

# The Origin of Animal Body Plans

*Recent fossil finds and new insights into animal development are providing fresh perspectives on the riddle of the explosion of animals during the Early Cambrian*

Douglas Erwin, James Valentine and David Jablonski

The barren Namibian desert in southern Africa, the dry outback of South Australia and the Winter Coast of the White Sea in northwestern Russia might seem unpromising Edens. But the rocks exposed in those far-flung areas hold the oldest record of animal life, a prelude to the evolutionary explosion of animal body plans that was to come. Preserved in those ancient marine sediments, which date from nearly 550 million years ago during an interval geologists call the Neoproterozoic, is a startling variety of frond-like fossils resembling sea pens, disc-shaped forms resembling jellyfish and a number of completely enigmatic forms that do not resemble any creatures living in modern oceans. The animals that left this ancient record were nearly all soft-bodied; hard skeletal remains are represented by only a few scraggy tubes whose biological affinities are uncertain. However, the activities of worms or slug-like animals are recorded by trails and

burrows left behind as they crawled and dug about on their ancient sea floor. These ancient traces of animal activity closely resemble those produced by present-day organisms, and thus provide insights into the expanding anatomical complexity and behavioral repertoires of these early forms, another piece of the puzzle posed by the spectacular appearance of a diversified skeletonized fauna over only a few million years, beginning nearly 530 million years ago—the Cambrian explosion.

The Cambrian record of life is in sharp contrast with that of the preceding eons. The remains of single-celled organisms can be traced back to nearly the oldest sediments on the planet, about 3.5 billion years ago. And for the next 3 billion years or so, the earth was chiefly populated by single-celled organisms, although algae achieved a multicellular grade about 1 billion years ago. About 565 million years ago, the larger, multicellular animals of the Neoproterozoic appear in the fossil record, with their striking variety of form, only to be overshadowed about 35 million years later by the explosion of body plans recorded in early Cambrian rocks: Nearly all known kinds of shelled invertebrates appear then, including clams, snails and arthropods (the group including crabs and trilobites), soon joined by echinoderms and soon thereafter by chordates, the lineage that gave rise to humans and all other vertebrates. All of the basic architectures of animals were apparently established by the close of the Cambrian explosion; subsequent evolutionary changes, even those that allowed animals to move out of the sea onto land, involved only modifications of those basic body plans. About 37 distinct body architectures are recognized among present-day animals and form the basis of the taxonomic classification level of phyla.

The fossil record of the last 3.5 billion years thus shows not a gradual accu-

mulation of biological form, but a relatively abrupt transition from body plans of single cells to those of a rich diversity of animal phyla. In geological terms, an explosion indeed. Was this explosion real, or is it an artifact of a strangely biased fossil record?

Over the past few years new fossil discoveries have greatly clarified the sequence of events up to and during the Cambrian explosion. This in turn has set the stage for integrating information from several fields that had once operated in near isolation. Modern techniques for extracting and analyzing molecular data have shed new light on the evolutionary relationships among the living animal groups whose roots extend back to, or even precede, the beginning of Cambrian time. Perhaps most extraordinary have been the discoveries in developmental biology. Molecular techniques have shown that the developmental systems that control patterns from eggs through embryos to adults, and thus determine animal architectures, are remarkably similar across a wide range of phyla. In spite of their similarities, which have persisted despite the long separation of the phyla, the systems produce very disparate body plans. Evolutionary biologists can now reconstruct basic aspects of the developmental control systems of long-extinct animals, and can attempt to track not only the diversification of animal form but also the establishment and evolution of the genetic controls that regulate it. Taken together, all these advances are permitting a new, multidisciplinary look at the early history of animals and into the mysteries of the Cambrian explosion.

## The Family Tree of Animals

Only 10 years ago many invertebrate biologists saw the reconstruction of relationships among the phyla as an insoluble dilemma; two centuries of

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Figure 1. Proboscis science fossilized re sediment about 530 skeletal spectacular the Camb that arose body plan invented just precede eular and evolution pects of the long-extir forms arose noted, pho

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Figure 1. With its five eyes and long, flexible proboscis, *Opabinia* resembles a creature out of science fiction. Yet once it was very real. Its fossilized remains, along with those of hundreds of other species, are found in ancient marine sediments dating back to a geological period about 530 million years ago. The diversity of skeletonized life forms from this time is so spectacular that the period has been dubbed the Cambrian explosion. Many of the creatures that arose then are now extinct. But the basic body plans of all animals on earth today were invented during the Cambrian or the period just preceding it. Advances in the fields of molecular and developmental biology are allowing evolutionary biologists to reconstruct basic aspects of the developmental control systems of long-extinct animals to understand how new forms arose from existing ones. (Except where noted, photographs courtesy of the authors.)



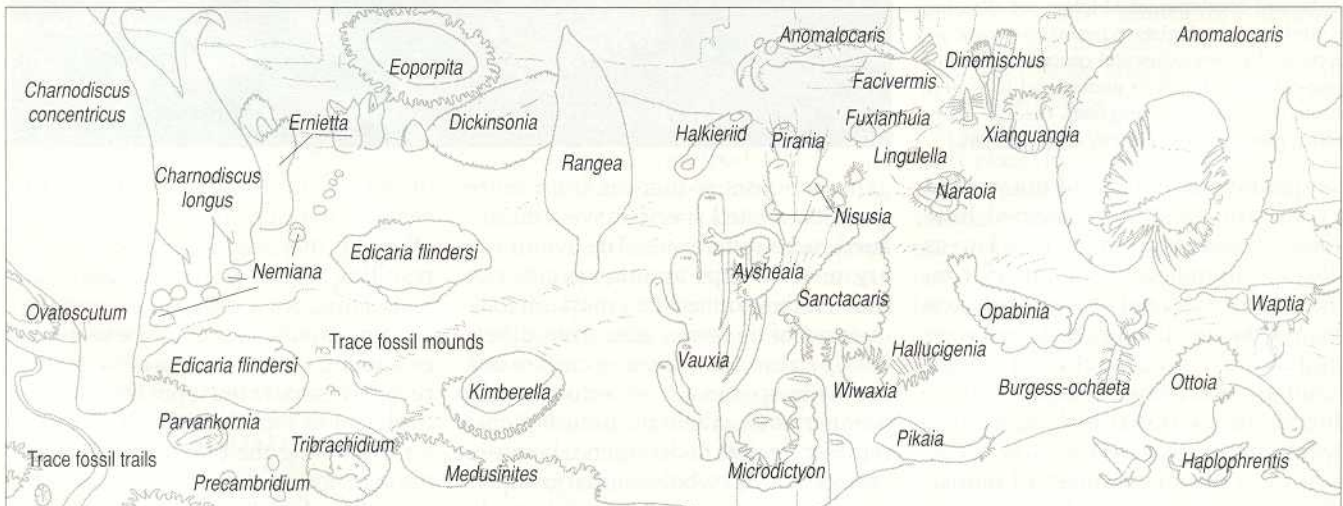
comparative anatomy had not yielded a consensus, and there seemed little hope of resolution. Indeed, as late as 1990 a comprehensive summary concluded that the relationships between most of the higher animal groups were entirely unresolved. Yet even as that summary was being written, the introduction of molecular techniques was beginning to provide the data necessary for a new assessment of animal affinities. The molecular data consist of long sequences of the four nucleic acids that make up the information encoded in DNA. Sequences from closely related species differ only slightly because of random mutations within a

