

Molecular clocks: Defusing the Cambrian 'explosion'?

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A recent molecular phylogenetic study argues against the orthodox view that metazoan phyla emerged abruptly during the Cambrian 'explosion', pointing instead to a protracted history for metazoans that arguably stretches back a billion years or more; the fossils, however, seem to tell a different story.

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You do not have to believe in punctuated equilibria — and given its status as ideological straw-man *par excellence*, why should you? — to accept that the history of life shows periods of rapid change separated by evolutionary longueurs of immense duration. In recent years, the so-called Cambrian 'explosion' has enjoyed the lion's share of attention from those interested in periods of apparently rapid evolutionary diversification, but equally dramatic, and less appreciated, is the evidence for a startling radiation of the eukaryotes, approximately a billion years ago. This episode only came to light with the advent of molecular phylogenetics, and especially the sequencing of ribosomal RNAs [1]. The sporadic fossil record of various algae [2] and organic molecules — the so-called biomarkers — recovered from sediments of about the same age [3], are broadly congruent with this phylogenetic scheme. Embedded somewhere, and exactly where remains controversial, in this welter of newly evolving eukaryotes are the multicellular animals, or metazoans. When exactly did they appear in geological history?

This apparently simple question has remained unresolved, and in the last few years the tensions between molecular and palaeontological data have been quietly gathering pace. The problem is straightforward. The earliest fossils that most people will accept as animals appear to be no older than about 600 million years (Fig.1). These are the Ediacaran faunas, whose role in understanding early metazoan evolution has in itself been controversial [4]. Nobody, however, takes the stratigraphic record so literally as to imagine that the first of these fossils are the first animals; there must be some sort of preceding history [5], but the question remains, is it very deep [6]?

Even staunch proponents of a protracted pre-Ediacaran history for metazoans might balk at an origin in excess of

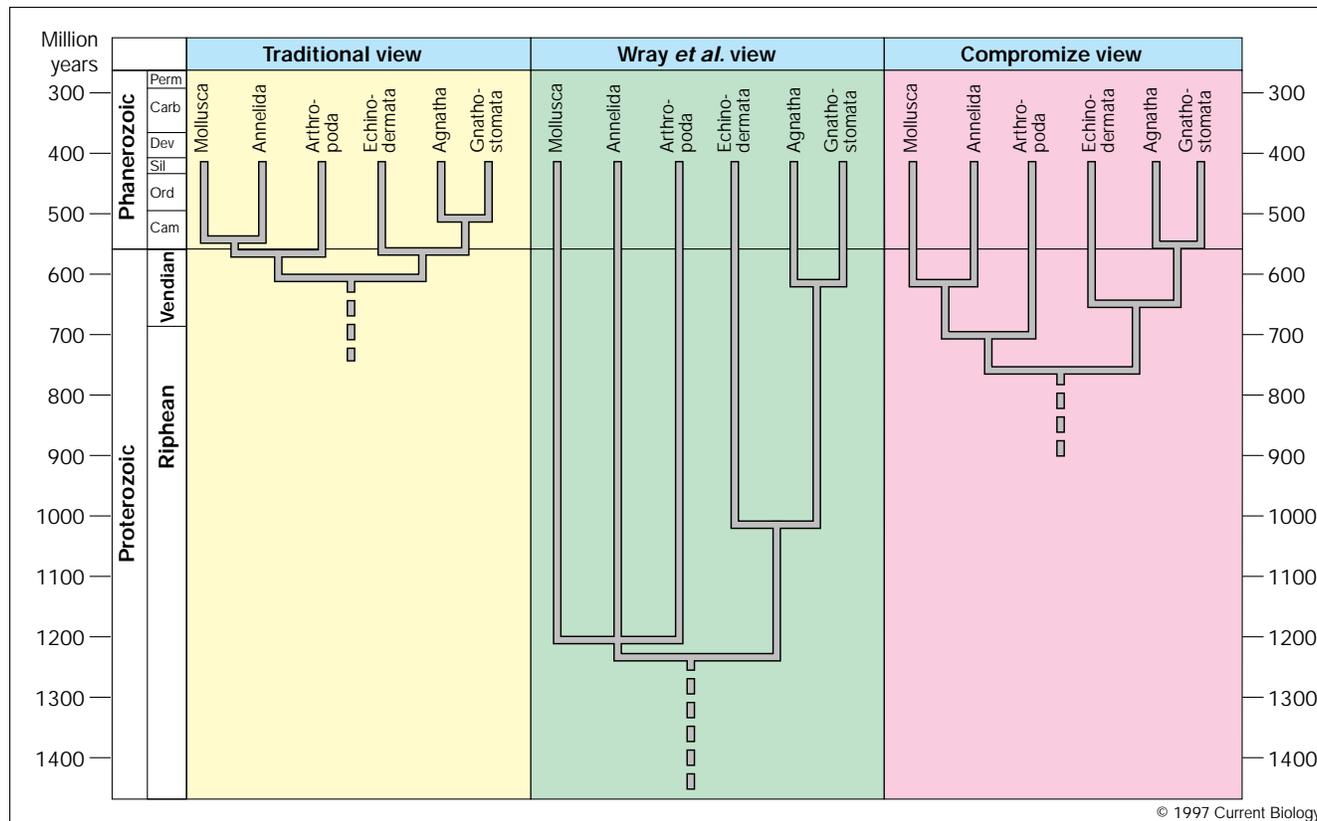
1200 million years ago (Fig. 1), but this is exactly what Wray *et al.* [7] propose in a recently published paper which takes as its fundamental basis the notion of the molecular 'clock' — the view that gene sequences evolve with a sufficiently regular rate for sequence differences to be used to date divergences between lineages. Are these molecular biologists naive to accept their clocks, or are the palaeontologists overlooking something obvious? Before anyone starts to polarize the debate, let alone demonize one side or the other, it might be fruitful to think of more subtle solutions to this apparent dilemma.

