13 The Small Picture Approach to the Big Picture: Using DNA Sequences to Investigate the Diversification of Animal Body Plans

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The Adaptive Radiation of the Metazoans

The Metazoa (animal kingdom) is divided into approximately three dozen phyla (figure 13.1). The first undisputed fossils of around half of the animal phyla appear in the Cambrian, the geological period that runs from around 543 million years ago (Myr) to 488 Myr. At least a third of animal phyla have no fossil record to speak of (Valentine 2004), but we can infer from phylogenetic relationships that many of these lineages must be at least Cambrian in age. On the basis of this fossil evidence, it has been suggested that all of the major kinds of animals were generated in a period of around 10 to 15 million years (e.g., Carroll 2005; Levinton 2001; Valentine 2004). This inferred explosive radiation of animals in the Cambrian has been considered the signature of a phenomenal rise in diversity and complexity of animal life, and creating more complex ecosystems (e.g., Bambach, Bush, and Erwin 2007).

An earlier Precambrian fauna, known as the ediacarans, were relatively simple, soft-bodied creatures (Xiao and Laflamme 2008). With the possible exception of *Kimberella*, which has been interpreted as having a muscular foot and scraping radula like a mollusc (Fedonkin and Waggoner 1997), none of the ediacarans show clear evidence of appendages specialized for locomotion, and there are relatively few complex trace fossils (marks made in the sediment) that would bear witness to directed bilaterian movement in the Precambrian period (Jensen, Droser, and Gehling 2005). Due to the general lack of evidence of mouths, claws, teeth, eyes, or other equipment associated with hunting or foraging, the ecology of ediacaran communities has also been regarded as being fairly simple (Bambach et al. 2007; Xiao and Laflamme 2008). By contrast, the Cambrian fauna provides abundant evidence of animals with sense organs, appendages for locomotion and feeding, and defensive structures. Unlike the floor-bound ediacarans, some Cambrian animals moved down into the sediment by active burrowing, and some moved up into the water column by directed swimming. For the first time, there is clear evidence of specialized, mobile animal predators.
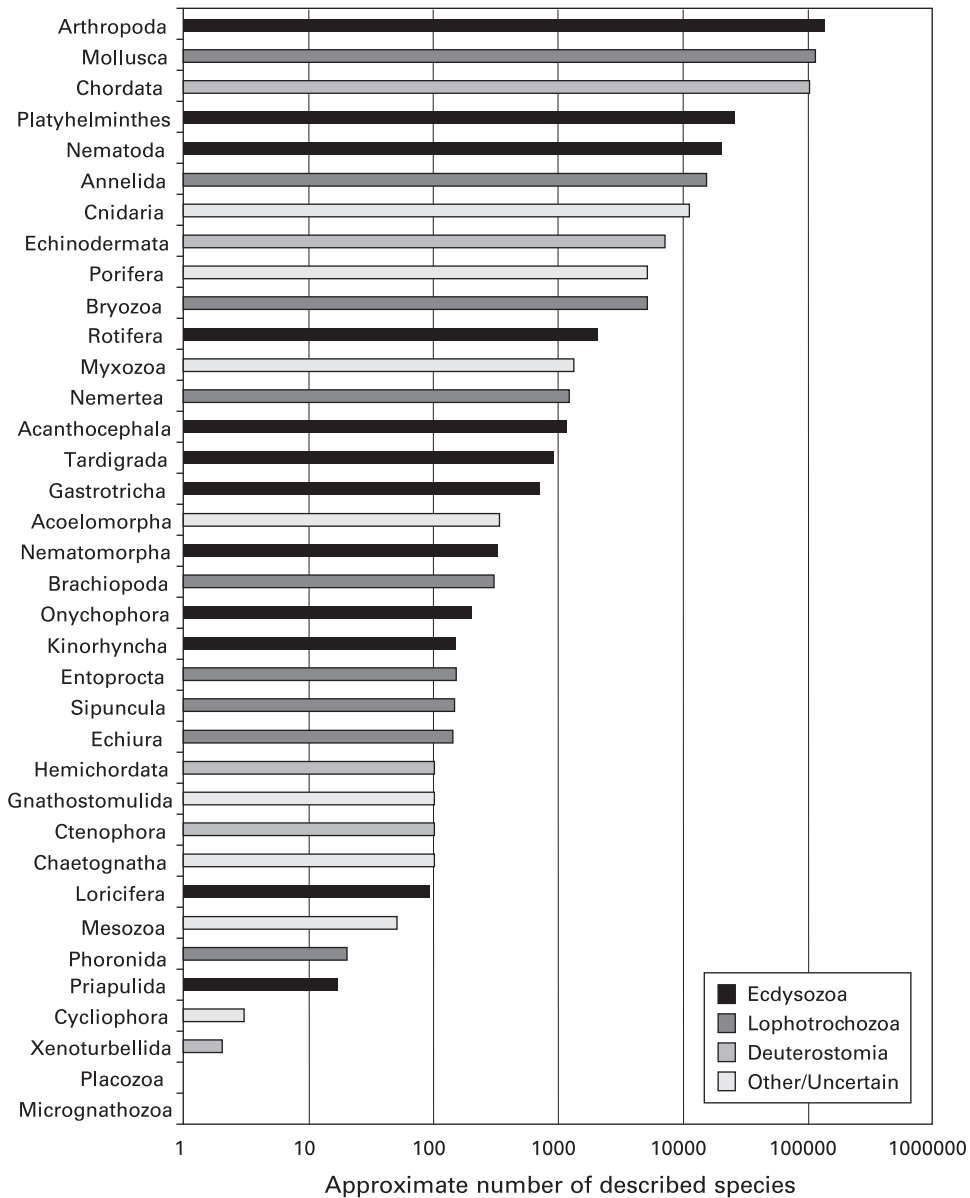
Figure 13.1
Approximate number of described species per metazoan phylum. There is no central database for described animal species, so these figures are open to debate. In most cases, it is a fair assumption that the number of described species will underestimate the actual diversity of the phylum, and in some cases only a relatively small proportion of the species thought to exist have been described. In addition, there is no definitive list of animal phyla, because there is disagreement over which taxa should be given phyletic status. Some taxa listed here are contained within other phyla in some systematic treatments (e.g., Echiura within Annelida). Some single species or genera have been elevated to phylum level on the basis of morphology (Micrognathozoa) or phylogeny (Xenoturbellida). Here, phyla are labeled according to superphyletic groupings (see figure 13.2). Assignment to superphyla is controversial in some cases. For example, Myxozoa (an important group of parasites of fish and other animals) have variously been classified as protists, cnidarians, or as a separate bilaterian phylum.

The metazoan radiation itself is not surprising. The great diversity of animals today must have been ultimately derived from a simple common ancestor, so we know the metazoans made the transition from blobs to bugs at some point. Adaptive radiations are common throughout evolutionary history, where a single ancestral lineage diversifies rapidly to produce a wide range of ecologically specialized descendents. We see evidence of rapid adaptive radiations on many oceanic islands, where a colonizing lineage radiates to fill a variety of ecological niches. For example, in as little as 10 million years, a single ancestral lineage of Hawaiian honeycreepers has radiated into more than fifty separate species, with a wide variety of colors and shapes, which occupy a range of niches including insectivores, seed-eaters, frugivores, nectarivores, and snail-eaters (Grant 2001; Lovette, Bermingham, and Ricklefs 2002). What is remarkable about the Cambrian radiation of metazoans is its apparent suddenness and uniqueness: It seems that more fundamental evolutionary change in animal complexity and diversity occurred in this relatively short period than in any equivalent time period before or since the Cambrian. In the time that it took Hawaiian honeycreepers to change the shape of their beaks or the color of their plumage, whole new body plans appeared in the fossil record.

Many hypotheses have been put forward to explain the sudden burst of animal diversity and disparity in the Cambrian. Some suggest an environmental trigger for the diversification: For example, animal evolution may have been constrained in earlier periods by a lack of environmental oxygen, so the rise in oxygen could have simultaneously released all metazoan lineages to develop large size and complex morphology (see Knoll, this volume). Others suggest that the driver of change was a kind of arms race in morphological or ecological complexity: For example, as some lineages became mobile predators, others had to develop defensive structures (see Bengston 2002). In this chapter, I want to consider only one particular kind of explanation for the Cambrian radiation, based on an "internal" trigger for the explosive evolution of diversity and disparity: that major innovations in body plan were generated from relatively few genetic changes of large phenotypic effect, particularly in the function of key conserved developmental genes such as those in the Hox cluster.

