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Darwin's dilemma: the realities of the Cambrian 'explosion'

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The Cambrian 'explosion' is widely regarded as one of the fulcrum points in the history of life, yet its origins and causes remain deeply controversial. New data from the fossil record, especially of Burgess Shale-type Lagerstätten, indicate, however, that the assembly of bodyplans is not only largely a Cambrian phenomenon, but can already be documented in fair detail. This speaks against a much more ancient origin of the metazoans, and current work is doing much to reconcile the apparent discrepancies between the fossil record, including the Ediacaran assemblages of latest Neoproterozoic age and molecular 'clocks'. Hypotheses to explain the Cambrian 'explosion' continue to be generated, but the recurrent confusion of cause and effect suggests that the wrong sort of question is being asked. Here I propose that despite its step-like function this evolutionary event is the inevitable consequence of Earth and biospheric change.

Keywords: Cambrian 'explosion'; Burgess Shale; Chengjiang; metazoan evolution; molecular clock; palaeontology

The reasons for the enduring interest in Darwin lie not only in our admiration of his genius, but also, I would suggest, his honesty. Few investigators were—or come to think of it, are—as ready to flag the glaring difficulties with a hypothesis. Yet in Darwin's case his not infrequent raising of 'manifest objections to my theory' were as often as not pointers to major, and yet unsolved, problems in evolution. In this context, a potentially crippling example to the acceptance of his theory, was what at the time was understood as the mysterious and abrupt appearance of skeletal remains. This, of course, is one part of the event we now colloquially refer to as the Cambrian 'explosion'. To be sure, the existence of ancient rocks devoid of evidence for life had been appreciated since at least the time of William Buckland (1784–1856), but it was Darwin who demanded a particular explanation. Were Darwin to emerge today from Westminster Abbey no doubt he would be gratified by the progress made. New insights into metazoan phylogenies, radiometric dating and exceptionally preserved fossils have greatly extended, and occasionally refined, our thinking. Progress, therefore, is palpable, but in briefly reviewing this demandingly large area I will suggest that much remains conjectural, some areas of received wisdom may require re-examination, and most significantly a comprehensive explanation for the Cambrian 'explosion' eludes us, but not for reasons we might imagine.

This event has conjured up a wide range of opinions, but at the risk of parody they can be divided into two camps. The 'ancient school' argues that animals evolved long before the Cambrian and that the 'explosion' is simply an artefact, engendered by the breaching of taphonomic thresholds, such as the onset of biomineralization and/or a sudden increase in body size. The alternative 'realist school', to which I largely subscribe, proposes that while the fossil record is far from perfect and is inevitably skewed in significant ways, none is sufficient to destroy a strong historical signal.

1. A DEEP AND CRYPTIC ORIGIN FOR ANIMALS?

Until recently the 'ancient school', looking to animals evolving at least one billion years ago (Gyr), was very much in the ascendancy. Such confidence was very largely based on divergence dates derived from molecular 'clocks' (e.g. Wray *et al.* 1996; Blair & Hedges 2005). Although the range of estimates is startlingly large, comfortably exceeding the duration of the entire Phanerozoic, a date for metazoan appearances well before 1 Gyr has become widely accepted in some quarters. Darwin's dilemma had apparently been solved; animals have a deep history and their appearance is indeed taphonomically controlled. There are, however, immediate difficulties. The absence of an obvious metazoan fossil record in these ancient sediments implies a cryptic and microscopic fauna. In this context it is not surprising that modern-day analogues, notably either larvae or meiofauna were suggested as possible guides to the most ancient metazoans. Such candidates, however, presupposed both ancestral states and courses of evolution that for good reasons remain very doubtful. For example, extant pelagic larvae showing maximal indirect development (i.e. a catastrophic metamorphosis, with the adult rudiment represented by stem (or 'set-aside' cells)) have been a particular focus of attention. This hypothesis supposes that the 'invention' of the 'set-aside cells' was subsequently utilized to allow

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One contribution of 14 to a Discussion Meeting Issue 'Major steps in cell evolution'.

the abrupt evolution of macroscopic adult forms which initiated not the appearance of animals but their fossil record. It seems more likely, however, that such larval types are not only highly derived but are almost certainly polyphyletic. In addition, as already pointed out (see Conway Morris 2000*a*,*b*), the functional context of such hypothetical Precambrian larvae, especially in terms of their 'set-aside' cells, remain unresolved. Moreover, at least one proponent of this 'planktonic-first' hypothesis has now abandoned it, and for a cogent list of reasons (Peterson *et al.* 2005). Correspondingly, in the case of the meiofauna not only did the list of potential Proterozoic candidates include groups such as the aplacophorans (Fortey *et al.* 1996) that given their size (see Giere 1993) would certainly leave discernible traces, but also more importantly no convincing functional argument exists that can explain how animals evolving at genuine meiofaunal dimensions would require the anatomical array of organs that is otherwise the expected complement of the macroscopic scale (Budd & Jensen 2000; Conway Morris 2000*a*).

Since then the evidence for a deep origination of animals has been steadily eroded. The reasons are complex and can only be touched upon very briefly. In essence, the operation of the molecular clock method has proved to be far more complex than initially anticipated, with many confounding factors that militate against simple extrapolations (Welch *et al.* 2005). Nevertheless, it has remained generally the case that divergence times based on molecular clocks significantly predate the first known appearances in the fossil record (e.g. Donoghue & Smith 2004). Nevertheless, in the immediate context of early animal evolution the divergence between molecular clocks and the fossil record is now considerably reduced (e.g. Peterson *et al.* 2005; Peterson & Butterfield 2005). A narrowing of the differences, however, does not mean reconciliation, and it is clear that this story is unfinished. For whatever reasons, the tensions between estimated divergence times and the known fossil record seem, in terms of constructive dialogue, to be a particular hallmark of a number of studies of plant evolution (e.g. Janssen & Bremer 2004; Rydin *et al.* 2004; Bell & Donoghue 2005; Lavin *et al.* 2005; Magallon & Sanderson 2005). Moreover, a satisfactory agreement between estimated molecular and actual fossil dates has been achieved in a number of instances, notably in a number of mammalian studies (e.g. Arnason *et al.* 2000; Adkins *et al.* 2001; Huchon *et al.* 2002; Dooley *et al.* 2004; Tuinen & Hadley 2004). Finally, repeated attempts have been made to find general principles that might permit rescaling of clocks. Some of these have met with mixed success, but the proposed scaling between metabolic rates, body size, and speed of clocks (Gillooly *et al.* 2005) is particularly relevant not only because some previously major discrepancies between fossils and molecular data were resolved, but because the principles of scaling speak to general principles that permeate all areas of biology (e.g. West & Brown 2005).

