Animal Phylogeny and Its Evolutionary Implications*

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Keywords

Metazoa, morphology, evolutionary developmental biology, fossils, anatomy

Abstract

In recent years, scientists have made remarkable progress reconstructing the animal phylogeny. There is broad agreement regarding many deep animal relationships, including the monophyly of animals, Bilateria, Protostomia, Ecdysozoa, and Spiralia. This stability now allows researchers to articulate the diminishing number of remaining questions in terms of well-defined alternative hypotheses. These remaining questions include relationships at the base of the animal tree, the position of Xenacoelomorpha, and the internal relationships of Spiralia. Recent progress in the field of animal phylogeny has important implications for our understanding of the evolution of development, morphology, genomes, and other characters. A remarkable pattern emerges—there is far more homoplasy for all these characters than had previously been anticipated, even among many complex characters such as segmentation and nervous systems. The fossil record dates most deep branches of the animal tree to an evolutionary radiation in the early Cambrian with roots in the Late Neoproterozoic.

INTRODUCTION

Since the publication of Haeckel's (1866) animal tree of life, zoologists have made great progress in understanding animal evolutionary relationships. Today's views of the animal tree of life are the result of decades of intense phylogenetic research, in terms of both data—first anatomical and developmental characters and then, more recently, molecular characters—and analytical developments. In the past ten years, phylogenetic analyses of genomes and transcriptomes have played a key role in refining animal relationships. Here we present recent advances that have led the community to approach consensus on many fundamental questions of animal phylogeny.

Animals (**Figure 1**, **Supplemental Figure 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**) are a clade of multicellular eukaryotic organisms characterized by several synapomorphies (**Table 1**). Here we use "animals" as a synonym for the members of Metazoa rather than in the broader historical sense that also included motile unicellular organisms referred to as protozoans. In recent years, our understanding of the relationships of animals to other eukaryotes has made remarkable progress (**Figure 1**, **Table 1**). Animals, fungi, and all the descendants of their most recent common ancestor form the clade Opisthokonta (Torruella et al. 2012). Within Opisthokonta, animals are united with the unicellular Ichthyosporea, Filasterea, and Choanoflagellata to form the subclade Holozoa. Within Holozoa, animals and choanoflagellates are sister groups (Torruella et al. 2012).

Animal phylogeny is interesting in its own right and is also fundamental to many other aspects of animal biology. The tree allows us to make informed comparisons among related taxa. Questions concerning character evolution, including the evolution of complexity (in terms of cell types, tissues, organs, etc.), cannot be answered without a sound phylogenetic tree. A well-resolved tree also allows us to better understand the history of life on earth, including the time of origin of the major lineages and the evolutionary rates and diversification patterns in different branches. Finally, a well-resolved animal phylogeny permits us to efficiently organize information about animals, and classify animal diversity, on the basis of shared evolutionary history. This helps us relate findings based on the study of particular animals, such as laboratory model systems, to findings on other animals, including humans.

THE ANIMAL PHYLOGENY

Recent Progress

The modern era of animal phylogenetics began with cladistic analyses of partial 18S rRNA sequences (Field et al. 1988) and anatomical traits (Eernisse et al. 1992, Nielsen et al. 1996, Schram 1991). Since then, many analyses of PCR-amplified molecular markers have ignited key debates, and a few combinations of molecular and morphological data have been undertaken (Giribet et al. 2000, Glenner et al. 2004, Zrzavý et al. 1998). These and dozens of other papers led to broad support for what was termed "the new animal phylogeny" (Adoutte et al. 2000, Halanych 2004), wherein some traditional groupings, such as the annelid-arthropod clade Articulata, were rejected in favor of novel hypotheses, such as Ecdysozoa. Most recent deep animal phylogenetic analyses have made use of transcriptomes and complete genomes. Initially, these analyses were based on Sanger sequencing (Bourlat et al. 2006, Delsuc et al. 2006, Dunn et al. 2008, Hejnol et al. 2009, Philippe & Telford 2006, Philippe et al. 2005), but new sequencing technologies that provide vastly more data are now becoming widely adopted (Kocot et al. 2011, Lemmon & Lemmon 2012, Smith et al. 2011).

The great progress made in recent decades on deep animal phylogeny is concentrating the attention of the field on a shrinking number of harder problems that have not been resolved with

