The Cambrian ‘‘explosion’’: Slow-fuse or megatonnage?

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Clearly, the fossil record from the Cambrian period is an invaluable tool for deciphering animal evolution. Less clear, however, is how to integrate the paleontological information with molecular phylogeny and developmental biology data. Equally challenging is answering why the Cambrian period provided such a rich interval for the redeployment of genes that led to more complex bodyplans.

William Buckland knew about it, Charles Darwin characteristically agonized over it, and still we do not fully understand it. ‘‘It,’’ of course, is the seemingly abrupt appearance of animals in the Cambrian ‘‘explosion.’’ The crux of this evolutionary problem can be posed as a series of interrelated questions. Is it a real event or simply an artifact of changing fossilization potential? If the former, how rapidly did it happen and what are its consequences for understanding evolutionary processes? The Cambrian explosion addresses problems of biology as diverse as the origin of metazoan bodyplans, the role of developmental genetics, the validity of molecular clocks, and the influence of extrinsic factors such as ocean chemistry and atmospheric oxygen.

The Framework. Stratigraphic sections spanning the Vendian-Cambrian boundary show a broadly similar pattern whereby the key events are bracketed by the ≈600-million-year (Myr)-old Neoproterozoic glacial deposits (tillites) and in the succeeding Cambrian diverse metazoan assemblages, typified by abundant skeletons, diverse trace fossils, and Burgess Shale-type faunas (Fig. 1). One key development is a series of accurate radiometric determinations (1). The Vendian-Cambrian boundary is now placed at ≈543 Myr, and the duration (≈45 Myr) of the Cambrian is substantially shorter than once thought. The preceding Ediacaran faunas have an approximate age range of 565–545 Myr. Accordingly, the overall time-scale for discussion is a relatively protracted 65 Myr, although the principal events of evolutionary interest are probably more tightly bracketed (550–530 Myr) between the diverse Ediacaran faunas of latest Neoproterozoic age (2) and the Chengjiang Burgess Shale-type faunas (3). Correlations are also assisted by emerging schemes of chemostratigraphy (2, 4), notably with reference to strontium (δ^{87}Sr) and carbon (δ^{13}C).

The First Metazoans. Ediacaran assemblages (2, 5) are presumably integral to understanding the roots of the Cambrian ‘‘explosion,’’ and this approach assumes that the fossil record is historically valid. It is markedly at odds, however, with an alternative view, based on molecular data. These posit metazoan divergences hundreds of millions of years earlier (6, 7). As such, the origination of animals would be more or less coincident with the postulated ‘‘Big Bang’’ of eukaryote diversification ≈1,000 Myr ago (8). The existence of some sort of pre-Ediacaran metazoan history is a reasonable assumption (9), but such animals must have been minute because anything larger than about one millimeter would leave a sedimentary imprint as a trace fossil. The literature is littered with claims for pre-Ediacaran traces, but the history of research has been one of continuous rebuttal. Will the most recent candidates avoid the same fate? If such examples as the ≈1,000-Myr-old structures from India are genuine (10), it is strange that there was not a rapid and global colonization of marine sediments. A failed adventure in metazoan history? Motility and hence the potential for sediment disturbance are not, moreover, automatically a prerogative of the metazoans. Conceivably, simple traces could be produced by strolling protistan ‘‘slugs,’’ analogous to slime-mold *Dictyostelium*.

The Way Forward. The key element in deciphering the Cambrian explosion (11) is to integrate the expanding insights of molecular phylogeny (12) and developmental biology with the totality of paleontological evidence, including the Ediacaran assemblages. Somewhere, and this is the tricky point, in the Ediacaran assemblages are animals that may throw particular light on key transitions. Of these, the most significant are those between sponges and diploblasts, cnidarians and triploblasts, as well as the early evolution of the three superclades of triploblast (deuterostomes, ecdysozoans, and lophotrochozoans) (Fig. 1). The overall framework of early metazoan evolution comes from molecular data, but they cannot provide insights into the anatomical changes and associated changes in ecology that accompanied the emergence of bodyplans during the Cambrian explosion. The fossil record provides, therefore, a unique historical perspective.

