

REVIEW

Developmental Evolution of Metazoan Bodyplans: The Fossil Evidence

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Evidence from the fossil record, developmental biology and metazoan phylogeny demonstrates that the rapid origination of major metazoan bodyplans during the late Neoproterozoic and earliest Cambrian was intimately associated with a series of innovations in developmental control mechanisms that included the *Hox* gene cluster. The interval between about 565 Ma (million years ago) and 530 Ma evidently includes the protostome-deuterostome branching, diversification of independent higher metazoan clades, diversification of important developmental control systems, and formation of higher metazoan bodyplans. Comparative paleontological and developmental studies will allow further tests of alternative models for the sequence of these events, illuminating the association between developmental and bodyplan evolution. © 1996 Academic Press, Inc.

INTRODUCTION

The similarity of developmental control systems found across a wide variety of animal phyla is extraordinary (Averoff and Akam, 1993; Akam *et al.*, 1994; Carroll, 1995) but tells us little about how the bodyplans of those phyla originated. The remarkable similarities represent an array of developmental mechanisms that were assembled early in metazoan history and thus were present in the common ancestors of the phyletic lineages that diverged subsequently. The key to the origin of the various bodyplans, however, lies in the rise of developmental differences associated with the major morphological novelties accumulated during their independent evolution. Establishing the shared legacy of the ancient developmental mechanisms and tracking their divergences during metazoan history will be a challenging task in the coming decade.

In this light we combine the flood of new data on molecular phylogenies, on developmental biology, and on the fossil record of early metazoan evolution to evaluate the origin of bodyplans of metazoan phyla. Phyla are Linnean taxa, and while they can be defined cladistically by using shared derived characters (synapomorphies), it is the combination

of primitive (plesiomorphic) and derived (apomorphic) design elements that form their unique bodyplans. For example, the arthropod bodyplan is triploblastic and possesses a blood vascular system, primitive features that are inherited from arthropod ancestors; it also includes jointed appendages, features that are derived. The data now clearly demonstrate that the origin of metazoan bodyplans did not coincide with the separation of the lineages that led to those bodyplans. Furthermore, the data suggest that the scope of developmental controls expanded and/or was modified as each bodyplan was assembled. The evolution of gene regulatory systems during the evolution of bodyplans is best illustrated by the highly conserved group of homeobox genes known as the *Hox* cluster, and we will use this cluster to discuss the process, although details of *Hox* cluster assembly must come from further rigorous comparative studies. Other developmental regulatory systems, for example, other homeobox gene classes, may show patterns similar to those of the *Hox* genes. It seems clear that the rise of the Metazoa and the elaboration of increasingly complex metazoan bodyplans was associated with the establishment and expansion of developmental control systems. Evolution within bodyplans, however (or perhaps among bodyplans of similar complexity), has often involved regulatory repatterning (Carroll, 1995).

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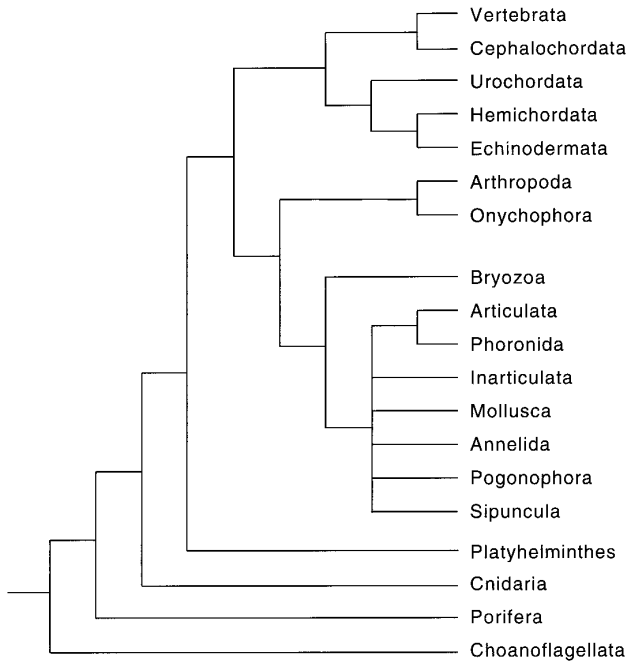


FIG. 1. Pattern of phylogenetic branching inferred to have led to selected metazoan phyla, representing a qualitative synthesis of 18S rRNA trees produced variously by algorithms based on maximum parsimony, evolutionary parsimony, maximum likelihood, and distance metrics. Branch lengths are not scaled to molecular distance measures or to geologic time. (Data chiefly from Lake, 1990; Turbeville, 1991; Turbeville *et al.*, 1992; Wainright *et al.*, 1993; Wada and Satoh, 1994; Sogin, 1994; and Halanych *et al.*, 1995.)