It is important to note that the various hypotheses for the cause of the metazoan radiation are not mutually exclusive; they may have all operated in concert to generate an extraordinary period of evolutionary change. However, here I concentrate only on a critical examination of the developmental genetic hypothesis of the origin and maintenance of body plans, which has garnered enthusiastic support in the last decade or two, because it has important implications for understanding macroevolutionary patterns.

Microevolution vs. Macroevolution: How Do Differences in Body Plan Arise?

The debate over the origin and evolution of animal body plans has a key role to play in evaluating claims about macroevolution. Broadly speaking, "microevolution" is used to describe the change in representation of heritable variants in a population over generations,

where new variants enter the population by mutation or migration, then rise or fall in frequency by selection and drift until one variant replaces all others. "Macroevolution" represents those changes that are not observable at the population level, but are detected by comparing different evolutionary lineages: Examples include the origins of major evolutionary adaptations, and differences in diversification rate. Darwin's genius was to connect the two: He explained macroevolution (differences between lineages, both past and present) using microevolutionary mechanisms (the observable change in frequency of variants in contemporary populations). He did this by demonstrating that variation is ubiquitous in populations; that there was a continuum of differences between populations, races, varieties, and species; and, most famously, by providing a plausible explanation of how the variation in populations could lead to the differences between lineages by the gradual accumulation of small changes over very long periods of time.

Darwin's argument rested on two related principles: uniformitarianism and gradualism. Darwin adapted Sir Charles Lyell's uniformitarian approach to geology, in which "the present is the key to the past" (Lyell 1830). The massive changes of the past, like building mountains or changing courses of rivers, could be explained by the continuous action over long time periods of forces we can witness today, such as uplift and erosion. This was Darwin's strategy for linking microevolution to macroevolution: The changes we can observe in populations today are sufficient, given immense time periods, to generate different lineages (Darwin 1859). But unlike geology, where occasional catastrophes can create sudden large changes, species-level differences do not tend to arise in contemporary populations. So to make the uniformitarian argument plausible, Darwin had to rely strongly on an argument from gradualism, such that large-scale changes are achieved by the accumulation of many small differences over long time periods:

As natural selection acts solely by accumulating slight, successive, favourable variations, it can produce no great or sudden modifications; it can act only by very short and slow steps. Hence the canon of 'Natura non facit saltum' . . . We can plainly see why nature is prodigal in variety, though niggard in innovation. (Darwin 1859, 489)

Darwin's insistence that macroevolution could be explained in terms of microevolution was his most controversial claim. Even die-hard supporters of Darwin, such as Thomas Henry Huxley and Alfred Russel Wallace, did not fully support this claim, suggesting that there may be some evolutionary changes that did not fit this framework. Nonetheless, this key aspect of Darwin's theory of evolution became the foundation of the neo-Darwinian synthesis, which bolstered Darwin's theory by basing it on population genetics (both theory and observation), strengthened by observations of natural selection in wild and experimental populations, and evidence of gradual change from paleontology. Thus, mainstream opinion in evolutionary biology has been that lineage differences can be explained in terms of population genetic processes: All evolution is microevolution, and macroevolution is a level of observation, rather than a separate process.

But there have always been challenges to this view. Two major arguments have been made against the "macroevolution equals microevolution plus time" hypothesis. First, the principle of gradualism has been challenged on the basis that the fossil record suggests, in some cases, discontinuities in the origin of lineage differences, rather than a continuous accumulation of small changes. Second, the principle of uniformitarianism has been challenged on the grounds that large changes to phenotype, rarely if ever witnessed in contemporary populations, may occasionally generate lineage-level changes, particularly in periods when lineages are somehow more responsive to such large changes. Both of these challenges are most evident in debates about the Cambrian explosion, where some researchers have explained the disjunction in forms in the animal fossil record in terms of large changes to phenotype generated through changes to developmental gene expression, which no longer arise in modern populations due to developmental and genetic canalization.

Recent advances in the understanding of the way changes in the genome are translated to different phenotypes through the process of development have fueled this challenge to neo-Darwinian gradualism. Studies of genes that play a fundamental role in early embryonic patterning have revealed surprising and exciting results. In particular, a common "toolkit" of developmental genes has been found in a wide range of metazoans. Sometimes these genes perform similar functions in very different organisms, such as the *Pax6* gene, which initiates eye formation in species as divergent as flies, humans, and flatworms. In other instances, the same genes perform different tasks, or are expressed in different places or times (see Garcia-Fernandez 2005). In some cases, changes in the expression patterns of these genes correspond with key differences in body plan, such as segment identity in arthropods with different numbers and types of appendages (Tour and McGinnis 2005). The role played by these genes in determining the development of body plan in animal embryos has led to suggestions that these genes were instrumental in the evolution of different body plans. This claim has given rise to the hypothesis that the evolution of the "toolkit" itself, or the changing patterns of usage of toolkit genes, triggered the Cambrian explosion (e.g., Garcia-Fernandez 2005; Gellon and McGinnis 1998). In particular, it has been suggested that changes to developmental genes offer a way of generating very different phenotypes from relatively few changes to genotype.

The role of developmental genes in the evolution of animal body plans has been interpreted in a number of ways that are relevant to the issue of whether macroevolution is wholly explained by microevolutionary mechanisms. In some discussions, there is an implicit or explicit assumption that evolutionary changes in development follow the same microevolutionary patterns as any other trait (e.g., Budd 1999; Carroll 2005). But in other cases, the claim is made that consideration of the influence of key developmental genes suggests that the evolution of major body plan changes occurred by a discrete macroevolutionary process, not by the microevolutionary processes that we can witness in action today (e.g. Arthur 2000; Baguna and Garcia-Fernandez 2003; Budd 2006; Carroll 2000). If it is

true that the Cambrian explosion is an example of a discrete evolutionary event that marks a jump to a new level of complexity, then processes we observe in contemporary organisms and ecosystems may not give a full account of macroevolution (Erwin 2004). For example, Butterfield (2007) interprets the Cambrian explosion as a sign that macroevolution before the Cambrian was of a fundamentally different type than that which occurred after the Cambrian, and therefore concludes that a uniformitarian approach to studying macroevolution is not appropriate. More generally, the emerging view of the link between developmental genes and body plan evolution has led to the idea that the neo-Darwinian synthesis has been critically incomplete without information on development or body plan change (e.g., Carroll 2000; Pigliucci 2007; Telford and Budd 2003). These claims are important because if they are true, we have been doing things wrong for quite a while. It is therefore important to test the hypothesis that past metazoan evolution was of a different type from currently observable microevolutionary processes, by considering the available evidence.

One way to explore the idea that the Cambrian explosion was caused by large changes to body plan, particularly through the action of developmental genes, is to ask why the Cambrian explosion is unique in animal evolution. The fossil record does not record any other periods of such radical change in form and complexity of so many animal lineages simultaneously. Why do body plan differences all seem to originate in this particular evolutionary period, and why have none arisen since? If major innovations in body plan can be generated from few genetic changes in key genes, then why do these changes not occur throughout animal history, generating new phylum-level differences after the Cambrian explosion? Should we not see such variants arising in contemporary populations? One common explanation is that animal evolution in the Cambrian period was in some way permissive, and that body plan variants either could not be generated (due to genetic canalization) or could not persist (due to competition) at later stages (e.g., Davidson and Erwin 2006; Erwin 2007; Levinton 2001). If this was true, then we should expect that once body plans were formed, they were unable to give rise to new body plans. This process may be analogous to the developmental canalization of stem cells that, once committed to becoming a specialized cell line like muscle, heart tissue, or bone marrow, can no longer return to the pluripotent state nor give rise to a fundamentally different kind of cell.

If we wish to know whether animal evolution in the Cambrian was by a special mechanism that was not able to operate in later ages, then it would be helpful to know how body plan variation is generated, and whether the capacity for body plan change has been limited or absent since the Cambrian. There are several ways of approaching this issue, and we could not hope to form a complete picture of body plan evolution without information from paleontology, population genetics, development, physiology, and so on. But here I wish to focus on just one line of evidence that has proved valuable in unraveling metazoan evolution: molecular phylogenetics (using DNA or protein sequences to uncover the evolutionary relationships between contemporary species).

