

## Seeing ghosts: Neoproterozoic bilaterian body plans

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**Abstract:** Bilaterians originated before 560 Ma. By 520–530 Ma, the fossil record reveals a fauna teeming with bilaterians with highly disparate body plans, in which most living phyla must have been represented. Between these dates, few bilaterian body fossil types have been found, although trace fossils indicate the presence of vermiform animals, small-bodied before the beginning of the Cambrian. The diversity of Cambrian lineages implies a branch-rich phylogenetic tree, yet organisms representing branch nodes of phyla and ancestral alliances of phyla are unknown, and most of the branches are inhabited by ‘ghosts’. The body plans of these ghosts must be precursory to the body plans of crown phyla, and their genomes must be precursory to crown genomes. Bilaterian Hox genes mediate anteroposterior regionation and are usually found in transcriptionally colinear clusters, a feature conserved even when clusters have been broken up during evolution. When body sections mediated by Hox genes are reduced during morphological evolution, the corresponding gene is sometimes deleted. It may be possible to reconstruct the anteroposterior regionation of ghost lineages from Hox clusters modifications. More information on Hox gene assemblages and functions in small-bodied crown phyla, such as acoelomorphs and others, is required to explore this possibility more fully.

The Neoproterozoic has yielded a fascinating, but enigmatic, fauna with marvellous, but mysterious, architectures. Despite indications of the presence of metazoans from *c.* 580 Ma (Xiao *et al.* 1998; Condon *et al.* 2005), it has proven difficult to locate many of the Neoproterozoic fossils on the tree of life. This situation is in contrast to the geologically abrupt appearance of crown phyla during the middle Early Cambrian. Certainly, enigmatic fossils also occur during that ‘Cambrian explosion’ interval, but the Tommotian and especially Atdabanian faunas demonstrate or imply the presence of most crown metazoan phyla, most of which are bilaterians. Clearly there were great radiations of body types following the origin of bilaterians, to produce the many ancestral branches along which the disparate Early Cambrian body plans were assembled. By analogy with radiations that occur when we can trace them in the fossil record, there are likely also to have been many branches arising from those radiations that do not have living or known fossil descendants, and among which the successful branches may actually be in the minority. The Neoproterozoic has not yielded much in the way of bilaterian body fossils. It is certainly possible that *Kimberella* is a stem branch of a lophotrochozoan taxon (Fedonkin & Waggoner 1997) and the sprigginids and vendomiids may have been ecdysozoans (e.g. Fedonkin 1985), but even these forms tell us little about the evolutionary pathways that led to the body plans of crown phyla. Is there any way that we can hope to recover at least

some information about the character of missing Neoproterozoic bilaterian clades in the near absence of a body plan record?

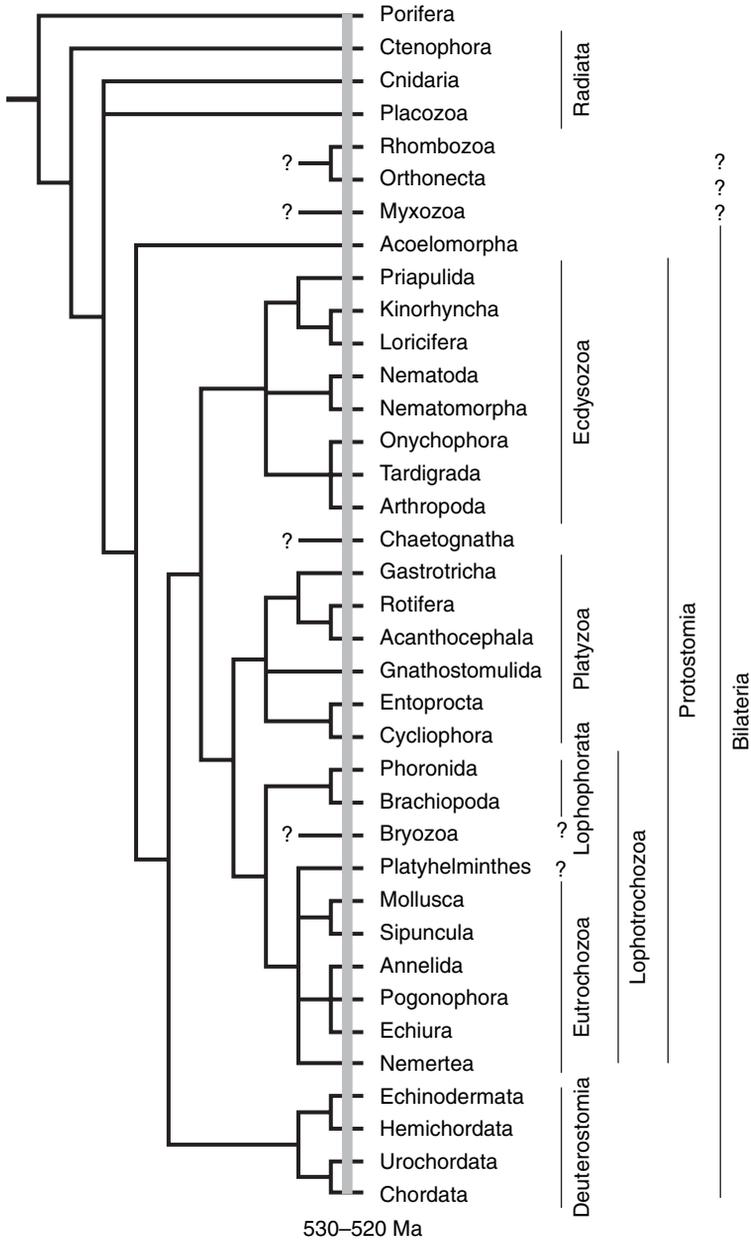
### The metazoan tree before the Cambrian explosion