gene, whereas sequences from more distantly related species have accumulated more differences. The evolutionary relationships among species can thus be determined by comparing sequences of the same gene from different species. After these comparisons are made, species are placed on an evolutionary tree, where the branch points represent points of divergence between species or even whole animal groups.

Choosing appropriate genes to study can be difficult, however, because different genes evolve at different rates. If the changes in sequence are too few, there is not enough difference among species to resolve the branching pattern

on an evolutionary tree; too many changes overwhelm or "saturate" the DNA, so that any original similarities resulting from common ancestry are lost. Thus, for example, a gene that changes rapidly enough to be useful for examining the differences between two recently separated species of mice evolves too rapidly to be appropriate for examining the differences between the ancestors of a mouse, an earthworm and a fly, which lived over half a billion years ago.

Even with the appropriate genes, the molecular tree of life is difficult to interpret. For one thing, many of the phyla appear to have branched within a rela-



Late Neoproterozoic		Cambrian		
Ediacaran		Early		Middle
		Manykaian	Tommotian	
570	543	530		7520
time (millions of years ago)				

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Figure 2. Fossils from the last 3.5 billion years show a relatively abrupt transition from body plans of single cells to a rich diversity of animal-body architectures. The first multicellular animals appear about 570 million years ago, shortly before the beginning of the Cambrian, and examples of them are shown on the left of this reconstruction. They did not have mineralized skeletons, but were instead soft-bodied creatures resembling sea pens or jellyfish. These were joined about 35 million years later by the animals represented in the center of the reconstruction—shelled invertebrates, including clams, snails and arthropods such as trilobites. Soon after, echinoderms such as starfish appeared, followed by chordates, the lineage that gave rise to humans and all other vertebrates. All of the basic architectures of animals were apparently established by the close of the Cambrian explosion. Subsequent evolutionary changes, even those that allowed animals to move out of the sea onto land, involved only modifications to those basic body plans.

tively short period of time. Therefore, the slowly evolving genes suitable for probing such ancient events changed relatively little between successive divergences, and it may be difficult or impossible to resolve the order of branching. Furthermore, with only four nucleic acids involved in the genes, similarities can arise by chance or through biases in substitutions of one nucleic acid for another that are unrelated to kinship among the species. More than 100 different numerical techniques have been developed to counter such problems, and whereas many of the divergences

among phyla remain uncertain, others seem to be well established by the new molecular analysis.

The pattern of divergence among the phyla does not solve the larger problem, for the branching sequence tells biologists too little about when the body plans themselves originated. This is because at the branchpoints—when the lineages split and the molecules began to change independently—each branch had precisely the same body plan, and it may have been many millions of years before a new body plan arose. Consider an evolutionary tree depicting a sword-

fish, a fly and Marilyn Monroe. Marilyn would be placed closer to the swordfish than to the fly. However, the divergence between Marilyn and the swordfish, which happened over 400 million years ago, did not immediately produce their disparate architectures. When these lineages first separated they shared nearly all morphologic characteristics and differed in very few; it would have taken an expert to distinguish them. Not any more. And when did these striking architectural changes take place? To reconstruct the events that led from the branchings to the various animal body

