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The Cambrian “explosion” of metazoans and molecular biology: would Darwin be satisfied?

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ABSTRACT The origins of metazoan bodyplans and the extent to which they are coincident with the Cambrian “explosion” are both areas of continuing debate. The fossil record has a unique advantage in terms of historical perspective, but remains highly contentious on account of the often controversial interpretations of particular groups (e.g. halkieriids, vetulicolians) and the heavy reliance on “windows” of exceptional preservation (e.g. Chengjiang, Burgess Shale). Molecular and developmental biology offer other unique insights, but may be problematic in terms of conflicting phylogenetic signals and questions revolving around gene co-option, evolution of developmental systems and even convergence. Such topics, far from frustrating the enterprise, actually widen our understanding of the nature of the evolutionary process with the exciting promise of the discovery of more general principles.

KEY WORDS: *Metazoa, Cambrian explosion, evolution, co-option, convergence*

Introduction

While in his triumph Caesar acknowledged the cheering crowds and basked in the reflected glory of Rome, a slave would periodically remind him of his mortality. So too, perhaps, when we acknowledge the triumphs of evolutionary biology we might also recall that acclamation and apparently immovable edifices can be surprisingly temporary. To maintain this creaking metaphor how might we expect the landscape of the evolutionary “city” to change, and from an historical perspective should we persist in the view that evolution is, to paraphrase, “one damn thing after the other” or rather does it show definite directions (e.g. Knoll and Bambach, 2000), if not a “manifest destiny” (Conway Morris, 2003). Whilst this review will very much deal with the inter-relations of palaeontology and molecular biology in the context of the Cambrian “explosion”, I should emphasize that ultimately like any other aspect of biology it can only command interest in as much as it remains relevant to our understanding of evolution. So further, I would argue, evolution only comes to age when there is a specific assessment of the substrate of possibilities (and constraints) upon which it can act.

The areas of developmental biology, bodyplan evolution and palaeobiology bring these problems into sharp focus, not least in the still unresolved questions of: (i) “molecules versus morphology”, that is exactly how do complex phenotypes emerge from the molecular substrate?, a question of some interest given the conservatism of at least some developmental genes; (ii) what I call “inherency”, whereby much of the potentiality of structures central to evolutionary advancement, e.g. mesoderm, neural crest, are already “embedded” in more primitive organisms, (iii) the phenomena of convergence (Conway Morris, 2003), and to some the unsettling question of the repeated recruitment of similar gene arrays to form complex structures that emerge independently of one another; (iv) the extent to which supposedly conserved genetic architectures allow inferences of ancestral form (e.g. Erwin and Davidson, 2002; see also Holland *et al.*, 2003); and finally (v) how much, and as importantly why, do developmental mechanisms themselves evolve?

These questions define an ambitious research programme, and it is necessary first to review very briefly our present understanding of metazoan evolution in the contexts of the geological time-scale, bodyplan construction, and phylogeny. Where then do we stand? Estimates of the timing of metazoan originations have oscillated wildly, from claims of very ancient divergences (e.g. Wray *et al.*, 1996; Bromham *et al.*, 1998) to values that are far more concordant with the fossil record (e.g. Ayala *et al.*, 1998; Ayala, 1999; Avis-Brosou and Yang, 2002; see also Rodriguez-Trelles, 2001, 2002). Comparable test cases can be found in many other groups, including birds, mammals and vascular plants. In each case there is a clear dichotomy of interpretation, but overall the evidence appears to be tending towards the notion that to the first approximation the fossil record is reliable (e.g. Foote *et al.*, 1999; Adkins *et al.*, 2001; Gaunt and Miles, 2002; Huchon *et al.*, 2002; Soltis *et al.*, 2002; Benton and Ayala, 2003). It seems, therefore, that those who argue for deep originations combined with convenient evolu-

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tionary crypsis are engaged in a mis-reading of the molecular and palaeontological evidence.

In the case of metazoan originations, if the fossil record provides an approximately reliable historical narrative this obviates the need to appeal to effectively unfossilizable forms. Such have been conjured up in a variety of forms, notably as either a meiofauna (e.g. Fortey *et al.*, 1996) or planktonic larvae with maximally indirect development (e.g. Davidson *et al.*, 1995). As such these types of organism would remain palaeontologically "invisible" until transformed by the respective expedients of body-size enlargement (in meiofauna) and invention of "set-aside" cells (in larvae). The substantial difficulties with either of these hypotheses are reviewed elsewhere (e.g. Conway Morris, 1998a, 2000a,b; Budd and Jensen, 2000).