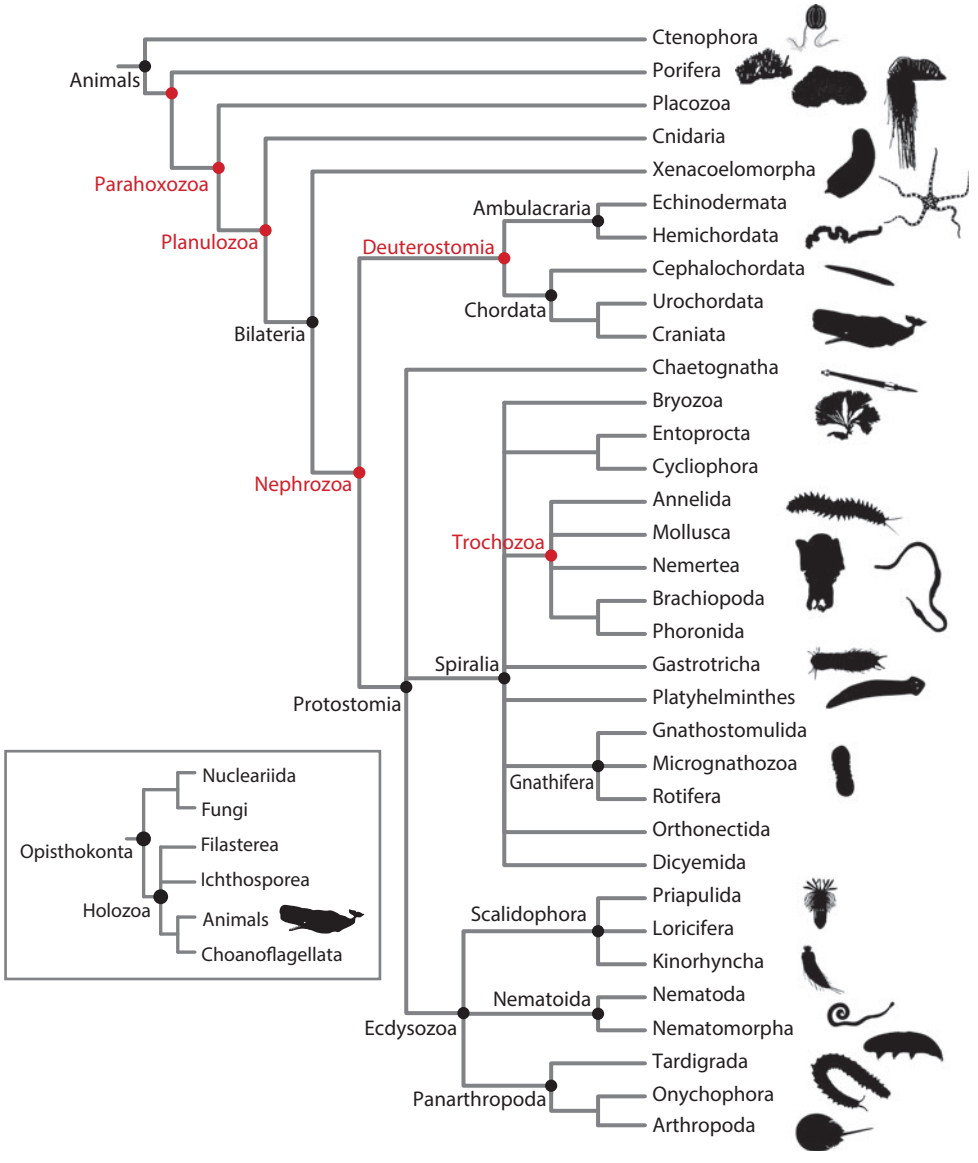

Figure 1

A hypothesis of animal phylogeny, compiled across multiple studies. Black dots denote clades that have broad consensus across studies. Red dots denote clades that have poor or conflicting support or whose exact composition is uncertain. The organism silhouettes were illustrated by Noah Schlottman and submitted to PhyloPic (**www.phylopic.org**). They are available for reuse under the Creative Commons Attribution-ShareAlike 3.0 Unported license.

previous approaches. Some of the relevant diversification events happened in quick succession hundreds of millions of years ago, which resulted in relatively few informative characters for these relationships (Rokas & Carroll 2006). Though some of these hard problems may never be resolved, there are several reasons to be optimistic that coming years will see continued progress.

Table 1 Some synapomorphies for the clades labeled in Figure 1

Clade	Synapomorphies
Opisthokonta	Chitin, single posterior flagellum
Animals (i.e., Metazoa)	Collagen, oogenesis, spermatogenesis (polar bodies), special sperm structure, mitochondrial genome reduction
All animals except Ctenophora	Paired domains linked to homeodomains (Ryan et al. 2010), NR2A genes include DNA binding domain (Reitzel et al. 2011), Drosha microRNA processing (Maxwell et al. 2012)
Parahoxozoa	Hox and ParaHox genes (Ryan et al. 2010)
Planulozoa (sensu Wallberg et al. 2004)	Serotonin
Bilateria	Mesoderm, bilateral symmetry, cephalization, circular and longitudinal musculature
Deuterostomia	Enterocoely, pharynx with ciliated gill slits, archimery
Ambulacraria	Dipleurula larva
Chordata	Notochord
Protostomia	Main neurite bundles ventrally localized
Spiralia	Spiral cleavage
Trochozoa	Larvae with a prototroch
Gnathifera	Special type of cuticularized jaws
Ecdysozoa	Molted cuticle, trilaminate epicuticle
Scalidophora	Scalids on the introvert
Nematoida	Longitudinal muscles only, cloaca in both sexes, sperm without flagellum
Panarthropoda	Paired segmental ventrolateral appendages with segmented leg nerves and muscles, *engrailed* expression in posterior ectoderm of each segment
Nephrozoa	Discrete excretory organs such as nephridia (Jondelius et al. 2002)

First, only a small fraction of the potential data has yet been examined. The PCR-based approaches used until recently were difficult and expensive to apply to more than a handful of genes. New sequencing technologies expand the number of genes that can be routinely examined into the thousands. Only now is it becoming feasible for laboratories to independently sequence whole animal genomes, which provides data on additional genes and enables the analysis of other features of genome evolution, such as gene gain and loss. Advances in imaging, such as X-ray microtomography and light sheet fluorescence microscopy, have accelerated morphological character description.

Second, data suitable for phylogenetic analysis have been collected for only a small fraction of living animals. Molecular data are almost entirely lacking for some important clades. In other cases, data are available for only one or two species, which are then used as the sole representatives of large clades. The improvements in sequencing technology noted above, in conjunction with concerted collecting efforts, will greatly expand taxon sampling of molecular sequence data (GIGA Community of Scientists 2014).

Last, data analysis methods have lagged behind advances in data acquisition but are now advancing at a rapid rate. There is a critical need for integrated computational workflows based entirely on explicit, reproducible methods (Dunn et al. 2013). Advances in phylogenetic inference, including the implementation of complex sequence evolution models (Lartillot et al. 2009) and greatly improved computational efficiency, will continue to be essential.

Broad Consensus

Many regions of the animal tree now have broad, consistent support across analysis methods, character sampling, and taxon selection (**Figure 1**). Animal monophyly is well supported, consistent with a single origin of multicellularity and some other characters (**Table 1**) in animals. All living animals belong to one of five clades: Porifera (sponges), Ctenophora (comb jellies), Cnidaria (corals, medusae, and their relatives), Placozoa (a small group of creeping marine animals), or Bilateria (most animals, including humans). The monophyly of each of these clades is strongly supported across well-sampled analyses. Some studies suggested that Porifera is paraphyletic (Sperling et al. 2009), but these studies considered a relatively small number of nuclear genes.

Bilateria (**Figure 1**) has more than a million described species, including the best-studied model animal species and nearly all the animals that humans regularly encounter. Bilateria is composed of Deuterostomia, Protostomia, and possibly the much smaller clade Xenacoelomorpha, which some studies place within Deuterostomia (see the next section). Apart from the placement of Xenacoelomorpha, there is broad consensus on the composition of and deep relationships within Deuterostomia (Delsuc et al. 2006, Dunn et al. 2008, Hejnol et al. 2009). These well-supported relationships include the sister-group relationship between Hemichordata and Echinodermata (together forming Ambulacraria). Recent analyses of gene sequence data have consistently supported the placement of Urochordata, rather than Cephalochordata, as the sister group to Craniata (Delsuc et al. 2006), though there is still active discussion about the congruence between these results and the morphological data (Stach 2008).

The clade Protostomia (**Figure 1**) is very diverse in terms of species numbers, morphological disparity, embryology, and many other attributes. Within Protostomia there are three well-supported clades: Chaetognatha, Ecdysozoa, and Spiralia. Ecdysozoa is split into three clades: Panarthropoda, Nematoida, and Scalidophora. Recent analyses have greatly clarified the relationships within Panarthropoda, including the placement of Tardigrada as sister to a clade comprising Onychophora and Arthropoda (Campbell et al. 2011). Relationships within Arthropoda were recently reviewed elsewhere (Giribet & Edgecombe 2012). Nematoida comprises the sister clades Nematoda and Nematomorpha (Schmidt-Rhaesa 2013). Scalidophora consists of several poorly known but fascinating taxa: Priapulida, which has both coelomate and pseudocoelomate members (Storch 1991); Loricifera, with extraordinary morphologies (Neves et al. 2013); and Kinorhyncha, composed of animals with a unique type of segmentation (Herranz et al. 2014).

Despite the many remaining questions about the relationships within Spiralia, there are several key relationships within this clade for which there is growing consensus (**Figure 1**). Several groups, including Myzostomida, Echiura, and Sipuncula, are nested within Annelida, expanding this already diverse clade to include additional animals with divergent body plans (Dordel et al. 2010, Dunn et al. 2008, Helm et al. 2012, Weigert et al. 2014). Trochozoa, a clade defined by the presence of a trochophore larva, includes at least Annelida, Mollusca, and likely Nemertea (Dunn et al. 2008, Nesnidal et al. 2013). The enigmatic Cycliophora, animals which live on the mouthparts of lobsters, forms a clade with Entoprocta (Hejnol et al. 2009, Nesnidal et al. 2013). Acanthocephala is now recognized as a derived clade of parasitic rotifers (Sørensen & Giribet 2006). Gnathifera, a clade of jawed animals consisting of at least Rotifera, Gnathostomulida (Wey-Fabrizius et al. 2014), and Micrognathozoa, is supported by morphological data but has not yet been thoroughly tested with molecular data (Witek et al. 2009).