The reliability of molecular clocks has been, to put it mildly, a matter for debate. Nevertheless, what Wray *et al.* [7] found in their analysis of seven genes was that, without exception, all pointed to a substantial history of pre-Ediacaran divergences. This is broadly in agreement with earlier molecular estimates based on the proteins haemoglobin [8] and collagen [9]. A worrying aspect of these calculations, however, is the enormous latitude in the figures for divergence times (Table 1). Thus, the minimum and maximum values, both as it happens for the annelid–chordate divergence, are respectively 773 million years (from cytochrome oxidase II sequences) and 1621 million years (from β haemoglobin sequences), an interval (848 million years) that is substantially longer than the entire Phanerozoic (the time from Cambrian to the present-day)!

There is, however, some sort of coherence in the divergence times, in as much as the echinoderm–chordate split is consistently younger, albeit slightly, than the split between protostomes (annelids, arthropods and molluscs) and chordates, a view that is consistent with most metazoan phylogenies. Unease persists, however. In particular, with the agnathan–gnathosome split (between jawless and jawed fish), the mean divergence time is 599 million years, but a closer look at the data reveals a possibly intriguing bimodality in the data. For three of the genes, the estimated divergence times cluster at a mean of 487 million years, whereas for the other two they average 767 million years. The former divergence time, equivalent to the geological interval of the lower Ordovician, does not do desperate violence to the known fossil record, whereas the latter figure certainly does.

The disinterested reader may well object to this pick-and-mix mentality, rejecting in the case of the agnathan–gnathostome divergence the evidence from cytochrome c (895 million years) and NADH 1 (638 million years) as being unconvincingly old. Nevertheless,

Figure 1



Differing views of metazoan phylogeny. Most palaeontologists follow the 'traditional view' (left), accepting the fossil record as a fairly reliable indicator of original events. Molecular clocks are interpreted by Wray *et al.* [7] (centre) as indicating very deep origins for the principal metazoan phyla. The recognition that some molecular clocks run much

faster than others (see Table 1) suggests a 'compromise view' (right), which implies that our search strategy for the first metazoans should be concentrated in the interval from about 750 million years onwards. Perm, Permian; Carb, Carboniferous; Dev, Devonian; Sil, Silurian; Ord, Ordovician; Cam, Cambrian.

some sort of pattern may yet emerge. Thus, β haemoglobin invariably gives the oldest divergence time, whereas ATPase 6 and cytochrome oxidase II are generally the

molecules giving the youngest dates (Table 1). A more extended analysis would hardly be justified given the acknowledged inaccuracies in the clocks, but should we

Table 1

Divergence times of major metazoan groups estimated from seven different gene sequences.

Divergence	Estimated divergence time in millions of years							Mean
	ATPase 6	Cytochrome c	Cytochrome oxidase I	Cytochrome oxidase II	β Haemoglobin	NADH 1	18S rRNA	
Echinodermata–Chordata	786	883	1160	608	1312	971	1288	1001
Arthropoda–Chordata	887	953	1272	803	1506	1338	1453	1173
Annelida–Chordata	1059	1078	1465	773	1621	1221	1214	1204
Mollusca–Chordata	1045	–	1333	788	1511	1492	1183	1225
Agnatha–Gnathostomata	462	895	511	487	–*	638	–*	599

Note that β haemoglobin (red numbers) gives consistently the oldest divergence times, and that cytochrome oxidase I and 18S rRNA also tend towards deep divergences. In marked contrast, cytochrome oxidase II (blue numbers) almost invariably gives substantially younger times for divergence, a tendency also apparent in ATPase 6. If molecular clocks run at markedly different rates, then the first point of enquiry is to decide

whether there are reasons for some genes to be more labile and/or more sensitive to environmental perturbations (for example, changes in atmospheric oxygen). In any event, a simple averaging may give too crude a resolution of divergence times to allow sensible strategies for a search of sediments that might confirm the existence of pre-Ediacaran metazoans. (Data from [7].) *Sequence unavailable

perhaps take the lower figures as a working hypothesis (Fig. 1) for sensible times of divergence?

