293 (1996).
21. Nachtigall, W. *Biological Mechanisms of Attachment* (Springer, Berlin, 1974).
22. Packard, A. in *The Mollusca. Form and Function* Vol. 11 (eds Trueman, E. R. & Clarke, M. R.) 37–67 (Academic, San Diego, 1988).
23. Conway Morris, S. *Typhloesus wellsii* (Melton and Scott, 1973), a bizarre metazoan from the Carboniferous of Montana, USA. *Phil. Trans. R. Soc. Lond. B* **327**, 595–624 (1990).
24. Johnson, R. G. & Richardson, E. S. Pennsylvanian invertebrates of the Mazon Creek area, Illinois: The morphology and affinities of *Tullimonstrum*. *Fieldiana Geol.* **12**, 119–149 (1969).
25. Holland, L. Z. & Holland, N. D. Developmental gene expression in *Amphioxus*: New insights into the evolutionary origin of vertebrate brain regions, neural crest, and rostrocaudal segmentation. *Am. Zool.* **38**, 647–658 (1998).

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## Environmental controls on the geographic distribution of zooplankton diversity

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Proposed explanations for the geographic distribution of zooplankton diversity include control of diversity by geographic variation in: physical and chemical properties of the near-surface ocean<sup>1–3</sup>; the surface area of biotic provinces<sup>4</sup>; energy availability<sup>5</sup>; rates of evolution and extinction<sup>6</sup>; and primary productivity<sup>7</sup>. None of these explanations has been quantitatively tested on a basin-wide scale. Here we used assemblages of planktic foraminifera from surface sediments to test these hypotheses. Our analysis shows that sea-surface temperature measured by satellite<sup>8</sup> explains nearly 90% of the geographic variation in planktic foraminiferal diversity throughout the Atlantic Ocean. Temperatures at depths of 50, 100 and 150 m (ref. 9) are highly correlated to sea-surface temperature and explain the diversity pattern nearly as well. These findings indicate that geographic variation in zooplankton diversity may be directly controlled by the physical structure of the near-surface ocean. Furthermore, our results show that planktic foraminiferal diversity does not strictly adhere to the model of continually decreasing diversity from equator to pole. Instead, planktic foraminiferal diversity peaks in the middle latitudes in all oceans.

We used the Brown University Foraminiferal Data Base (BFD, 33 species and 6 subspecies >150 μm; 1,252 samples) to document the global pattern of planktic foraminiferal diversity and to evaluate the long-standing hypothesis of a latitudinal diversity gradient. We used planktic foraminifera for this study because all of the living species are known and are included in the BFD, unlike other plankton groups (such as radiolaria or copepods), which have hundreds of species and greater taxonomic uncertainty. Our results clearly show that, throughout the world ocean, planktic foraminiferal diversity peaks in middle latitudes, is lowest at high latitudes and is inter-