Notwithstanding these questions, and the muted response to them, there is a parallel activity in the form of periodic announcements of putative trace fossils (i.e. tracks, burrows and other signs of animal activity), often dating in excess of a billion years (e.g. Breyer *et al.*, 1995; Seilacher, 1998; Rasmussen *et al.*, 2002). This too supports a lively industry of claim and refutation. Whilst an attempt to call a moratorium on this area is futile, the sceptical view is that: (i) these ancient "traces" are typically highly restricted in distribution and sometimes only known from a single slab of rock; (ii) no explanation is offered as to the failure of the "organisms" to diversify in what would otherwise appear to be an ecological "vacuum"; (iii) the structures in question are almost all remarkably different from one another; (iv) all other evidence (e.g. Logan *et al.*, 1997) points to a "microbial world" uneffected by a putative macroscopic ecology; and (v) the important fact that even in late Neoproterozoic sediments yielding exquisitely preserved soft-bodied algae, there is no corresponding preservation of metazoans (Xiao *et al.*, 2002). It is only fair to point out that much older candidates for metazoan body fossils do exist (reviewed in Fedonkin 2003), but in all cases detailed comparisons are suspect. In particular specific claims, such as a similarity to annelids, are questionable, although the possibility that some taxa are representatives of fungal-metazoan stem-groups (see below) is certainly worth entertaining. In any event, each and every claim requires exceptional scrutiny, in the spirit of Cloud (1986), not least in terms of exact geological age and biological affinity (if not biogeneticity).

Metazoan evolution: first steps

Here I will proceed on the assumption that: (i) metazoans did not originate much earlier than c. 700 Ma; (ii) their effective record begins c. 600 Ma within the Ediacaran assemblages, and (iii) the Cambrian "explosion" is synonymous with much of triploblastic diversification. The following outline can only be whet the imagination and is also highly selective, if not idiosyncratic. To provide first a perspective of earth history it needs to be stressed that the roles of forcing factors, notably global glaciations (e.g. Hoffman and Schrag, 2002), are controversial. Thus in this particular example despite arguments that "Snowball Earths" imposed major evolutionary bottlenecks, the contrary evidence in the form of: (i) significant pre-glaciation eukaryotic diversity; (ii) the likelihood of biological oases during glaciation (including perhaps an ice-free equatorial zone; e.g. Hyde *et al.*, 2000; Poulsen, 2003); (iii) an active hydrological cycle (e.g. Kellerhals and Matter, 2003); and, (iv) most tellingly, the discovery of complex microbiotas coeval with the glaciations (Corsetti *et al.*, 2003; see also McKay, 2000), suggest that while the evolutionary effects of "Snowball", or probably "Slushball", Earth were significant they were not catastrophic.

Whether these, or other environmental drivers such as atmospheric oxygen (Canfield and Teske, 1996; Shen *et al.*, 2003), had important evolutionary consequences will become more apparent not only with improved data, such as stratigraphic correlations and refinement of geochemical proxies (e.g. Jacobsen and Kaufman, 1999; Evans, 2000; Lund *et al.*, 2003), but also by exploring new metazoan phylogenies (e.g. Giribet, 2002). Here some spectacular advances in our understanding need to be set against other areas that have remained refractory. The latter include both interpretations of fossil material, especially the Ediacaran assemblages, and lack of present evidence for key transitions, notably the transformations involving those between diploblast-triploblast, protostome-deuterostome, and ur-chordate-vertebrate. While the combined strengths of molecular biology and palaeontology give reasons to be optimistic, it is also worth recalling that (i) effectively unfossilizable organisms, perhaps like *Symbion* (Winnepenninckx *et al.*, 1998); (ii) extinct major clades, perhaps like the petalonamids (Grazhdankin and Seilacher, 2002), and most importantly (iii) evolving developmental systems (see below), mean that some evolutionary questions may remain intractable for the foreseeable future.

Nevertheless, at the least the emerging framework will help to pinpoint new questions. While the Fungi are widely regarded as the sister-group of Metazoa (e.g. Baldauf, 1999), more specific hypotheses of the phylogeny of this group and its closest relatives (e.g. Atkins *et al.*, 2000; Cavalier-Smith and Chao, 2003) ultimately may indicate which key novelties, such as receptor systems or cell binding (e.g. Morris, 1993; Schütze *et al.*, 2001) underpin metazoan success. As long thought the choanoflagellates may be the nearest living equivalent to a pre-metazoan (e.g. Snell *et al.*, 2001). Both their molecular equipment (King and Carroll, 2001) and also evidence for very early episodes of gene duplication (Miyata and Suga, 2001), possibly roughly coincident with the choanoflagellate-poriferan split, may help to define the groundfloor of metazoan evolution.

As pointed out by Medina *et al.* (2001) a resolution of sponge, cnidarian and ctenophore relationships is still problematic, although their suggestion of a possible Calcarea-Eumetazoa (see also, for example, Kruse *et al.*, 1998; Borchiellini *et al.*, 2001) and Cnidaria-Bilateria connection are both important, if controversial. The continuing problems in the phylogenetic resolution of these major groups were stressed by Manuel *et al.* (2003), although their suggestion that the axial symmetry of some Calcarea might be plesiomorphic to the Metazoa is certainly intriguing. The molecular insights to metazoan phylogeny are of crucial importance, but it is still necessary to reiterate the point that given the disparity of these groups (or any other superclade, not least the deuterostomes; see below) the molecular data are necessarily silent as to the anatomy, function and ecology of the various stem-groups and common ancestors.