Open Questions

Although many relationships described above now find broad support, some critical deep animal relationships still have poor or conflicting support across analyses. The progress enumerated

above greatly facilitates work on these remaining questions, as most of them can now be clearly articulated as a smaller number of specific, alternative hypotheses (e.g., **Figure 2**). Increased taxon sampling, improved analytical methods, and the consideration of new genome-level data, such as the gain and loss of genes, will help resolve many of these questions in coming years.

Root of the animal tree. Placing the root of the animal tree (**Figure 2*a***) has been one of the most difficult and controversial challenges in animal phylogenetics (Medina et al. 2001). This is not surprising given that these relationships represent the deepest splits in the tree. This challenge comes down to testing the relationships among five clades: Porifera, Ctenophora, Cnidaria, Placozoa, and Bilateria (Edgecombe et al. 2011). Traditionally, Porifera has been thought to be the sister group to all other animals, the latter grouping collectively named Epitheliozoa (**Figure 2*a***, *right*). This is because sponges lack some features found in other animals [e.g., epithelia with belt desmosomes (Leys & Riesgo 2011)], and their choanocytes superficially resemble choanoflagellates. Detailed investigations of choanocytes and choanoflagellates, however, reveal many differences and their homology has been questioned (Mah et al. 2014). Despite widespread acceptance of Porifera as the sister group to all other animals, early molecular analyses (Medina et al. 2001) did not strongly support this relationship, and until quite recently it had not been tested in well-sampled trees. Nonetheless, it was surprising when the first phylogenomic analyses to include both sponges and ctenophores recovered ctenophores, not sponges, as the sister group to all other animals (Dunn et al. 2008, Hejnol et al. 2009) (**Figure 2*a***, *left*).

Subsequent studies found support for the traditional hypothesis of Porifera as the sister group to all other animals (Philippe et al. 2009, Pick et al. 2010), but only when most out-groups were excluded or a reduced set of slowly evolving genes was considered. A more recent phylogenomic analysis of the base of the animal tree (Nosenko et al. 2013) reiterated the conclusion that the placement of the root is sensitive to gene sampling, taxon sampling, and analytical methods. The challenges of resolving these relationships through analyses of gene sequence evolution have inspired hope that other kinds of character data, such as the gain and loss of genes (Osigus et al. 2013b), could advance the field. The recently sequenced genomes of two ctenophores (Ryan et al. 2013, Moroz et al. 2014) now makes this possible, and analyses of gene gain and loss support the placement of ctenophores, rather than sponges, as the sister group to all other animals.

Hox and ParaHox genes are found in Placozoa, Cnidaria, and Bilateria, but clear orthologs are absent in Porifera and Ctenophora (see Genome Evolution, below, for more details). This finding led to the hypothesis that these first three groups form a clade, Parahoxozoa (Ryan et al. 2010). Phylogenomic analyses that place sponges as the sister group to all other animals tend to place Ctenophora as the sister group to Cnidaria, reviving the old clade Coelenterata (Nosenko et al. 2013, Philippe et al. 2009). This construction would reject Parahoxozoa and indicate that Hox and ParaHox genes had been lost in Ctenophora (Osigus et al. 2013b). The sequencing of the ctenophore genome has allowed scientists to extend gene content analyses well beyond Hox and ParaHox genes. These new, much broader analyses find strong corroboration for Parahoxozoa (Ryan et al. 2013), which suggests that the placement of ctenophores with cnidarians in some analyses may be an artifact. Within Parahoxozoa, there is strong support (Ryan et al. 2013) for Planulozoa, a clade composed of Cnidaria and Bilateria (Wallberg et al. 2004) (**Table 1**).

The placement of Xenacoelomorpha. Though many of the broad features of relationships within Bilateria find strong, consistent support, many open questions remain. One question concerns the very deepest relationships within Bilateria (**Figure 2*b***). Some analyses have placed Xenacoelomorpha as the sister group to Protostomia and Deuterostomia (Hejnol et al. 2009) (**Figure 2*b***, *left*), whereas others have placed Xenacoelomorpha within Deuterostomia (Philippe