METAZOAN PHYLOGENY AND THE ORIGIN OF EARLY METAZOAN BODYPLANS

Despite more than a century of work by anatomists and developmental biologists on the phylogenetic relationships among the animal phyla, the field has been divided into several major camps (Willmer, 1990). Molecular data now provide an independent source of phylogenetic information. At present, small subunit (SSU) rRNA (18S rRNA in metazoans) appears to be the most appropriate molecule for which a significant amount of comparative data are available to infer the branching pattern of metazoan phyla (Field *et al.*, 1988; Lake, 1990; Turbeville *et al.*, 1991, 1992; Sogin, 1991, 1994; Wainright, 1993; Wada and Satoh, 1994; Halanych, 1995; Halanych *et al.*, 1995; Winnepenninckx *et al.*, 1995; Cohen and Gawthrop, in press). A variety of phylogenetic methods has been applied to the growing catalog of sequences, revealing the pattern of branching relationships in Fig. 1. Some branchpoints remain unresolved or weakly supported, however. Much of the uncertainty probably reflects a paradox inherent in rRNA (or rDNA) sequences.

The SSU rRNA molecules are used to investigate ancient branches within metazoan phylogeny because they evolve only slowly, but their rate of change can be too slow to resolve the order of branching for the metazoan clades that diverged within a geologically short time interval (Erwin, 1991; Turbeville *et al.*, 1992; Philippe *et al.*, 1994); this may account for the unresolved cluster of protostome phyla in Fig. 1. Uncertainties can also arise when clades with different rates of rRNA evolution are compared (Lake, 1987), and some other problems in interpreting molecular sequence data are reviewed by Raff *et al.* (1994). Most of the branchings indicated in Fig. 1, though provisional, have been evaluated by several methods and the tree represents a plausible interpretation of the available SSU rRNA data.

The genealogical branchpoints provide an essential framework for analyzing metazoan evolution, but they cannot be used to infer the establishment of novel bodyplans. Rather, the nodes are points at which the molecule first became isolated in separate lineages. The branchings reflect speciation events that separated two sister lineages sharing the same suite of characters—genomic, morphologic, and developmental—that had evolved prior to the divergence (i.e., that are plesiomorphies). Obviously these clades have come to differ importantly in characters that changed *after* the divergence (i.e., they have accumulated apomorphies), but there is no good reason to suppose that their initial divergences involved morphological steps on the way towards novel bodyplans, although some may have. The earliest representatives of diverging branches, however, clearly had the same bodyplan. Reconstruction of the bodyplan of the common ancestor represented at such branchings requires data from comparative morphology and the fossil record. The branching sequence is quite important in considering the history of developmental control.

The origin of the Metazoa has generally been assigned dates that range chiefly from just under 1000 to over 1700 Ma (million years ago), by extrapolation from various rates of morphological and molecular change inferred for the Phanerozoic (e.g., Durham, 1971; Runnegar, 1982). The pattern of branching among protistan and multicellular clades that is emerging from SSU rRNA sequence data indicates that the nearest living protistan relative of the Metazoa (and sponges, regardless of whether they fall within the formal definition of Metazoa) is the Choanoflagellata (Fig. 1). Unfortunately, the age of that branchpoint, which could set a maximum age for the origin of metazoans, is poorly constrained; probably it lies between 1200 and 600 Ma. A minimum age is set by the earliest generally accepted metazoan fossil remains, described from rocks dated at about 565 Ma ("Vendian" or "Ediacaran" time; Fig. 2) (Grotzinger *et al.*, 1995).