Consider first the sponges, which present many problems. Despite lacking a nervous system, but interestingly possessing neuronal-like receptors (Perovic *et al.*, 1999), and effectively showing an absence of other tissues, sponges show considerable sophistication, not least in the evolution of carnivory (e.g. Kübler and Barthel, 1999) and their ability to sequester cnidarian nematocysts (Russell *et al.*, 2003). In addition, whilst their early geologic appearance, established on the basis of body fossils (Gehling and Rigby, 1996), spicules (Brasier *et al.*, 1997) and chemical fossils (e.g. McCaffrey *et al.*, 1994), is consistent with their primitiveness, apart from some embryological hints (Leys and Degnan, 2002) the details of the presumed transformation to a diploblastic organization are effectively conjectural. Here is one transition that may have been effectively microscopic and larval. In this sense the Placozoa (i.e. *Trichoplax*) is perhaps our best guide amongst living animals (e.g. Syed and Schierwater 2002; Ender and Schierwater, 2003; cf. Cavalier-Smith and Chao, 2003) to the first Eumetazoa, although a yet more primitive position is also possible.

Amongst the key innovations of the cnidarians is the nervous system (e.g. Grimmelikhuijzen *et al.*, 2002), culminating in such features as the remarkable nerve ring in some species in *Hydra* (maintained, incidentally, despite the dynamic displacement of cells; Koizumi, 2002; Fig. 10) and the extraordinary camera-eye bearing cubozoan jellyfish (e.g. Martin, 2002; see also Conway Morris, 2003). The now widely-accepted basal position for the anthozoans (e.g. Bridge *et al.*, 1995; Odorico and Miller, 1997; see also Müller *et al.*, 2003) may be congruent with the abundance of pennatulacean-like fronds in the Ediacaran assemblages (e.g. Jenkins and Gehling, 1978; Narbonne and Gehling, 2003), as well as the identification of possible Cambrian "survivors" (Conway Morris, 1993; Jensen *et al.*, 1998). It is quite possible, however, that the Ediacaran "fronds" are polyphyletic (D. Grazhdankin pers. comm.), and even if some are anthozoan cnidarians, a place in the Pennatulacea *per se* is open to debate (Williams, 1997).

It is equally likely that at least some of the other Ediacaran fossils, including the sac-like *Inaria* (Grazhdankin, 2000), are of diploblast, if not a cnidarian, grade. Whether there were any genuine "jellyfish" is much more conjectural. *Kimberella*, once interpreted as a possible cubozoan, is now reconstructed as a mollusc-like animal (Fedonkin and Waggoner, 1997). The fate of the possible chondrophorine (Hydrozoa), *Kullingia*, is even more extraordinary, because this strikingly concentric structure is now interpreted as a scratch-mark, produced by a tube rotating around its anchor on the sea-bed (Jensen *et al.*, 2002). Other "discs" may include medusiform organisms, but are more likely to be hold-fasts of "fronds" or even protistan.

Other vaguely cnidarian-like fossils may be something different. Thus, it is equally plausible that rather than being any sort of animal the enigmatic bag-like petalonamids (e.g. *Ernietta*, *Pteridinium, Ventogyrus*) are multicellular (or plasmodial) analogues of metazoans (e.g. Crimes and Fedonkin, 1996; Ivantsov and Grazhdankin 1997; Grazhdankin and Seilacher, 2002; Seilacher *et al.*, 2003), arising independently from one or more protistan clades. This is, of course, effectively equivalent to the Vendozoa hypothesis, as proposed by Seilacher (1989; see also Runnegar 1995). Whilst the phylogenetic details are only beginning to be explored, perhaps the Ediacaran interval should be interpreted not so much as the dawn of animal life (Glaessner, 1984), but as the first effective exploration of macroscopic multicellular morphospace (or equivalent syncitial constructions) by various protistan groups (see Seilacher *et al.*, 2003), one of which happened to evolve into the Metazoa.

There is another possible line of fossil evidence into the early evolution of cnidarians, albeit in a form very different from the classic Ediacaran record. These are the remarkable discoveries of phosphatized embryos from the Neoproterozoic Doushantuo Formation of South China (e.g. Xiao and Knoll, 2000; Xiao, 2002). The interpretations are complicated by both the fact that the embryos may derive from several distinct groups, and also remarkable claims for specific features of embryology such as gastrulation (Chen *et al.*, 2000). This latter analysis has been received with justified caution (Xiao *et al.*, 2000), but undeterred Chen *et al.* (2002) have presented further claims for phosphatized embryos showing such features as blastopores and internal cellular structures. Such structures, they would argue, are consistent with these fossils being cnidarian gastrulae. These, however, are equally questionable interpretations. Not only are the purported blastopores relatively enormous, but at least some of the supposed internal anatomy is clearly mineral growths of botyroidal phosphate that grew during diagenesis. In this latter case there is no compelling reason to think that they replicate pre-existing internal structures. To echo the points made so cogently by Xiao *et al.* (2000), this is not to say that some of the structures identified by Chen *et al.* (2000, 2002) are incorrectly identified, but simply to observe that for the most part a diagenetic origin seems both more plausible and parismonious.