Only those aspects of the Ediacaran record relevant to the Cambrian diversification are noted here. Sponges, anthozoan cnidarians, and stem-group triploblasts can all be identified with reasonable confidence. Anthozoans, which are perhaps best known from such animals as sea anemones, are represented by frond-like fossils. These types persisted into the Cambrian (Fig. 2*e*) (13, 14) and are similar to the living sea-pens (pennatulaceans). Despite the widespread onset of biomineralization, it is curious that an authenticated record of Cambrian cnidarians is relatively sparse but does include some primitive corals. Jellyfish, which belong to the scyphozoans, are virtually unknown. A benthic scyphozoan shows, however, an astonishingly complete ontogenetic sequence that can be traced from the early embryo (15). Remarkably, given their very delicate and gelatinous construction, representatives of the sea gooseberries (ctenophores) are also known (Fig. 2*b*).

Lophotrochozoans. The ancestral lophotrochozoan may have looked slug-like, creeping across the seafloor on a muscular foot. The Ediacaran *Kimberella* may be an early representative (16), and the armored halkieriids (Fig. 2*c*) from the Lower Cambrian are possibly a subsequent development (17). A surprising discovery is fossil embryos (Fig. 2*d*), from the Lower Cambrian of Siberia, that are reasonably attributed to the halkieriids (18). From a halkieriid-like stock, it may be possible to derive not only the molluscs, but more

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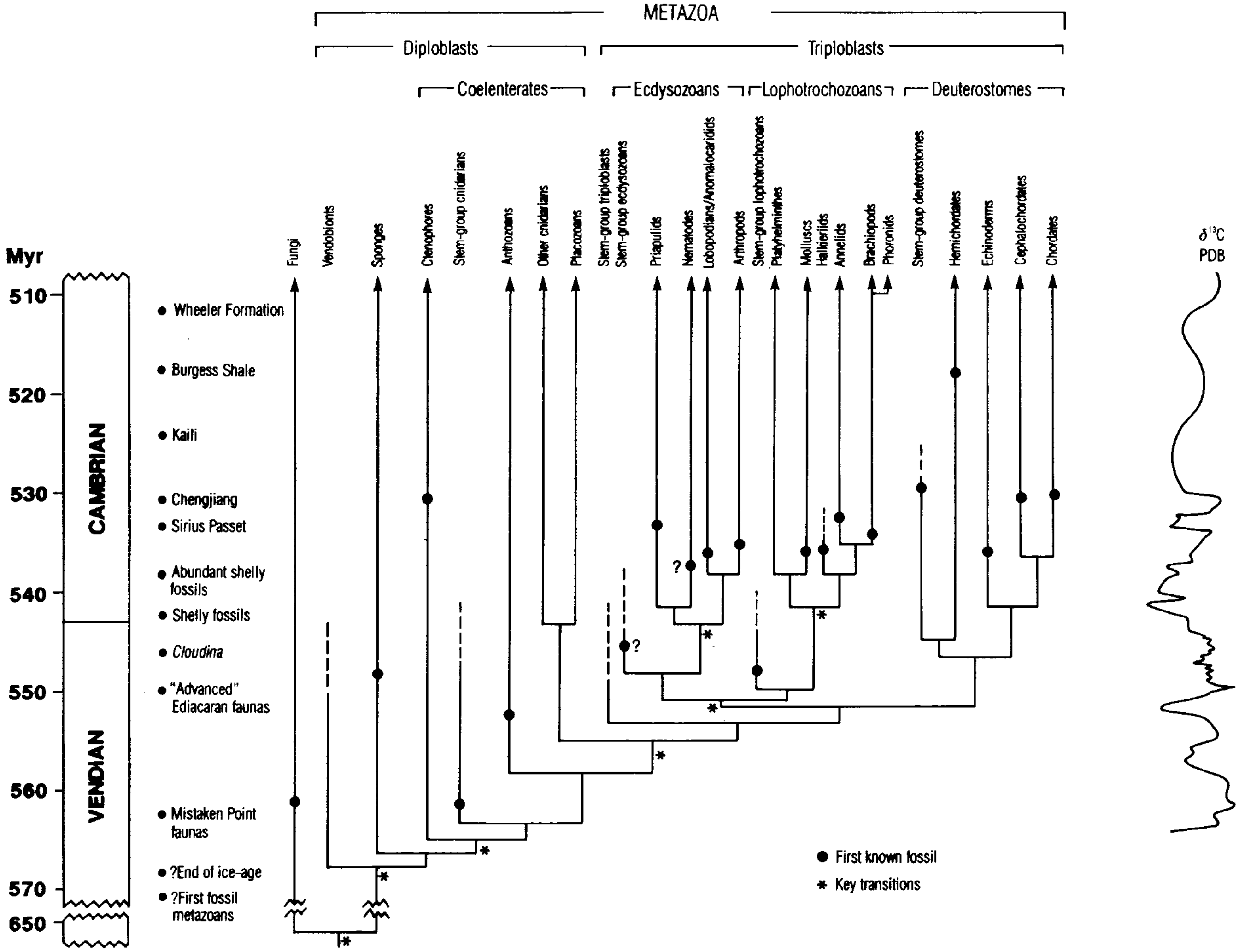