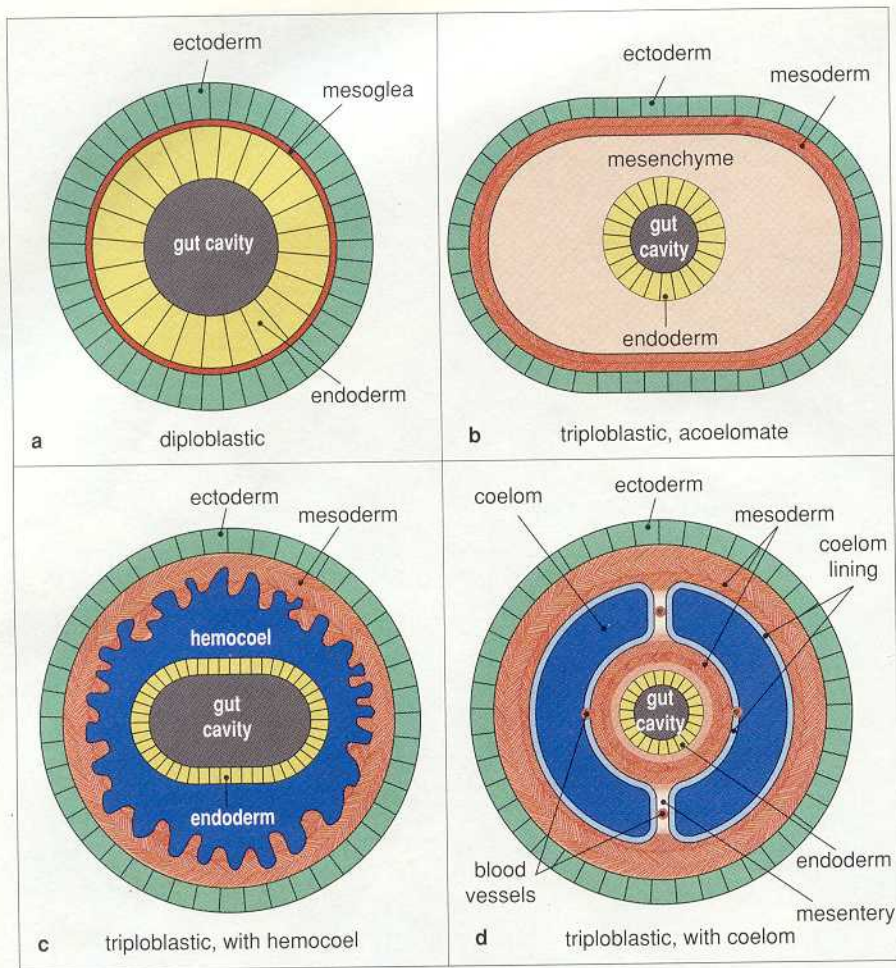


Figure 3. Body cavities of animals become increasingly more complex as one ascends the evolutionary tree. Ctenophora and Cnidaria are diploblastic (a) and have two thin but well-differentiated tissue layers separated by mesoglea, a gelatinous material that protects the body and lines the gut. Flatworms have three primary tissue layers and are triploblastic but are without an inner cavity called a coelom (b). Ectoderm is the outer tissue layer, mesenchyme and mesoderm are the middle tissue layers, and endoderm is the inner layer; mesoderm is the tissue layer that produces most muscles. Flatworms lack a circulatory system, so oxygen must be transported to their inner tissue layer by diffusion, and thus their bodies must remain flat. Animals with the next most complicated body plan have three tissue layers as well as hemocoelic, or blood, spaces between the tissue layers (c). The most complicated body plans have both hemocoelic spaces and coelomic spaces, which develop inside the third or innermost layer (d). In general, animals with only blood spaces are found in lower branches of the tree than are animals with coelomic spaces.

plans we must leave the molecules and turn to the fossil record.

#### Body Plans: A Neoproterozoic Prologue

Molecular data indicate that the metazoa—multicellular animals—arose from single-celled organisms related to choanoflagellates, a group that apparently originated about one billion years ago; the date is not closely constrained. Just when the first animals evolved is also uncertain, but it must have been sometime before the oldest traces of wormlike forms appeared, about 565 million years ago. Morphological and molecular evidence agree that the most primitive of living animal phyla are the

sponges (Phylum Porifera). Sponges have only a few cell types differentiated to perform specialized functions, and they lack the sort of cell-to-cell junctions that form sheets of tissues in higher forms. Fossil sponges have recently been discovered in Neoproterozoic sediments.

The next most advanced phyla are Ctenophora (comb-jellies) and Cnidaria (jellyfish and sea anemones), which have two thin but well-differentiated tissue layers separated by a gelatinous material: a protective one surrounding the body and a digestive one lining the gut. The majority of the late Neoproterozoic soft-bodied fossils most resemble representatives of these two phyla.

Most analyses suggest the next major branch produced a body type with three primary tissue layers, the flatworms (Platyhelminthes), whose inner tissue layer produces muscles and some other organs. However, flatworms do not have a circulatory system, so oxygen must be transported to their inner tissue layer by diffusion, and thus they must be flat in order to keep these tissues near their surface oxygen supplies. Flatworm guts, like those of jellyfish, contain only one opening, so all of the contents enter and exit through the same aperture. Although most molecular and morphologic evidence indicates that flatworms evolved very early in the history of animals, they are small and soft-bodied; consequently no fossil flatworms are definitely identified in the fossil record.

The meandering trails and burrows of the Neoproterozoic were made by organisms capable of displacing sediments to form grooves and tubes, sometimes marked by structures that indicate pulses of creeping or burrowing, and in some cases containing pellets that are interpreted as fecal remains. Most of these are traces that cannot be attributed to sponges, anemones, or even flatworms; some of those animals can disturb sediments, but they do not produce elongate rounded burrows or fecal pellets. To produce such traces requires an organism that is not flat, can propel itself by generating peristaltic waves (waves of contraction and expansion moving along the body or along its ventral surface, as a "foot") and has a complete gut. Thus the fossil record puts a minimum age on an important branchpoint in metazoan evolution: The earliest known animal traces must have been produced by lineages more advanced than flatworms.

The kind of peristaltic locomotion that must have produced the early traces requires a "skeleton" of fluid-filled spaces inside a muscular sheath that can be deformed into waves to displace sediment. Two main kinds of fluid-filled spaces that could act as such hydrostatic skeletons are found within animal bodies: hemocoelic (blood) spaces, which develop *between* the tissue layers mentioned above, and coelomic spaces, which develop *inside* the third or innermost layer. In general, animals with only blood spaces are found in lower branches of the tree than are animals with coelomic spaces.