Much of the focus on the use of molecular phylogenies to understand the Cambrian explosion has been on molecular dating. Most estimates of divergence dates made from molecular data point to a substantial Precambrian history of the major metazoan lineages. These molecular dates are increasingly being interpreted as being compatible with the fossil record of ediacarans and Precambrian metazoan embryos (e.g., Budd 2008; Peterson et al. 2008). However, the large degree of variation between published estimates have made molecular dates difficult to interpret (Bromham 2006): Molecular dates have been presented as being both compatible (e.g., Aris-Brosou and Yang 2003) and incompatible (e.g., Blair and Hedges 2005) with an explosive radiation of animal phyla in the early Cambrian. Any interpretation of molecular date estimates must be done with a weather eye to the potential for imprecision and error in molecular estimates, and the results must be considered in light of evidence from all other lines of inquiry (Bromham 2006; Wray 2001).

Less controversially, molecular phylogenies provide an alternative record of the relationships between metazoan lineages, independent of traditional systematics based on morphological and developmental characters. These molecular phylogenies have an important role to play in testing ideas about body plan evolution. Molecular phylogenies have dramatically reshaped ideas about animal evolution. In particular, molecular phylogenetic analyses have split the animal kingdom into four main groups (figure 13.2). The first group, the diploblasts, contains the oldest extant phyla of the animal kingdom, Porifera (sponges) and Cnidaria (jellyfish, corals, etc). The Cambrian explosion is generally considered to represent the earliest diversification of the remaining phyla, collectively referred to as the Bilateria. Molecular phylogenies have been used to group the bilaterian phyla into three superphyla: the Lophotrochozoa (annelids and molluscs and their kin), Ecdysozoa (arthropods, nematodes, and relatives) and Deuterostomia (echinoderms, chordates, and friends). Each of these superphyla contains a diversity of forms and ways of life.

In addition to revealing novel superphyletic groupings in the animal tree, molecular data has also revolutionized the systematics of the "minor phyla": types of animals that are recognized as being representatives of ancient lineages, yet whose modern members are typically neither diverse nor disparate. Many of these minor phyla consist of, to be blunt, fairly unexciting little marine worms. In fact, a good proportion of metazoan phyla consist of dull little worms of one kind or another, even if explanations of the Cambrian Explosion tend to focus on the more charismatic body plans. Molecular phylogenetic analyses have been crucial in reconstructing the origins of the minor phyla and their relationships to the sexier phyla. To quote Levinton (2001, 465):

Until the advent of molecular sequencing techniques, it was often difficult to establish relationships among apparently distantly related groups; this falsely highlights the multiple weirdo-evolutionary lawn hypothesis. No set of groups has been more victimized by this shortcoming than the "wormy" groups.
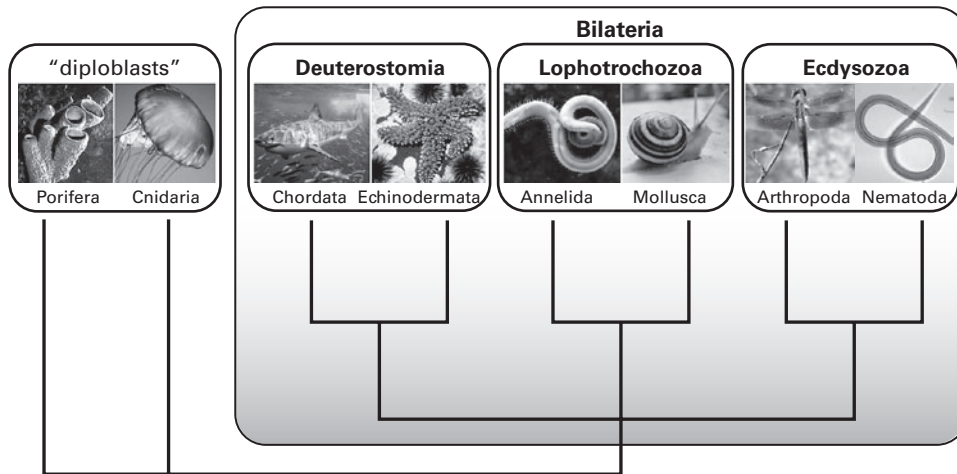
Figure 13.2
The relationships between some of the most species-rich metazoan phyla. Molecular phylogenies have caused the animal kingdom (Metazoa) to be divided into four superphyletic groups. The relationships between the basal groups, including Porifera (sponges) and Cnidaria (including jellyfish and corals), is uncertain (for example, there has been some suggestion that Porifera is paraphyletic and Cnidaria is descended from the bilaterian lineage). The bilaterian phyla (not all of which are bilaterally symmetrical) are divided into three superphyla. The Deuterostomia includes the chordates, echinoderms, and a number of minor phyla such as Hemichordata. The Lophotrochozoa are named for the lophophore (a tubelike feeding appendage found in some of the phyla, such as bryozoans, brachiopods, and phoronidans) and the trochophore type of larvae. Lophotrochozoan phyla, most of which show evidence of spiral cleavage in early embryological cell divisions, include annelids, molluscs, sipunculids (peanut worms), echiurans (spoon worms), pogonophorans (tube worms), and nemerteans (ribbon worms). The Ecdyzosozoa are named for the habit of molting their outer cuticle (a process referred to as ecdysis). The major ecdysozoan phyla are the arthropods and nematodes, but an array of other phyla are also part of this group, such as tardigrades, onycophorans, and rotifers.

The Evolutionary Lability of Body Plans

Phylogenies that reveal the evolutionary relationships between major animal groups are essential for placing both body plans and developmental genes in an evolutionary framework, to allow prediction of ancestral states, reconstruction of patterns of character evolution, and establishment of homology of traits (e.g., Baguna and Garcia-Fernandez 2003; Fortey, Briggs, and Wills 1996; Jenner 2000; Telford and Budd 2003). Molecular phylogenies play a particularly useful role because they provide a means of avoiding the circularity of inferring phylogeny from body plan characters, then using those same phylogenies to infer patterns of body plan evolution (see Jenner 2003). However, molecular phylogenies are not without error, as any comparison of published phylogenies of metazoan phyla will attest. Therefore, the use of molecular phylogenies in testing ideas about body plan evolution must be done within a statistical framework that assesses the robustness of the conclusions (e.g., Bromham and Degnan 1999). Inclusion of minor phyla is essential to

completing our picture of metazoan evolution, as these minor phyla often provide the intermediates that make the "unbridgeable gaps" between the major phyla look less severe, and help to reconstruct the order of acquisition of key body plan characteristics.

In order to illustrate how relatively modest systematic or comparative case studies can shed light on the big picture of animal evolution, I will present some cases studies of body plan evolution. I will focus specifically on the question of the fixity of animal body plans, rather than their origins, since this seems the most tractable part of the mystery to explore. The case studies presented here are not necessarily the most fascinating or conclusive case studies, they just happen to be the ones I have a passing familiarity with because members of my research group have worked on these taxa. No doubt someone else would choose a different set of taxa, and different body plan characteristics. As it happens, we will consider some of the less lovable metazoans: peanut worms, acorn worms, and cockroaches.

Lessons from Acorn Worms: Body Plans Are Not Immutable

Deuterostomia, one of the three bilaterian superphyla, contains the chordates, echinoderms, and a number of minor phyla. The members of the deuterostome superphylum are united by key developmental features, although the adult body plans of the two major deuterostome lineages could hardly be more different. The chordates, including our good selves, have a head-and-tail body plan, with the brain, sense organs, mouth, and breathing apparatus located up one end of the body, a muscularized post-anal tail at the other end, with a hollow dorsal nerve cord running down the back. They get their name from the notochord, a stiffened internal rod that runs from the head to the tail (this is replaced during development by the backbone in vertebrates). Echinoderms, on the other hand, have no head and no tail. Instead, they develop by pentaradial growth, giving rise to the iconic five-pointed symmetry of many echinoderms, such as starfish. Echinoderms do not have a linear nerve cord or a brain, but a ring-shaped nervous system (thus, reminiscent of a zombie movie, some echinoderms are efficient mobile predators with no brains). Echinoderms also have a water-vascular system that is used for both circulation and locomotion.

What would the ancestor of two such wildly different body plans have looked like? It is commonly assumed that the deuterostome ancestor possessed the basic bilaterian characteristics such as a front and back end, but none of the specific body plan characteristics of the modern deuterostome phyla, like a dorsal nerve cord or a water vascular system. Under this scenario, only after the split of the deuterostome stem lineage did the two major branches develop the characteristic body plans we see today: The chordates retained bilateral symmetry and developed a pharynx and dorsal nerve cord, the echinoderms lost their heads and developed pentameral symmetry, radial nervous system and water vascular system. But molecular studies of the minor phyla in the deuterstomes have challenged this picture.