THE FOSSIL RECORD OF EARLY METAZOAN BODYPLANS

The Earliest Preserved Metazoans

The fossil record helps to pinpoint the events in morphologic evolution that gave rise to the spectacular biodiversity

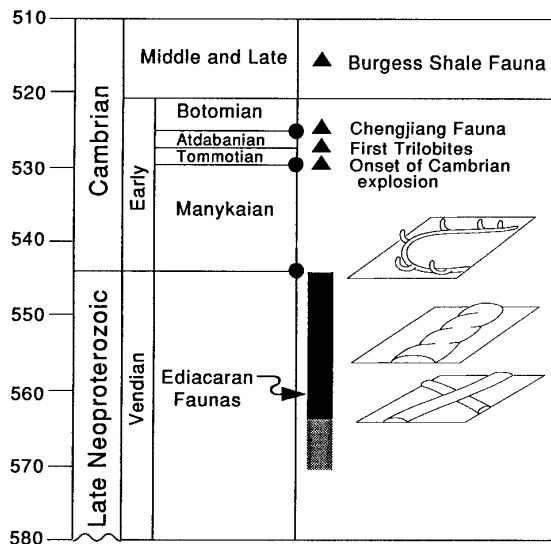


FIG. 2. Geologic time scale for late Neoproterozoic (Vendian) time and the Cambrian Period, with some trace fossil types and other major fossil occurrences indicated. Stages are from the Russian column. Filled circles indicate the approximate stratigraphic location of dates based on U/Pb geochronology (Bowring *et al.*, 1993); the ages of other boundaries are less well-constrained. The internationally recognized boundary between the Vendian and Cambrian has recently been placed at the base of the Manykaian Stage, well before the Cambrian explosion, which is largely confined to the Tommotian and Atdabanian Stages. New data from Namibia (Grotzinger *et al.*, 1995) indicate a date for the base of the Ediacaran fauna at about 565 Ma, younger than previously believed, and also suggest that the Ediacaran fauna ranges to the Vendian/Cambrian boundary. Correlation of the widespread Vendian assemblages has been difficult, but carbon-isotope chemostratigraphy has provided significant improvements. The stippled area indicates the occurrence of less complex fossils which may be early metazoans.

that has been this planet's hallmark over the past half-billion years. Knowledge of the early metazoan record has increased significantly in recent years (Simonetta and Conway Morris, 1991; Lipps and Signor, 1992; Bengtson, 1994; Grotzinger *et al.*, 1995). The oldest body fossils, as well as trace fossils (signs of animal activity such as trails) that can be certainly assigned to the Metazoa, make their appearances at about the same time, late in the Neoproterozoic (a time unit that extends from 1 billion years ago to the beginning of the Cambrian Period). The earliest traces, from rocks of Vendian age (Fig. 2), are rather simple, gently curved to meandering furrows that suggest the presence of bilaterian worms, but the traces become more complex and diverse later in the Neoproterozoic (Crimes, 1992a, b, 1994). Some of the trails exhibit relatively sophisticated search patterns, display transverse furrows and longitudinal ridges or grooves, and contain pellet-like structures interpreted as fecal in origin. A few rare traces penetrate the sediment as

shallow burrows (Fedonkin, 1994). The more complex traces must have been produced by organisms that were centimeters in length and rounded rather than flat, and which therefore must have had circulatory systems of some sort to provide oxygen to and remove metabolites from internal tissues; the pellets suggest that at least some of the forms had complete guts. The traces also indicate locomotion by pedal or peristaltic movement, and the trace-makers must therefore have had some means of antagonizing the musculature involved; a tissue or fluid skeleton, such as a hemocoel, would have sufficed. These features indicate that the trace-makers were more advanced than flatworms, which lack these attributes and cannot leave trails of the sorts described (Fedonkin and Runnegar, 1992). Indeed, no trace markings of flatworms seem to have been recorded from marine sediments, although trails interpreted as sub-aerial flatworm traces are described from the nonmarine Permian by Alessandrello *et al.* (1988). While those trails resemble locomotory patterns of land planarians (Pantin, 1950), they are quite unlike any of the early marine traces discussed here. The simplest bilaterians capable of making the Vendian trails might be placed within the Mollusca if found alive, though the trace-makers were probably less derived than any living molluscan clade (Valentine, 1994).