Traditionally, hypotheses of metazoan phylogenies at the phylum and class levels have been based on developmental and morphological similarities, ranging from sperm morphology and cleavage patterns to the gross and microscopic anatomies of adults. As different features have different patterns of resemblance, many different hypotheses were possible, depending on which features were deemed most important—that is, most informative of relationships. For example, the notion that segmentation has arisen once and segmented animals are, therefore, closely related was once widely held, and is still held by some today, although morphologic evidence that segmentation is not homologous among major groups is strong (see Eernisse *et al.* 1992). The molecular phylogenetic tree, although still provisional, also argues against this idea (see below).

As it has become possible to compare DNA sequences among organisms and to erect phylogenetic trees based on mutual sequence similarities of particular genes, such molecular phylogenetics have provided a new dataset with which to evaluate animal relationships that is independent of developmental or morphological data *per se*. However, some genes evolve at different rates than

others, while genes in some animal groups evolve at different rates from those in other groups, and some animal groups evolve at different rates at different times. Such rate variations can result in the same genes in closely related taxa looking rather different

(see Hendy & Penny 1989). Another problem arises if an early radiation is rapid, for those genes not under direct selection for the changes will not evolve many differences, and it may not be possible to resolve the branching pattern (Valentine 2004;



**Fig. 1.** A provisional hypothesis of the phylogenetic relations among metazoan phyla, based chiefly on the SSU rRNA molecule but supplemented by data from other molecules and, when the often scanty molecular data seem erroneous, on developmental and morphological criteria. The vertical line near the branch tips represents the Cambrian explosion; all of the earlier nodes and most of the risers are occupied by ghosts. After Valentine 2004.

Rokas *et al.* 2005). For these, and somewhat similar reasons, some of the branching patterns of metazoan phyla have not yet been established with certainty from molecular evidence; some of the molecular branchings are likely to be artefacts. However, three major groupings of phyla identified by molecular trees have been supported by numerous studies using varied genes and treeing techniques, and while not thoroughly corroborated, appear presently to be standing the test of time. Some important early contributions to the establishment of these groupings were by Field and others in 1988 (the pioneering study); Lake 1990; Halanych and others 1995; and Aguinaldo and others 1997; important later contributions are far too numerous to list here.