The echinoderms and chordates account for around 95 percent of all deuterostome species. But there are a number of less charismatic lineages in the superphylum, including the

cephalochordates (lancelets), urochordates (sea-squirts), and hemichordates (acorn worms and pterobranchs). As their names suggest, it has generally been considered that these three groups arose from the chordate lineage, based on the shared chordate-like features of the dorsal nerve cord and pharynx (basically a head with gill slits). Whether the urochordates and cephalochordates should be considered phyla in their own right or subphyla of the Chordata is a matter of debate (Cameron, Garey, and Swalla 2000). This debate over phyletic status serves as a healthy reminder that while phyla are typically considered to represent discrete body plans separated by unbridgeable gaps, ongoing debate about whether certain lineages represent phyla or not illustrates that, in at least some cases, the distinction between "body plans" is less obvious. An extreme example is the deuterostome genus, *Xenoturbella*, consisting of two species of marine worms with virtually no distinguishing features (no brain, no central nervous system, no through-gut, no excretory system, not even any gonads), which was elevated to phylum status by phylogenetic studies that suggested it was a basal lineage within the deuterostome superphylum (Bourlat et al. 2006). The debate over phyletic status of deuterostome lineages illustrates that phyla (and thus "body plans") are not always discrete and obvious, but can grade into each other, an observation that could be interpreted as support for a gradualist model of body plan evolution in these lineages.

Hemichordates have traditionally been regarded as an early-branching lineage of chordates on the basis of shared chordate-like features, particularly the dorsal nerve cord and pharynx. But molecular sequence data consistently places hemichordates on the echinoderm lineage of the deuterostomes (figure 13.3). This conclusion has been supported by virtually all molecular phylogenetic analyses, including a large-scale study of 170 nuclear genes (Bourlat et al. 2006) and analysis of whole mitochondrial genomes (Castresana et al. 1998). So DNA sequence data provide statistically significant support for the hemichordates and echinoderms sharing a more recent common ancestor than either does with the chordates, a conclusion supported by some gene expression data (see Bromham and Degnan 1999).

The reader could be forgiven for thinking this is a bewilderingly dull example to include in a book on the rather more exciting topic of major transitions. Who really cares where acorn worms fit in the big scheme of things? But determining the phylogenetic position of hemichordates can tell us a lot about the evolution of the extremely different body plans in the major deuterostome lineages, Chordata and Echinodermata. If both of the major branches of the deuterostomes clade contain phyla with the classic chordate body plan features of a pharynx and dorsal nerve cord, then it implies that these features were present in the common ancestor (or gained independently in two lineages, which seems less likely given the shared developmental patterns; see Bromham and Degnan 1999; Hinman and Degnan 2000). This means that the ancestor of all deuterstome phyla had a chordatelike body plan (figure 13.3). The corollary of this is that the echinoderm lineage began with one body plan, lost those body plan features, and gained an entirely new set. Whenever this
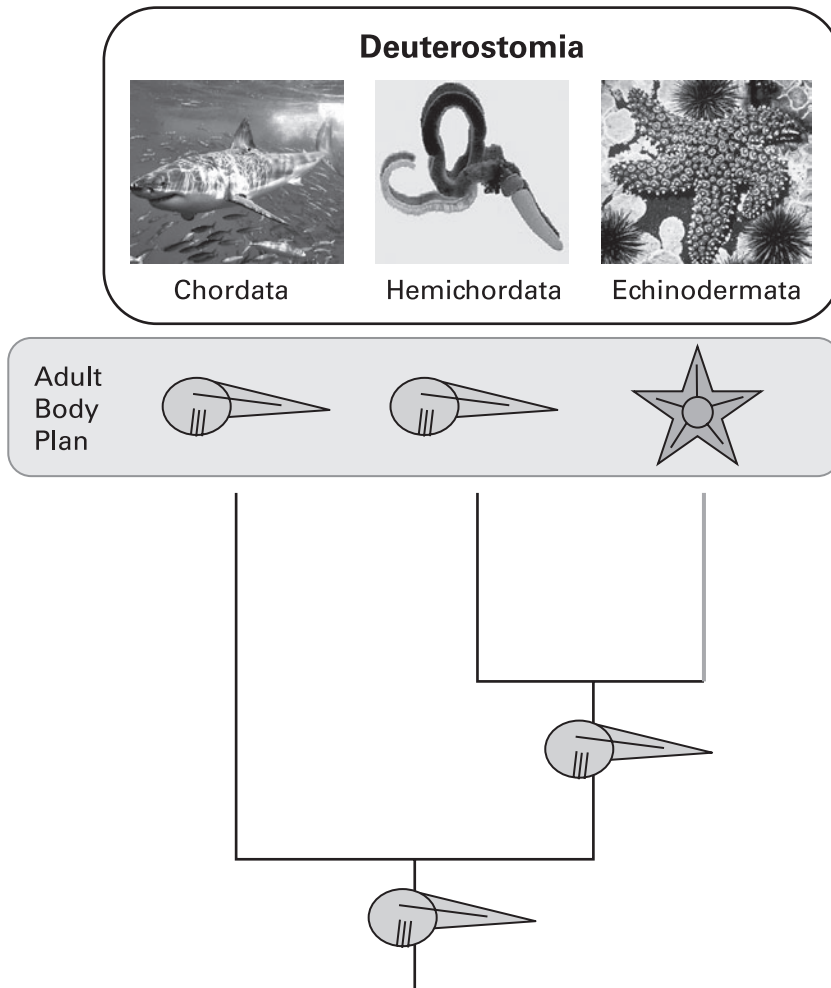
Figure 13.3
Chordates and hemichordates share key elements of their adult body plans, most notably the pharynx (throat with gill slits) and a dorsal nerve cord. So when taxa are grouped on the basis of shared body plan characters, the Chordata and Hemichordata have been considered to be more closely related to each other than either is to the pentamerally symmetrical echinoderms, which have no pharynx or dorsal nerve cord. However, molecular data unambiguously supports a grouping of hemichordates and echinoderms, suggesting that the chordate body plan features might be ancestral for this superphylum.

transition happened, it runs counter to the prevailing notion that, once a body plan has evolved, it would not have the evolutionary flexibility to give rise to an entirely different body plan (e.g., Davidson and Erwin 2006; Levinton 2001). Yet echinoderms seem to have done it in spades. While this is only one example, it does suggest that we cannot make the general claim that body plan characteristics were formed in a discrete event, or by some discontinuous mechanism, then were resistant to further change.

Lessons from Cockroaches: The Developmental Basis of Body Plan Is Labile

The evolution of segmentation provides a useful illustration of how molecular phylogenies can shed new light on the evolution of animal body plans. Segmentation refers to the repetition of structural units, either in the formation of body parts in the embryo or in features of the adult body plan; thus, it is one of the most fundamental aspects of body plan. One of the most obviously segmented phyla is Annelida (earthworms and their kin), where the tubelike body consists of repeated "rings." Chordates (the phylum containing the vertebrates) are less obviously segmented, but skeleton and muscles form in the embryo by the development of segmented blocks of tissues called somites. Segmentation in arthropods has been cited as one of the reasons for their evolutionary success, by providing a flexible way of patterning bodies that leads to diversification of limb morphology. But while these "big three" are often considered the only truly segmented (eusegmented) phyla, there is no clear definition of what should be called segmentation and what shouldn't. Chitons (basal molluscs), for example, have rows of plates down their backs, which some have interpreted as segments. Furthermore, even in the eusegmented taxa, some parts of the body are segmented, and some parts aren't: For example, in chordates, skeleton, muscles and skin form from a series of segments (somites), but other body parts, such as the internal organs, do not.

Some earlier animal taxonomies grouped segmented phyla together on the grounds that sharing such a fundamental body plan character must reveal a shared ancestry. However, molecular phylogenies do not group the three "eusegmented" phyla together. Instead, the eusegmented phyla (chordates, arthropods, and annelids) occur in each of the major lineages of animals (deuterostomes, ecdysozoans, and lophotrochozoans; see figure 13.4). This observation has led to the suggestion that segmentation was a feature of the last common ancestor of all bilaterian phyla, because it is assumed that the presence of this fundamental body plan character in all three major superphyla must reveal common inheritance of an ancestral segmented body plan. Thus segmentation is often cited as one of the features of the urbilaterian, the ancestral bilaterian possessed of all the genetic and developmental equipment necessary to give rise to the radiation of animal phyla (e.g., Balavoine and Adoutte 2003).