Fig. 1. Principal events across the Vendian-Cambrian boundary, spanning an interval of approximately 60 Myr (570–510 Myr), in the context of the early evolution of metazoans. On the left are denoted a series of important fossil assemblages, e.g., Burgess Shale, and various other significant events, e.g., cessation of ice age. To the right is the carbon isotope curve (redrawn from ref. 4), which provides an independent tool for correlation by chemostratigraphy and may also indicate substantial changes in ocean state with possible implications for evolutionary diversification. The evolutionary framework is largely based on molecular data (12, 19, 20), but the available fossil record not only gives a temporal perspective but also indicates major anatomical transitions that mark the emergence of distinct bodyplans. The sister-group of the Metazoa are the Fungi (35), and a possible time of divergence was ≈650 Myr ago. No fossil evidence for this event is yet available, and the early history of animals (≈650–570 Myr) is also cryptic. This is presumably because the earliest metazoans were microscopic and too fragile to fossilize readily. The most primitive animals in the fossil record may be represented by the vendobionts (36). Metazoans are otherwise divided into various major groupings, of which the most significant depends on the number of germ layers: respectively, two in the diploblasts and three in the triploblasts. The Ediacaran faunas postdate episodes of major glaciation and, with the exception of a few mineralized taxa (e.g., *Cloudina*), lack hard-parts. These Vendian-age assemblages comprise the problematic vendobionts, various coelenterates, and stem-group representatives of the three main groups of triploblast, referred to, respectively, as the ecdysozoans, lophotrochozoans, and deuterostomes. The process of exoskeleton molting, known as ecdysis, is a characteristic of the ecdysozoans. The most important group is the arthropods, and, possibly, they derive from a priapulid-like worm. Lophotrochozoans derive their name from a tentacular feeding organ (lophophore) found in some groups and the most widespread occurrence of a type of ciliated larva known as the trochophore. Lophotrochozoans are a diverse group encompassing the molluscs, annelids, and brachiopods. The ancestral form was probably rather slug-like. The deuterostomes are notably disparate and include the echinoderms and chordates.

surprisingly two more bodyplans, specifically in the form of the brachiopods and annelids (17) (Fig. 1).

Although molecular data define the lophotrochozoans, with some exceptions (19) internal resolution of the phylogeny is limited. This makes the Cambrian fossil record of potentially key importance. Nevertheless, several phyla remain "floating," arising from unresolved polychotomies. Most surprising, perhaps, is a changed status for the platyhelminthes (free-living flatworms and various parasitic groups) (12). Classically regarded as primitive triploblasts, the flatworms appear now to be anatomically degenerate, dispensing with such features as an anus.

Ecdysozoans. If the concept of the Lophotrochozoa overthrows some long-cherished beliefs, it remains consistent with some earlier lines of evolutionary thinking and is at least partly congruent with the Cambrian fossil record. In contrast, the notion of the ecdysozoans (20) is much more revolutionary. Its principal phyla are the arthropods, nematodes and priapulids, all of which molt (or ecdyse) their cuticle (or exoskeleton) at some point in their life cycle. The unusual nematode bodyplan, based on a hydrostatic "skeleton," and the reduced complement of *Hox* genes (12) suggest these worms, of central importance in molecular science in the form of *Caenorhabditis elegans*, are