Figure 1 is a tree of metazoan phyla which approximates our knowledge of their interrelationships, based on molecular data but supplemented by developmental and morphological evidence when that seems particularly strong. The grey vertical bar just below the branch tips represents the Cambrian explosion, when body fossils of stem members of many crown phyla first appear. All (or at any rate nearly all) of the nodes representing last common ancestors of major clades occur before we see many body plans—the living phyla are simply represented by a line of distinctive lineages at the crown, and the incredible and unparalleled divergence and branching of the myriad ancestral bilaterian lineages are essentially all ghost lineages. At the base is Acoelomorpha, comprising the formerly flatworm orders Acoela and Nemertodermatida; the acoels appear to be the more basal. Those radiations must have produced large numbers of branches, including stems from the earliest bilaterian radiations, stems from each of the early radiations of the major groupings of phyla, stems from early branchings of sisters within these groupings, and stems from the phyla themselves, some of which we do have from Cambrian faunas. The bilaterian fossils predating the Cambrian explosion must be scattered within the tree, but we are not even sure what nodes they lie between; the possibility that any of them happen to represent any of the nodes in Figure 1 is small indeed.

### Neoproterozoic trace fossils

The evidence from much significant work on Neoproterozoic trace fossils indicates the presence of small organisms with the ability to creep on the sea floor or to burrow horizontally, probably just below the sediment surface; some of these organisms could form penetrating burrows, which are minute and rare. The traces first occur *c.* 555–600 Ma. Neoproterozoic trace widths tend to be measured in millimetres (e.g. Crimes 1989; Droser *et al.* 1999),

suggesting the presence of vermiform bodies of perhaps several millimetres or less in length. The lack of significant bioturbation of Neoproterozoic sediments likely indicates that the sea floor was firmer, with less water content in the sediments, thus more likely to preserve traces than is the norm with modern sediments in analogous habitats (Droser *et al.* 2002). Furthermore, some of the trails are likely to have been preserved under algal mats (see Gehling 1999; Dornbos *et al.* 2004). All other things being equal, larger trails and, especially, deeper burrows are more likely to be preserved than small trails and shallow burrows, yet larger traces are the rare ones. Therefore the traces tell us that most benthic ghosts were very small-bodied and most did not burrow or were poor burrowers.

Today, trails that resemble these horizontal Proterozoic traces can be formed by non-coelomate bilaterians using mucociliary locomotory techniques (Collins *et al.* 2000). While organisms with diploblastic body plans are able to produce similar trails, they are not known to do so under normal circumstances, and none of those are yet known that were likely to have been present in the Neoproterozoic. As for the burrows, they could have been formed by small bilaterians via push-pull locomotion, involving anterior and posterior anchors, or via weak forms of peristaltic locomotion. It is well established that the size of traces increased into the centimetre range, and penetrating burrows became more common, at or near the onset of the Early Cambrian (e.g. Crimes 1989; Dzik 2005). The onset of penetrating burrows suggests the presence of fluid skeletons, which could have been either hemocoelic (perhaps something like priapulids) or coelomic (perhaps something like enteropneusts).

### Small-bodied crown phyla

The usual way of inferring the body plans of ghosts is to determine the morphological features common to descendant branches that the ghosts must, therefore, have had, although because phyla have such disparate body plans this strategy commonly yields only very general reconstructions at that level. Among living phyla, there is a variety of organisms that might well leave traces similar to those of the Neoproterozoic. However, as there is no record of large bilaterians preceding the earliest Neoproterozoic traces, it is reasonable to eliminate from consideration those small-bodied forms that are descended from benthic ancestors significantly too large to have formed the early traces. Unfortunately, many of the entirely small-bodied phyla have proven difficult to place in the metazoan tree. Some molecular phylogenetic studies have recovered a clade of small-bodied phyla, Platyzoa

(Fig. 1; see Cavalier-Smith 1998; Giribet *et al.* 2000), most members of which were formerly included in the defunct grouping of Aschelminthes. Because Platyzoa originally included acoeles, which significant evidence now indicates are basal bilaterians, as well as several groups of flatworms, including rhabditophorans, which have the classic cleavage and 4d mesentoblasts of spiralian lophotrochozoans, this grouping seems likely to be an artefact, at least in part. What can be done at present is to examine the architectural features that are widespread among these small-bodied taxa and that can be imputed to have been common among the small-bodied Proterozoic trace-makers.