But there are fundamental differences in the way that members of these eusegmented lineages build their embryos (see Tautz 2004). A chick (chordate) embryo generates waves
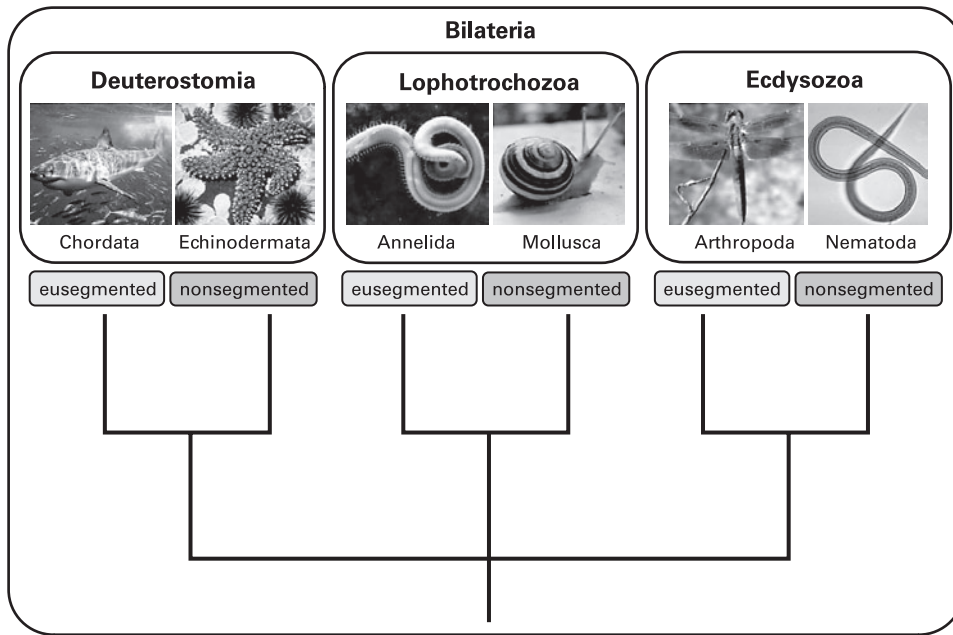
Figure 13.4
Three phyla are widely considered to be "eusegmented," though there are other phyla that show some degree of segmental construction. These eusegmented phyla occur in each of the bilaterian superphyla.

of gene expression, and as each new wave moves along the embryo, it creates an additional segment boundary. In a leech (annelid) embryo, new segments are defined by rounds of cell division. The fruitfly (arthropod) embryo uses an "inelegant" and complex interaction between the expression patterns of gap, pair-rule, and segment polarity genes to divide the embryo into stripes that develop specific segment identities (Akam 1989; Peel, Chipman, and Akam 2005). So at first glance it seems that each of the major bilaterian lineages has a unique way of creating a segmented body.

But filling in the gaps between these developmental exemplar species blurs the boundaries between the ways of forming the basic ground plan of the body. It transpires that the mechanism of segmentation in the fruitfly, the darling of arthropod genetics, is not typical of other arthropods. For example, the spider *Cupiennius salei* employs a mode of segmentation that is more similar to that of vertebrates than flies, in which waves of expression create sequential segments (Stollewerk, Schoppmeier, and Damen 2003). The spider even uses some of the same genetic pathways (e.g., the *Notch-Delta* pathway) to drive this "clock and wave-front" method of segmentation. Studying the pattern of segmentation in other arthropod lineages might shed light on the evolutionary process that changed the underlying mechanism of segmentation in fruitflies (Peel et al. 2005).

So why study cockroaches? The phylogenetic position of the Blattodea (cockroaches) makes them informative for studying the evolution of segmentation, since they sit between the wave-front spiders and the pair-rule flies. Blattodea contains at least 4,500 species, and, despite their bad reputation, many of them are quite charming creatures. I once kept a very attractive little native Australian cockroach as a pet, a teardrop-shaped animal less than a centimeter long, with a segmented carapace, delicate yellow stripes, and cute little cerci (the sensory appendages that stick out of the back end and detect air movements, a distinctive feature of blattodeans). I asked an entomologist what these native cockroaches ate, and he said no one knew, so I fed it lasagne. So not all cockroaches are shudder-inducing nuclear-holocaust-surviving global pests.

It turns out that American cockroaches (*Periplaneta americana*), like spiders and millipedes, use the *Notch* pathway to produce segments (Pueyo, Lanfear, and Couso 2008). This suggests that the wavefront method of segmentation is ancestral to the arthropods and insects, but that some insect lineages, including the flour-beetle *Tribolium castanateum* and the fruitfly *Drosophila melanogaster,* then evolved a new developmental pathway to make segmented embryos (figure 13.5). In other words, these lineages have rewired the developmental pathways used to make their segmented bodies, even though the end product looks much the same as in other insects. In fact, different parts of arthropod bodies are segmented by different means: For example, the *Notch* pathway has been coopted into specifying the development of leg segmentation in flies (see Pueyo et al. 2008).

This lability of the genetic architecture underlying segmentation tells us that even this fundamental aspect of body plan has been able to change since the Cambrian explosion. Flies and beetles are post-Cambrian creatures, descendents of the metazoan colonization of the land and sky. The first fossil insects are Devonian (approximately 420 to 360 Myr), winged insects do not appear until the Carboniferous (approximately 360 to 300 Myr), and fossil flies don't appear until the Triassic (approximately 250 to 200 Myr). If the basic developmental processes underlying body plan formation were able to change so dramatically in these lineages long after the Cambrian explosion, it would seem that the genetic architecture underlying body plans was not set during the Cambrian and has been immutable since.

Lessons from Peanut Worms: Body Plan Characters Come and Go

The examples given in the previous sections show that, on the one hand, there is evidence that members of two superphyla, Ecdysozoa and Deuterostomia, share aspects of the developmental basis of body plan formation because of the common use of the *Notch* pathway in determining segmentation in chordates and some arthropods. But, on the other hand, some arthropods have ditched this fundamental aspect of developmental genetics and use an entirely different way of making segments. What can we learn from looking at the third superphylum, the Lophotrochozoa, which contains the eusegmented annelids?
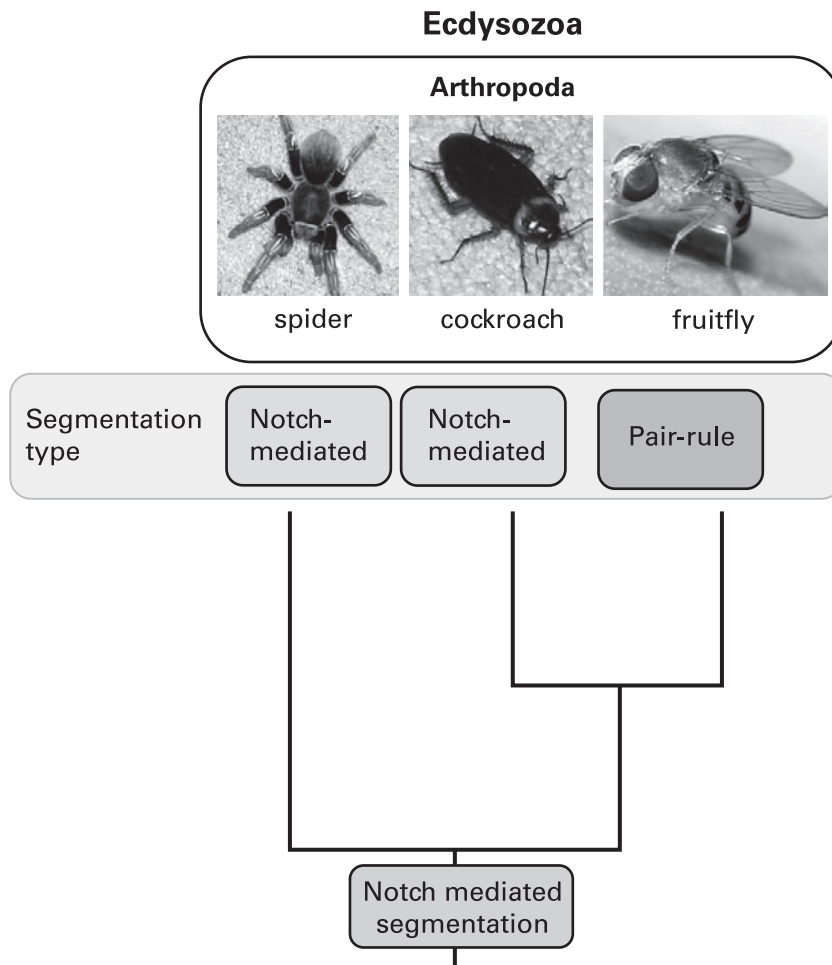
Figure 13.5
Spiders (*Cupiennius salei*) and cockroaches (*Periplaneta americana*) both employ the Notch-signaling pathway to define segments in the growing embryo. This pathway is also used in segmentation in vertebrate embryos, suggesting that either Notch-mediated segmentation is ancestral for two of the bilaterian superphyla, or that the Notch pathway has been independently coopted into defining segments in more than one lineage. Flies and beetles have evolved an entirely different means of defining body segments, independent of the Notch pathway.