What of the fossils themselves? To the first approximation palaeontologists—perhaps naively—remain confident that the fossil record of their respective groups is reliable (see the great majority of chapters in Donoghue & Smith 2004), and in their view it is the molecular clocks that require scrutiny. This is not to deny that claims for significantly deeper divergence times are a vital spur against palaeontological complacency, not least in either revising search strategies or reinterpreting previously problematic fossils. Nevertheless some existing claims for such divergence times, if accepted, will necessitate radical reappraisals of evolutionary history. Heckman *et al.* (2001), for example, have argued for the appearance of land plants hundreds of millions of years before the first fossil appearance in the Late Ordovician–Early Silurian. It appears that other molecular data are not only inconsistent with this estimate, but broadly in line with the fossil record (Sanderson 2003). Such agreement seems sensible simply because the transition to land involved key characters, such as the evolution of sporopollenin, cuticular hydrocarbons and tracheids. All of these display an enhanced fossilization potential, but have apparently few if any counterparts in even Cambrian sediments. Even if land plants were coeval with Burgess Shale-type faunas, and for a questionable record of bryophytes from the Lower–Mid-Cambrian Kaili Lagerstätte of Guizhou, South China (see Yang *et al.* 2004), this would leave unexplained the lag in diversification until the earliest convincing records from the Late Ordovician, an interval of *ca* 50 Myr. Similar arguments may be applied to the estimated divergence times of birds (and mammals) where a good fossil record is very difficult, if not impossible, to reconcile with molecular data (e.g. Fountaine *et al.* 2005). Naturally such examples are always predicated against the future possibility of discovering new exceptionally preserved fossils and the revision of phylogenies, yet at least in the case of the Cretaceous birds new finds (e.g. Zhang *et al.* 2003*a*) reinforce earlier conclusions that the radiation of the 'modern' birds was very largely a latest Cretaceous (e.g. Clarke *et al.* 2005) or Early Tertiary affair, and in any event a genuinely explosive event (e.g. Poe & Chubb 2004).

What then of the palaeontological record of the earliest metazoans in the context of molecular clocks? As already noted, the evidence for deep origins is increasingly questionable, and correspondingly the divergence in estimates of origination has been considerably reduced. Nevertheless, it still exists. Peterson & Butterfield (2005), for example, offer an interesting synthesis that ties together geological, molecular and palaeontological data. Yet their analysis begs several questions. Consider, for example, the notable development of acritarch ornamentation. This is certainly in striking contrast to the simple morphology of most earlier acritarchs, and may have arisen as a response to metazoan predation, especially by a mesoplankton. It remains the case, however, that the functional link between fluid flow around acritarchs and capture remains to be explored, as does the discovery of faecal pellets containing such acritarchs. Peterson & Butterfield (2005) estimates of metazoan diversification still significantly predate the bulk of the Ediacaran record, which as noted below has many problematic aspects. To date the links between these assemblages and the proposed synthesis of Peterson & Butterfield (2005) are somewhat tenuous. Nor is the typical Ediacaran taphonomy particularly conducive to preserving the delicate grazers and other metazoans that are posited to have existed. Nevertheless, what we presently know may not be too encouraging. Superbly preserved algae from the latest Neoproterozoic Miaohe-type biotas (e.g. Xiao *et al.* 2002; Yuan *et al.* 2002; Zhao *et al.* 2004) are accompanied by questionable sponges, which in any event are very widely assumed to be the most basal metazoans, but to date no more complex metazoans.

There is one further line of evidence that has been widely cited in support of deep divergence times for the metazoans, in the form of putative trace fossils (e.g. Seilacher *et al.* 1998; Rasmussen *et al.* 2002). In the case of the material from the Stirling Range Formation of southwestern Australia (Rasmussen *et al.* 2002), an earlier age of *ca* 1.2 Gyr was subsequently extended to at least 1.8 Gyr (Rasmussen *et al.* 2004). Nor is this the only reason to be sceptical. As noted elsewhere (Conway Morris 2003), despite the attention that greets many of the new announcements, their occurrences are distinctly puzzling. Such putative traces are extremely sporadic, which show within the limits of a relative simplicity a considerable range of morphologies, and they span a huge age range. One solution, of course, is that the 'worm' that ostensibly made these sedimentary markings evolved independently several times, and conceivably from different protistan ancestors. Nevertheless, this still fails to explain why such an evolutionary invention failed to radiate into a vacant ecosystem.

2. THE EDIACARAN ASSEMBLAGES: A CONTINUING CONUNDRUM

The earliest macroscopic fossils, which may represent metazoans, post-date all glacial units (tillites), which evidently represent major, possibly global, glaciations. Present estimates suggest there were three such glacial episodes (e.g. Halverson *et al.* 2005), and it is the latest of these (generally referred to as the Gaskiers, after the tillite sequence in southeast Newfoundland) which predates the first definitive Ediacarans (Narbonne & Gehling 2003). In fact, discoidal fossils from intertillite units in northwest Canada (Twitya Formation) are known (Hofman *et al.* 1990), are widely accepted as the earliest fossil metazoans, but they are just as likely to be microbial in origin (D. Grazhdankin 2005, personal communication). In addition, the tillite above these discs appears to correlate with the second of the glacial episodes (referred to as the Marinoan; see Halverson *et al.* 2005), and therefore significantly predates the Gaskiers, perhaps by about 40 Myr.

In any event, the post-tillite Ediacaran interval is justly famous for its more or less soft-bodied assemblages, but in terms of both phylogenetic placement and functional biology they have proved to be remarkably recalcitrant (see Narbonne 2005). Discussion has broadly divided into two schools. The first regards them as largely metazoans, whereas the alternative group, initiated by A. Seilacher (1989), argues for a unique body construction, effectively mattress-like, possibly syncitial, and by implication some sort of giant protistan. This intriguing hypothesis is enshrined in the concept of Vendobionta. As is often the case, neither side is likely to have a monopoly on the truth, but the continuing intractability in the interpretations suggests that any hypothesis on the table will continue to beg as many questions as it answers. The likelihood that we are dealing with assemblages markedly different from those found in the Phanerozoic is reinforced by Grazhdankin's (2004) seminal synthesis. In addition to identifying three principal ecotypes he made two cardinal observations. First, so far as the constraints of stratigraphic correlation and radiometric dating allow, it appears that the assemblages show negligible evolutionary change over protracted geological intervals. Second, and equally intriguingly, there is no evidence that diversity was much influenced by latitudinal gradients. Given the near-universality of such gradients (Hillebrand 2004), this is curious. The fact, however, that the species richness in recent microbial communities also shows little control by latitudinal gradients (Finlay & Fenchel 2004) may represent a significant analogue, hinting that the ecology of the Ediacarans has important similarities.