Let us accept, for the sake of the argument, that the protostome–chordate divergence was pre-Ediacaran, but happened about 750 million years ago. This opens what may transpire to be an even more contentious area, because Wray *et al.* [7] explicitly assume that the dates of molecular divergence apply to recognizable lineages, and by implication defined bodyplans, such as those of the molluscs or the echinoderms. This proposal may be premature, and needs urgent palaeontological investigation. At first sight, the evidence is hardly convincing. The renowned American palaeontologist Preston Cloud made part of his reputation by consistently, and convincingly, debunking claims for pre-Ediacaran metazoans [10].

For the most part Cloud's view has prevailed, and the few examples cited by Wray *et al.* [7] fall well short of widespread acceptance. For example, they speak of "various carbonaceous compressions (of) annelids and pogonophorans", yet these particular fossils are in fact more likely to be algae [11]. Not that we should rush to be over-dismissive, and each case, such as the recently announced 1100 million-year-old trace fossils from northern India [12], requires careful and sympathetic scrutiny. Nevertheless, appeals to gaps in the rock record and pervasive metamorphism of the sediments are not going to work: if there were large metazoans capable of either fossilization or leaving traces, they had an uncanny knack of avoiding areas of high preservation potential.

The obvious compromise view is that there were indeed abundant pre-Ediacaran metazoans, but that they were small in size — in the millimetre range. Some may wish to invoke the occupation of meiofaunal habitats — the interstices between sand grains which can be inhabited by minute metazoans — even though the primitiveness of this remarkable ecosystem is not widely accepted, at least so far as most extant metazoans are concerned. Others would not necessarily seek a benthic nursery for the first metazoans, but would turn to the pelagic realm and the venerable notion that larval morphologies are primitive. This has received a new lease of life with the proposal that the primitive larva-like animals were equipped with 'set-aside' cells that provided the rudiments of adult form, and whose developmental potential facilitated the Cambrian 'explosion' [13].

With our eyes properly open, such pre-Ediacaran metazoans may well be recognized in the fossil record, but the fact remains that, in the context discussed by Wray *et al.* [7], it seems difficult to envisage a millimetre-long chordate or echinoderm with anything like the bodyplan that characterizes their irruption as part of the Cambrian 'explosion'. Would a metazoan a few millimetres long

'need' a notochord or water vascular system? In any event, the pre-Ediacaran metazoans would have inhabited an effectively protistan world, one of low Reynolds numbers (where viscous forces predominate over inertial forces) and sensitive to chemical gradients. Perhaps our nearest glimpse of this vanished world comes not so much from recent meiofauna but by comparison with such complex protistans as the ciliates.

It would be tempting to invoke the Cambrian 'explosion' as being as much the response to the lifting of some external constraint, most popularly thought to be levels of atmospheric oxygen, as any genetic breakthrough. After all, if Wray *et al.* [7] are correct in their basic analysis of ancient metazoans, then the *Hox* genes that seem to play such a general role in specifying the body plans of metazoans during development should also have a deep Neoproterozoic history. Any exploration of this possibility still needs to be put into the context of the known fossil record, and perhaps most crucially a further consideration of the links between the Ediacaran faunas and the rest of metazoan history. The fact remains that these very late Neoproterozoic fossils comprise a distinctive assemblage whose place in most of the existing phylogenies is controversial. One way forward may be to consider how these Ediacaran faunas might have emerged from the microscopic milieu of their ancestors.

Perhaps the most important aspect of the paper by Wray *et al.* [7] is one that receives no direct mention. This is effectively a philosophical problem, and concerns the notion of inherency. Thus, if we concede a significant pre-Ediacaran history for the metazoans, we need to discuss to what extent metazoan history was *implicit* a billion years ago, at least in outline, as opposed to what was *inevitable* 500 million years later at the onset of the Cambrian 'explosion'. Even if metazoans have a deep history, which palaeontologically remains cryptic, the actual organisms would have been of millimetre size and perhaps without the potential for macroscopic size and complex ecology. Thus, it may still be true that the architecture of today's world owes its basis to the Cambrian 'explosion', and not least the onset of neural complexity as witnessed by such features as the complex optical systems in Cambrian arthropods, and more obliquely by the remarkable efflorescence of trace fossils. It is these latter behavioural manifestations that point as clearly as the body fossil record to the emergence of a new order. Wray *et al.* [7] may be correct in tracing the trail of gun-powder back far into the mists of the Neoproterozoic, but the keg itself still looks as if it blew up in the Cambrian.

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