Like the deuterostomes, the lophotrochozoans are united by shared developmental traits despite the fact that the major lineages—Mollusca and Annelida—have very different adult body plans. The molluscs are a very diverse phylum, including snails, bivalves (e.g., clams), and cephalopods (squid and octopus). The soft part of the molluscan body (the mantle) supports a muscular foot, a rasping radula (feeding appendage) and, in many taxa, secretes a calcareous shell. Annelids—including marine polychaetes, terrestrial earth-worms, and leeches—all have a generally vermiform (wormy) construction, essentially a tube with a hole at each end, but their key defining feature is segmentation. Annelid bodies are built from a series of "rings," each of which contains a portion of the internal structures such as muscles, nerves, and digestive organs. So one of the major lineages of the Lophotrochozoa (Annelida) is highly segmented, and the other major lineage (Mollusca) is essentially unsegmented. Based on this information alone, it is difficult to predict whether the ancestral lophotrochozoan was segmented or not. But consideration of the minor lophotrochozoan phyla such as Echiura (spoonworms) and Sipuncula (peanut worms) might make the path of evolution of segmentation clearer.

Peanut worms have been described as "astonishingly unprepossessing creatures" (Tudge 2000). Shaped essentially like a shelled peanut with a tail, they generally live in shallow marine sediments. The sipunculid body plan is predominantly taken up with the digestive tract: The tentacle-surrounded mouth at the end of the "tail" leads to the gut, which is twisted around within the "peanut," with simple eyespots, chemoreceptors, muscles, and a brain (if fused pair of cerebral ganglia can be called a brain; Cutler 2001). Developmental studies show that, although sipunculan larvae show serially repeated structures, like muscle rings, these form simultaneously, not by the serial addition of segments (Wanninger et al. 2005). So sipunculan development does not follow the same pattern as annelids, where the segments are added sequentially to the growing embryo. At this point, you may well be tempted to say "well who cares how sipuncula grow their wormy little bodies?" But the importance of this finding becomes evident when it is combined with molecular phylogenetic data.

Although sipunculans have classically been considered to be most closely related to molluscs, particularly on the basis of similarity in the pattern of cells in early embryonic stages (referred to as the "molluscan cross"), molecular phylogenies tend to group sipunculans with the echiurans and annelids (Boore and Staton 2002; Schulze, Cutler, and Giribet 2007; Wanninger et al. 2005). If Sipuncula are more closely related to annelids than they are to molluscs, then there are two ways of explaining the patterns of segmentation in the metazoan tree. One possible explanation is that segmentation is a shared ancestral feature of bilaterians, present in the lophotrochozoan ancestor, then two or three lophotrochozoan phyla all independently lost annelid-style segmentation (Mollusca, Sipuncula, and Echiura; see Bleidorn 2007; Stuck et al. 2007). New results suggesting a role for the *Notch* pathway in annelid segmentation may support this hypothesis (Rivera and Weisblat 2008). The alternative explanation is that the lophotrochozoan ancestor was unsegmented, and

segmentation was independently derived in the annelid lineage (figure 13.6), thus not ho-mologous to segmentation in arthropods and chordates (see discussions in Jenner 2000; Seaver and Kaneshige 2006; Tautz 2004). Either way, these case studies suggest that seg-mentation, a fundamental body plan character, seems to evolve along lineages just as other characteristics do.

What Is Special About Body Plan Characters?

Each of the case studies described in this chapter has a relatively small focus, such as de-termining the phylogenetic position of a fairly unsexy marine worm, so it may seem that they have little to tell us about the big picture of the evolution of complex animals. How-ever, if the results of the case studies are reliable, then they point toward some important conclusions. The hemichordates (acorn worms) suggest that animal body plans were not fixed once they arose; instead, a lineage can begin with one body plan, then evolve an entirely different one. The Sipuncula (peanut worms) tell us that fundamental body plan characters such as segmentation can evolve along lineages, being lost, gained, or remod-eled, just like other aspects of phenotype or development. The cockroaches show that the developmental mechanisms that specify fundamental body plan characters can change dra-matically, so were not all fixed in the early diversification of animal phyla.

Of course, I may have chosen examples where body plan characters are mutable, and ignored cases where they appear to have a discrete origin in the Cambrian. But it is difficult to think of an example where body plan characters do not behave as any other character does, being conserved in some lineages and changed in others. For example, genes under-lying the formation of the anterior-posterior body axis formation are remarkably conserved in function in flies and vertebrates, so these genes have been considered fundamental to the bilaterian body plan (hence the rainbow-colored diagram comparing hox gene expression in fly and mouse embryos now found in every biology textbook). Because phyla may differ in their *Hox* gene complements or patterns of expression, changes in *Hox* number or ex-pression have been proposed as a mechanism for generating different body plans in animal phyla (e.g., Tour and McGinnis 2005). But *Hox* genes were not invented in the Cam-brian explosion: They were present in the metazoan lineage from the beginning (Garcia-Fernandez 2005). Nor are changes in *Hox* gene number, expression patterns, or functions peculiar to the Cambrian explosion, as all of these aspects of *Hox* genes have changed be-fore, during, and after the Cambrian explosion (e.g. Lanfear and Bromham 2008).

Hox genes, though clearly important and fascinating, do not appear to have a pattern of evolution that suggests their creation or modification provided a special basis for the evo-lution of body plans, generating large changes during a particular evolutionary period and then being immune to subsequent change. The same may be said for other develop-mental genes: while some are highly conserved, it is possible to find enough exceptions to show that they are evolutionarily labile, even for fundamental patterns set very early in

Lophotrochozoa

| | Annelida | Sipuncula | Mollusca |

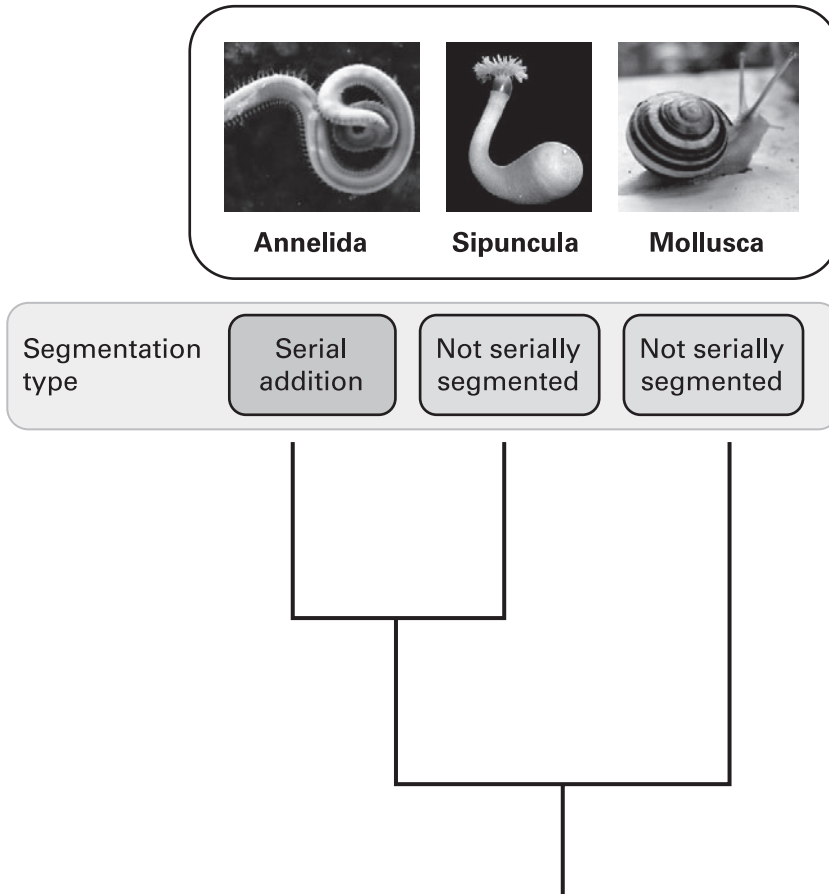| Segmentation type | Serial addition | Not serially segmented | Not serially segmented |

Figure 13.6
The molecular evidence for the phylogenetic placement of the Sipuncula is, like many minor phyla, still equivocal; however, several studies suggest that they are more closely related to annelids than to their traditional allies, molluscs. If true, this suggests that the annelid-style segmentation, formed by the serial addition of segments in the embryo, has been derived within the Lophotrochozoa and is not homologous to eusegmentation in the arthropods and chordates.

embryonic development. For example, one of the key developmental genes involved in dorsoventral patterning in flies is highly conserved among insects, but no homologs of this gene have been found in other arthropods (Copley 2008). This suggests a new gene that has arisen in insects has formed the basis of the adoption of an entirely new way of forming the fundamental axes of the embryo. So, although we cannot fail to be impressed by the conservation of developmental genes between disparate phyla, even very early embryonic developmental programs are able to change dramatically between related animal lineages.