There has been a wide range of interpretation of Vendian body fossils, with some placed in extinct phyla or even kingdoms (e.g., Pflug, 1972; Seilacher, 1989; but see Gehling, 1991). Many can be interpreted as metazoans of cnidarian grade and indeed some are likely to be Cnidaria or close relatives (Conway Morris, 1993b); some may represent a sister group to Cnidaria plus higher metazoans (Buss and Seilacher, 1994). Still other Vendian fossils may be bilaterians (Fedonkin, 1994; Sun, 1994), but assignment of certain forms to the Annelida, Echinodermata, and Arthropoda is based on general similarities or putative evolutionary scenarios rather than specific derived characters that place the fossils within these higher metazoan phyla. Thus, there is no compelling evidence that either protostomes or deuterostomes occur in the Vendian, although some of the early members of those clades would surely have been capable of forming Vendian-style traces. Probable bilaterian material has been described from the Manykaian Stage (Fig. 2), but the earliest undisputed body fossils of living bilaterian phyla appear at the base of the Tommotian, near 530 Ma. By that time the last common ancestor of the protostomes and deuterostomes had certainly evolved, for early Tommotian fossils include derived protostome phyla.

The Cambrian Explosion

Forms with mineralized skeletons (chiefly of uncertain affinity) begin to appear in the Manykaian Stage (Khomentovsky, 1986), and a wide array of higher metazoan body fossils first appears during the Tommotian and Atdabanian Stages of the Lower Cambrian (Conway Morris *et al.*, 1987; Dzik and Lendzion, 1988; Hou *et al.*, 1991; Bengtson and Conway Morris, 1992; Conway Morris, 1993) (Fig. 2), when

trace fossils also increase in abundance and diversity (Seilacher, 1956; Crimes, 1994). This burst of evolutionary invention gave rise to many of the derived features of metazoan bodyplans. Phylogenetic evidence indicates, for example, multiple independent origins of segmentation and of coelomic cavities during this period (see Fig. 1; Valentine, 1994).

Some of the more intriguing fossils from this explosive evolutionary episode possess morphological features not found among the bodyplans of extant groups. While these forms cannot be unequivocally assigned to living phyla, most exhibit characters relating them in some way to living groups, many to arthropods, some to molluscs, some to aschelminths, and so on; others remain enigmatic. These problematic forms further underscore the morphologic breadth of the Cambrian explosion. The only living phyla with durable skeletons absent from the Early Cambrian roster are the bryozoans and the chordates, but these groups do not require mineralized skeletons in support of their bodyplans and may have been soft-bodied during their early histories. The earliest known chordates are in slightly younger Middle Cambrian rocks (near 515 Ma) and the first bryozoan fossils occur in the Early Ordovician. These oldest known bryozoans are sufficiently derived to require an earlier phase of diversification (P. D. Taylor, personal communication, July 1995). The paleontological data are consistent with the view that all of the currently recognized phyla had evolved by about 525 Ma.

The Post-Explosion Record

Despite half a billion years of evolutionary exploration by the clades generated in Cambrian time, no new phylum-level designs have appeared since then. This decrease in evolutionary inventiveness has recently been quantified without recourse to taxonomic rank. For example, the array of Cambrian arthropods and associated lineages—which is surely undersampled—occupies as large a volume of morphospace (a multidimensional volume defined by morphological variables, within which taxa or lineages can be compared and tracked over evolutionary time) as does the entire present-day marine arthropod fauna in all its diversity (Briggs *et al.*, 1992; Foote and Gould, 1992). Two long-debated explanations for this trend are that (a) developmental mechanisms became canalized or at least constrained so as to preclude the specification of great novelty and (b) the filling of the environment by early Phanerozoic diversifications preempted the ecological opportunities that were once available to organisms with distinctive bodyplans (Valentine, 1986; Jablonski and Bottjer, 1990; Erwin, 1994). The relative significance of these respectively internal and external controls is difficult to determine at present; new paleontological and developmental evidence will be required to assess their relative strengths (see Hughes, 1991; Smith, 1994; Valentine, 1995).

THE EARLY EVOLUTION OF DEVELOPMENTAL REGULATION

The extraordinary conservation of developmental control systems concerned with differentiation reflects the fact that the origin and early elaboration of these systems lies within the early history of the Metazoa itself; the systems are neither relevant to nor known within the ancestors of metazoans (Erwin, 1993), though their genes must have their roots there. The inferred history of metazoan diversification, with branching topology from molecular phylogenies and bodyplan assembly from fossil evidence, provides a context for the burgeoning data on metazoan development (Valentine, 1994; Conway Morris, 1994). The *Hox* cluster exemplifies, for the evolution of a particularly significant control system, both the promise and problems of comparative developmental studies.