Bona fide embryos do exist (e.g. Xiao and Knoll, 2000; Xiao, 2002), are possibly cnidarian, and conceivably are associated with the co-occurring coralliform *Sinocyclocyclicus*. There is, however, a curious anomaly between these late Precambrian embryos and the spectacular examples from the Cambrian, including the probable cnidarian *Olivooides* (Yue and Bengtson, 1999). In all these cases the mode of fossil preservation is via the agency of very early diagenetic phosphatization, yet in the Cambrian examples the smallest embryos are effectively always larger than the 64 cell-stage, whereas the Doushantuo material is always preserved in material that never exceeds the 64 cell-stage. This has two implications. First, laboratory experiments attempting to replicate these diagenetic processes (Martin *et al.*, 2003) may be of rather marginal relevance, not only because they throw little light on the specific process of phosphatization, but also because they do not offer a reason for presumably similar embryos in similar diagenetic environments being preserved at mutually distinctive stages of growth. Second, and more importantly, it is possible that the life-cycles of the Doushantuo ?cnidarians were radically different from the Cambrian equivalents (Conway Morris, in press), possibly hinting at a type of metazoan rather different from expectation.

The case of the ctenophores is also intriguing, both because of their extraordinary bodyplan and possible links to the Bilateria (reviewed by Martindale *et al.*, 2002, who also discuss the evidence for the more likely Cnidaria-Bilateria link; see also Martindale and Henry, 1999). Just as in the Cnidaria the emerging evidence of ctenophoran developmental genes indicates both harbingers of bilaterian organization, but also puzzling exceptions such as the lack of expression of a forkhead gene in the sensory apical organ (Yamada and Martindale, 2002). It is apparent that ctenophores were widespread in the Cambrian (e.g. Chen and Zhou, 1997), and the remarkable but poorly known Chengjiang taxon *Trigoides aclis* (see Luo *et al.*, 1999, see p. 56, pl. 8, Fig. 5), with its comb-rows attached to prominent vanes, is a reminder that the early stages in ctenophoran evolution may be different, perhaps very different, than sometimes imagined (see also Odorico and Miller, 1997). Another unresolved problem is the peculiar protistan *Ctenoctophrys chattoni*, single-celled but with eight ciliated rows (see Conway Morris, 1998b). That this resemblance is a rather striking example of convergence (see Conway Morris, 2003), as originally suggested by Weill (1946), may be consistent with the suggestion that the stereotypical arrangement of eight comb-rows is a reduction from what primitively may have been a larger number in the Cambrian (Conway Morris and Collins, 1996).

Metazoan evolution: the next step

The nature of both the diploblast-triploblast transition and the earliest bilaterians is still largely conjectural. In principle, some constraints may be inferred from the developmental biology of various cnidarians. This indicates that a significant part of the molecular machinery seen in triploblasts is already in place (e.g. Müller *et al.*, 1999, 2003; Zhang *et al.*, 2001; Miller *et al.*, 2003; Scholz and Technau, 2003). This echoes, of course, the repeated observation that "primitive" animals do not so much lack the genetic "switches" and "levers", but rather the appropriate "instruction manuals". The latter, of course, are effectively to be sought in the realm of protein chemistry at a level quite far removed from the genomic substrate (see Ryoo *et al.*, 1999). Thus just as amphioxus (and perhaps tunicates; see below) is "a vertebrate in waiting" (Conway Morris, 2000b) so cnidarians may have an equivalent status with respect to the bilaterians. The details of any cnidarian-bilaterian transformation, however, are far from clear, and it is not surprising that topical questions of diploblast-triploblast equivalences in terms of such structures as "head", "body axes" and "mesoderm" are still rather inconclusive. Nor should we forget (see also below) that at least some genes are subject to rampant co-option and re-deployment, so that identifying an "original function" may be more problematic than is sometimes realized. In conclusion, at the least it would be naïve to think of these "primitive" animals as some sort of "genetic museum".