Lessons from Eyes: Body Plans and Developmental Genes Are Normal Evolutionary Traits

The effect of conservation and change on body plan characters can be illustrated by considering the evolution of the wonderfully metazoan invention, the complex eye ("complex" refers to some level of spatial vision, where the direction and intensity of light can be detected, as opposed to simple light sensitivity). The pre-Cambrian ediacarans show no sign of having eyes, but many Cambrian animals have gloriously large and complex eyes (though, of course, many have no obvious eyes at all). The appearance of sight in the Cambrian has even been proposed as the primary cause of the animal radiation (Parker 1998). The most notable feature of metazoan eyes is their remarkable diversity. At first glance, the body plans of the different phyla seem to be characterized by fundamentally different kinds of eyes, such as the single-chambered eyes of vertebrates or the compound eyes of arthropods. But a closer inspection reveals a pattern of evolution like any important trait: a great deal of conservation, yet a surprising frequency of change. For example, compound "flies-eyes" are a key feature of Arthropoda, but arthropod visual systems have been remarkably labile. Not only has the form of the compound eye varied substantially between lineages (see the following discussion of lepidopteran eyes), but some arthropod lineages have independently evolved entirely different forms of eyes, such as the mirror-based eyes of the deep-sea ostracod *Gigantocypris,* or the camera-type (single chamber) eyes in spiders. New types of eyes appear at all levels of the arthropod phylogeny, from species to subphyla. Conversely, compound eyes have evolved independently in a number of other phyla, and can be found in a family of tube worms, some genera of bivalves, and also in some starfish (see Land and Nilsson 2002).

How could such a fundamental and highly engineered aspect of body plan as the complex eye evolve from one kind to another? Land and Nilsson (2002) present an extreme example. Most butterflies and some moths have classic "apposition" compound eyes, where the eye is made of many separate units, each with a lens that forms a separate image. But some moths and butterflies have an entirely different arrangement, the "superposition" compound eye, where the single retina is deep within the eye and multiple lenses work together to form a single erect image. "It is not very easy to see how it is possible to get from one type of eye to the other, without going through an intermediate that doesn't work." Yet this switch between apposition and superposition eyes has happened many

times in the Lepidoptera (butterflies and moths), and also several times in other insect groups. Land and Nilsson describe a possible path between the two types of eyes that involves incremental changes: "[T]o become nocturnal, the powers of the distal and proximal lenses must become more equal, the receptor later moves to a deeper location, and gradually more and more facets contribute to the image. There are no blind intermediaries." Complex eyes that seem discontinuously variable are apparently as able to be altered by evolution as other key aspects of phenotype.

The developmental genetics of eyes shows a similar pattern of conservation and change to that of the morphology. Much excitement has been generated by the demonstration that some of the genes that trigger eye development are conserved between animal phyla, most notably the homeobox-containing *Pax6* gene. The homeobox sequence of the *Pax6* gene is sufficiently conserved between taxa that the sequence from one species can trigger eye formation in a very distantly related species. For example, the *Pax6* sequence of a mouse can cause the formation of eye tissue in flies. The *Pax6* transfer experiments produced some of the most exiting scientific images of the past century, with unfortunate flies with ectopic (out-of-place) eyes on their limbs, antennae, wings, foreheads, and wherever else *Pax6* was expressed (Halder, Callearts, and Gehring 1995).

But *Pax6* is not a simple "master switch" for eye formation (Wilkins 2002). A number of other developmental genes are required to generate functioning eyes; there are at least half a dozen genes in *Drosophila* that can trigger ectopic eye formation, and, in both flies and vertebrates, part of the eye can still develop even when *Pax6* is knocked out (Pichaud and Desplan 2002). Interestingly, while the expression of *Pax6* may promote eye development, in some cases the presence of an eye can promote *Pax6* expression: *Pax6* expression can be induced in eyeless cavefish by transplanting a lens from a related species with a functional eye (Yamamoto and Jeffrey 2000).

The conservation of the *Pax6* gene across phyla is striking, but not unusual. The *Pax* gene family plays many important roles in nervous system development and organogenesis, so it is not surprising that these genes tend to be well conserved. But it is only the 60-amino-acid active site that is conserved between phyla; the rest of the gene sequence has acquired so many changes that it has lost any recognizable similarity (Morgan 2004). Many other genes with important roles in metabolism, physiology, and development show much greater levels of sequence conservation than *Pax6*, otherwise we would not be able to use DNA sequence data to uncover metazoan relationships. For example, there is a thirteen-amino-acid sequence in one of the active sites of DNA polymerase that has been stable for billions of years, such that it is virtually identical in a wide range of bacteria and similar in most other prokaryotes and eukaryotes (Bromham 2000; Patel and Loeb 2000). And although the transfer of *Pax6* between phyla is mightily impressive, the ability to move genes between distantly related species and have the genes function normally is not confined to developmental genes, as can be noted from frequent horizontal gene transfers, both natural and artificial. Genetic engineering would be a nonstarter if this were not so.

Nonetheless, the strikingly similar role of *Pax6* in eye development in many disparate metazoans has been taken as evidence that this gene is part of a developmental toolkit that evolved in the bilaterian stem lineage that enabled the evolution of complex eyes. But the invention of *Pax6* was neither necessary nor sufficient for the evolution of complex eyes in metazoans. Cnidarians have *Pax*-like genes that appear to be related to the *Pax* genes in bilateria. Indeed, two different *Pax* genes (*paxB* and *paxC*) from the coral *Acrospora* can cause the formation of ectopic eyes in *Drosophila* (despite the fact that these genes do not, of course, trigger eye formation in *Acrospora* itself; Miller et al. 2000). Conversely, the cnidarian hydromedusa produces a complex lens eye without the involvement of its *paxB* and *paxC* genes (Sun et al. 2001). If cnidarians have *Pax* genes that can trigger eye formation, but they can develop complex eyes without them, then this suggests the acquisition of a bilaterian developmental toolkit was not a prerequisite for the formation of complex eyes. Furthermore, post-explosion metazoans that have inherited the *Pax6* gene can find alternative ways of directing eye formation; for example, the development of adult eyes in the polychaete *Platynereis dumerilii* (Arendt et al. 2002) and eye regeneration in planarians (Pineda et al. 2002) are apparently *Pax6* independent. The association of *Pax6* with eye development in different metazoans is truly fascinating, but it seems to have all the characteristics of a "normal" evolutionary trait: conserved in many related taxa, yet changed in others.

Is the Cambrian Explosion Incompatible with Darwinian Gradualism?

When we stand back and look at the big picture of animal evolution, we see unbridgeable gaps between the phyla that appear to have their origin in a single evolutionary event. This has led some researchers to the conviction that body plan characters had a discontinuous origin, forming by the acquisition of a few large changes rather than the gradual accumulation of many small changes. Here, I have argued that it is sometimes helpful to take a small-picture approach, seeing if the predictions of the discontinuous hypothesis hold true for particular case studies, in addition to fitting the overall big picture. The small pictures presented here suggest it is possible for a lineage to begin with one body plan and evolve an entirely new one, and that even fundamental body plan characters like segmentation can evolve along lineages. These small pictures call into question some explanations for the suddenness and uniqueness of the metazoan radiation by showing that body plan characters and the genetic architecture that governs their development did not all arise in a single evolutionary event and then were unable to change further.