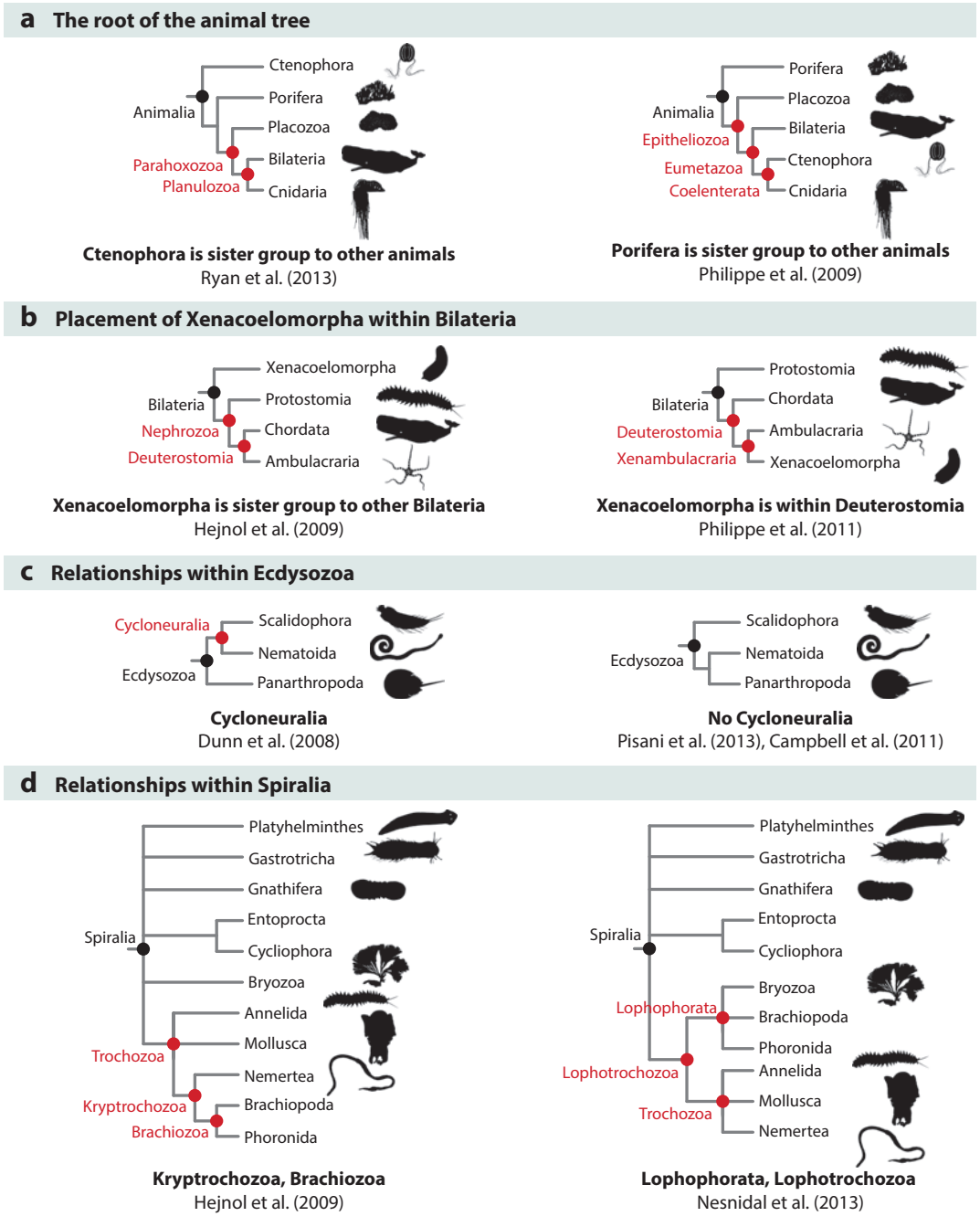

Figure 2

Key questions in animal phylogenetics. Each panel shows two alternative hypotheses for (*a*) the placement of the animal root, (*b*) the placement of Xenacoelomorpha, (*c*) relationships within Ecdysozoa, and (*d*) relationships within Spiralia. Not all alternatives are shown for each case. Black dots denote nodes that have broad consensus across studies. Red dots denote nodes that have poor or conflicting support across studies, or whose exact composition is uncertain. The animal images are a subset of those shown in **Figure 1**, which were illustrated by Noah Schlottman and submitted to PhyloPic (**www.phylopic.org**). They are available for reuse under the Creative Commons Attribution-ShareAlike 3.0 Unported license.

et al. 2011) (**Figure 2*b***, *right*). It was only in the past five years that the union of *Xenoturbella* and Acoela received support from molecular data (Hejnol et al. 2009, Philippe et al. 2011). Several morphological characters, such as distinctive epidermal ciliary rootlets (Lundin 1998), suggested their affinity. The organisms within Xenacoelomorpha are worm-like creatures without an anus or any form of excretory organs; they also lack many other characters found in other members of Bilateria.

Protostomia. Protostomia consists of Chaetognatha, Ecdysozoa, and Spiralia. Although it is now clear from molecular data and characters of the nervous system that chaetognaths are protostomes, they fall outside both Ecdysozoa and Spiralia, and it is not yet known how these three clades relate to each other (Marlétaz et al. 2006, Matus et al. 2006, Perez et al. 2014). The interpretation of chaetognaths as a deep-branching lineage of protostomes is consistent with the appearance of their grasping spines among the earliest skeletal animal fossils near the base of the Cambrian (Kouchinsky et al. 2012), as well as the presence of some deuterostome-like features during their development (deuterostomy, enterocoely, radial cleavage).

Despite strong support for each of the three clades that compose Ecdysozoa (Scalidophora, Nematoida, and Panarthropoda), their interrelationships remain uncertain (**Figure 2*c***). Campbell et al. (2011) found a polytomy for the relationships between these ecdysozoan clades. A clade composed of Scalidophora and Nematoida, called Cycloneuralia (**Figure 2*c***, *left*), has been recovered in multiple analyses, though often with poor support (Dunn et al. 2008). Cycloneuralia is generally favored by morphologists because most members share a circumoral, collar-shaped brain composed of a ring neuropil with anterior and posterior somata that contrasts with the circumoral commissures found in other ecdysozoans (Richter et al. 2010, Schmidt-Rhaesa & Rothe 2014). Other molecular analyses suggest that Cycloneuralia is paraphyletic relative to Panarthropoda (**Figure 2*c***, *right*), with Nematoida more closely allied to Panarthropoda than to Scalidophora (Pisani et al. 2013), though anatomical support for a nematoid-panarthropod group is not obvious. Genomic resources are not yet available for important ecdysozan groups, notably Loricifera and Kinorhyncha.

The internal relationships of Spiralia are in many respects the most poorly resolved of the animal tree (**Figure 2*d***), as many open questions overlap in complex ways. Most spiralian species fall in Trochozoa, a clade defined by trochophore larvae that include at least Mollusca and Annelida. Each of these two clades has tens of thousands of species. Most analyses also place Nemertea within Trochozoa (Dunn et al. 2008, Giribet et al. 2000, Glenner et al. 2004, Hejnol et al. 2009, Paps et al. 2009, Zrzavý et al. 1998). The prototroch of the trochophores and a band of nonciliated cells of arrested development in the nemertean pilidium are proposed to be homologous (Maslakova et al. 2004), consistent with this phylogenetic hypothesis and the derivation of nemertean larvae from trochophore larvae. A recent study (Nesnidal et al. 2013) instead placed Nemertea with Platyhelminthes, outside Trochozoa, in some analyses.

The question of which clades falls within Trochozoa is inseparable from a related topic, the hypothesized clades Lophophorata and Lophotrochozoa. Lophophorata consists of a set of organisms (Brachiopoda, Phoronida, and Bryozoa) with a rake-like feeding structure. Several analyses suggested that Lophophorata is polyphyletic (**Figure 2*d***, *left*), placing Brachiopoda and Phoronida within Trochozoa and Bryozoa outside Trochozoa (Funch & Kristensen 1995, Hejnol et al. 2009). Other analyses, in contrast, resolve Lophophorata as monophyletic and falling outside Trochozoa (Nesnidal et al. 2013) (**Figure 2*d***, *right*). Depending on the placement of lophophorate taxa within Spiralia, Lophotrochozoa, defined as a clade composed of Mollusca, Annelida, and Lophophorata (Halanych et al. 1995), is either a subclade of Spiralia (**Figure 2*d***, *right*) or a synonym of Spiralia.

Animals within Spiralia that clearly fall outside Trochozoa include Gnathifera (Gnathostomulida, Rotifera, and likely Micrognathozoa), Bryozoa, Platyhelminthes, Gastrotricha, and the clade comprising Entoprocta and Cycliophora. Their relationships to each other and to Trochozoa remain unclear. Conflicting results suggest that Platyhelminthes, Gnathifera, Gastrotricha, and perhaps several other of these organisms either form a clade, referred to as Platyzoa (Giribet et al. 2000, Hankeln et al. 2014), or are paraphyletic with respect to Trochozoa. Likewise, the clade Polyzoa has been proposed for Bryozoa, Cycliophora, and Entoprocta. These animals have similar asexual budding (Funch & Kristensen 1995), but molecular support for this clade has been weak (Hejnol et al. 2009).