So far as the earliest bilaterians are concerned, it seems increasingly likely that whilst many of the platyhelminthes are derived lophotrochozoans, the acoels (and nemertodermatids) are genuinely basal (e.g. Jondelius *et al.*, 2002; Ruiz-Trillo *et al.*, 2002; Telford *et al.*, 2003). Excavating the roots of the Bilateria, however, may be more complicated than is often supposed. Thus, whilst the phylogenetic position of the chaetognaths – an orphan-phylum if there ever was one – has long been conjectural, recent work suggests that they too have a basal position (Papillon *et al.*, 2003). What of their fossil record? The preservation potential of acoels must be very low, but there is a Cambrian fossil record of possible chaetognaths (e.g. Szaniawski, 1982; Chen and Huang, 2003).
It may also be worth considering a number of Ediacaran taxa, which although quite unlike the living acoels and chaetognaths, possibly have some bearing on the earliest bilaterians. These include the relatively well-known *Dickinsonia* and the more recently described *Yorgia* (Ivantsov, 1999; Dzik and Ivantsov, 1999). Both are segmented, but the anterior unit of *Yorgia* is remarkable for its asymmetry and also canal-like structures. Another curiosity is that rock slabs bearing this fossil are often associated with imprints (see Fedonkin 2003, Figs. 10-12). Ivantsov (1999; see also Dzik and Ivantsov, 1999) interpreted these as post-mortem structures, although the alternative possibility is that *Yorgia* was locomotory (possibly by the action of ciliary gliding). Such is the view of Fedonkin (2003), who suggested the individual imprints represented protracted periods of immobility. A further possibility is that these stationary episodes were also times of feeding. In any event Fedonkin (2003) suggested that food acquisition may have been by ciliary transfer along the ventral grooves to the mouth. Despite the likely phylogenetic closeness of *Yorgia* and *Dickinsonia* (and several other taxa, such as *Vendia*; see Ivantsov 2001), and their inclusion in the Proarticulata (or Dipleurozoa), neither this nor the recent descriptions of both possible internal anatomy (Dzik and Ivantsov, 2002) and locomotory abilities (Ivantsov and Malakhovskaya, 2002) do much to resolve more precisely their wider phylogenetic relationships.

Metazoan evolution: the triploblast stories

So far as our understanding of the evolution of the three superclades of Bilateria (the lophotrochozoans, ecdysozoans, and deuterostomes) is concerned, there have been many interesting developments. Arguments for an annelid-brachiopod relationship via the Cambrian halkieriid-wiwaxiid clade are rehearsed elsewhere (Conway Morris and Peel, 1995). It has, however, recently received support from studies of Lower Cambrian brachiopod-like shells (Ushatinskaya, 2002; Holmer *et al.*, 2002; see also Parkhaev, 1998), although to describe the central idea of brachiopod origin, that is the folding together of two formerly separate shells, as "a neglected bodyplan hypothesis" (Cohen *et al.*, 2003) is perhaps a slight exaggeration (Conway Morris, 1998c).

The slug-like halkieriids, and presumably the more primitive siphogonuchitids, each armoured with calcareous sclerites, are also at least vaguely reminiscent of primitive molluscs, specifically chitons and aplacophorans. Details of the principal evolutionary transitions that led from a halkieriid-like animal to a mollusc are, however, still largely conjectural. More primitive still may be the Ediacaran *Kimberella* (Fedonkin and Waggoner, 1997), and it is interesting that some specimens co-occur with prominent scratch marks, perhaps representing grazing traces (?radulate) on the microbial mat, as well as what appear to be short trails (Fedonkin 2003, Figs. 14 and 16; see also Seilacher *et al.*, 2003; Fig. 3).
Even though there is some glimmer of understanding concerning the origins of annelids, brachiopods and molluscs, it is still the case that lophotrochozoan evolution presents numerous conundra. Not least of these are the (i) origin of nemerteans; (ii) precise relationships between brachiopods, bryozoans and phoronids; (iii) details of the "regressive" evolution of platyhelminthes; (iv) surprising discovery that myzostomids are probably not aberrant annelids (Eeckhaut *et al.*, 2000) and (v) position of sipunculans.

In terms of ecdysozoan evolution there have been important realignments amongst the arthropods, drawing on both molecular (e.g. Regier and Shultz, 1997; Giribet *et al.*, 2001; Hwang *et al.*, 2001) and palaeontological (e.g. Budd, 2002; Hughes, 2003) data. So too the widely accepted inclusion of priapulids and nematodes has revitalized conjectures of their evolution. The former group has a rich and still incompletely documented Cambrian record (e.g. Chen and Zhou, 1997; Conway Morris, 1998c). It is tempting to envisage a priapulid-lobopodian transition, as presciently envisaged by Dzik and Krumbiegel (1989; see also Budd 2001). By taking onychophoran lobopodians as the most primitive arthropods, such a transformation becomes interesting in the functional context of a locomotory shift from infaunal burrowing to epifaunal walking (and gait adjustment). As such it is somewhat analogous to the hypothesized crawling to leg-like transition in the halkieriid/ wiwaxiid –annelids (Conway Morris, 1998c).