Conserved similarities in the ground plan of members of a phylum may impress, but conservation exists at all levels of the taxonomic hierarchy. We can pick any level of metazoan organization and choose characters that are largely invariant within groups at that level. All metazoans have wall-less cells joined by particular kinds of cell junctions. Within the metazoans, all ecdysozoans have a cuticle that is molted as the animal grows. Within the ecdysozoans, all arthropods have a chitinous exoskeleton. Within the arthropods, all

insects have three body segments, the middle of which bears three pairs of jointed append-
ages. Within the insects, all flies are defined by having one set of wings and one set of
halteres, and so on. This hierarchy of conservation and change produced by continuous
evolution is the basis of systematics and phylogenetics. To classify organisms, we select
characters with a rate of change appropriate to the depth of divergence we wish to delin-
eate. This is most obvious with molecular systematics: Choose a fast-changing gene to
distinguish populations, a slow-changing gene to distinguish phyla, and an extremely
highly conserved gene to study the relationships between kingdoms. But it is also the basis
of morphological systematics: Choose highly labile traits like color, mating call, or bristle
number to distinguish species; choose conserved traits like number of legs, shell material,
or embryological characters to define phyla. Traits that define animal phyla are those traits
that change at an appropriate rate so that they tend to differ between phyla but are more
likely to be constant within phyla. There is no reason to be surprised that body plan char-
acters are conserved within phyla, since that is commonly how they are defined in the first
place (see also Budd 1999).

The continuous scale of conservation and change can be seen for most evolved charac-
ters, including genes and developmental patterns. The homeobox-containing genes are by
no means unusual in their level of conservation between phyla, as a great many genes have
this level of conservation between animal phyla, involved in metabolism, physiology, cell
function, and so forth. Not surprisingly, these are the genes typically selected for phylum-
level phylogenetic studies. Yet, as far as I know, nobody is proposing that we need a mac-
roevolutionary mechanism to explain the conservation of form and function of metabolic
genes. All we need to do is assume that these enzymes are so important that changes are
rare. As with any other evolutionary character, we cannot assume that differences in genes
or expression patterns between lineages played a causal role in the formation of the lin-
eages, as they may have accumulated subsequent to lineage divergence. Similarly, it is
possible to trace the history of languages by comparing the pattern of shared words (Gray
and Atkinson 2003); we do not expect that the origin of new words actually caused the divi-
sion of humans into separate language groups, but that language differences are simply an
inevitable consequence of population divergence.

Recognition of distinct differences between the way arthropods, annelids, echinoderms,
and chordates are put together does not mean that body plan characters evolved in a dis-
tinctly different way to other aspects of phenotype or development. Indeed, "unbridgeable
gaps" between ancient lineages are expected under a gradual model of divergence, due to
the extinction or modification of the intermediate lineages. As lineages diverge, some traits
remain similar and some change, whether by drift or by selection. The longer two lineages
have been separated, the more different they will be, and the more likely that lineages
showing gradations between them will have gone extinct. Long-separated lineages are
likely to have some conserved traits in common, potentially some convergent traits, and
very many traits that differ. The impression of unbridgeable gaps may also be heightened

by the way that body plan differences are categorized. Body plan characters tend to be discrete, such as number of limbs, presence of eyes, type of skeleton, developmental origins of organs, and so on. Discrete traits such as these can, by definition, change only by whole numbers or entire categories, so may appear to evolve by "jumps."

Conclusion

There is clearly a remarkable increase in animal complexity from the Precambrian to the Cambrian periods. The rate of body plan evolution across the Precambrian-Cambrian boundary may have been high, but there is currently a lack of evidence to suggest that the pace of evolutionary change during this period depended critically on the formation of a genetic architecture that then constrained future innovation in body plan or development.

Raff (1996) explores the notion of inflexible body plans with the following thought experiment:

Suppose that through some incredibly bad luck, all animal phyla became extinct except echinoderms. Could the survivors eventually evolve into new phyla? They would start from within a unique and unpromising body plan with tube feet, a water vascular system, a circular "brain" and pentameral symmetry. Could they evolve bilaterian symmetry and various features that we associate with the other phyla, or would they go on munching algal mats until the Sun swells into a red giant and parboils the entire lot? There is a lot of variability within the echinoderms, and they have done some remarkable things. One group of sea urchins, the heart urchins, has evolved a secondary bilateral symmetry. Who in Paleozoic times would have predicted that one group of crinoids, the comatulids or feather stars, would lose their stems and become highly motile, swimming or walking with their arms and clinging to their perches with cirri that resemble multiple articulated appendages? I don't know the answer to this question, but I'm sure that in the right circles a lot of beer and peanuts could be consumed while it was being debated.

Could one body plan give rise to a radically different one? Yes, the chordate body plan gave rise to the echinoderm body plan. Could bilateral symmetry evolve again? Yes, it has several times in the deuterostomes (e.g., sea cucumbers, heart urchins). Could aquatic creatures with a water vascular system ever hope to colonize the land? Well, plenty of other aquatic lineages did so in the past (and some are in the process of doing so today if the land-based crayfish that live in the mud in some Australian forests are anything to go by).

How, then, do we explain the near-simultaneous appearance of phylum-level differences in the Cambrian, and the failure to generate any similar level of variation since? Under a gradualist model, there is no need to worry about the lack of new phyla arising since the Cambrian, because this is explained by the positive relationship between time and divergence: A phylum is the amount of change you expect to accumulate over half a billion years or so, therefore they cannot appear overnight (but come back half a billion years from now, and those Australian crayfish may have given rise to a new phylum). But the gradualist

model still requires an explanation of why the speed of the increase in animal diversity and disparity over the Cambrian boundary is so much greater than that witnessed at other times.

Three key areas of investigation are needed to explore the adequacy or otherwise of a gradualist model of phylum divergence. One is the timing and duration of the radiation. Both paleontological and molecular studies have been used to suggest that bilaterian lineages arose and began diversifying well before the Cambrian. This makes the radiation of metazoan lineages look less explosive but raises more unanswered questions: If many bilaterian lineages existed in the Precambrian, then why did obvious body plan features like legs, eyes, and shells not appear in the fossil record until the Cambrian? Similarly, we cannot attribute differences between these lineages to a causal role in the original speciation event that created the two lineages without a way of determining which of the differences occurred at the original divergence and which were accumulated afterwards. Second, we need an expectation of how much change we could expect under a gradualist model in this time period, so that we can judge what observed level of change would be incompatible with a continuous model. This is not easy, but some attempts have been made to create biologically-informed models of body plan character changes, such as the evolution of a complex eye (Nilsson and Pelger 1994). If we wish to reject a neo-Darwinian explanation of patterns of conservation and change, we need a clearer picture of what any given period of microevolutionary divergence can produce, rather than relying on gut feeling. Third, we need to know if body plan–level characters could arise today and be perpetuated. This seems intuitively unlikely, but a dispassionate exploration would need a taxonomy-free definition of what constitutes a body plan character.

Any investigations of body plan evolution rely critically on using an unbiased way of recording change between lineages over evolutionary time, to avoid the circularity of defining as body plan difference only those that have a discontinuous distribution between phyla. We need a definition of a body plan that is not tied up with taxonomic level or depth of divergence. For example, a naïve observer might suggest that the sausagelike sea cucumbers, flowerlike crinoids, spiky sea urchins, and five-pointed starfish all had different basic body plans. Of course, a zoologist would counter that these animals all do share the common features of the Echinodermata. But the examples given in this chapter demonstrate that, at least in some cases, the relationship between body plan and phylum can become blurry when the minor phyla are considered. Hemichordates, for example, have some of the body plan characteristics of chordates, and some of echinoderms. Sipuncula are currently classed as a phylum, but some consider that they should be subsumed within the phylum Annelida. Insects have body plan innovations not seen in other lineages, such as wings, yet are nested within the phylum Arthropoda. Consideration of the unsexy minor phyla tempers some of the apparent "unbridgeable gaps" between phyla and counters some of the claims about discontinuous body plan evolution.

An unbiased assessment is also required when testing the consequences of the evolution of certain body plan features. For example, the three eusegmented phyla—Arthropoda,

Chordata, and Annelida — are among the most diverse and ubiquitous of the metazoan phyla, so segmentation has sometimes been considered a key innovation that, at least in part, accounts for the evolutionary success of these lineages, by giving them a kind of developmental flexibility that has allowed the evolutionary of many forms and ways of life. But then the molluscs, nematodes, and platyhelminths are just as successful, and they are not eusegmented (see figure 13.1). In fact, the two "preexplosion" metazoan phyla, the diploblasts Porifera (sponges) and Cnidaria (corals, jellyfish, and allies), both make it into the top ten most diverse phyla, despite their presumed lack of any inventions that could have triggered the bilaterian radiation. Molecular data, which records evolutionary history essentially independently of the record in phenotypes, developmental patterns, or fossil forms, might provide a level playing field in which all taxa are equal and body plan characters can be traced as they evolve along the evolutionary tree.

Acknowledgments

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