Flatworms lack both sorts of body spaces, but above them on the animal

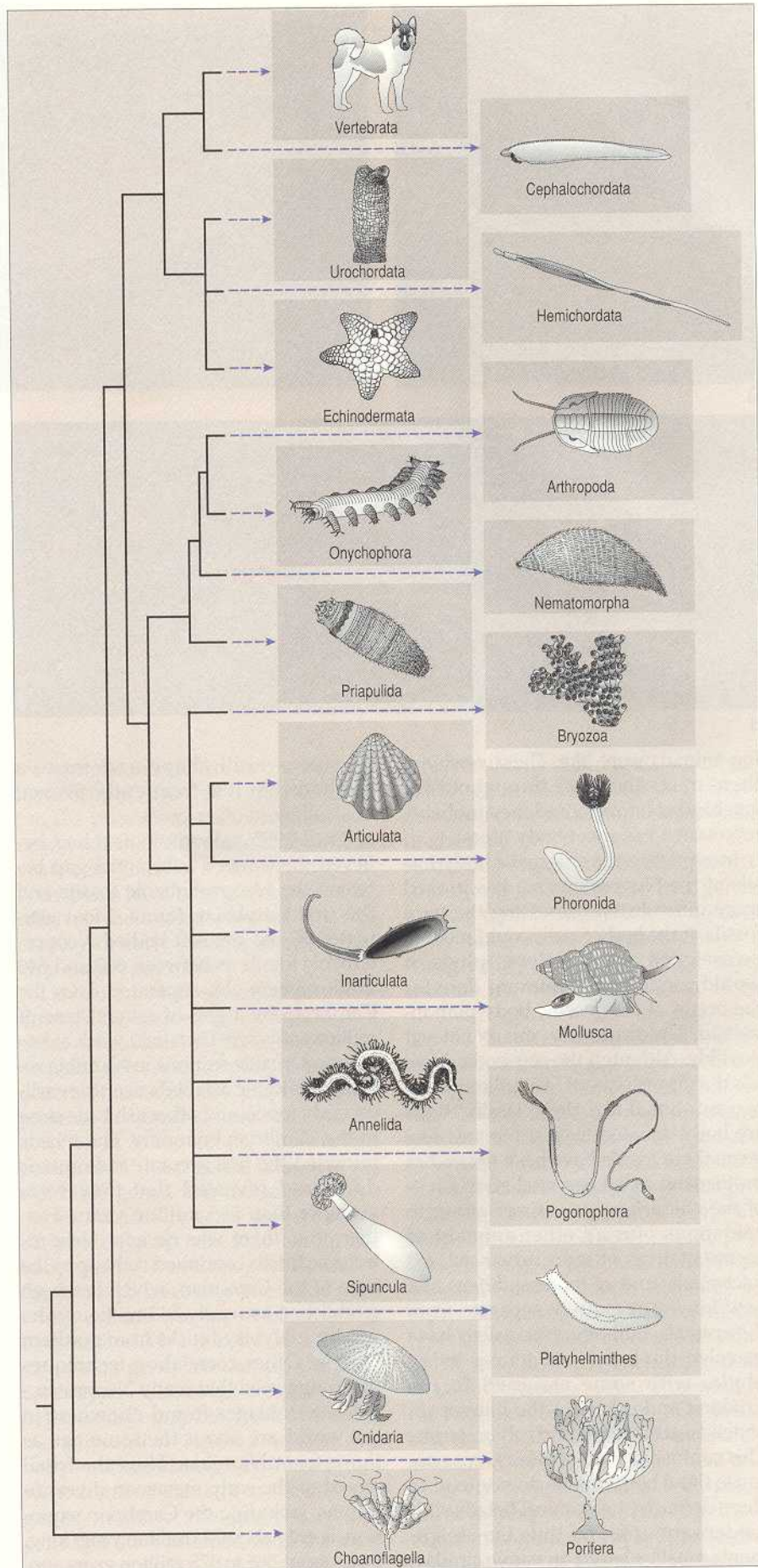
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tree is the most famous branchpoint of all, a division that gave rise to a wealth of more complex animals that have one or both types of body space. One branch, the deuterostomes, includes echinoderms (starfish and sea urchins), chordates (from fish to mammals) and a number of minor groups. The second branch, the protostomes, contains most of the familiar invertebrate animals, including arthropods (crabs and insects), annelids (earthworms), molluscs (snails, clams and squid) and a host of other phyla known mostly to those lucky enough to have had an in-depth course in invertebrate zoology. It is quite likely that most or all of the Neoproterozoic traces were made by organisms with hemocoel-based locomotive systems.

Among living phyla, a simple body plan that could be responsible for some of the traces is that of the phylum Priapulida, which has a complete gut surrounded by a capacious hemocoel that is sheathed in turn by the muscles of the body wall. Priapulids burrow in soupy sediments at the surface of the sea floor. Other traces look as if they were formed by creeping snail-like animals of the phylum Mollusca, although, as snails themselves do not appear until significantly later, the Neoproterozoic traces may have been made by a common ancestor of molluscs and their relatives. Just such a form, known as *Kimberella*, has recently been reconstructed from a large number of body fossils from the White Sea of Russia. This is the first solid indication of what some of the creep-

Figure 4. Multicellular animals arose from single-celled organisms related to choanoflagellates, a group that originated about one billion years ago. Animals probably appeared more than 565 million years ago. The most primitive of living animal phyla are the sponges, forms of which have been found in Neoproterozoic fossils dating back 565 million years. Following the sponges are animals such as comb-jellies (phylum Ctenophora) and jellyfish and sea anemones (phylum Cnidaria), fossils of which date to the late Neoproterozoic period. The next major branch produced the flatworms (phylum Platyhelminthes). After the flatworms came a division that gave rise to a wealth of more complex animals—the split between protostomes and deuterostomes. The protostomes include most of the familiar invertebrates, including crabs and insects (phylum Arthropoda), earthworms (phylum Annelida), and snails, clams and squids (phylum Mollusca), as well as others. Deuterostomes include starfish and sea urchins (phylum Echinodermata), and the group that encompasses fish to mammals (phylum Vertebrata).





a



b



c



d

Figure 5. Simple, architecturally unsophisticated animals of the Ediacaran fauna represent the first phase of the radiation of animals. Some of these animals are known only from their burrows (a) and fossil traces (b). Others, such as *Dickinsonia* (c) and *Kimberella* (d) are known from their body fossils. (Photograph of *Kimberella* courtesy of M. A. Fedonkin and B. M. Waggoner.)

ing animals were like. The diversity of these traces increases throughout the late Neoproterozoic, and they probably represent a variety of body types.

Interpreting the enigmatic body fossils of the Neoproterozoic has proved more difficult than assessing the trace fossils. If the body fossils could reliably be assigned to some living phyla, it would pinpoint a minimum date for the origin of the specific body plan involved. Unfortunately, this is not yet possible. Although the soft-bodied fossils that appear about 565 million years ago are animal-like, their classifications are hotly debated. In just the past few years these fossils have been viewed as protozoans; as lichens; as close relatives of the cnidarians; as a sister group to cnidarians plus all other animals; as representatives of more advanced, extinct phyla; and as representatives of a new kingdom entirely separate from the animals. Still other specialists have parceled the fauna out among living phyla, with some assigned to the Cnidaria and others to the flatworms, annelids, arthropods and echinoderms. This confusing state of affairs arose because these body fossils do not tend to share definitive anatomical details with modern groups, and thus the assignments must be based on vague similar-

ities of overall shape and form, a method that has frequently proved misleading in other cases.