As with the other groups, however, the Ediacaran record of possible ecdysozoans is problematic. While it has long been recognized that animals like *Spriggina* are vaguely arthropodan, attempts to arrive at a specific arthropodan phylogeny on the basis of Ediacaran material (e.g. Waggoner, 1996) have not won wide support. Indeed, if the problems of understanding the Ediacaran assemblages needed any emphasis, one can simply note that Seilacher *et al.* (2003) regard *Spriggina* as a member of the Vendobionta, along with such forms as *Vendia* and *Vendomia*, while Fedonkin (2003; see also Ivantsov, 2001) place them within the Bilateria. An interesting recent development, however, is the suggestion that the Lower Cambrian Chengjiang arthropod *Primacaris* is related to the Ediacaran *Parvancorina* (Zhang *et al.*, 2003). Another possibility worth entertaining is the fact that a "skeletal" *Primacaris*, that is, with its carapace reduced to central and flanking spines, would be intriguingly similar to the Burgess Shale arthropod *Marrella*. In any event, if arthropods with jointed appendages had evolved by late Ediacaran times, and if the hypothesis of a priapulid→lobopodian→ anomalocaridid→CCT (chelicerate, crustacean, trilobite) sequence is valid (Budd, 1998), then this has obvious implications for the early timing of ecdysozoan diversification. The position of nematodes, and presumably the related nematomorphs (e.g. Bleidorn *et al.*, 2002), is rather problematic, but most evidence suggests that within the ecdysozoans (e.g. Manuel *et al.*, 2000) they are derived. Whether, however, they arose from a priapulid or arthropod-like ancestor is still conjectural.

What then of the deuterostomes? This super-phylum exemplifies most clearly the question of bodyplan disparity, be it the bizarre echinoderms that have thrown away their gill slits (and perhaps their brains; but see Lowe *et al.*, 2003), while plumping for pentaradiality, the still enigmatic enteropneusts, the strange cellulose-encased tunicates, or the radical innovations of the vertebrates with their neural crest tissue, sensory sophistications, and apparently unique duplication of the *Hox* clusters. This medley of evolutionary questions has spawned a vast, sometimes contradictory, literature, but here too some possible signs of order are emerging. Because it is practically impossible to imagine what, to take one example, the common ancestor of the echinoderm-hemichordates looked like, it is necessary to turn again to the fossil record. Here we have argued that the two key morphological features in the primitive deuterostomes are a bipartite body and the anterior bearing gill slits, as manifested in the Lower Cambrian group known as the vetulicolians (Shu *et al.*, 2001). The alternative view, that vetulicolians are some sort of strange arthropod has been bolstered by reconstructions showing prominent eyes and antennae (Chen and Zhou, 1997). These features appear, however, to be hypothetical and have not been observed in the thousands of specimens collected.

The implications of vetulicolians as primitive deuterostomes, if confirmed, will take some time to sort out. Here it is only possible to discuss briefly a couple of points. One is that the voluminous internal cavity in the anterior section and the prominent openings are consistent with the latter's original function being associated with disposal of excess water, as hypothesized by Gilmour (1979). A second point is a potentially significant similarity to the enigmatic group of echinoderms, known as the calcichordates. The hypothesis of Jefferies (1986) revolves around the notion that amphioxus, tunicates and vertebrates are all derived from calcichordates and independently lost their calcareous skeleton. These interpretations, however, depend upon contentious reconstructions of soft-bodied anatomy (including features e.g. brain and eyes, that are remarkably advanced for their supposed evolutionary position). The calcichordate hypothesis is also difficult to reconcile with many other aspects of the fossil record, not to mention stratigraphic order, as well as molecular biology. As such Jefferies' ideas have been greeted with scepticism (e.g. Lefebvre, 2003), although it has to be acknowledged that apart from being described as "aberrant" by nearly all other workers, their place in echinoderm phylogeny is so uncertain that in any wider context they are effectively ignored, regarded as derived off-shoots, of uncertain ancestry.

Apart from the strange asymmetries, notably in the cornutes, the most remarkable feature of the calcichordates is the possession of apertures, interpreted as gill slits on the anterior section (Jefferies, 1986; Dominguez *et al.*, 2002) and a segmented "tail". This possession of a bipartite body and gill slits suggests that the origin of the calcichordates, and thereby the echinoderms, could be with a vetulicolian-like animal that developed the ability to secrete the diagnostic stereom skeleton of high magnesium calcite. In passing we should note that although molecular evidence strongly supports echinoderms and hemichordates as sister-groups (e.g. Bromham and Degnan, 1999; Cameron *et al.*, 2000) the origins of the hemichordates, of which the enteropneusts are probably the most primitive, is still enigmatic.

The fossil record, however, may help to resolve at least one step towards the resolution of the other major deuterostome clade, that of cephalochordate-tunicate-vertebrate (CTV). This involves contentious interpretations surrounding the yunnanozoans, another important component of the Chengjiang faunas. Whilst the general consensus has been that these animals are craniates (e.g. Chen *et al.*, 1999; Mallatt and Chen, 2003), this interpretation suffers from a series of difficulties, not least concerning the supposed identification of putative myomeres and a notochord. In describing a new species (Shu *et al.*, 2003) we suggested a possible evolutionary relationship to vetulicolians, as well as a more controversial argument concerning the possibly composite origin of the pharyngeal gills. In our view the yunnanozoans may well be an important staging post towards the CTV clade, but the existing evidence suggests they are substantially closer to the vetulicolians than the craniates.