The phylogenetic position of Gastrotricha is especially unstable across analyses. The presence of ciliation, protonephridia, and other characters suggests, as do molecular analyses, that Gastrotricha falls within Spiralia (Schmidt-Rhaesa 2013), though it is not clear where exactly. In addition, data are scarce for several taxa that are difficult to obtain. The position of Mesozoa (Orthonectida and Dicyemida) is still unsettled, although recent analyses suggest an affinity to protostomes (Ogino et al. 2010, Suzuki et al. 2010). Diurodrilida was traditionally considered an aberrant group of annelids with some convergent similarities to Gastrotricha (Kristensen & Niilonen 1982) until detailed anatomical studies brought annelid affinities into question (Worsaae & Rouse 2008). However, a recent analysis of mitochondrial DNA sequence data suggests that the molecular affinity of Diurodrilida to platyzoans may be a systematic artifact (Golombek et al. 2013). Molecular data from Micrognathozoa are still restricted to a few Sanger-based gene fragments (Giribet et al. 2004), and the group's position remains untested in the newer phylogenomic analyses. No molecular data on the enigmatic *Lobatocerebrum psammicola*, formerly believed to be closely related to annelids and flatworms (Platyhelminthes) (Rieger 1980), have yet been published.

THE EVOLUTION OF MORPHOLOGY AND DEVELOPMENT

The growing consensus regarding many aspects of animal phylogeny provides the opportunity to evaluate hypotheses about character evolution. Concurrent improvements in imaging and sequencing technology have made available morphological and developmental data across a broader set of animal taxa. These advances provide a sharper and more detailed picture of character evolution in animals and indicate extensive homoplasy in characters of central interest (**Figure 3**).

Epithelia

In the broadest sense, an epithelium is a continuous sheet of cells that are connected to each other by junctions. Such structures are a synapomorphy for animals (**Table 1**). Epithelia form barriers between the organism and the outside world, as well as between internal organismal structures. They are selectively permeable or nearly impermeable and are critical to the compartmentalization of the animal body.

The term epithelium is sometimes used to more narrowly refer to tissue that fits the above criteria but is also attached to an extracellular basement membrane. Ctenophora, Cnidaria, and Bilateria include animals whose epithelia fit this more stringent definition. The members of Placozoa do not have basement membranes, although their genome includes genes for many extracellular matrix proteins found in the basement membranes of other animals (Srivastava et al. 2008). The lack of a basement membrane in placozoans could be explained by secondary loss, as observed in Acoelomorpha. The nature of epithelia in sponges has been somewhat confused in the literature, in part because sponge epithelia are diverse. Because sponges have often been presented as lacking tissue

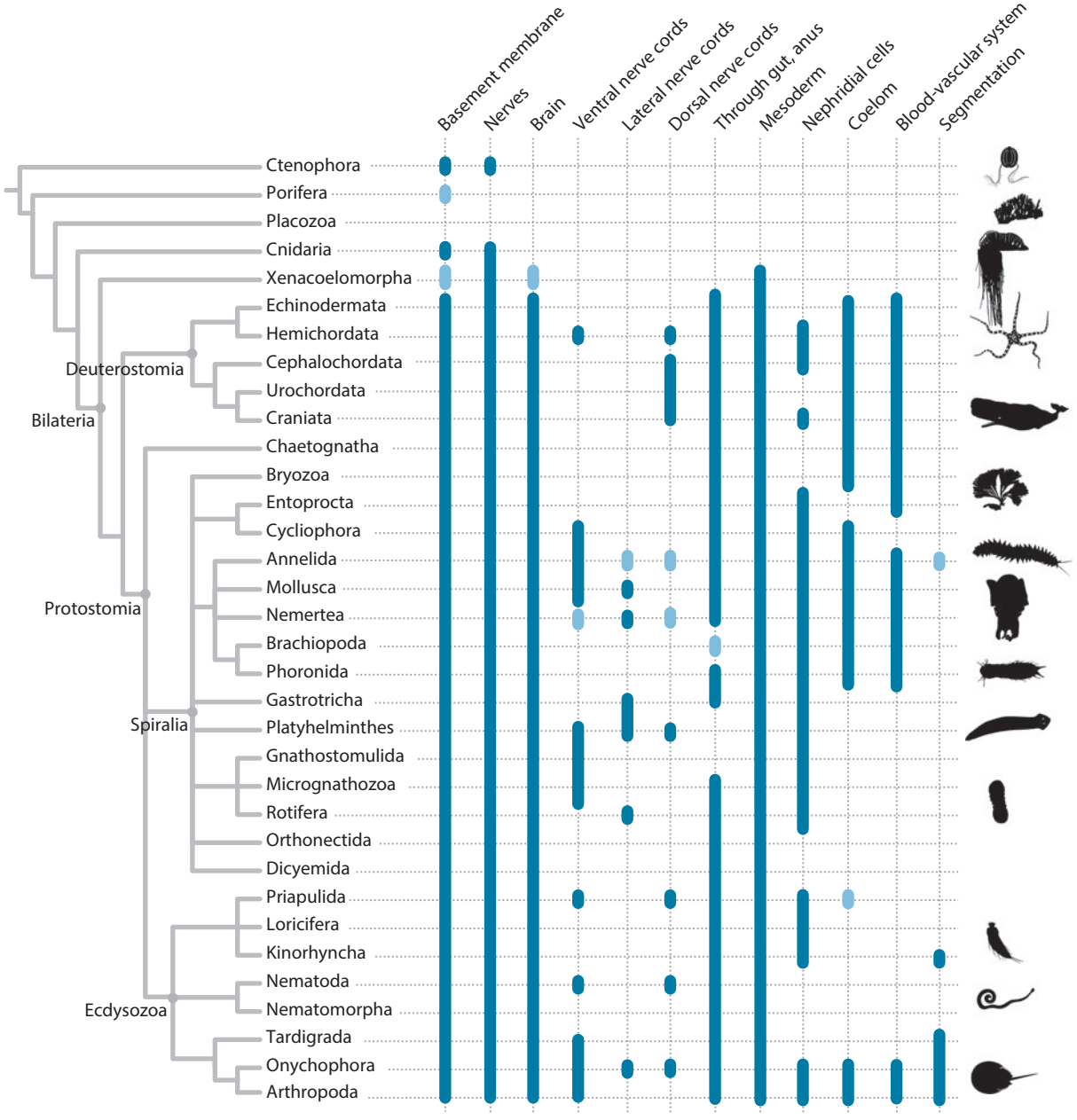

Figure 3

Select morphological characters mapped onto the tree from **Figure 1**. Dark blue bars indicate characters that are present, and light blue bars indicate clades with mixed presence/absence of characters. See **Table 1** for additional characters that are synapomorphies of clades. The animal images are a subset of those shown in **Figure 1**, which were illustrated by Noah Schlottman and submitted to PhyloPic (**www.phylopic.org**). They are available for reuse under the Creative Commons Attribution-ShareAlike 3.0 Unported license.

that fits the stricter definition of epithelia, and because the position of Placozoa has been unstable, the hypothetical clade of all animals, not including Porifera, has been named Epitheliozoa (Ax 1995) (**Figure 2*a***, *right*). Further work has revealed that the complexity of sponge tissues has often been underappreciated (Leys & Riesgo 2011). Sponges clearly possess cell junctions that seal the tissue layer, and the homoscleromorph sponges have basement membranes (Leys & Riesgo 2011).