The Hox Cluster

Metazoan development is mediated by regulatory genes that possess DNA-binding sequences through which they control the activities of other genes. In many metazoans, perhaps all, maternal and early nuclear regulatory gene products set up embryonic body axes and provide a framework within which further development occurs (Gilbert, 1994). Many of these patterning genes have a characteristic sequence termed the homeobox (Duboule, 1994). In some metazoans, pattern-formation genes are known to mediate the expression of a few classes of highly conserved homeobox genes termed *Hox* genes, which are homeotic genes that in turn mediate the identity of a region of the body. In arthropods, a cluster of homeotic genes mediates the expression of genes that specify legs, wings, or antennae on different body segments, for example (Akam, 1987). In nematodes, which are unsegmented and lack such elaborate structures, a *Hox* cluster mediates the identity of particular cell lineages along the body axis (Salser and Kenyon, 1994). Orthologous *Hox* genes in these phyla, and in chordates (Garcia-Fernandez and Holland, 1994), have a similar order and are expressed colinearly along the anteroposterior (AP) body axis.

The extensive sequence conservation of the *Hox* genes does not necessarily extend to conservation of their patterning effects, so that the present regulatory roles of *Hox* genes do not necessarily correspond to those of their ancestral genes. For example, the *Hoxa* and *Hoxd* genes are sequentially activated during the development of the vertebrate limb (Duboule, 1992; Morgan and Tabin, 1993), but they are related not only to the *AbdB* gene in *Drosophila* but to the *egl-5* gene in the nematode *Caenorhabditis* (Salser and Kenyon, 1994), and thus their evolutionary origins predate that of limbs. Other regulatory genes display similar sorts of histories. For example, the homeobox variant *Pax6* appears to be a master control gene for eye development in both vertebrates and *Drosophila* (Quiring *et al.*,

1994), which have very different and very complicated eyes, but the last common ancestor of those organisms, at the protostome–deuterostome divergence, must have possessed only simple light-sensitive receptors.

The *Hox* cluster in a nematode (*Caenorhabditis*) has 4 genes (Kenyon and Wang 1991; Salser and Kenyon 1994; Kenyon, 1994), and there are 8 in an arthropod cluster (*Drosophila*) (Akam, 1987; Averoff and Akam 1993), 10 in a cephalochordate cluster (*Branchiostoma* or amphioxus) (Garcia-Fernandez and Holland, 1994), and 38 in four clusters in a vertebrate (*Mus*) (Krumlauf, 1994). Each phylum or class in which the *Hox* cluster has been well-characterized exhibits a unique pattern of gene duplication or loss, relative to other phyla or classes (and each of the four vertebrate clusters is unique as well, although ultimately traceable to duplication from a single ancestral cluster). *Hox* genes have been detected in many other phyla and classes, but chiefly through polymerase chain reaction (PCR) surveys that may not provide reliable information on the number present (because failure to detect genes is difficult to assess) and do not always permit the unambiguous identification of paralogs or orthologs. Nevertheless, the surveys have demonstrated the presence of *Hox* genes in all major phyla except sponges (Coutinho *et al.*, 1994; Seimya *et al.*, 1994), and the number of *Hox* genes so detected tends to be greater as their bodyplans become more complex (see Ruddle *et al.*, 1994). The clusters in phyla which can be located within the SSU rRNA phylogeny, and *Hox* genes identified by PCR surveys in some other phyla, are placed within the phylogenetic framework provided by Fig. 1 and illustrated in Fig. 3.

It is still unknown whether the earliest metazoan node—the last common poriferan–cnidarian ancestor (Fig. 1)—possessed any genes of the *Hox* classes. However, *Hox* genes tentatively identified in cnidarians have been inferred to form a cluster, and at least two other homeobox classes also occur (Shummer *et al.*, 1992; Miller and Miles, 1993; Shenk and Steele, 1993). At least one of the genes in Fig. 3 (*Cnox2*) is inferred to be involved in axial patterning (Shenk *et al.*, 1993). The extinct common ancestor of cnidarians and higher metazoans may well have been a planuloid form (a minute flagellated organism with a solid, cellular interior from which both primitive diploblastic and triploblastic body plans may have evolved; see Salvini-Plawen, 1978), and if so the early *Hox* gene(s) may have mediated patterning therein. Numbers of *Hox* genes have been found in flatworm species by PCR survey techniques (Bartles *et al.*, 1993; Belavoine and Telford, 1995). Homologues have been identified to genes of the *lab*, *Dfd*, and *Antp* classes or subclasses, and questionably to other *Hox* genes known in higher metazoans.