Until 1995 paleontologists had believed there was a substantial gap between the Neoproterozoic fossils and the first Cambrian fauna. Most estimates placed the soft-bodied Neoproterozoic fossils as between 600 and 640 million years old, separated from the Cambrian by a gap of several tens of millions of years. Then field work at late Neoproterozoic sections in Namibia revealed volcanic ash beds near the earliest body fossils and other ash beds close to the Cambrian boundary. These beds provided the first accurate radiometric dates and revealed that they were younger than 565 million years. Furthermore, there was no gap: Neoproterozoic fossils continued right up to the base of the Cambrian, which has been established as nearly 543 million years ago by analyses of rocks from northern Siberia. Other correlation techniques have suggested that many Neoproterozoic assemblages found elsewhere in the world are about the same age as those from Namibia. Thus the fossil record of the early metazoan diversification, including the Cambrian explosion, is only about 40 million years long, from about 565 to 525 million years ago.

### The Cambrian Explosion

Although abrupt geologically, the divergence of the early animal groups was somewhat more drawn out than paleontologists recognized even a decade ago. Recent fieldwork in Siberia and Mongolia has demonstrated that skeletal fossils gradually became more common and diverse in the earliest part of the Cambrian (known as the Manykaian Stage). At the same time, trace fossils increased in diversity and abundance, including the first trace fossils that reflect the presence of animals with limbs. However, it is in rocks of the later Tommotian and Atdabanian stages of the Early Cambrian, between about 530 and 525 million years ago, that fossil assemblages first include most of the basic body plans of living animals. This is the "Cambrian explosion," with the first appearance of mineralized skeletons of such phyla as the Mollusca, Brachiopoda (lamp shells), Arthropoda and Echinodermata. Trace fossils exhibit a dramatically expanded range of animal activities, suggesting that as skeletonized forms diversified, soft-bodied groups expanded as well. Furthermore, soft-bodied phyla, such as Annelida, Onychophora and Priapulida, which do not have mineralized skeletons, also make their appearance, thanks largely to a beautifully preserved soft-bodied fauna from the Late Early Cambrian of Chengjiang, Yunnan Province, China. A number of forms from now-extinct phy-



a



b

Figure 6. Earliest representatives of arthropods include these unusual Cambrian lobopods, members of the phylum Onychophora. Shown here are *Ayshaeia* (a), *Hallucigenia* (b) and *Microdictyon* (c).



c

la occur in these beds. The Middle Cambrian Burgess Shale fauna from British Columbia, Canada preserves many soft-bodied fossils similar to those of the Chengjiang fauna, indicating that these forms were widespread and persisted for many millions of years. These faunas serve to emphasize the spectacular morphologic breadth that was achieved so early in animal history. This fossil record raises many questions as to how new body plans evolve and just how rapidly such novel evolutionary innovations may be produced. Answering these questions requires information from the field of evolutionary developmental biology.

#### Ancient Developmental Systems

One of the most remarkable discoveries of the past few years is that the major elements controlling animal development are quite similar across a wide range of body plans. Most animals start from a single cell, the fertilized egg or zygote. However, during development their cells multiply and differentiate into specialized cell types that make up muscles, nerves, glands and all the other tissues and organs. This is an extraordinary process, given that each and every cell in a developing embryo has exactly the same genetic information in its DNA. Unlike their unicellular ancestors, multicellular animals need a genetic regulatory system to specify different gene activities in the different cell types as development unfolds to produce an adult body plan. Many of the regulatory genes in butterflies, giraffes and squid,

for example, are similar, having been inherited from their last common ancestor, the protostome–deuterostome ancestor, which lived at least half a billion years ago. Thus the striking changes in body plans have been accompanied by relatively modest tinkering with the machinery of early development of that long-extinct precursor.

Developmental regulation proceeds through the sequential activation of a series of regulatory switches that in turn activate networks of other genes. In general, the regulatory genes produce proteins that bind to and influence the activity of other genes. The protein products of these genes then activate still other genes, and the cascade continues. Regulatory genes that are active early in development help set up the body axes by determining which end of the embryo becomes the head and which the tail, which part becomes the back and which the belly. These early expressing genes also set up the basic tissue types. Genes that are active later in the cascade help block out distinctive morphological regions within the body—differentiating, say, a head from an abdomen. Later still in the cascade, genes mediate the growth of appendages such as limbs, until the most refined morphological details have been

achieved. Many different classes of regulatory genes share a common DNA sequence known as the homeobox, which predates the origin of animals.

The best-studied class of homeobox-containing genes are the *Hox* genes, usually found clustered next to each other along animal chromosomes. In complex organisms the *Hox* cluster specifies the developmental fate of individual regions within the body, and usually the genes are activated and expressed in the body in the same order as their position in the cluster. Thus, in arthropods, the first genes in the cluster mediate the expression of the head and associated structures, those in the middle of the cluster control genes that produce legs and wings on appropriate body segments, and so on. In the phylum Nematoda, which lacks limbs or wings, the cluster simply mediates the expression of a series of different cell types along the body (along with other functions). Obviously such sophisticated control systems were not needed in the single-celled ancestors of animals, and thus their evolution is intimately associated with the establishment and initial elaboration of animal body plans.