Are there any metazoans within the Ediacaran assemblages? While unlikely, it is possible to argue that everything is some sort of vendobiont, and the recurrent modular architecture remains a striking feature (e.g. Narbonne 2004). Against this extreme view is the apparently reasonable evidence for sponges (e.g. Gehling & Rigby 1996), although the record of co-eval spicules is at least in some cases more circumspect (e.g. Zhou *et al.* 1998). Cnidarians are also an expected component of these assemblages, but Grazhdankin (2000) addresses some continuing difficulties of interpretation. Nevertheless, there are candidate cnidarians. Perhaps the most convincing are in the form of conulariids (van Iten *et al.* 2005), as well as some of the frond-like forms that also occur as Ediacaran 'survivors' in the Cambrian (Conway Morris 1993). Another apparently reliable metazoan is the quasi-mollusc *Kimberella*, which is associated with tracks and apparent feeding traces in the form of scratch arrays (e.g. Fedonkin 2003, fig. 14–16). The roster of putative metazoans is considerably longer, but the placement of such well-known taxa as *Dickinsonia* (e.g. Dzik & Ivantsov 2002), *Spriggina* and *Parvancorina* is problematic, although the last genus has an interesting resemblance to certain Cambrian arthropods (Zhang *et al.* 2003*b*). These difficulties of placement are exemplified by *Yorgia* (e.g. Ivantsov 1999). This intriguing organism shows a complex bodyplan, albeit asymmetrical about the left–right axis. Evidently, it had the ability to move across the seabed, where it left behind a series of resting impressions (Ivantsov 1999; Ivantsov & Malakhovskaya 2002; Fedonkin 2003). How it moved, and the reason for a succession of imprints—feeding, and if so by absorption through the ventral surface?—are open questions. How best to treat *Yorgia* and presumed relatives? The first possibility is to dispatch them to the vendobiont camp (see below), but this perhaps raises more questions than it answers. If taken to be metazoans, we can as a second possibility unhelpfully dismiss them as 'failed experiments', enigmatic offshoots within the animals. A third possibility is that these are not only animals but have a level of organization seemingly more complex than cnidarians and conceivably fall within the stem-group triploblasts. The difficulties with this proposal are self-evident in as much as the little we can infer about the diploblast–triploblast transition, and the apparently basal position of the acoels (e.g. Baguna & Ruitort 2004; Cook *et al.* 2004), have no obvious connection to these Ediacaran taxa. On the other hand, both this historical transition and the nature of the primitive triploblasts are speculative. Extant forms are highly derived, and may be relatively uninformative in this regard. Could the common ancestor of all triploblasts be represented by animals similar to *Dickinsonia* and *Yorgia*?

What of the vendobionts? Recent work, including evidence for an infaunal habitat (e.g. Grazhdankin & Seilacher 2002), and even the possibility that the tissue (or syncitial equivalent) could grow through the sediment (see Crimes & Fedonkin 1996), combined with earlier observations on the organisms' pronounced modularity, sac-like construction and relative simplicity, suggests that they may have been giant protistans (see Seilacher *et al.* 2003). This too leads to some interesting conjectures. Where within the protistans (or as some have even argued the fungi; see Peterson *et al.* 2003) should the vendobionts be placed? To what extent can they be regarded as analogous to metazoans, attaining a multicellular grade independently? What was their embryology and developmental biology? The well-defined symmetries and metamerism may also have arisen independently, but it is also possible that some of the homeotic genes known in metazoans may derive from a common ancestor.

The interpretation of Ediacaran assemblages constitutes one of the major challenges to palaeontology. It is, perhaps, worth concluding this section with a couple of apparently anomalous reports. Ediacaran assemblages are notable for discoidal fossils, which have variously been interpreted as medusoids, holdfasts and microbial colonies. In at least one case, that of the strikingly concentric *Kullingia*, the disc is now reinterpreted as a series of annular scratches imposed by a tethered benthic object that presumably was some sort of tubicolous organism (Jensen *et al.* 2002). A somewhat different example is a striking array of fractal-like branching structures, preserved in carbonate (Xiao *et al.* 2005). While these have a certain similarity to other fractally constructed Ediacaran organisms, an alternative possibility is that these are of diagenetic structure, possibly mediated by microbial activity.

Such Ediacaran material, irrespective of its controversial nature, is macroscopic. There is, however, another important new avenue to our understanding of Ediacaran assemblages. This is in the form of embryos, remarkably preserved and recovered in quite extraordinary abundance, from the Doushantuo Formation in the Weng'an area of Guizhou, South China. Although earlier dated as *ca* 600 Myr (Barford *et al.* 2002), the most recent results suggest an age only about 10 Myr before the Precambrian–Cambrian boundary (see Condon *et al.* 2005). Even though these embryo fossils are, therefore, exactly contemporaneous with typical Ediacaran assemblages, their interpretations are not free of difficulties. For example, the most convincing examples are only found up to the *ca* 64-cell stage. Yet the diagenetic environment of what must have been very early phosphatization seems otherwise to be similar to those examples of Cambrian embryos (e.g. Bengtson & Yue 1997; Dong *et al.* 2004, 2005), but in the latter case far more complete ontogenies are known. One possibility, therefore, is that the developmental pathway diverged radically from that found in at least directly developing Cambrian embryos (see Conway Morris 2004). Associated with the Doushantuo embryos is a cylindrical organism, possibly a cnidarian (e.g. Yuan *et al.* 2002; Chen 2004, fig. 117), which conceivably might have produced some of these embryos. Other alternatives, including vendobionts or other early metazoans are possible, but in the associated strata no direct evidence exists for these groups. In addition to what are almost universally accepted as embryos, there are, however, other forms whose status is more controversial. Some phosphatic spheres, for example, have been interpreted as showing such embryological features as gastrulation and blastopores (e.g. Chen *et al.* 2002*a*; Chen 2004), but it seems more likely these structures are diagenetic. This may also apply to supposed minute bilaterians where phosphatic crusts are interpreted as ostensible cell layers (Chen *et al.* 2004; Chen 2004). Here too a diagenetic interpretation seems preferable, and it is difficult to accept the detailed reconstructions offered in terms of cellular sheets and internal organs. Nevertheless, it remains the case that these complex histories of phosphate precipitation are not fully understood.