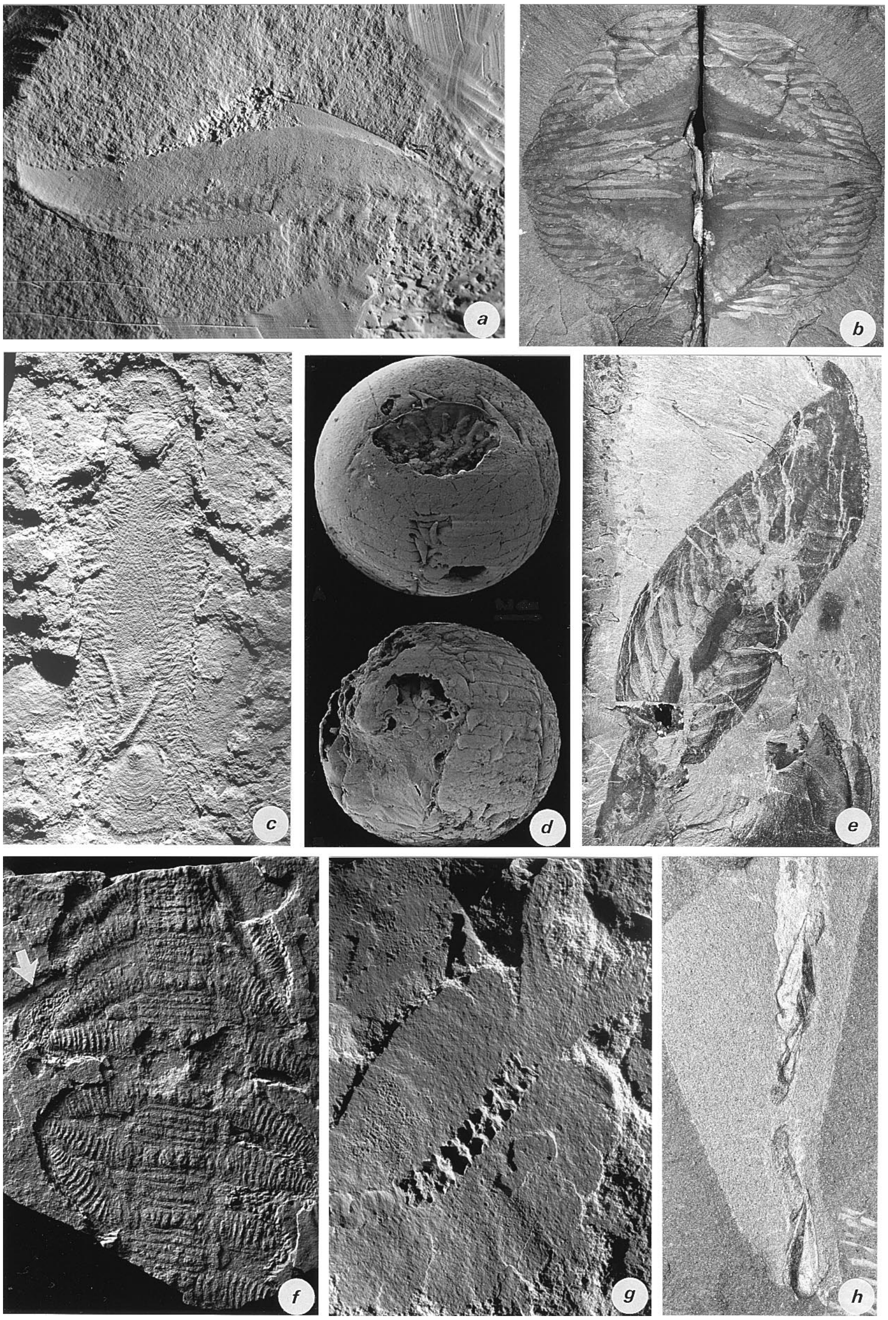

Fig. 2. Representative Cambrian animals from Burgess Shale-type deposits (all except *d*) and an example of early phosphatization (*d*). (*a*) The agnathan chordate *Myllokunmingia fengjiao* from the Lower Cambrian (lower Botomian) Chengjiang lagerstätte, at Haikou near Kunming, Yunnan, China. The photograph is courtesy of D. Shu (North-West University, Xilan, People's Republic of China). (*b*) The holotype and only known specimen (part and counterpart) of the ctenophore *Fasciculus vesanus* from the Middle Cambrian Burgess Shale lagerstätte, at Field in British Columbia, Canada. (*c*) The halkieriid *Halkieria evangelista* from the Lower Cambrian (upper Atdabanian) Sirius Passet lagerstätte in Peary Land, North Greenland. (*d*) Phosphatized embryos, possibly of a halkieriid, and referred to as *Markuelia secunda* from the Pestrotsvet Formation (Tommotian) of south-east Siberia. The figures show views of two embryos that are wrapped around the surface. The photograph is courtesy of S. Bengtson (Swedish Museum of Natural History, Stockholm). [Reprinted (abstracted/excerpted) with permission from ref. 37. Copyright 1997, American Association for the Advancement of Science.] (*e*) The Ediacaran survivor and presumed anthozoan (Cnidaria) *Thaumaptilon walcotti* from the Middle Cambrian Burgess Shale lagerstätte, at Field in British Columbia, Canada. (*f*) The lobopodian *Hadranax augustus* from the Lower Cambrian (upper Atdabanian) Sirius Passet lagerstätte in Peary Land, North Greenland. The photograph is courtesy of G. Budd (Uppsala University, Uppsala). (*g*) The primitive arthropod *Kerygmachela kierkegaardi* from the Lower Cambrian (upper Atdabanian) Sirius Passet lagerstätte in Peary Land, North Greenland. The photograph is courtesy of G. Budd. (*h*) The posterior trunk of the priapulid worm *Ottoia prolifica* from the Middle Cambrian Burgess Shale lagerstätte, at Field in British Columbia, Canada. The specimen shows the intestine and three hyoliths, interpreted as ingested prey. (*a*, ×2.0; *b*, ×0.3; *c*, ×0.8; *d*, ×55; *e*, ×0.3; *f*, ×0.8; *g*, 0.9; *h*, ×1.9.)

highly derived. Nematode origins, however, remain unresolved, although possible connections between some Cambrian priapulid-like fossils and the group of "nemathelminthes" (which includes the nematodes) have been made (21).