The number of genes in the *Hox* cluster varies among animal phyla. Sponges, the most primitive of animals, have at least



one *Hox* gene, whereas arthropods have eight. In mammals, the cluster has been repeatedly duplicated to form four clusters, all slightly different, with a total of 38 genes. It looks very much as if the *Hox* clusters become larger with increasing body plan complexity, although this cannot be the entire story. Some primitive forms have clusters unlike the *Hox* cluster of higher forms. Furthermore, mammals and arthropods both display a striking diversity of morphologies within each of their body plans, but this diversity is generated chiefly by genes active after the *Hox*-cluster genes have done their work. Many different body plans can be specified by similar genes early within a cascade, whereas morphological complexity can be achieved by regulatory evolution in many parts of the cascade. What seems clear is that morphological evolution of body plans, such as is documented by Neoproterozoic and Cambrian fossils, involved increases in the complexity of both the body plans and the regulatory systems that specified them. With each

new variation, there is an alteration in the relation between the regulatory genes and the so-called structural genes that actually produce the proteins and eventually the lipids and other building blocks that make up an organism.

Combining molecular views of animal phylogeny with the trace-fossil record helps evolutionary biologists reconstruct the primitive body plans that gave rise to the living phyla. As the important findings of developmental biology lead to a greater understanding of gene regulation, scientists can begin to reconstruct primitive developmental systems and their pattern of evolution. The synthesis of these fields, which is just beginning, will yield a much more complete picture of the early evolution of animal life.

#### Early Evolution of *Hox* Clusters

As a first step towards a developmental history of animal architectures, we can begin to reconstruct the evolution of the *Hox* clusters using information from de-

velopmental biology and knowledge of the relationships between different phyla. Any gene found in both flies and mice, for example, must have evolved prior to the last common ancestor of the two lineages. As each key developmental control gene is discovered, developmental biologists quickly search for its cognate gene in distantly related groups, effectively peering back in time to the ancestors of each lineage.

Six *Hox* genes are shared between mice and flies, indicating that their common ancestor, which lived before the Cambrian explosion, had a *Hox* cluster composed of at least six genes. As living arthropods have eight *Hox* genes, two of them must have originated by duplication after the divergence of the ancestors of arthropods and vertebrates. Today these two newer *Hox* genes mediate the development of segments in the middle of the arthropod body. *Hox* genes mediating the development of the midbody, in addition to other developmental features, were also duplicated within the lineage



Figure 7. Ecological interactions between animals increased during the Early and Middle Cambrian. For some animals, predation became a problem, as it was for *Haplophrentis* (a), which made a meal for the *Ottoia* shown here. Both predator and prey were fossilized together (b). Expanding numbers of predators led to the widespread appearance of protective armor, such as the spines on *Marella* (c), which might have effectively thwarted a predator such as *Jianfangia* (d). (Photograph of *Jianfangia* courtesy of Chip Clark.)

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leading to mammals. Although not all phyla have been studied, and the quality of the data remains variable, *Hox* clusters within phyla that have been well studied are distinctive, produced by unique patterns of gene duplication and loss.

Both mammals and arthropods have segmented body plans, and one might reasonably conclude that their common ancestor might also have been segmented, for each group employs the *Hox* gene array to control segmentation. However, the evolutionary tree suggests that these two groups arose from a nonsegmented ancestor in which *Hox* genes probably helped to specify the production of a series of structures repeated along the body axis, but not of segments, just as they mediate cell differentiation along the axis of nematode worms today. A similar situation is found with the genes that control the development of limbs: Some regulatory genes, such as *distalless* and its relatives, help generate both arthropod and mammal legs, yet both the family tree and the fossil record indicate that the common ancestor of these groups lacked limbs, which evidently arose just before the Cambrian explosion and thus after the groups diverged. Eyes provide still another example: The regulatory gene at the top of the cascade that produces eyes in mice (*Pax-6*) is so similar to that in insects that the genes can be interchanged and still function correctly. Yet insect and mammal eyes are both complicated structures and each quite different. Each eye has clearly evolved independently from a very simple common precursor.

These examples begin to give biologists a picture of how body plans, and the genetic machinery that generates them, actually evolved. As animals emerged, developmental control genes evolved that regulated the architecture of their multicellular, differentiated bodies. The fundamental job of these genes was to mediate the production of various cell types by other genes farther down the cascade of gene expression, and to array the cell types within tissues and organs in the appropriate order. Even as body plans changed and anatomical structures evolved, the basic regulatory genetic system nevertheless remained intact. Doubtless, as body plans became more elaborate and more cell types were required, the gene-regulatory systems were enlarged. Still, it seems that regulatory genetic modules were conserved during evolution and suites of genes already pre-

sent were deployed to generate novel structures. Thus the genes that direct animal development evolve in the same quirky, opportunistic ways as the morphologies that they produce.

Perhaps the relative abruptness with which metazoan body plans were elaborated to produce the Cambrian explosion can be explained by this organizational structure. A cascade of developmental signals, perhaps organized into a complicated hierarchy of gene expression, was able to alter the network of structural gene expressions and interactions, rapidly producing distinctive body plans.

#### *Hox* Genes and Early Body Plans

Although those of us who study evolution can infer a great deal about the body plans of the first animals that left traces on the seafloor, we obviously do not have their actual genes and cannot evaluate their relationships from molecular evidence. We are sure that they were moderately complex forms with three tissue layers, but we have no evidence of their relationship to the many living phyla that came afterwards. For example, we do not know whether the animals that made these early traces are more closely related to vertebrates or arthropods, or include ancestors of both groups. It is also quite possible that these early tracemakers originated well before the last common ancestor of arthropods and vertebrates. We can infer some of the developmental control genes that must have been present in the common ancestor of arthropods and vertebrates, but, as these do not specify particular structures, they do not constrain the morphology of that ancestral form, and so we are not sure whether or not it was like the early trace makers. The data that we do have permit us to frame three possible scenarios for the relative timing of the evolution of the *Hox* genes and of the body plans of animal phyla near the time of the Cambrian explosion.