Nervous Systems

The nervous system and the origin of its different architectures in various animal lineages are one of the best-studied aspects of animal morphology. This is due both to functional interest and to its diverse morphology across taxa. Nerve cells are present in Ctenophora, Cnidaria, and Bilateria but are absent in Placozoa and Porifera. It has been thought, then, that there was a single origin of nerves prior to the diversification of Eumetazoa (a clade hypothesized to consist of Ctenophora, Cnidaria, and Bilateria) and no losses. Support for Parahoxozoa as opposed to Eumetazoa, however, indicates that there has been homoplasy in nerve cell evolution (Ryan et al. 2013, Moroz et al. 2014). This is because animals with and without nerves are found both within and outside Parahoxozoa, requiring multiple evolutionary gains or losses of nerves. There are many patterns of nerve gain and loss that could explain their presence and absence in living animals. Nerves may have arisen independently in Ctenophora and the clade composed of Cnidaria and Bilateria. Alternatively, nerves may have had a single origin followed by loss in Placozoa alone (if Porifera is the sister group to all other animals) or both Placozoa and Porifera (if Ctenophora is the sister group to all other animals).

Ctenophores lack many genes that are essential for nervous system development and function in cnidarians and bilaterians, suggesting that ctenophores have nervous systems that are quite different from those of other animals (Ryan et al. 2013, Moroz et al. 2014). The nervous systems of ctenophores and cnidarians are net-like, with some regional specialization (Jager et al. 2010, Schmidt-Rhaesa 2008). Within Bilateria, a central question about nervous system evolution concerns the number of times that a complex brain and a centralized nervous system with multiple cords arose from a nerve net or that a centralized nervous system became reduced back to a nerve net (Holland et al. 2013, Holland 2003, Northcutt 2012). All bilaterians possess more nerve and sensory cells in the anterior part of the body than in other parts, so it is widely agreed that cephalization is a synapomorphy for Bilateria. The complexity of the ancestral bilaterian brain, however, is debated (Northcutt 2012). The number of evolutionary events that led to the formation of mushroom bodies and subdivisions of the brain (bipartite/tripartite) and the reductions in many animal lineages remains poorly understood (Holland et al. 2013). However, all bilaterians use similar genes to control brain formation (Holland et al. 2013), which is consistent with a single origin of the brain, although the exact number of cell types and the structure of a putative ancestral brain remain unclear (Tessmar-Raible 2007). A small condensation composed of a small number of multifunctional cell types is a likely possibility, as many lineages have either a nerve ring (Cycloneuralia) or a small assemblage of neurons and sensory cells (Polyzoa, Platyzoa).

A related question of great interest is, how many times did the complex chordate, annelid, and panarthropod nerve cords evolve from either an orthogon-like or net-like nervous system (Holland et al. 2013, Lowe 2008)? An orthogonal nervous system is composed of multiple ventral, lateral, and dorsal cords connected by more or less regular commissures, as found in Platyhelminthes and Acoela. Basiepidermal nerve nets, in addition to the cord-like structures, are located in the epidermis and are found in hemichordates, *Xenoturbella*, nemertodermatids, and many other bilaterians. Phylogeny clearly indicates multiple independent condensation events even though similar molecules are used to develop these structures, suggesting that the molecular networks had an

ancestral function in (neuro-)ectodermal patterning and were co-opted for the patterning of advanced structures (Pani et al. 2013). Ventrally condensed nervous systems can be derived from an orthogon by the loss of dorsal cords, leaving ventral and ventrolateral cords as remnants—a neural architecture found in nemerteans and molluscs. Conversely, both multiple independent condensations of axon tracts and subepidermal relocation are probable mechanisms accounting for multiple evolutionary origins of more complex dorsal or ventral nerve cords.

Gut and Gastrulation

Gastrulation is the process by which cells become internalized to produce the endoderm, a tissue layer that forms the gut and other associated structures. Gastrulation has been described in detail for Ctenophora, Cnidaria, and Bilateria. The embryology of Placozoa is unknown, and it remains unclear how internal cells arise and whether this process is homologous to gastrulation in other animal lineages. Whether gastrulation is present in Porifera has been a source of extensive debate (Degnan et al. 2005, but see Ereskovsky & Dondua 2006). Even though sponge embryology lacks many features of gastrulation seen in other animals, they may be derived from animals that did have gastrulation.

The animal gut can have one opening, the base of which is functionally blind (ctenophores, sponges, cnidarians, xenacoelomorphs, platyhelminths, gnathostomulids, and some brachiopods), or two openings, including those cases in which the gut is a tube that opens externally at both ends. Phylogenetic, developmental, and morphological data suggest that the most recent common ancestor of Cnidaria and Bilateria had a gut with a single opening that functioned as both a mouth and an anus, and that this opening is homologous to the mouth of animals with a through gut (Hejnol & Martindale 2009). In this scenario, the through gut arose with the novel origin of an additional posterior opening, the anus. The number of times a posterior opening has evolved is under debate (Schmidt-Rhaesa 2008). The anus and a through gut may have arisen only once, which would require subsequent losses in clades including Gnathostomulida and Platyhelminthes, or they may have arisen independently multiple times.

Mesoderm, Coeloms, and Excretory and Circulatory Systems

The mesoderm is the embryonic layer in bilaterians that gives rise to coeloms, blood vascular systems, hemolymphatic fluid, bones, connective tissue, and individual muscle cells. Most of these tissues and organ systems are associated with larger body sizes, facilitating nourishment of the cells or stabilization of the body, and are often reduced in smaller animals. The homology of the mesoderm within Bilateria was once under dispute (Ruppert 1991), but molecular and developmental studies now indicate a single origin. There is consensus that in Bilateria (Chiodin et al. 2013, Ladurner & Rieger 2000) the mesoderm originated from the endoderm (Martindale 2004). Nephridial cells are present in protostomes and deuterostomes (Ruppert & Smith 1988). They are hypothesized to share a single common origin (Bartolomaeus & Ax 1992, Jondelius et al. 2002) and to be a synapomorphy for the clade Nephrozoa (**Figure 2*b***, *left*). There is substantial variation among these cell types (protonephridia and metanephridia) across Bilateria, as well as in the excretory systems of which they are a part. A close relationship of protonephridia and metanephridia to the complex metanephros of the vertebrate kidney has been hypothesized, although the metanephros is of mesodermal origin whereas nephridial cells originate from the ectoderm (Ruppert 1994). Interestingly, a recent molecular study of planarian regeneration showed that orthologs of genes that pattern the metanephros in vertebrates are responsible for the regeneration of planarian protonephridia (Scimone et al. 2011) despite their different ontogenetic

origin. A closer molecular examination of protonephridia and metanephridia of other protostome lineages is thus warranted.

Advances in animal phylogeny and in imaging tools now make clear that vasculature and coelomic cavities, two key mesodermal derivatives, show extensive homoplasy within Bilateria. This differs markedly from classic perspectives that presumed that these traits were too complex to show convergent gain and loss (Koch et al. 2014). Results from these advances suggest that larger body sizes that are present in several lineages (Arthropoda, Annelida, Nemertea, Chordata, Ambulacraria) have independent evolutionary origins.