All of the small-bodied, vermiform bilaterian phyla lack coeloms. These phyla are differentiated along anteroposterior and dorsoventral axes and are triploblastic, with body-wall muscles, usually layered. Some of them are acoelomate, some pseudocoelomate, and some both, inspiring the term paracoelomate for these forms (Inglis 1985). None of the paracoelomates, even those with pseudocoels, have blood vascular systems. Most acoeles do not even have a gut lumen, but most of the paracoelomates do have guts and most guts are entire (the exceptions being obligate parasites that lack guts, and gnathostomulids and flatworm taxa with blind guts). Mucociliary creeping is common, and some paracoelomates can swim, although others are meiofaunal and of these some attach to particles in the substrate. Most paracoelomates have ganglionic brains from which nerve cords run longitudinally, and also proceed to sense organs, but acoeles do not (Raikova *et al.* 1998). Acoels do have a subepidermal nerve plexus, and although many have several longitudinal nerve cords, it is not certain that the cords participate in integrating and coordinating functions. Paracoelomate excretory organs are protonephridia, which however are absent in Acoelomorpha, Gnathostomulida and the parasitic Nematomorpha.

Even among these small-bodied and relatively simple organisms, acoeles stand out as being simpler. Lacking body cavities and both circulatory and excretory organs, with subepidermal nerve plexuses and 'brains' represented, if at all, by thickened anterior commissures, and with simple reproductive set-ups, acoeles come close to representing a model stem ancestor for bilaterians. The last common radiate-bilaterian ancestor is likely to have had a subepidermal nerve plexus as a coordinating system, with muscle cells not well developed into muscle (mesodermal) tissues, and may have lacked bilaterian body axes. Presumably the lineage leading to bilaterians developed axial features, a creeping habit, and mesodermal muscles as adaptations to benthic life. Little more is needed to produce an acoel, which certainly fits

the bill as representing a very early bilaterian body plan.

Inspecting nodes leading to crown phyla (Fig. 1), it is not until the body plans of stem ancestors require hydrostatic coeloms that we can be certain of synapomorphies associated with the last common ancestors of some alliances of phyla. Such a requirement occurs in the annelid/echiuran/pogonophoran stem (schizocoely, and very possibly including the sipunculan stem; the alliances in Figure 1 are, of course, provisional); in the deuterostome stem (enterocoely, pharyngotremy); and perhaps in the phoronid/brachiopod stem (a separate enterocoely?). Perhaps we can squeeze more detail into interpretations of the ghostly early bilaterian architectures if we use genes as well as morphology.

### Regulatory genes in early bilaterians

During ontogeny, the gene products that make up parts of a body, such as blood or tissue layers, or that perform physiological processes, such as enzymes, are coded by structural genes. The expression patterns of the structural genes are mediated by regulatory genes, which play the dual roles of architects and skilled artisans in specifying the body plan and insuring that materials are available and correctly assembled during development. It turns out that many of the same regulatory genes are present across a whole array of bilaterian phyla; some are present even in choanoflagellates, more in sponges and many in cnidarians, implying their presence in the last common cnidarian-bilaterian ancestor. The best known and probably most important of the regulatory genes are the Hox genes, a cluster of genes which code for transcription factors that, so far as is known, mediate anteroposterior axial patterning in all Bilateria. As Hox genes are known in Radiata (but not in choanoflagellates or sponges), they were presumably present in the last common ancestor of Radiata and Bilateria (see, for example, Finnerty & Martindale 1999).

A problem in using regulatory genes to interpret morphology is that many have been recruited down through bilaterian history to perform a variety of different functions and thus may affect morphology very differently in different lineages. However, there is a possibility that some aspects of Hox gene expression may prove useful in interpreting Neoproterozoic body plans. Although Hox gene products are certainly used for different developmental functions in different organisms, Hox genes are expressed colinearly when used in anteroposterior axial patterning. That is, they are usually transcribed in the same order that they occur in the cluster, and their domains of expression along the body seem to always be in the same order,

starting anteriorly. Although the Hox clustering is assumed to be the primitive condition—it hardly seems likely that scattered Hox genes would be assembled into a cluster—some of the clusters are broken up, as in the fly *Drosophila*, in which the cluster is in two sections, and in the ascidian *Ciona*, in which the cluster is entirely dispersed. In both these cases, however, the Hox genes remain transcriptionally colinear (Ikuta *et al.* 2004). The reason for this conservation is not resolved.