The first scenario proposes an ancestor common to protostomes and deuterostomes that lived nearly 565 million years ago, before the advent of trace fossils. In this case, the ancestor was not capable of making the sorts of trace fossils found later and must have been either tiny or flat, or both. The presence of at least six *Hox* genes at this early stage implies that *Hox*-cluster sizes and *Hox*-gene duplications are not closely linked to morphological innovations, and in-

deed that some of the genetic evidence may be misleading. The Cambrian explosion, then, must be related to some pervasive environmental change, the evidence for which is still lacking, which permitted or encouraged developmental evolution among many independent lineages. Explanations range from an increase in atmospheric oxygen

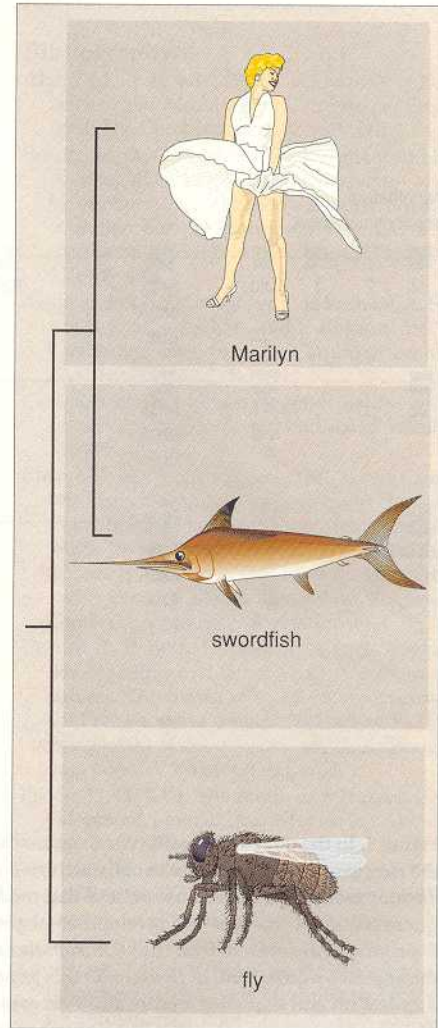


Figure 8. Evolutionary trees show relationships between phyla, but not when and how the body plans diverged. This is because at the moment where lineages split and begin to change independently—represented by the branch points on an evolutionary tree—each branch had precisely the same body plan, and it may have been many millions of years before independent body plans arose. Consider this tree, showing a swordfish, a fly and Marilyn Monroe. Marilyn is more closely related to the swordfish than to the fly, but when the two lineages diverged—over 400 million years ago—they shared almost all of their morphological characteristics and differed in very few. This branching pattern cannot in itself tell us when the characteristics unique to the fly, fish or human lineage actually arose, and for this scientists turn to the fossil record.