Segmentation

Segmentation, the anteroposterior repetition of body units, is an important feature of some animals in Bilateria. A clear definition of segmentation has been difficult to come by (Hannibal & Patel 2013, Scholtz 2002), but it is usually distinguished from metamery and seriality. Panarthropods and annelids, which are distantly related and phylogenetically embedded among many nonsegmented animals, have true segmentation, in which the substructures of segments (e.g., muscles, nephridia) have specific spatial patterns. Only a broader definition of segmentation can include additional taxa, such as vertebrates (subdivision of the backbone and somites), kinorhynchs (serially repeated zonites), and some molluscan clades (e.g., multiple shell glands in chitons, and serially repeated nephridia and dorsoventral muscles in chitons and monoplacophorans). Even broader definitions of seriality can also include serially arranged ring musculature similar to that found in acoelomorphs. A closer look at the molecular mechanisms of segmentation shows that they are superficially similar (clock-like expression) but very different in the details (Sarrazin et al. 2012). Further resolution of the internal relationships in Spiralia and Ecdysozoa will specify when segmentation emerged therein, and molecular investigations may clarify how these segmentation processes were modified.

GENOME EVOLUTION

Nuclear Genomes

In addition to helping resolve animal phylogeny, sequenced animal genomes have revealed several patterns of prime importance to our understanding of animal evolution. In particular, many genes initially thought to be specific to particular innovations, such as multicellularity, precede these innovations (Suga et al. 2013). This finding erodes the expectation that we should look for novel genes associated with each novel morphological, developmental, or functional character. Many novel phenotypes arise through modification of the functions of and interactions between existing genes, and the number of genes inferred to be present in ancestral genomes is much greater than previously thought.

Most sequenced animal genomes belong to a few clades within Bilateria, especially vertebrates, insects, and nematodes (GIGA Community of Scientists 2014). Ctenophora has two sequenced genomes (Ryan et al. 2013, Moroz et al. 2014). Porifera (Srivastava et al. 2010) and Placozoa (Srivastava et al. 2008) have one sequenced genome apiece. The sampling of cnidarian genomes is only slightly better (Chapman et al. 2010, Putnam et al. 2007, Shinzato et al. 2011). Sequencing the genomes of the animals' closest unicellular relatives is also critical to understanding the evolution of animal genomes—genome sequences are now available for two choanoflagellates, *Monosiga brevicollis* and *Salpingoeca rosetta*, and the filasterean *Capsaspora owczarzaki* (Suga et al. 2013).

The animal genomes sequenced to date, though still limited in taxonomic scope, make it possible to reconstruct aspects of some key events in the history of genome evolution. A comparison

of animal genomes to those of unicellular holozoans reveals that many cellular adhesion and transcriptional regulation genes essential to animal multicellularity precede animals (Suga et al. 2013). In contrast, many intercellular signaling genes appear to be specific to animals.

The gene contents of ctenophore and sponge genomes are similar in many respects (Ryan et al. 2013). For example, both sets of animals have some genes that have neural functions in Bilateria and Cnidaria, even though sponges lack a nervous system. Other genes essential for nervous system development in Bilateria and Cnidaria are absent in ctenophores and sponges, even though ctenophores have a nervous system. This suggests that the ctenophore nervous system is quite different from that of other animals. Many genes are specific to Parahoxozoa, a clade initially defined by the presence of Hox and ParaHox genes (Ryan et al. 2013). Some scientists have argued that signatures of Hox and ParaHox genes are present in all animal clades, but that these genes have been lost or extensively altered in some groups (Mendivil Ramos et al. 2012).

The first animal genomes to be sequenced were of ecdysozoans and vertebrates. Many genes that were present in vertebrate genomes but not in ecdysozoan genomes were thought to be unique vertebrate innovations. The sequencing of the first cnidarian genome, that of *Nematostella vectensis* (Putnam et al. 2007), radically altered this belief. Many of the vertebrate-specific genes were in fact present in cnidarians, and thus were not vertebrate-specific at all, but had been lost in ecdysozoans.

Genomes, of course, include many features other than protein-coding genes. These include microRNAs, small molecules that modulate the degradation and translation of messenger RNA. MicroRNAs are present in all animals except Ctenophora (Maxwell et al. 2012) and Placozoa (Srivastava et al. 2008). MicroRNA-processing genes are not present in Ctenophora, consistent with the possible divergence of this group from other animals prior to the origin of microRNA (Maxwell et al. 2012). Some components of microRNA-processing machinery are present in Placozoa (Srivastava et al. 2008), suggesting that microRNA may have been secondarily lost in this group. Once the microRNA-processing machinery was in place, different microRNAs have been gained in different animal lineages, and it has been inferred that, once present, they are only very rarely lost (Tarver et al. 2013). A low level of homoplasy would make the presence or absence of particular microRNAs highly informative phylogenetic markers. As taxonomic sampling has improved, however, it has become increasingly clear that microRNAs, like many other characters, are more homoplastic than initially thought (Fromm et al. 2013). A recent reanalysis of microRNA studies indicates that homoplasy, heterogeneous rates of gain and loss, sampling artifacts, and modeling inadequacy can impact the utility of microRNAs for phylogenetic analysis of animal relationships (Thomson et al. 2014).

Mitochondrial Genomes

The mitochondrial genomes of animals (**Figure 4**) are much smaller than those of closely related eukaryotes (Lavrov 2007), which greatly facilitates their sequencing and assembly. Mitochondrial genome sequences for thousands of animal species sampled across all major animal clades are now available. The evolution of animal mitochondrial genomes is interesting in its own right and can provide phylogenetically informative characters. Although mitochondrial genomes have improved our understanding of the internal relationships of some animal clades, their utility for resolving deeper phylogenetic relationships has been limited. Recent mitochondrial sequence analyses that targeted Bilateria (Bernt et al. 2013) and the root of the animal tree (Osigus et al. 2013a), for example, recovered some well-recognized clades but were poorly resolved at other nodes of particular interest. This was due in part to the very few genes in mitochondrial genomes, which limits the number of available sequence characters (Bernt et al. 2013).