The priapulids (Fig. 2*h*) are a diverse and prominent group in the Cambrian (11). As a group newly recruited to the ecdysozoans, can we find a link with the arthropods? One interesting proposal (22) looks to a distinctive group of priapulids with an armored cuticle, known as the palaeoscolecidans, as potential precursors. The key step is to affect a functional transition from the peristaltic burrowing action of priapulids to a walking cycle based on the leg-like lobopods (Fig. 2*f*) that are found in the first arthropods. Functional interpretations of the subsequent evolution of early arthropods can be put in a context of changing ecology, linked to defense and shifts in feeding style. In this scenario (23), a number of hitherto enigmatic taxa, notably *Kerygmachela* (24, Fig. 2*g*) and the large and active predator *Anomalocaris*, are seen as key staging posts leading from the primitive lobopodians (Fig. 2*f*) to the somewhat more familiar clade of advanced arthropods (CCT = crustacean-chelicerate-trilobite). Morphometric and phylogenetic studies (25) have shown that the supposedly "bizarre" Burgess Shale-type arthropods fall into a phylogenetic scheme that gives no support to the idea that they are outliers in morphospace awaiting the grim reaper of contingent extinction.

Deuterostomes. Although there seems to be some congruence between the fossil record and molecular phylogenies with respect to the ecdysozoans and lophotrochozoans, in the case of the deuterostomes, matters are less clear-cut. One difficulty is the extreme morphological distinction of the component phyla, so that plausible functional intermediates between echinoderms, hemichordates, and chordates remain effectively ad hoc constructions (26). Molecular data are certainly yielding important insights, most notably in terms of amphioxus (27) and the developmental biology of ascidians (28). With the addition of the fossil record, there may now be the glimmerings of a resolution (Fig. 1).

Arguably the basal deuterostome bodyplan is best conceived as basically consisting of two sections: a head with pharyngeal perforations (gill-slits) and, to the posterior, a segmented unit. The most primitive of living deuterostomes are taken to be the hemichordates, although living representatives, such as the acornworms, are evidently derived. Chengjiang fossils, such as *Yunnanozoon* (29) and the almost identical *Haikouella* (30), possess a segmented body, with incomplete cuticular rings, and an anterior section with prominent gill slits. Although interpreted as advanced chordates, in the artist's reconstruction (30) of *Haikouella*, the supposed myotomes show a subtle "enhancement" of a sigmoidal profile when compared with the illustrated fossils. The supposed notochord is also in a biomechanically peculiar position, inconsistent with its role as an antagonist to the purported myotomes. These strange-looking taxa from Chengjiang may be our best glimpse of the first deuterostomes.