Placing the available *Hox* gene data in a phylogenetic context indicates that the last common protostome–deuterostome ancestor had a cluster of at least six *Hox* genes (Fig. 3). Judging from its phylogenetic position, this organism probably had more AP differentiation than the last common ancestor of the flatworm and higher invertebrate lineages; it may well have been seriated and was probably

hemocoelic (Valentine, 1994). As the higher invertebrates diversified during the Cambrian radiation the *Hox* genes in the center of the cluster (cognate groups 6–8) were evidently duplicated independently in lineages in which trunk complexity subsequently increased. In the deuterostome line, duplications of the *Antp/abdA/Ubx* gene produced the genes belonging to the sixth, seventh, and eighth ortholog groups present in amphioxus (Garcia-Fernandez and Holland, 1994). Amphioxus genes 9 and 10 were duplicated from an *AbdB*-type precursor prior to the cluster duplication events in the vertebrates (Garcia-Fernandez and Holland, 1994). Independently of these duplications, the *AbdB*-type precursor may also have given rise to at least two additional genes in echinoderms (Ruddle *et al.*, 1994). However, some clades exhibit a range of body-type diversities but possess identical clusters, as for example within the arthropods (Warren *et al.*, 1994), illustrating the importance of regulatory repatterning downstream of the *Hox* genes within major clades (Carroll, 1995).

Determining gene homologies in the protostome line is difficult from the available PCR survey data. A plausible interpretation based on this preliminary data is that arthropods, annelids, and mollusks experienced independent duplications of the ancestral *Antp/abdA/Ubx* gene, giving rise to these three genes in ancestral arthropods (Kappen and Ruddle, 1993; Schubert *et al.*, 1993), prior to the divergence of chelicerates and mandibulates (Bartles *et al.*, 1993). Independent duplication of the same ancestral gene in the annelid line may have given rise to three *Antp*-class genes and separate *Ubx* and *abdA* homologs in polychaetes (Dick and Buss, 1944). A survey of an oligochaete annelid suggested that as many as five genes may have derived from the ancestral *Ant/abdA/Ubx* gene (Snow and Buss, 1994). The *Hox* cluster inferred from a PCR survey of the gastropod *Haliotis* (Degan and Morse, 1993) is indistinguishable from that inferred for the protostome–deuterostome ancestor. However, unpublished data cited by Ruddle *et al.* (1994) suggest the presence of “several” *Antp*-class genes in *Aplysia* and/or cephalopods (mollusks more derived than *Haliotis*), which may represent another independent duplication of the medial genes of the cluster, either in all mollusks (if *Haliotis* has them or has lost them) or only in more derived groups.

Other Genes

Other regulatory genes also evolved prior to the Cambrian explosion, of course. For example, Bürglin (1994) recognized 21 classes of homeobox genes, and 2 more have been added since (Bürglin, World-Wide Web). The phylogenetic distribution of these gene classes demonstrates that all of them originated prior to the last common protostome–deuterostome ancestor, and many must have evolved much earlier, becoming established early in the evolution of metazoan bodyplans.

A similar situation holds for several important cell-signaling molecules. The sequences of the *Drosophila* gene *hh* and a vertebrate counterpart *Shh* and the regulatory cas-