3. OPENING THE DOOR INTO THE CAMBRIAN

The Cambrian fossil record has seen highly significant advances, notably in the study of Burgess Shale-type and Orsten faunas, but the context of the various discoveries requires continuous reappraisal in the light of on-going developments in the molecular phylogenies that address metazoan relationships. This latter field, however, remains fluid, with many unresolved issues. For example, despite strong evidence for the concepts of Ecdysozoa (Aguindaldo *et al.* 1997) and Lophotrochozoa (Rosa *et al.* 1999), respective voices favouring both the older concept of the Coelomata (Almeida *et al.* 2003; Wolf *et al.* 2004; Philip *et al.* 2005; see also Telford 2004) and the directly related theme concerning the expulsion of the Nematoda from the Ecdysozoa (Blair *et al.* 2002) have been raised. In either case, however, the counter-arguments appear more persuasive (e.g. Haase *et al.* 2001; Anderson *et al.* 2004; Copley *et al.* 2004; Philippe *et al.* 2005; Roy & Gilbert 2005).

Here, I will touch briefly on a few potentially key issues, fully aware that new data may necessitate radical revision of existing frameworks. In this context, palaeontological evidence is problematic, because some widely differing interpretations of fossil material lead to disparate phylogenies. The yunnanozoans, a case in point, are discussed below. In addition, while there has been some success in accommodating hitherto problematic fossils in a phylogenetic framework, a number of fossil taxa still remain enigmatic. A number of examples could be given. One is the eldoniid/rotadiscid/parapsonemid group, discoidal fossils which range from the Lower Cambrian to Middle Devonian (e.g. Clarke 1900; Chen *et al.* 1995*b*). It has long been realized that this group has some similarities to the echinoderms, but our present understanding of the latter's phylogeny (see below) still leaves the eldoniids (and relatives) in limbo. Equally, enigmatic are the chancelloriids. These are sponge-like organisms, but they build their skeletal elements in a coeloscleritophoran mode, that is as hollow spicules which are typically connected to other parts of the body by a restricted aperture. The presence of an obvious integument (Bengtson & Hou 2001) also argues against a poriferan affinity (but see Butterfield & Nicholas 1996), while Randell *et al.* (2005) make an interesting argument for a place in the cnidarians.

Correspondingly, among extant faunas there are a number of still-enigmatic groups. Most famous are the chaetognaths, whose phylogenetic position has proved recalcitrant, although a place in the basal protostomes is most likely (Helfenbein *et al.* 2004; Papillon *et al.* 2004). Very useful as this is, it tells us nothing about the origins of their distinctive and notably conservative bodyplan. Can the fossils assist? There is a convincing fossil record from the Lower Cambrian Chengjiang Lagerstätte (Chen & Huang 2002; Chen *et al.* 2002*b*, fig. 8-1.3, pl. 17, fig. 6; Chen 2004, fig. 347, 348; Vannier *et al.* 2005; and also the Burgess Shale; D. Collins 2000, personal communication), and the case for the Cambrian to Ordovician protoconodonts being equivalent to the grasping spines is also strong (e.g. Szaniawski 2002). The suggestion, however, by Szaniawski (2005) that the Burgess Shale animal *Oesia disjuncta* is a chaetognath is untenable (Conway Morris, in preparation).

In §5, brief remarks are made on the possible early history of the lophotrochozoans. While the fossil record appears to be highly informative, nevertheless interesting questions remain. For example, while not enigmatic in terms of being a lophotrochozoan (see Anderson *et al.* 2004), how the distinctive bodyplan of the nemerteans arose is conjectural. Similar remarks apply to the sipunculans, and in this case probable fossils from the Chengjiang Lagerstätte (Huang *et al.* 2004*a*) are not otherwise especially informative. In the case of the echiurans, once treated as a separate phylum, it is clear that they nest within the Annelida (e.g. Bleidorn *et al.* 2003), although the fossil record is almost mute. A somewhat different category of enigmatic metazoans are the quasi-flatworm or even quasi-protistan groups. Notable examples include the myxozoans, mesozoans, symbions and xenoturbellans. The latter, for example, are evidently deuterostomes (see Israelsson & Budd 2005), and while their being primitive seems less likely, how they arrived at what may be a highly derived position is conjectural. Similar remarks apply to the other groups just listed, and while their overall phylogenetic positions are reasonably clear, again the details of their phylogenetic history and the functional reasons for massive simplification await elucidation.

4. THE MOST PRIMITIVE METAZOANS

The earliest radiations of the sponges and coelenterates (i.e. cnidarians and ctenophores) can only be briefly touched upon. The record of sponges in the Cambrian is rich and diverse (e.g. Rigby & Collins 2004), and they appear to have been of particular importance in deep-sea habitats (e.g. Steiner *et al.* 1993). Their phylogeny remains largely dependant on molecular data (e.g. Borchiellini *et al.* 2004; Nichols 2005), but palaeontology yields important insights. Botting & Butterfield (2005), for example, identify the genus *Eiffelia* as a stem-group hexactinellid but with important links to calcareans. As already noted, the status of the sponge-like chancelloriids, however, remains more enigmatic, with the principal competing hypotheses arguing for retention within the poriferans (Butterfield & Nicholas 1996; Botting & Butterfield 2005) as against a possible cnidarian affinity (Randell *et al.* 2005). Despite their primitive status the record of Cambrian cnidarians is relatively sporadic, but includes possible sea-pens (Conway Morris 1993), probable octocorals (e.g. Ausich & Babcock 1998), anemone-like creatures, such as *Xianguangia* from the Chengjiang Lagerstätte (e.g. Chen 2004, fig. 246) as well as early corals (e.g. Jell 1984; Debrenne *et al.* 1987; Lafuste *et al.* 1991; Sorauf & Savarese 1995). No convincing scyphozoans (or cubozoans) are yet documented, although the newly proposed class of staurozoans may have as fossil representatives the conulariids (Marques & Collins 2004). This extinct group had generally been placed in the scyphozoans, but is known to have an Ediacaran (see above) and Cambrian record (e.g. Conway Morris & Chen 1992). They are also of considerable interest because of a spectacularly documented ontogenetic series from the Lower Cambrian of China that includes embryonic stages (Yue & Bengtson 1999).

Despite their reputation for delicacy, the fossil record of ctenophores is quite impressive (Conway Morris & Collins 1996; Chen 2004, fig. 254–256). The number of comb-rows is surprisingly variable. Some Chengjiang taxa have the eight (or in one case apparently four) comb-rows which characterize all extant ctenophores, whereas the Burgess Shale taxa have what appears to be multiples of eight. With one possible exception all these Cambrian ctenophores apparently lacked feeding tentacles. All of these ctenophores at least approximate to the extant fauna in being more or less globular, probably in life largely gelatinous and it has been assumed pelagic. This may be premature when one considers what is perhaps the most interesting taxon, that is *Trigoides*. In this animal, from the Chengjiang Lagerstätte (Chen *et al.* 2002*b*, pl. 21, fig. 3), the comb-plates seem to be attached to plate-like structures. The origin of ctenophores is presently completely unknown, but one possibility would be to envisage a benthic ancestry, whereby the ciliated comb-rows acted to generate feeding currents. *Trigoides* might be instructive in this regard, because one implication of this suggestion would be that the extant ctenophores are much more derived than generally thought, highly adapted to a pelagic existence and dependant on the ciliary rows for effective locomotion.