The first definite echinoderms do not appear until the Lower Cambrian. The riot of ensuing forms has proved difficult to place in a coherent phylogeny. Nevertheless, the classic five-fold symmetry is apparently a derived feature and as such is consistent with marked redeployment of a number of developmental genes (31). What then did the first echinoderms look like? The concept of a basic deuterostome bipartite bodyplan of head with gill slits and tail could reinvigorate the status of the otherwise highly controversial fossils known as the "calcichordates" (32), which show a puzzling combination of echinoderm and chordate characters.

The fossil record of the earliest chordates remains sporadic, but new fossil discoveries are beginning to fill in the picture. From Chengjiang, these include the cephalochordate *Cathaymyrus* and, more sensationally, two types of agnathan fish (33) (Fig. 2*a*). The proposal (3) that *Cathaymyrus* is synonymous with *Yunnanozoon* verges on the whimsical. The more famous *Pikaia*, from the Burgess Shale (11), remains more of a conundrum. It has myotomes and a notochord, but a peculiar bilobed head. Neither *Cathaymyrus* nor *Pikaia* are particularly similar to the living amphioxus, suggesting that, although genomically primitive (27), this living representative is anatomically derived.

What Triggered the Cambrian Explosion? Isotopic and chemical indicators (2, 4), notably δ^{13}C (Fig. 1), δ^{32}S, δ^{87}Sr, and phosphogenesis, suggest substantial changes in ocean chemistry and circulation on various time-scales. Despite repeated speculation, the extent to which these changes in the oceans influenced, let alone stimulated, the Cambrian explosion is obscure. The motor of the Cambrian explosion was largely ecological, notably with the rise of macroscopic predation (and defense) and effective filter-feeding on the seafloor and in the pelagic zone. Skeletal hard-parts, the most tangible expression of this event, seem to have been largely protective, even though the proportion of animals with robust hard-parts in the original communities was small (11).

There is also continued interest in the role of genomic change, especially with respect to the homeotic genes. Although they are clearly of central importance in the definition of bodyplan architecture, there is a risk of losing the overall evolutionary context (34). It is evident that at least some components of a given bodyplan are assembled by virtue of a genetic "toolbox." This, in turn, has provoked extensive discussions on definitions of homology, but perhaps deflects the interesting question of how such toolboxes are recruited. This is no trivial point because there is increasing evidence for extensive co-option and redeployment of genes. Not only that, but there are intriguing mismatches between genomic architecture and bodyplan complexity. To complicate matters further, a substantial proportion of the metazoan genome was probably available well before the Cambrian explosion. Genes make bodies and bodyplans require a corresponding genetic architecture, but we are still far from understanding either their interconnections or evolution.

To conclude: The Cambrian explosion is real and its consequences set in motion a sea-change in evolutionary history. Although the pattern of evolution is clearer, the underlying processes still remain surprisingly elusive.

I thank Sandra Last for typing numerous versions of this manuscript, Sharon Capon and Dudley Simons for technical assistance, and Stefan Bengtson and Graham Budd for generously providing photographs (Fig. 2*d* and Fig. 2 *f* and *g*, respectively). Critical remarks by Nick Butterfield and an anonymous referee are appreciated. My work is supported by the Natural Environment Research Council, Leverhulme Trust, Royal Society, and St. John's College (Cambridge, U.K.). This is Cambridge Earth Sciences Publication 5933.