Amphioxus has already been described as "a vertebrate in waiting" (Conway Morris, 2000b). It is significant that both this group and the tunicates have genes that in the vertebrates are associated with neural crest expression (e.g. Holland *et al.*, 2000; Manni *et al.*, 2001), but evidently they lack the necessary genetic networks. Although the tunicates are the centre of intense research (e.g. Satou and Satoh, 2003, and accompanying papers), for several reasons their wider relevance to the origin of the vertebrates is perhaps questionable. To the first approximation agnathan-amphioxus- tunicate form an evolutionary trichotomy; in other words it is not clear if either amphioxus or tunicate is the more primitive. In particular, it is arguable whether the celebrated tunicate "tadpole" is any more relevant to understanding vertebrate origins than is amphioxus. In fact, in many respects it is as simple to regard the tunicates as highly derived, with primitively a sessile mode of life and short-lived larvae whose anatomy is relevant to the functional needs for dispersion rather than a template for phylogenetic ascent to the vertebrates. This view also assumes that the fascinating pelagic oikopleurans are heterochronic derivatives of more primitive forms (see Stach and Turbeville, 2002). Finally, the tunicates show a series of remarkable idiosyncracies, not least the ability to synthesize cellulose for the tunic and the employment of the respiratory protein haemocyanin (but see Ebner *et al.,* 2003). Both of these may have been acquired by gene transfer (see Dehal *et al.*, 2002).

Vertebrate origins, therefore, are still contentious, with neither amphioxus nor tunicate larvae likely to provide a complete picture. There has, however, been dramatic new information with the discovery of stem-group craniates from the Chengjiang Lagerstätte (Shu *et al.*, 1999, 2003; Shu, 2003). A parallel publication (Hou *et al.*, 2002), however, diverges significantly in its interpretations. Apart from the inability to identify a notochord and a tentative identification of "sensory structures" (cf. Shu *et al.*, 2003), the overall emphasis by Hou *et al.* (2002) on an amphioxus-like appearance (apart from possibly metameric gonads; see Shu *et al.*, 1999) is also questionable. For example, Hou *et al.* (2002) identify an extensive set of "arches" posterior to the unequivocal set of anterior branchial pouches and supporting bars (Shu *et al.*, 1999, 2003), and also V-shaped myotomes. In neither case, however, is this consistent with our evidence. Moreover, the functional context of unequivocal branchial pouches combined with a posterior set of presumed branchial arches is somewhat problematic, while contrary to Hou *et al.* (2002) there is unequivocal evidence that the myotomes had a Z-shape rather than a V-shape.

An emphasis on V-shaped myotomes would be significant not only because it would facilitate comparison to amphioxus, but also the putative basal craniate group known as conodonts. It is intriguing, however, to speculate that rather than conodonts being integral to vertebrate origins (e.g. Donoghue *et al.*, 2000), they are actually a parallel development arising independently from the cephalochordates (see also Kemp and Nicoll, 1995, 1997). Thus while conodonts possess phosphatic teeth that have what are claimed to be vertebrate-like fabrics (e.g. Sansom *et al.*, 1992; Armstrong and Smith, 2001), other studies question this conclusion (e.g. Kemp and Nicoll, 1997; Kemp, 2000a,b; see also Schultze, 1996). So too the architecture of the feeding apparatus is markedly at odds with any known vertebrate, as indeed is evidence for the "enamel organ" being "repeatedly reformed throughout [the] life" in at least some conodonts (Armstrong and Smith, 2001, p. 819). If indeed amphioxus (or tunicate) is "a vertebrate in waiting" then it seems quite possible that neural crest, biomineralized tissue, and perhaps features such as camera eyes (see Purnell, 1995; Donoghue *et al.*, 2000), evolved several times independently.

Conclusion

The ways in which biological "space" is explored, be it at the level of proteins or social systems, is arguably one of the two central problems in evolution (Conway Morris, 2003). The other, and by no means unrelated question, is how the molecular substrates are translated into operational phenotypes and the constraints that might accompany these processes. In the context of this review, these points return both to the five questions I listed near the beginning of this review and the specific problem of how animal bodyplans evolve.

Whilst there is no over-arching theory of developmental biology, some generalities are emerging. First, while it is reasonable to suppose that genes and regulatory processes had original functions, in reality these may be lost in the mists of history. Either way co-option and redeployment are rampant both in a developmental context (e.g. Eizinger *et al.*, 1999; Heanue *et al.*, 1999 (see also Relaix and Buckingham, 1999); Merlo *et al.*, 2000; Damen, 2002; Locascio *et al.*, 2002; Lowe *et al.*, 2002; Fabrizio *et al.*, 2003) and in related topics such as those concerned with enzymatic pathways (e.g. Peregrin-Alvarez *et al.*, 2003). The realities of conservation are not, of course, in dispute; a fact that applies not only to animals, but also to plants (e.g. Kirst *et al.*, 2003) and beyond. What we are beginning to see, however, is evidence for a far more dynamic system than might be supposed from the classic examples of gene conservation. Thus, writing of one specific instance Locascio *et al.* (2002) remark that "The present analysis of *Snail/Slug* duplicated genes during vertebrate evolution reveals a much higher degree of plasticity and complexity than expected" (p. 16845). Just how labile these systems will prove to be is still largely conjectural. Nevertheless, all the signs are that developmental frameworks are often far from static. To take a specific case, that of a cnidarian gene referred to as *cnox-2,* Schierwater *et al.* (2002) emphasize how it appears that this putative ParaHox gene is both "multicolored" and "polygenealogical", that is *cnox-2* has a diversity of expression patterns in different body regions in different cnidarian lineages.