5. THE TRIPLOBLAST STORY

The possibility that certain Ediacaran taxa might represent stem-group triploblasts was alluded to above, but otherwise the available Cambrian record appears to shed no obvious light on either the diploblast–triploblast transition or the earliest history of the triploblasts. It is just as likely, however, that the fossils have already been collected, but have not yet been recognized for what they represent. With respect to the three triploblast superphyla, that is the ecdysozoans, lophotrochozoans and deuterostomes (the order in which they will be dealt with here), there does appear, however, to have been some progress.

Within the ecdysozoans there have been impressive advances in the documentation of an extensive range of arthropods (e.g. Zhang *et al.* 2000; Chen *et al.* 2001; Chen 2004; Hou *et al.* 2004; Liu *et al.* 2004) and priapulids (e.g. Chen 2004; Huang *et al.* 2004*b*,*c*). To date, however, the fossil record throws no useful light on the origin of the nematodes. The welter of Cambrian arthropods has been placed in a number of phylogenetic schemes (e.g. Budd 2002; see also Maxmen *et al.* 2005), which in certain cases seek to make also functional and ecological sense (e.g. Budd 1998). It is widely proposed that lobopodians are among the most primitive arthropods, and it is possible that they in turn derived from an early priapulid, conceivably a palaeoscolecidan. Direct evidence of such a transition appears not to be available, but it is consistent with molecular evidence pointing towards a basal position for the priapulids (Mallatt *et al.* 2004). The priapulids include forms with various sorts of armature, including button-like sclerites whose functional significance is largely unexplored. A number of phylogenies have been proposed (e.g. Huang *et al.* 2004*c*), and in addition it is worth noting that some worms identified as phoronids (*Eophoronis*, see Chen 2004, fig. 331, 332; and *Iotuba,* see Chen & Zhou 1997, fig. 49, 50) may well be synonymous, and are similar to the priapulid *Louisella*.

Interpretation of the lophotrochozoans continues to excite debate at a number of levels. While the suggestion, based on molecular data, that annelids and molluscs were related was broadly in line with existing thinking, this emphatically was not the case with the brachiopods whose placement in this super-clade was greeted with suspicion by some organismal biologists. So far as stem-groups are concerned, potentially key groups include the halkieriids and wiwaxiids. The former, as the articulated *Halkieria evangelista* (Conway Morris & Peel 1995), was argued to be instructive with respect to several lophotrochozoan phyla, including the annelids, brachiopods and molluscs. Vinther & Nielsen (2005), however, preferred to shoe-horn the halkieriids back into the molluscs, but in setting this essentialist agenda failed to grasp the evolutionary importance of stem groups and the nature of transitional organ systems. First, it is not in dispute, as had already been pointed out, that molluscs may well have arisen from something fairly similar to halkeriids, that is in the form of a slug-like animal with a coating of dorsal spines or plates. The difficulty, however, is that the secretion of the spicules in what are presumably the primitive aplacophorans and polyplacophorans bears no particular resemblance to the assumed mode of growth of the complex halkieriid sclerites. To be sure, one can envisage a hypothetical transition between halkieriid sclerite and molluscan spicule, but such a transformation is unsupported by any evidence. A key part of Vinther & Nielsen's (2005) argument, however, was to compare halkieriids to a number of multi-plated chiton-like animals from the Palaeozoic (e.g. Hoare & Mapes 1995; Vendrasco *et al.* 2004). Yet this is doubtful in many respects. First, these Devonian–Carboniferous animals are substantially younger than the last-known halkieriids (Porter 2004), and the reasonably good record of Lower Palaeozoic chitons (e.g. Pojeta *et al.* 2003, 2005) suggests no obvious link between these multi-plated chitons and the halkieriids. Second, the comparisons made by Vinther & Nielsen (2005) between the hollows spicules/spines of various molluscs and the complex canal system of the halkieriid sclerites is seriously misleading. Even in the Carboniferous multiplated chiton *Diadeloplax* the canal system of the lateral spines (see Hoare & Mapes 1995, fig. 7 J-R) is completely unlike the halkieriid arrangement, and no convincing homology exists. Third, in at least this genus the porous microstructure of the spines is the same as the plates, raising the possibility that these marginal structures are better interpreted as derived shells.

Halkieriids have also attracted attention on account of the hypothesis that the prominent shells at either end of the body are precursors of the dorsal and ventral valves of the brachiopods (Conway Morris & Peel 1995). It has long been known that a number of otherwise enigmatic tommotiids, a diverse group of phosphatic shelly fossils from the Lower Cambrian, have shell structures that are strikingly brachiopod-like (e.g. Conway Morris & Chen 1990). In addition, in the case of forms such as *Micrina* and *Tannuolina*, there are two distinct morphs referred to as the sellate and mitral sclerites. These, it has been argued (Holmer *et al.* 2002; Williams & Holmer 2002), might have a comparable location to the shells of *H. evangelista*, and as such would be interpreted as stem group brachiopods. On the basis of some associated ontogenetically merged material Li & Xiao (2004) argued, however, for a multiplated configuration. Such fused sclerites are, however, extremely rare and a teratological alternative may be worth exploring. Although otherwise markedly different, the apistoconchs, originally nicknamed pseudobrachiopods and assumed to be bivalved animals despite the incongruence of fit between either shell (Bengtson *et al.* 1990, pp. 171–181), may have also occupied halkieriid-like positions (Parkhaev 1998). In contrast to the tommotiids, however, apistoconchs evidently had a calcareous shell, as possibly did the Burgess Shale taxon *Oikozetetes* which was tentatively reconstructed as a halkieriid animal (Conway Morris 1994). There are a number of other Lower Cambrian shells, of various shapes, which are assigned with different degrees of confidence to halkieriid-like animals. It is likely that there was a plexus of armoured slug-like animals in the Cambrian that gave rise to a number of groups, including the brachiopods and molluscs.