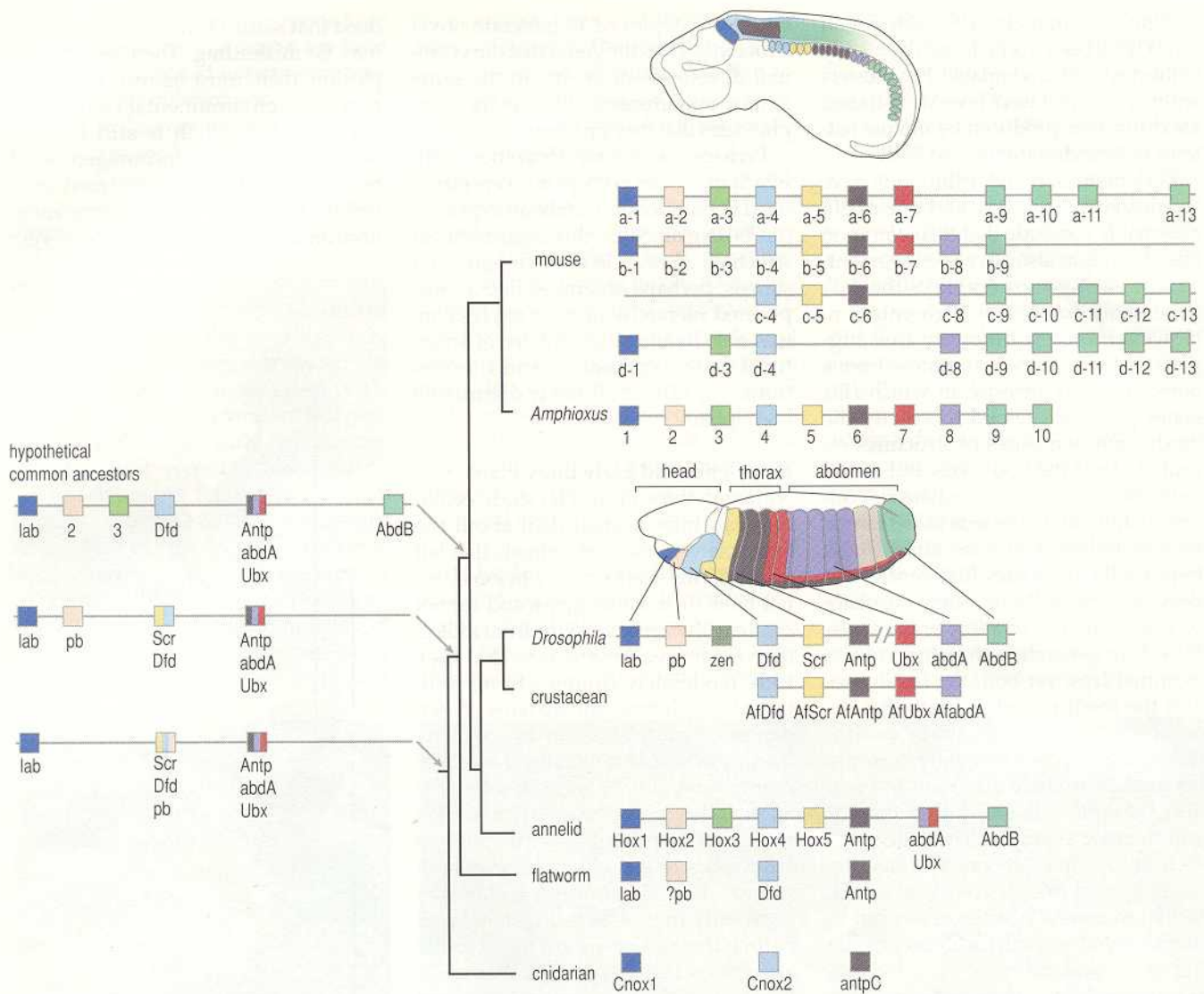


Figure 9. In the developing embryo, an animal's body plan emerges under the guidance of developmental control genes, including a cluster called the *Hox* genes. *Hox* genes are usually activated and expressed in the animal body in the same order as their position in the cluster. Molecular and developmental biologists now believe that modifications in body plans arise from modifications—for example, duplications of genes and subsequent sequence changes—of developmental genes, such as those found in *Hox* clusters. Mapping *Hox* genes on the evolutionary tree suggests that the common ancestor to fruit flies (*Drosophila*) and mice had one gene (*gray, red and violet striped*) that presumably controlled the development of the animal's midsection. In *Drosophila* this gene has become three separate genes (*gray, red and violet*). These genes underwent further expansion, duplication and sequence modifications in evolution, so that in the mouse there are a greater number of related genes to control and direct the formation of an abdominal region that is much more complex than those of more primitive animals. Similar expansions and modifications can be seen in other *Hox* genes as one goes from more primitive to more advanced animals and body plans. (The *Drosophila zen* gene is hatched to indicate that it does not have the same developmental role as genes of the *Hox* cluster.) (Adapted from Carroll 1995.)

content above some critical constraint, to an ecological arms race in which the mutual evolutionary responses of predators and prey drove a host of lineages independently to elaborate skeletons and behavioral repertoires.

Another possibility is that lineage divergence, *Hox*-gene duplications and body-plan formation were spread through the 35-million-year interval between the early traces and the Cambrian explosion. The last ancestor common to vertebrates and arthropods could have lived nearly 565 million years ago or even somewhat later. As in the previous scenario, devel-

opmental controls in this ancestor presumably evolved first, reaching a level of sophistication that permitted the rise of major morphological innovations and culminating in the explosion of body plans during the late Neoproterozoic and early Cambrian. This scenario might also include an environmental trigger to the explosion.

The final scenario assumes a tight linkage between lineage diversification, the duplication of the *Hox* cluster and the formation of the body plans, all taking place rapidly nearly 535 million years ago. In this case the Neopro-

terozoic traces were produced by animals that predated the last ancestor common to mammals and arthropods. This rather extreme view of the Cambrian explosion was held by some paleontologists until fairly recently, and increasingly accurate radiometric dating of fossil-bearing beds has actually shortened the timespan during which the explosive appearance of body plans took place. At the same time however, intensive collecting has produced fossils that tend to smear out the metazoan diversification and to indicate that moderately complex body

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plans were present at classic Neoproterozoic fossil localities.

Choosing between these three hypotheses, which are not mutually exclusive, is difficult at present, although a growing body of evidence leads paleontologists to discount the third scenario. We suspect that the answers will eventually lie within the second scenario, with major innovations appearing neither in the dim past before fossil evidence is available, nor at the very instant that the fossils leap to our attention, but rather at various times within the relatively brief late Neoproterozoic interval now under such heavy study. By extending the perspective beyond the *Hox* cluster to the myriad of other regulatory genes, biologists can begin to reconstruct the regulatory architecture at other critical branch-points. For example, the same set of genes is responsible for head formation in both arthropods and vertebrates, but it is unclear what the head of the ancestor common to protostomes and deuterostomes was like. Similarly, the heart and blood-vascular system in both lineages are also controlled by a set of conserved regulatory genes, but the role of these genes in the ancestor of protostomes and deuterostomes remains unknown.

These uncertainties culminate in the two very different visions of the ancestor common to protostomes and deuterostomes. It is possible to visualize this ancestor as the simplest animal permitted by this sort of molecular evidence, assuming the conserved regulatory genes are relegated to general functions but not to specific structures, even those that are widespread in the body plans of their descendants. In this event the protostome-deuterostome ancestor was a simple worm, lacking segmentation, with minimal differentiation from head to tail and from back to belly and no blood-vascular system. At the other extreme is a much more complex protostome-deuterostome ancestor, with features associated with similar control genes in living descendants, including a well-developed head, nervous system and circulatory system and perhaps even limbs.

The differences between these two models are great, and the course of body-plan evolution is likely to have involved a mosaic of changes intermediate between these two extremes. The coming decade is sure to bring a much deeper understanding of the evolutionary interplay between developmental control genes and the morphologies they help to construct. A partnership of paleontology,

developmental biology and molecular systematics has enormous potential to reveal the evolution of the fundamental body plans that characterize all animals.

### The Next Questions about Body Plans

Clearly many difficult questions remain about the early radiation of animals. Why did so many unusual morphologies appear when they did, and not earlier or later? The trigger of the Cambrian explosion is still uncertain, although ideas abound. If the evolutionary trees are right and the fossil record is not deceptive, then many different lineages must have acquired complex anatomies and hard parts at about the same time. Whether the burst was the result of an increase in oxygen, an ecological arms race or something else, the elaboration of *Hox* complexes may have been necessary, but it was not sufficient, to drive the evolutionary creativity of the Cambrian.

It is also difficult to explain why the innovation declined. Possibly, the ecological barrel become full, so that major novelties could no longer readily gain a foothold. Alternatively, the integration of regulatory controls reached a point where major restructuring of body plans became exceedingly difficult. These debates are ongoing and reflect both the difficulties inherent in resolving such complex problems and the health of a fast-moving, intellectually ambitious set of once-disparate disciplines.

Throughout these debates, the timing of events as recorded in the rocks has been vital in shaping our understanding of the Cambrian explosion. New geological evidence has both spread out the stratigraphic interval over which these new morphologies appear and simultaneously constricted the duration of the radiation. The new dates for the late Neoproterozoic restrict the entire radiation, from the beginning of the radiation with the trace and body fossils of the Ediacaran through the basal Cambrian explosion of the first good skeletal fossils and the explosion of trace fossils, to a mere 40 million years. This is the most extraordinary pace of morphologic innovation yet recognized in the fossil record, and there are strong suggestions that the origin of the regulatory controls that underpin animal development played an important role in these events. Clearly we have much to learn about the behavior of developmental-control genes during morphologic evolution, but just as clearly, there is potential in this partnership of paleontology, developmental biology and

molecular systematics for profound advances in our understanding of the origin and diversification of body plans.

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