From this perspective the search for an "original function" becomes almost an irrelevance, if not positively distracting. For example, Mineta *et al.* (2003) observe that c. 30 per cent of the genes related to the nervous system in planarians have equivalents in *Aradiopsis* and yeast, neither of which has any pronounced mental capacities. So too the apparent examples of genomic conservation not only need to consider examples of co-option but the increasing evidence that the developmental systems themselves evolve. Rather than remaining embedded in an essentialist framework – with iconic reference to *Pax-6*, *tinman*, *otx*, and so on – we need to discover, given the degrees of variability, how it is that new pathways, interactions and networks evolve in selective and functional regimes (e.g. Collazo, 2000; Grenier and Carroll, 2000; Gibert, 2002; Ronshaugen *et al.*, 2002; Shiga *et al.*, 2002; Vervoort, 2002). Such a programme is, of course, familiar to those concerned with the mapping of epigenetic landscapes, and the still-remarkable fact that embryos "navigate" towards the same complex structures via markedly different routes.

Such a view undermines the reductionist perspective of genes "for something"; rather it is context and association that matter. Moreover, much of the developmental conservation may be little more than skin deep, reflecting the economy of using that which is already available. To imagine also that this constrains evolutionary possibilities is refuted in examples where for one reason or another a gene is "unavailable", yet the "desired" structure still emerges. Thus in the development of the snout of the star-nosed mole, possibly because of pre-existing neural requirements, the embryological pathway is radically different and suggests a novel developmental pathway, yet the spectacular appendages still emerge (Catania *et al.*, 1999).

This welter of examples may be individually fascinating, but they hardly present a coherent picture. So far as general patterns are concerned, one of the most productive ways forward, I believe, is in the study of convergence (Conway Morris, 2003). The immensity of molecular "space" and the variety of developmental systems might suggest that this is the one area of biology where convergence is of marginal relevance. That this may be a premature assumption is apparent from some intriguing evidence in both expression patterns and phenotype studies. In the former case Nielsen *et al.* (2003) demonstrate a rather extraordinary example of evolutionary convergence in terms of *otx* expression in echinoids with direct larval development. This mode has evolved a number of times from indirect larval development, where it is already known that *otx* has at least two distinct expression patterns. In a result that Nielsen *et al.* (2003) describe as "most surprising" (p.74) (cf. Conway Morris, 2003, p. 128), each independent lineage of direct developers employs *otx* for a new and specific purpose (in the primordial tube feet). The implication is that somehow this gene may play a central and irreplaceable role. Nor is this the only such example, and in an overview of developmental evolution in the echinoderms Wray and Lowe (2000) have an absorbing discussion of potential examples of molecular convergence. Of equal importance is the report by Wittkopp *et al.* (2003) concerning similar pigmentation patterns in *Drosophila* that emerge by at least two distinct regulatory mechanisms (see also Hoekstra and Nachman, 2003).

These examples of molecular co-option and convergence (see also, for example, Bull *et al.*, 1997 and Cooper *et al.*, 2003) should give us pause for thought for at least two reasons. First, it reinvigorates the discussion of homology and what biological similarity really means. For example, are the tripartite brains of insects and vertebrates (Hirth *et al.*, 2003) similar because of the ancestral condition in some sort of ur-bilaterian (as these authors argue), or is it because the pathways of evolution are far more constrained, if not pre-ordained, than is generally supposed? This second possibility is, I suspect, an uncomfortable thought for many evolutionary biologists, yet in the immediate context of tripartite brains some support for this may come from the polychaete annelids. As lophotrochozoans this group is, of course, far removed from either insects or vertebrates. Yet, in the polychaetes, as Rouse and Pleijel (2001, p. 26) note, the brain structure varies widely, with the most complex arrangements being found in the mobile and active groups, notably the eunicids and nereidids. Here the brain is again tripartite, sometimes with mushroom-like bodies, yet annelid phylogeny suggests that at least here the tripartite brain must have arisen independently.

The second reason is that despite all the talk of constraints and conservation, the evidence for dynamic and evolving systems suggests that not only can very specific areas of the phenotype be precisely tailored (e.g. Stern, 2003), but in addition the relevant target and number of cells involved can be remarkably small (e.g. Weber, 1992). In the final analysis we are what we are because of the process of natural selection rather than any internal specific and over-riding constraint (e.g. Beldade *et al.*, 2002). Process, however, can only operate on a substrate, and I would argue that far from evolution being chaotically contingent in fact the way in which biological "hyperspaces" are navigated points to a deeper, and to date largely unrecognized, structure.

And so to answer the subtitle of this paper, "Would Darwin be satisfied?": fascinated, certainly; but satisfied?, not yet.

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