What of the annelids? Apart from the Burgess Shale (Conway Morris 1979), the record is very sporadic. Perhaps surprisingly, no definite example is known from the richly fossiliferous Chengjiang deposits, and a possible annelid briefly described by Chen *et al.* (1996) is a very questionable assignation. The somewhat enigmatic *Myoscolex*, from the Emu Bay Shale of Kangaroo Island, South Australia, was also interpreted as a polychaete by Dzik (2004), but this too appears to be a forced comparison and although not free of its difficulties a comparison to the anomalocaridids is more persuasive (Briggs & Nedin 1997). Reasonably, Eibye-Jacobsen (2005) regarded all the Burgess Shale polychaetes as stem-group annelids, but he excluded *Wiwaxia*. His arguments revolved around the supposed lack of segmentation, absence of parapodia and equivalence of the sclerites to chaetae. In a way analogous to the disputed phylogenetic position of the halkieriids, much depends on character determination and expectations of a stem-group. Thus, not only did Butterfield (1990) convincingly demonstrate a microstructure in wiwaxiid sclerites similar to that of annelid chaetae, but Eibye-Jacobsen's (2005) mention of other setal-like structures is not immediately relevant because of the proposed homology of ventral and dorsal wiwaxiid sclerites to the neurochaetae and notochaetae of polychaetes. Neither is the absence of parapodia germane, because these (especially in the neuropodia) are posited as crucial to the emergence of walking gait in the first polychaetes as against the crawling mode of wiwaxiids. The wiwaxiids show clear segmental repetition of the dorsal and ventral sclerites (Conway Morris 1985, e.g. fig. 61 and 137–140) and here too the shift to a complete metameric segmentation is plausibly linked to a more active stepping locomotion requiring precise co-ordination of movement. I have also argued for an evolutionary relationship between wiwaxiids and halkieriids, principally on the basis of overall sclerite similarity and their arrangement in comparable zones across the body (Conway Morris & Peel 1995). Clearly, these hypotheses require further testing, and may be critically dependant on recovery of new articulated material and further study of sclerite microstructure, especially the extent to which the wiwaxiid sclerites are hollow.

Deuterostome phylogeny has particular interest both on account of the disparity of forms, and also questions surrounding the early evolution of vertebrates. The sister-group relationship between the echinoderms and hemichordates is largely accepted, but the phylogeny of the chordates and their near-relatives the cephalochordates and tunicates remains more confused. With respect to the hemichordates, on the basis of unpublished observations on the Burgess Shale material (E. Boulter 2004, personal communication), it seems more likely that the balanoglossids (rather than the rhabdopleurids and extinct graptolites) are primitive, but whether they arose from the stem-group echinoderms or vice versa is conjectural. There is, moreover, a quite general problem, by no means restricted to this case, in as much as the evolutionary transformations involved stem-group bodyplans that often had little resemblance to any crown-group representative. A recurrent stumbling block in the zoological literature has been the effectively arbitrary invention of 'ur-phyla', representing a supposedly convenient amalgam of character states. These are fictions, but if taken seriously make the interpretation of the actual fossils a yet more daunting task.

The early history of the echinoderms may, however, be somewhat closer to resolution. Arguments hinge around the vetulocystids (Shu *et al.* 2004) and a series of decidedly enigmatic echinoderms that include the cinctans, stylophorans and solutes. So far as the stylophorans, which are divided into cornutes and mitrates, are concerned, the focus of debate has been Jefferies' arguments that there was a threefold loss of the diagnostic calcitic stereom, to give rise respectively to the tunicates, cephalochordates and chordates (Jefferies 1986, 1997). The range of observational detail that Jefferies has obtained concerning these strange organisms is impressive, but the wider conclusions, e.g. identification of nervous systems, notochord, etc., have, for the most part, been greeted with considerable reservation (see Clausen & Smith 2005), indeed in places with incredulity. One solution is to regard them as highly derived echinoderms, with the stylophorans, for example, being related to the crinoids (e.g. David *et al.* 2000). This, however, poses many problems and is also somewhat inconsistent in terms of stratigraphy. Their possible place as stem-group echinoderms may, however, receive some support from the vetulocystids, given they also have a bipartite body, with a swollen anterior section bearing probably gut openings and gill, and a tail-like structure that was possibly segmented. In this respect, the sequence of vetulocystids, stylophorans (as cornutes), cinctans and solutes suggests that the order of acquisition in this stem group may have been: acquisition of mesodermal skeleton (stereom), change of function of the segmented tail from propulsion to first attachment and then ultimate loss, development of an ambulacral feeding tract (first attached, then as free arm) and by implication the water vascular system with hydropore, complete loss of gill slits and subsequently pentameral symmetry (Shu *et al.* 2004, fig. 4; similar conclusions are arrived at by Smith 2005). The last feature has attracted much comment, but given the strikingly asymmetric nature of the stem-group, the choice of a fivefold symmetry may reflect the transition to sessility and the replacement of a central nervous system with a diffuse nerve net.

The origin of the vertebrates is now known to be substantially earlier than thought, and to date three fishes (*Haikouichthys*, *Myllokunmingia* and *Zhongjianichthys*) have been reported (Shu *et al.* 1999, 2003*a*; Shu 2003). The proposed synonymy of the first two taxa (Hou *et al.* 2002) seems unlikely, because although *Myllokunmingia* is known only from a single specimen, the anterior, and especially the gills, is very different in arrangement from *Haikouichthys* where there is a striking array of branchial supports (Shu *et al.* 2003*a*). The interpretation of the supposed gill areas in a single specimen of *Haikouichthys* (Hou *et al.* 2002) is also not free from difficulties. While the anterior set with well-defined branchial supports is clearly identical to those in other specimens of *Haikouichthys*, the more posterior set of 'arches' are difficult to interpret in this functional context and may be myotomal. The description of forwardly pointing fin rays in this latter taxon was also greeted with scepticism, including arguments that they were an imposed cleavage fabric (Hou *et al.* 2002). Our earlier observations have, nevertheless, been confirmed with the additional information that this fin extended as a fold around the posterior of the body with the fin rays also changing direction towards the tail (Zhang & Hou 2004).

The Cambrian fossil record of the related tunicates and cephalochordates does, however, continue to pose a number of questions. For example, two types of tunicate have been recorded, both from the Chengjiang Lagerstätte but otherwise distinctly different (Shu *et al.* 2001*a*; Chen *et al.* 2003). Thus, *Cheungkongella* is strikingly similar to extant stylid tunicates, but critics (e.g. Chen 2004) have drawn attention to the otherwise enigmatic *Phlogites* (see Chen *et al.* 2002*b*; Chen 2004), which has a somewhat similar body form, but is also equipped with prominent tentacles, a feature unknown in tunicates. My own view, having examined the only known specimen of *Cheungkongella* closely, is that the similarity to *Phlogites* is most likely superficial. *Shankouclava* (see Chen 2004, fig. 512–514) is not quite as well preserved, and the putative branchial basket is somewhat difficult to resolve, and I regard its status as a tunicate as more provisional. Unfortunately, but unsurprisingly, the question of whether these putative tunicates include a 'tadpole' larva in their life cycle is conjectural.

