New developments on an ancient front: pre-Cambrian evolution of animal life

To anybody not committed to the motto "bigger is better", the most spectacular episode in the history of life preserved in the fossil record has to do, not with dinosaurs, but with the appearance in the Cambrian era [beginning about 450 million years (My) ago] of an astounding variety of complex multicellular animal life. The Cambrian fauna included not only representatives of all the major modern phyla, but also an amazing array of taxa—from genera to phyla—which never made it beyond that early phase of metazoan evolutionary exuberance: only a small fraction of this Cambrian diversity survived into later times. The sudden appearance and elaboration of the Cambrian fauna, in the geologically brief span of a few tens of millions of years has frequently been described as the "Cambrian explosion". Cambrian animals sported a variety of skeletal structures such as shells, carapaces and sclerites, which lend themselves more readily to fossilization than soft-bodied animals.

Does the Cambrian explosion therefore represent the extremely rapid evolution of a diversity of entirely novel body plans? Or does it represent the acquisition of skeletal structures (and subsequent diversification) among different groups whose appearance in the fossil record was preceded by a protracted period of pre-Cambrian evolution, during which the different basic body plans represented among these groups had already evolved? In other words, how much of an evolutionary explosion really occurred during the Cambrian? The belief that such major evolutionary developments could not have occurred in so short a span of time encouraged the search for pre-Cambrian metazoan life, leading to the discovery of the Ediacaran fauna from the late Vendian period just preceding the Cambrian. However, the Ediacaran fauna are modest compared to Cambrian finds, and do not greatly extend the period of early metazoan evolution, the upper limit being about 580 My ago. There is no unambiguous fossil evidence in support of the evolution of complex metazoan body plans prior to this. Is this because none existed? Or is it because the prevailing geochemical and ecological conditions did not favour the preservation of soft-bodied and likely microscopic forms? Or is the fossil evidence somewhere out there, but we have not known what to look for and where?

Several papers appearing over the last year or so have shed new light on—or at least added fresh fuel to—the debate about early metazoan evolution. These represent three lines of argument and evidence:

(i) Comparisons of protein and rRNA sequences have been used to estimate the times at which different lineages diverged. However, the use of genes as molecular clocks in this way can be problematic; this is tellingly illustrated by the vastly different times that have been arrived at for the origin of metazoans by different groups. In an influential paper, Wray *et al* (1996) analysed rates of sequence evolution of 18S rRNA and seven protein-coding genes, to derive a metazoan origin between 1000 and 1200 My ago. This supported a time of origin about 500 My earlier than palaeontological estimates. In a recent paper, Ayala *et al* (1998) take issue with this estimate. Using a similar data set, but different statistical methods to eliminate biases arising from non-uniform rates of molecular evolution, they arrive at the more conservative figure of a metazoan origin some 670 My ago, which can be reconciled with the fossil record. Other papers published this year arrive at yet other figures, such as that of 830 My ago (Gu 1998). Back to square one?

(ii) Following an earlier report (Zhang and Pratt 1994) of fossil metazoan embryos from the middle Cambrian, two more recent papers (Bengtson and Zhao 1997; Xiao *et al* 1998) report even older fossil embryos. Bengtson and Zhao present beautifully detailed evidence on metazoan embryogenesis from early Cambrian deposits, including a reconstruction of an entire developmental

sequence running from early cleavage stages to newly hatched individuals. Xiao *et al* (1998) go even further back in time, with evidence of pre-Cambrian metazoan embryos from about 570 My ago, making these contenders for the oldest pre-Cambrian fossils to date. What makes these two papers significant, apart from the awe-inspiring detail visible in these fossil embryos, is the fact that it is at all possible to obtain well-preserved invertebrate fossil embryos. This points the way for one important approach to the further study of early metazoan life: fossil embryos will be able to provide invaluable information on the evolution of development—a central concern in the attempt to reconstruct early metazoan evolution. Furthermore, the direct mode of development inferred from two of these fossils (Bengtson and Zhao 1997) suggests that, contrary to a widely-held view, the evolution of major invertebrate phyla may not have needed to proceed through the agency of free-floating, plankton-feeding larval stages (Morris 1998), and may therefore not have required the longer period of pre-Cambrian evolutionary "preincubation" implied by this view.

(iii) A very recent paper (Seilacher *et al* 1998) should hold special interest for Indian readers, since it reports findings from Churhat in Madhya Pradesh, of collaborative work by an Indo-German team. Seilacher *et al* (1998) claim that the traces they found in the Churhat sandstone represent burrows formed by triploblastic, probably worm-like, animals tunnelling beneath bacterial mats. What makes this claim dramatic is that the Churhat sandstone has been dated at 1100 My, which would make this by far the oldest evidence of metazoan life. Not surprisingly, this claim is attracting critical scrutiny. In a commentary (Brasier 1998) on their paper, it has already been pointed out that the diameter of the burrows does not necessarily imply the activity of triploblastic animals; that it is very strange that no other evidence of metazoan life has been found over the huge time span of 500 My separating this date from the earliest subsequent metazoan fossils; and most importantly, that the dating of the Churhat sandstone is in doubt. Clearly, convincing evidence on the age of the Churhat sandstone will have to be forthcoming before the interpretation of Seilacher *et al* (1998) finds wide acceptance. Should it turn out to be supported by new information on the age of the Churhat sandstone, it would have profound implications for our view of the course of early metazoan evolution, and should lead to an intensive search for further fossil evidence from deep time. In the absence of such finds, we would be left with the intriguing possibility that multicellular animal life made one false start, and that it took another half a billion years or so before a successful second attempt.

References

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