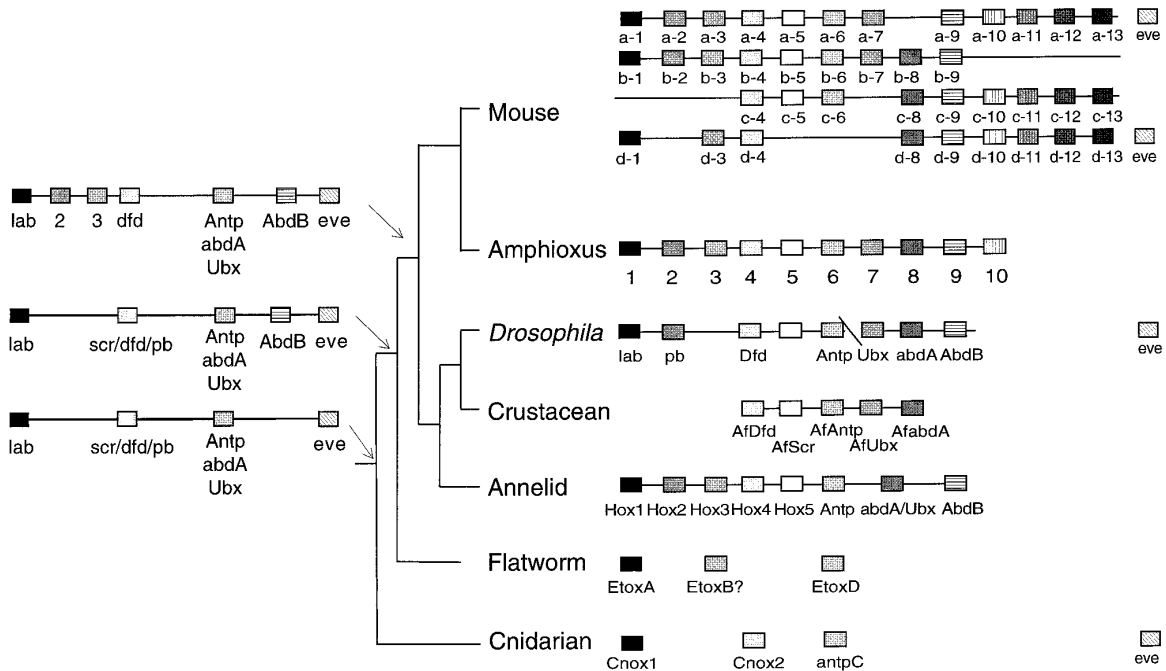


FIG. 3. *Hox* genes that have been identified in selected metazoan phyla. On the right, those genes established as belonging to clusters are linked by horizontal lines. On the left, hypothetical clusters are inferred for the last common ancestors of: cnidarians and bilaterians; the flatworm line and higher metazoans; and the protostomes and deuterostomes. The flatworm cluster may contain additional paralogous *Hox* genes but is not yet worked out. The annelid cluster is based on studies of polychaetes, leeches, and oligochaetes (Shankland, 1994; Dick and Buss, 1994; Snow and Buss, 1994). *Haliotis*, a fairly primitive gastropod, may have a *Hox* cluster indistinguishable from that of the protostome–deuterostome ancestor (see Degnan and Morse, 1993), although the cluster in more advanced mollusks may be more complex (Ruddle *et al.*, 1994).

acades through which they act are highly conserved (Laufer *et al.*, 1994). Both genes encode extracellular signaling proteins that mediate pattern formation in adjacent tissues. Each gene seems to control another highly conserved cell-signaling gene (*wg* in *Drosophila* and *Wnt-1* in vertebrates) and plays a critical role in the patterning of developing limbs. The striking conservation of both expression and regulatory function in these homologs suggests that proximodistal axis formation in vertebrate and arthropod limbs share a common developmental control mechanism (Feitz *et al.*, 1994) despite their separate origins from a common ancestor that lacked limbs.

MODELS OF DEVELOPMENTAL HISTORY FOR THE CAMBRIAN EXPLOSION

Because the precise timing of bodyplan originations remains unclear, we frame rival models for their origins in relation to the Cambrian explosion (Fig. 4). Each model is constrained paleontologically; the fossil record contains no indications of bodyplans higher than the flatworm grade prior to about 565 Ma, and an array of higher metazoan

bodyplans appears near 530 Ma. Therefore, the interval between 565 and 530 Ma most likely accommodates the split between protostomes and deuterostomes, the subsequent branching of numerous independent metazoan lineages, and the evolution of derived bodyplans within many of those branches. Alternative hypotheses on the relationship between morphological and developmental evolution within this interval have dramatically different implications for the evolution of metazoan body patterning.

Model I incorporates the maximum time lag between the splitting of the lineages and the origin of the bodyplans. Two submodels can be envisioned, depending on the timing of *Hox* cluster assembly. In the first submodel, the bulk of the *Hox* cluster is assembled early in metazoan history and is not usually enlarged during subsequent bodyplan originations. This submodel thus requires that the PCR analyses are misleading and that the breadth of phylogenetic information is insufficient at present to reveal an early large *Hox* cluster. In the second submodel, although *Hox* cluster formation of perhaps six genes is completed early, expansion to perhaps eight or more genes occurs in some lineages during the Cambrian explosion, to underpin some novel bodyplans. In Model II, lineage splitting and *Hox* gene duplications occur in sequence during the Vendian and Many-