Cathaymyrus has been described on the basis of a single specimen (Shu *et al.* 1996*a*), but it may be our best candidate for a Cambrian cephalochordate. More fragmentary cephalochordate material is known (Shu Degan 2004, personal communication and personal observation), and so far as can be told *Cathaymyrus* is not particularly similar to the extant amphioxus animal. The Burgess Shale *Pikaia* has also attracted considerable attention. Its chordate credentials rest on what are interpreted as myotomal segmentation and a prominent rod-like structure, presumably the notochord. This animal shows, however, several distinctive features (especially in the head region). It may be better interpreted, therefore, as an independent development of a chordate-like anatomy, albeit from a common ancestor whose descendants include amphioxus and the fish. Nor may this be the only possible example. Cladistic methodology routinely embeds the conodonts not only within the chordates, but also within crown-ward of the agnathans (Donoghue *et al.* 2000). Yet the conodonts show a number of distinctive features. These include simple V-shaped myomeres (as in amphioxus), and a feeding apparatus which has no clear homologies in structural arrangement to the vertebrate jaw. In addition, it is also questioned whether the microstructural similarities of conodont element histology are genuine homologies with some tissues of vertebrate teeth (e.g. Kemp 2002*a*,*b*). It seems that in a way analogous to *Pikaia*, conodonts could be another parallel development to a vertebrate-like form, again arising from a cephalochordate-like ancestor. Given the earliest conodonts are Mid-Cambrian, this development of teeth would be another example of convergence (see also Smith & Johanson 2003), significantly pre-dating that of the vertebrates.

From this perspective, it is not obvious that amphioxus need be directly implicated in vertebrate ancestry and its apparent proximity may be more a result of the extinction of other lineages. This is not to deny its major genomic relevance, most famously in terms of the single set of *Hox* genes, but this genetic architecture (e.g. Holland *et al.* 2004) may in itself be more primitive. It does, however, suggest that attempts to establish direct phylogenetic and functional links in terms of key features, such as myomeres, notochord construction, hyper-pharyngometry, sensory systems and possibly body asymmetries, may be difficult to achieve. Similarly, despite the major investment into tunicate genomics, it seems possible that this group is very specialized and genomically it shows various peculiarities (e.g. Edvardsen *et al.* 2004; Gissi *et al.* 2004; Ikuta *et al.* 2004; Seo *et al.* 2004). One consequence of this may be the widespread assumption that the 'tadpole' larva is instructive with respect to vertebrate origins. This claim may be wide of the mark. Indeed, it is yet another attempt to place a phylogenetic burden on the metaphorical shoulders of larval forms, a burden they were never intended to bear.

Clearly, deuterostome phylogeny will remain an active area of debate for many years. This applies also to particular fossil taxa, notably the vetulicolians and yunnanozoans. The former were initially described as arthropods, and this possibility was reiterated as one phylogenetic solution to a discovery of what appears a new example from the Middle Cambrian of Utah (Briggs *et al.* 2005). If accepted, this would point to some radical re-thinking of arthropod phylogeny. Just how radical is apparent from the fact that such a scheme would also have to accommodate other members of the vetulicolians, such as *Didazoon* and *Xidazoon*, and almost certainly *Banffia* (Shu *et al.* 2001*b*). The absence, in particular, for any evidence of any appendages, jointed or lobopodian, is perhaps surprising and at present the arthropod-like features most clearly expressed in the abdomen may be better interpreted as convergent. The alternative scheme of interpreting vetulicolians as primitive deuterostomes does, therefore, seem to have more merit. In particular the perforations along either lateral margin, and associated structures which show their most complex development in *Vetulicolia*, seem to represent gill openings. The bipartite body may also provide a link with the vetulicystids, as well as to the chordates via the somato-visceral hypothesis of Romer (see Shu *et al.* 2001*b*, 2003*b* for further explanation).

Yunnanozoans were first identified, albeit as a highly enigmatic group, more than 15 years ago (Hou *et al.* 1991), and although now generally accepted as deuterostomes (e.g. Chen *et al.* 1995*a*; Shu *et al.* 1996*b*, 1999, 2003*b*; Mallatt & Chen 2003; Chen 2004) have attracted major controversy in terms of their position and so importance. One possibility is that they are allied to the hemichordates (Shu *et al.* 1996*b*), but the alternative hypothesis that they are effectively pre-vertebrates (Mallatt & Chen 2003) has also attracted support. In commenting on the strengths of this latter view, Briggs & Fortey (2005) noted that in the cladistic analysis of Mallatt & Chen (2003) no less than 40 characters supported a chordate affinity. All depends, of course, on the usefulness and reliability of these characters. For example, although eyes have been identified (e.g. Mallatt & Chen 2003; Chen 2004), and reconstructions accordingly equipped, the illustrated specimens indicate at best vague structures, sometimes only seen on one side of the head. In the Chengjiang Lagerstätte, however, unequivocal eyes are routinely preserved and often prominent, as in the fish *Haikouichthys* (see Shu *et al.* 2003*a*). In the many exquisitely preserved specimens of *Haikouella jianshanensis* (Shu *et al.* 2003*b*), no eyes were identified. Similar remarks apply to such features as supposed mouth, tentacles and teeth. The structure identified as a notochord has neither the preservation nor functional position to be convincing, while the putative myomeres are very unlikely to be constructed in the diagnostic cone-in-cone structure of vertebrate muscle blocks. In all yunnanozoans, the segmental boundaries are at best gently arcuate, having neither a V let alone a W shape. In addition, the anterior-most segment of the trunk series, which has the same style of preservation, has an approximately triangular shape, which again is very difficult to reconcile with a myomere. Finally, the surface of this trunk region was evidently cuticular, to judge from its sometimes wrinkled texture. This is consistent with a relationship to the vetulicolians (Shu *et al.* 2001*b*), but has no counterpart in unequivocal chordate material from Chengjiang (Shu *et al.* 1999, 2003*a*). Extraordinarily, a relatively enormous tripartite brain has been identified (Mallatt & Chen 2003, fig. 5; Chen 2004), even though it is at least an order of magnitude larger than any equivalent structure in animals of broadly comparable organizational complexity. In conclusion, although rare, even unique, specimens may fortuitously display structures 'expected' in a primitive chordate, larger suites of material repeatedly throw severe doubt on many of these interpretations.