1. Bowring, S. A. & Erwin, D. H. (1998) *Geol. Soc. Am. Today* **8,** 1–8.
2. Narbonne, G. M., Kaufman, A. J. & Knoll, A. H. (1994) *Geol. Soc. Am. Bull.* **106,** 1281–1292.
3. Chen, J.-Y. & Zhou, G.-Q. (1997) *Bull. Natl. Mus. Nat. Sci. Taiwan* **10,** 11–105.
4. Shields, G. (1999) *Eclogae Geol. Helv.* **92,** 221–233.
5. Narbonne, G. M. (1998) *Geol. Soc. Am. Today* **8,** 1–6.
6. Wray, G. A., Levinton, J. S. & Shapiro, L. H. (1996) *Science* **274,** 568–573.
7. Bromham, L., Rambaut, A., Fortey, R., Cooper, A. & Penny, D. (1998) *Proc. Natl. Acad. Sci. USA* **95,** 12386–12389.
8. Sogin, M. L. (1994) in *Early Life on Earth*, ed. Bengtson, S. (Columbia Univ. Press, New York), Nobel Symposium 84, pp. 181–192.
9. Conway Morris, S. (1993) *Nature (London)* **361,** 219–225.
10. Seilacher, A., Bose, P. K. & Pflüger, F. (1998) *Science* **282,** 80–83.
11. Conway Morris, S. (1998) *The Crucible of Creation* (Oxford Univ. Press, Oxford).
12. de Rosa, R., Grenier, J. K., Andreeva, T., Cook, C. E., Adoutte, A., Akam, M., Carroll, S. B. & Balavoine, G. (1999) *Nature (London)* **399,** 772–776.
13. Jensen, S., Gehling, J. G. & Droser, M. L. (1998) *Nature (London)* **393,** 567–569.
14. Conway Morris, S. (1993) *Palaeontology* **36,** 593–635.
15. Yue, Z. & Bengtson, S. (1999) *Lethaia* **32,** 181–195.
16. Fedonkin, M. A. & Waggoner, B. M. (1997) *Nature (London)* **388,** 869–871.
17. Conway Morris, S. & Peel, J. S. (1995) *Philos. Trans. R. Soc. London B* **347,** 305–358.
18. Conway Morris, S. (1998) *BioEssays* **20,** 676–682.
19. Cohen, B. L., Gawthrop, A. & Cavalier-Smith, T. (1998) *Philos. Trans. R. Soc. London B* **353,** 2039–2061.
20. Aguinaldo, A. M. A., Turbeville, J. M., Linford, L. S., Rivera, M. C., Garey, J. R., Raff, R. A. & Lake, J. A. (1997) *Nature (London)* **387,** 489–492.
21. Hou, X.-G. & Bergström, J. (1994) *Lethaia* **27,** 11–17.
22. Dzik, J. & Krumbiegel, G. (1989) *Lethaia* **22,** 169–181.
23. Budd, G. E. (1997) in *Arthropod Relationships*, eds. Fortey, R. A. & Thomas, R. H. (Kluwer, Dortrecht), pp. 125–138.
24. Budd, G. E. (1999) *Trans. R. Soc. Edinburgh Earth Sci.* **89,** 249–290.
25. Wills, M. A., Briggs, D. E. G. & Fortey, R. A. (1994) *Paleobiology* **20,** 93–130.
26. Gee, H. (1996) *Before the Backbone* (Chapman & Hall, London).
27. Holland, N. D. & Holland, L. Z. (1999) *Am. Zool.* **39,** 630–640.
28. Nishida, H. (1997) *Semin. Cell. Dev. Biol.* **8,** 359–365.
29. Shu, D.-G., Zhang, X.-L. & Ling, C. (1996) *Nature (London)* **380,** 428–430.
30. Chen, J.-Y., Huang, D.-Y. & Li, C.-W. (1999) *Nature (London)* **402,** 518–522.
31. Lowe, C. J. & Wray, G. A. (1997) *Nature (London)* **389,** 718–721.
32. Jefferies, R. P. S. & Jacobsen, A. G. (1998) *Intergrative Biol.* **1,** 115–132.
33. Shu, D.-G., Luo, H.-L., Conway Morris, S., Zhang, X.-L., Hu, S.-X., Chen, L., Han, J., Zhu, M. & Chen, L.-Z. (1999) *Nature (London)* **402,** 42–46.
34. Conway Morris, S. (2000) *Cell* **100,** 1–11.
35. Baldauf, S. L. (1999) *Am. Nat.* **154,** Suppl., S178–S188.
36. Buss, L. W. & Seilacher, A. (1994) *Paleobiology* **20,** 1–4.
37. Bengtson, S. & Yue, Z. (1997) *Science* **277,** 1645–1648.