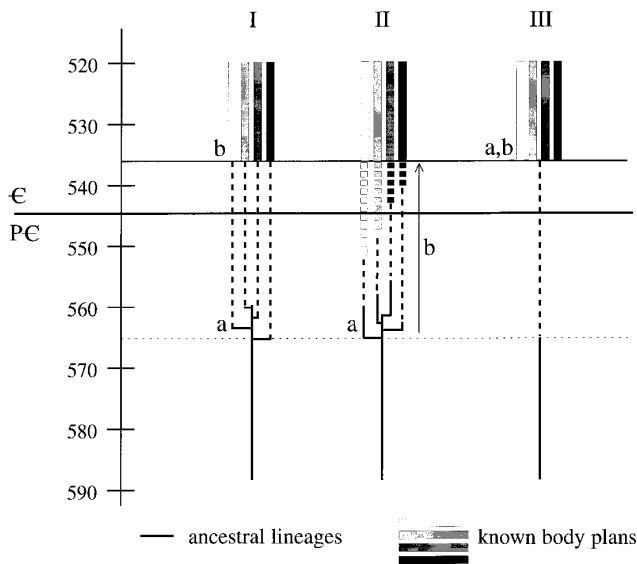


FIG. 4. Models of the sequence of evolutionary events surrounding the Cambrian explosion as constrained by the fossil record. The events include: (a) the protostome–deuterostome split and divergence of the major lineages and (b) the origin of bodyplans. *Model I*: The lineages that eventually lead to higher metazoan phyla branch early, but a burst of bodyplan diversification occurs near 530 Ma. Genomes achieve complexity early, but undergo possible secondary expansions near 530 Ma. *Model II*: Metazoan lineages, genomes, and bodyplans branch, diversify, and increase in complexity progressively during the Vendian and Manykaian, achieving a threshold in developmental controls that permits a final burst of advanced bodyplan diversification near 530 Ma. *Model III*: Higher metazoan lineages, genomes, and bodyplans all diversify explosively near 530 Ma. Model II, which we prefer, can in principle be distinguished from the others by fossil and molecular evidence.

kaian separation of numerous protostome and deuterostome lineages and the origin of higher invertebrate bodyplans (with, of course, appropriate splittings preceding duplications); the Cambrian explosion then marks the attainment of a threshold in the complexity of gene regulation that permitted a cascading radiation of advanced invertebrate bodyplans, commonly by regulatory repatterning. Finally, in Model III, the last common ancestor of protostomes and deuterostomes occurs near 535 Ma, followed immediately by lineage and bodyplan diversification. This is the most extreme version of the Cambrian explosion, proceeding (as a limit) from a single lineage that may have had fewer than six *Hox* genes and expanding the genomic repertoire and morphologic diversity all in a single burst.

These models can be tested as further data become available. The two varieties of Model I can be distinguished from each other and from Model II by thorough molecular studies of *Hox* genes among the phyla, especially if lower metazoans are targeted. Model II best accords with the *prima facie* evidence. The increases in the diversity and complexity of

trace fossils through the crucial Vendian–Lower Cambrian interval is consistent with both Models I and II, and the large number of *Hox* genes found in clades that branch higher on the phylogenetic tree is consistent with Model II. However, Model II will be falsified if large *Hox* clusters homologous with those of higher invertebrates are found in clades that branched early. Model III seems to be the least plausible, implying that the Vendian traces by and large represent dead-end clades. Model III also requires nearly simultaneous duplications of *Hox* genes in multiple independent lineages. Such synchronicity would best be explained by environmental forcing factors. Many such factors have been proposed (reviews in Valentine *et al.*, 1991; Signor and Lipps 1992), but none has been convincingly supported by subsequent research. Model III is further undermined by requiring the near-coincidence not only of independent *Hox* gene duplications but of lineage splitting and bodyplan origination of most living phyla.

Even if *Hox* clusters prove to have expanded during the Vendian, favoring Model II, we will still not know whether the increasing diversity of Vendian and Manykaian trace fossils corresponds to the cladogenetic events leading to higher metazoans. Molecular data are incapable of resolving this question, placing the burden on paleontologists to scour the Neoproterozoic fossil record in search of metazoan bodyplans. On the other hand the determination of *Hox* clusters within the thirty-odd phyla in which they are not yet known, and evaluation of the roles of homeobox and other regulatory genes, can only be done in the molecular laboratory, where appropriate tools already exist. Understanding the sequence of events that led from the origin of the metazoans to the evolution of their enormous architectural diversity will require a creative combination of these disciplines.

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