It is evident, therefore, that many of these fossils will continue to attract controversial interpretations. In addition, there are a number of enigmatic forms whose position in early metazoan phylogeny is still conjectural. These include the eldoniids (and rotadiscids), nectocaridids, odontogriphids, amiskwiids and vetustovermids. This is not to say we lack some existing proposals. As noted above, eldoniids and their relatives have some intriguing similarities to the holothurians, but seem to be at variance with our current models of echinoderm phylogeny. New material of odontogriphids and possibly nectocaridids has been collected by the Royal Ontario Museum expeditions to the Burgess Shale locality (J. Caron & D. Collins 2005, personal communication), and their reinterpretation is eagerly awaited. The amiskwiids are particularly intriguing, and although reported from the Chengjiang Lagerstätte (e.g. Chen *et al.* 2002*b*, pl. 27, pp. 174–175, fig. 7) our principal evidence still comes from the Burgess Shale (Conway Morris 1977). Although Butterfield (2003) attempted to smuggle *Amiskwia* back into the chaetognaths, his argument that the taphonomic environment was unconducive to the preservation of the diagnostic grasping spines is negated by just this sort of preservation in the chaetognaths from Chengjiang (and also the Burgess Shale; see above). While rejecting any close similarity between *Amiskwia* and nemerteans (Conway Morris 1977), this possibility might still bear further investigation. The nemerteans were also proposed as a possible home (among many others) for the vetustovermids (Chen *et al.* 2005), but in describing what is obviously the synonymous *Petalilium* (not *Petalium* as spelt in Chen *et al.* 2005), the authors of this description (Chen *et al.* 2002*b*, pl. 21, fig. 1 and 2) suggested this animal was some sort of arthropod. Indeed, this animal may have more significant similarities to some primitive arthropods, notably *Kerygmachela* (see Budd 1999). Many of these ideas are still provisional and will require major, even radical, change, but the discovery and description of new material clearly suggests that in a few years a number of existing hypotheses will have been confirmed, or entirely dismissed.

6. CONCLUSIONS

In this review I have most touched on current controversies in animal phylogeny, as well as trying to describe an outline of evolutionary events in post-glacial ('snow-ball') times. There are, of course, numerous ancillary questions which can only be touched upon. Among the most significant are the proposed roles of developmental genes, both in explaining transformation into new bodyplans and providing a guide to the likely organization in primitive animals, now long extinct. The growing realization, however, of major redeployment and co-option of genes, as well as evidence that closely related forms may employ surprisingly different developmental pathways to produce phenotypically very similar structures suggests that the attempt to define genetic archetypes may not be straightforward. Put simply, genomic systems are probably highly dynamic, that is they evolve. This is not to deny there will be phylogenetic footprints, but to infer various organ systems, e.g. eye, heart, mesoderm, on the basis of inferred gene possession in Neoproterozoic and Cambrian animals may be more conjectural an exercise than expected. Possibly 'unexpected' configurations of anatomy in fossil material may be helpful in this regard.

My main conclusion is that the Cambrian 'explosion' is a real event. This does not mean, however, Darwin's dilemma is quite the problem it may at first appear. It does seem most likely that for the vast bulk of the Precambrian there were no animals, for reasons reviewed above. One alternative, which I consider unlikely but still needs to be entertained, is that animals are very ancient indeed, perhaps evolving in excess of 2 Gyr ago, but existed as extremely scattered and sparse populations, unable to expand because of environmental constraints. In one sense, if metazoans were the 'sleeping beauty' of such a world, it is more or less academic when and where they appeared. It does, however, suggest a line of investigation to see whether they are convincing environmental signatures which might be associated with the extremely problematic claims for very early animals.

Taking, however, the first view as correct, the next step is to suggest that the latest Neoproterozoic advanced eukaryotic assemblages did include animals, but also a number of protistan groups, some of which possibly rivalled the organismal complexity of these primitive animals. This, of course, raises intriguing questions concerning protistan evolution. The Ediacaran animals are for the most part problematical, but properly understood they will provide historical evidence as to the initiation of the Cambrian 'explosion', an initiation which may only predate the Cambrian faunas by *ca* 15 Myr. The massive burst of diversification we see in the Cambrian itself is a real event, and is brought home forcibly from three perspectives. First, there is what we might call 'phylogenetic telescoping', whereby primitive and advanced groups co-existed. If, for example, our ideas on deuterostome evolution are in any way accurate then vetulicolians, vetulicystids, yunnanozoans, echinoderms, cephalochordates and fishes are all effectively contemporaneous. Second, the essentialist view adopted by some zoologists, whereby Cambrian fossils are either familiar, e.g. mollusc, or weird, i.e. to be ignored for all intents and purposes, is not likely to be helpful. Rather this medley of forms, often admittedly puzzling and controversial, surely gives us our best clue as to not only how certain bodyplans were actually constructed, but what the functional and ecological contexts might have been. Third, what are now seen as widely disparate groups arose from a plexus of forms which in the Lower and Middle Cambrian showed little difference among themselves. The halkieriids suggest, for example, that groups as diverse as annelids, brachiopods, molluscs and possibly other lophotrochozoans evolved from a group whose differences were at that time little more than generic. The implications for this in terms of the debate of supposedly macroevolutionary processes operating in the origin of 'phyla' should be obvious.

Does this course of events create a problem for Darwinism, even for evolution? I do not think so. In particular, the search for any sort of trigger may be to misunderstand the problem. Rather than invoking an almost endless litany of possibilities, among which some of the more popular include the invention of a *Hox* gene, eyes, cell signalling, extracellular matrix, nerve cells, armour, guts and so on, it may be more useful to regard this event as the natural and inevitable result of the continuing evolution of a planetary system that shows cumulative and irreversible biogeochemical changes. As and when the conditions are appropriate, the opportunism and flexibility of the evolutionary process will exert itself. This is hardly surprising given both adaptive advantage and the fact that much of the molecular architecture necessary for complex organisms had evolved much earlier. In the context of thresholds that had to be passed, it is tempting to consider, as indeed many have already, either rising levels of atmospheric oxygen (e.g. Canfield & Teske 1996) or falling surface temperatures (e.g. Schwartzman 1999). However, given that much of evolution is conducted in terms of organismal interactions, it may be the resilience or more probably the vulnerability of Precambrian microbial systems that will be informative.

Once the first animal appeared, and recall that on the metaphorical 'day one' this was just another protistan experiment, then the ecological ball automatically began to roll. The complex ecologies which rapidly developed were subject to both continuing expansion and feedback, and as others have argued that in essence was the Cambrian 'explosion', the reverberations of which continue until the present day. The final point of which to speculate is to whether what transpired on this planet had parallels on other Earth-like planets. That is, however, another question.

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