Not all of the known clusters contain the same Hox genes; in fact, none of the known clusters have the same Hox gene composition in any two phyla, and in the mammals, which have four clusters, each cluster is unique. Some of the differences among phyla are probably owing to paralogy, but some are due to Hox gene loss. In some cases, these losses seem to be correlated with morphology. For example, there is a basic set of 14 Hox genes in chordates, exemplified in the single cluster of *Amphioxus* (Ferrier *et al.* 2000). In *Ciona*, Hox 7, 8 and 9 are missing (Dehal *et al.* 2002). These genes mediate the development of posterior parts of the trunk region in bilaterians and 7 and 8 (presumed orthologs of *abdominal-A* and *Ultrabithorax*) were present in the last common protostome-deuterostome ancestor (de Rosa *et al.* 1999). This region has evidently been lost in ascidians, which certainly display reduced axial differentiation. Further, *abdominal-A* is lost in cirripedes, but is present in other crustaceans, and it has been suggested that this correlates with the reduction in the abdomen of these highly derived creatures (Mouchel-Vielh *et al.* 1998). And finally, the nematode Hox cluster is small, and the genes are scrambled (Kenyon & Wang 1991), yet they remain transcriptionally colinear, and nematode bodies are surely reduced morphologically. Thus in these cases, the loss of Hox genes appears to have a morphological counterpart in the loss of body sections associated with morphological reduction. And, the colinearity of Hox expression domains sometimes enables one to locate the region where the reduction has taken place. This raises the possibility that Hox gene absences in crown bilaterians might yield clues as to the body plans of their Neoproterozoic ancestors.

According to a plausible model of Hox-type gene evolution, the last common radiate-bilaterian ancestor had at least four Hox genes (see Finnerty & Martindale 1999). Three Hox cluster genes are reported in acoels (Baguna *et al.* 2001; Salo *et al.* 2001; Cook *et al.* 2004), representing one anterior, one central, and one posterior Hox type. A *Caudal*-like gene is also present, a Hox-type gene that is, however, not clustered in higher bilaterians. Thus, unless Hox genes have been missed, acoel clusters may have lost at least one, implying that they may be somewhat morphologically reduced from the

stem bilaterian ancestor. The Hox cluster of the last common protostome-deuterostome ancestor (PDA) had at least 7 genes, and possibly more (de Rosa *et al.* 1999), indicating significant growth in the cluster, possibly post-dating the last common acoel-PDA ancestor. During the radiations following the PDA, some Hox genes were lost from the clusters in many phyla.

The timing of these losses is uncertain, but most may have been between the PDA and the rise of crown bilaterian phyla. The reasoning for this notion (Valentine & Jablonski 2003; Valentine 2004) is partly based on the use of the Hox cluster for axial specification, even in cases where axially differentiated organs are absent, as in nematodes. In the relatively simple bodies of early bilaterians, exemplified by acoelomorphs, Hox domains would presumably directly regulate cell or perhaps tissue types along the anteroposterior axis, without an elaborate cascade of regulatory gene expressions following, as there were no appendages or other organs to be built. Deletion of a cell type or some other change in the simple axial pattern would be mediated directly by Hox genes, and thus could involve deletion of the Hox gene itself. So, as the PDA radiated into what was doubtless a wide variety of lineages on, within, and above the Neoproterozoic sea floor, which included subsequent stem ancestors and ancestors at nodes below the stems of living phyla, Hox gene domains were modified as anteroposterior differentiations varied. As those axial patterns were modified in response to the varied requirements of the distinctive marine habitats, some Hox genes were lost, and in different patterns in different lineages. At any rate, these losses had to occur between the PDA, with its cluster, and the crown ancestors of the phyla that display losses in PDA Hox genes. Of course, the addition of Hox genes to some clusters, as may have occurred between the clade ancestor of Rhabditophora and the crown ancestors, further differentiated the Hox gene assemblages.

A major difficulty in further speculation along these lines is that the Hox gene content of the genomes of the small-bodied living phyla is generally unknown, and for such phyla in which Hox genes have been detected, which include rhabditophoran flatworms, the development of the morphologies and functions that they mediate have not been much investigated. Although with the exception of acoelomorphs the living paracoelomates postdate the PDA (Fig. 1), correlation of body-part development with Hox gene function in a variety of paracoelomates could lead to useful models of early body plan differentiation. The comparative study of other key developmental genes in these groups is also likely to greatly improve understanding of the Neoproterozoic evolution of metazoans. Such data are now well within the capacity of molecular

developmental laboratories to acquire; whether these studies will be done at all and soon is simply a matter of priorities.

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