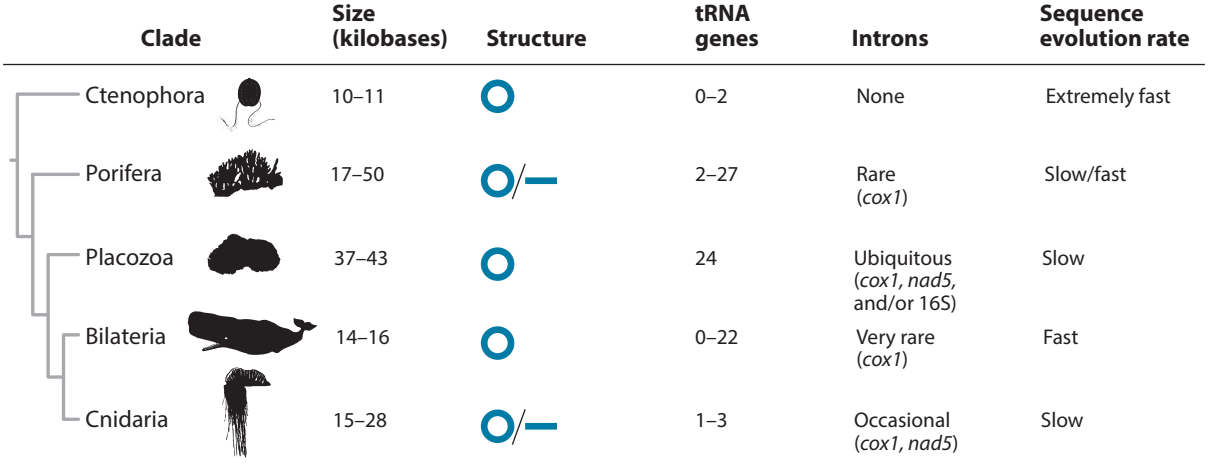

Figure 4

Diversity of mitochondrial genome features, largely from Bernt et al. (2013), Osigus et al. (2013a), Papillon (2004), and references therein. The topology is a simplification of that shown in **Figure 1**. This summary is affected by some outliers within each clade. The poriferan *Clathrina clathrus* is extreme in several respects: it is the only sponge known to have a linear mitochondrial genome, and its mitochondrial genome is much larger (50 kb) than the next largest known for sponges (28 kb). The mitochondrial genome of the chaetognath *Spadella cephaloptera* has no transfer RNA (tRNA) genes (Papillon 2004), whereas most other bilaterians have 22 tRNA genes. In the Structure column, a circle indicates a circular genome organization and a line indicates a linear genome organization The animal images are a subset of those shown in **Figure 1**, which were illustrated by Noah Schlottman and submitted to PhyloPic (**www.phylopic.org**). They are available for reuse under the Creative Commons Attribution-ShareAlike 3.0 Unported license.

The size, gene composition, gene order, and other structural features of mitochondrial genomes vary greatly across the animal tree (**Figure 4**). There has been considerable interest in using these features to help resolve animal relationships. As more animal mitochondrial genomes are sequenced, however, it is becoming increasingly clear that many of these structural characters exhibit extensive homoplasy (Lavrov 2007, Stöger & Schrödl 2013). Animal mitochondrial genomes have at least a fivefold variation in size, from ~10 kb in a ctenophore (Pett et al. 2011) to >50 kb in a sponge (Lavrov et al. 2013). Mitochondrial genomes have different shapes (circular versus linear), gene composition, gene order, and gene orientations. There have been at least two independent shifts from circular to linear mitochondrial genomes, one in Medusozoa (Kayal et al. 2012), a subclade of Cnidaria, and another in Porifera (Lavrov et al. 2013).

Differential gene loss is a major structural feature of animal mitochondrial genomes. There are several categories of mitochondrial genes: protein-coding genes, ribosomal RNA (rRNA) genes, and transfer RNA (tRNA) genes. Animal mitochondrial genomes have a relatively small number of protein-coding genes, and some have been lost in particular groups but retained in others (Lavrov 2007). There have also been a small number of gene gains in animal mitochondrial genomes (Bilewitch & Degnan 2011). The evolution of tRNA content has been particularly dynamic (**Figure 4**), with multiple reductions in tRNA number and important implications for changes in the mitochondrial genetic code (Lavrov 2007). The evolutionary history of introns in animal mitochondrial genomes is also complex (**Figure 4**). Mitochondrial introns have not been found in ctenophores, whereas all sequenced placozoans do have mitochondrial introns. Mitochondrial introns are found within isolated clades in other animals: within Hexacorallia in Cnidaria, within Homoscleromorpha in Porifera, and within an annelid (*Nephtys* sp.) in Bilateria (Vallès et al. 2008). The variation of sponge mitochondrial genomes is particularly striking

(Lavrov 2007, Osigus et al. 2013a, Wörheide et al. 2012), and this variation may be informative for resolving difficult internal phylogenetic relationships in this group.

THE EARLY FOSSIL RECORD OF ANIMALS

Most major lineages of animals first appear in the fossil record in the Cambrian (**Figure 5**), and the compression of most of these first appearances between 541 (the base of the Cambrian) and 520 million years ago (Ma) is the empirical basis for the Cambrian explosion. Some shell-bearing animals such as molluscs first appear among so-called small shelly fossils in the earliest Cambrian. Chaetognaths appear as the first biomineralized protostomes, represented by protoconodonts in rocks as old as 535 Ma (Kouchinsky et al. 2012). Other biomineralized bilaterian animal groups such as arthropods and echinoderms are first represented in the body fossil record in Cambrian Stage 3 (about 520 Ma). For some groups, such as arthropods and priapulids, trace fossils provide evidence for earlier origins than body fossils do, in this case extending back to near to the base of the Cambrian (Vannier et al. 2010). The discrepancy between when nonbiomineralized groups appear in the body fossil and trace fossil records suggests a preservational bias in the former, constrained by the appearance of conditions that favor the preservation of soft anatomy as carbonaceous compressions, known as Burgess Shale–type preservation (Gaines et al. 2008). The combined knowledge from body and trace fossils, however, provides a coherent picture of rapid animal diversification in the early Cambrian.

The search for stem- or crown-group animals in the Neoproterozoic has long focused on macrofossil remains from between approximately 575 and 541 Ma, in the Ediacaran Period, and the identification of particular Ediacaran fossils as metazoans continues to have its advocates. For example, recent arguments have been made that *Dickinsonia* is a placozoan-grade animal (Sperling & Vinther 2010), *Kimberella* is a mollusk (Fedonkin et al. 2007), *Eoandromeda* is a ctenophore (Tang et al. 2011), and *Thectardis* is a sponge (Sperling et al. 2010). None of these metazoan identifications has been emphatically embraced. Paleontologists are split over whether most if not all Ediacaran macrofossils represent extinct clades allied to each other rather than metazoans or include a phylogenetically varied assemblage of animal stem-groups (Xiao & Laflamme 2009).

The discovery of microfossils of Ediacaran age from the Doushantuo Formation in China (Xiao et al. 1998) led to identifications of animals dating back at least 580 million years. Doushantuo fossils have been assigned to various cnidarian groups, to Demospongiae on the basis of putative spicules (later reinterpreted as abiogenic), and to Bilateria. Metazoan interpretations of Doushantuo fossils have received criticism because putative anatomical structures have been subjected to extensive taphonomic alteration (Cunningham et al. 2012). The interpretation of putative embryos has been especially contentious, as these fossils have been identified as stem- or crown-group metazoan embryos, algae, bacteria, or protists (Huldtgren et al. 2011).

Other kinds of biochemical and paleontological data have been cited as evidence for Neoproterozoic animals. Sterane biomarkers have been argued to indicate the existence of Demospongiae in the Cryogenian (Love et al. 2009), vastly predating the first reliable sponge spicules in the early Cambrian. Caution has been urged regarding this interpretation, because other organisms, including algae, can produce these compounds (Antcliffe 2013). Another proposed indicator of metazoans in the Ediacaran is acritarchs known as large ornamented Ediacaran microfossils, some of which have been interpreted as the encysted resting stages of Metazoa (Cohen et al. 2009). These acritarchs have a temporal range from approximately 635 to 560 Ma. Their precise affinities are unclear and appear to be phylogenetically varied (Liu et al. 2014), although some of these ornamented acritarchs encase the embryo-like Doushantuo fossils discussed above (Yin et al. 2007). This association bolsters the case that such acritarchs may be egg cysts.

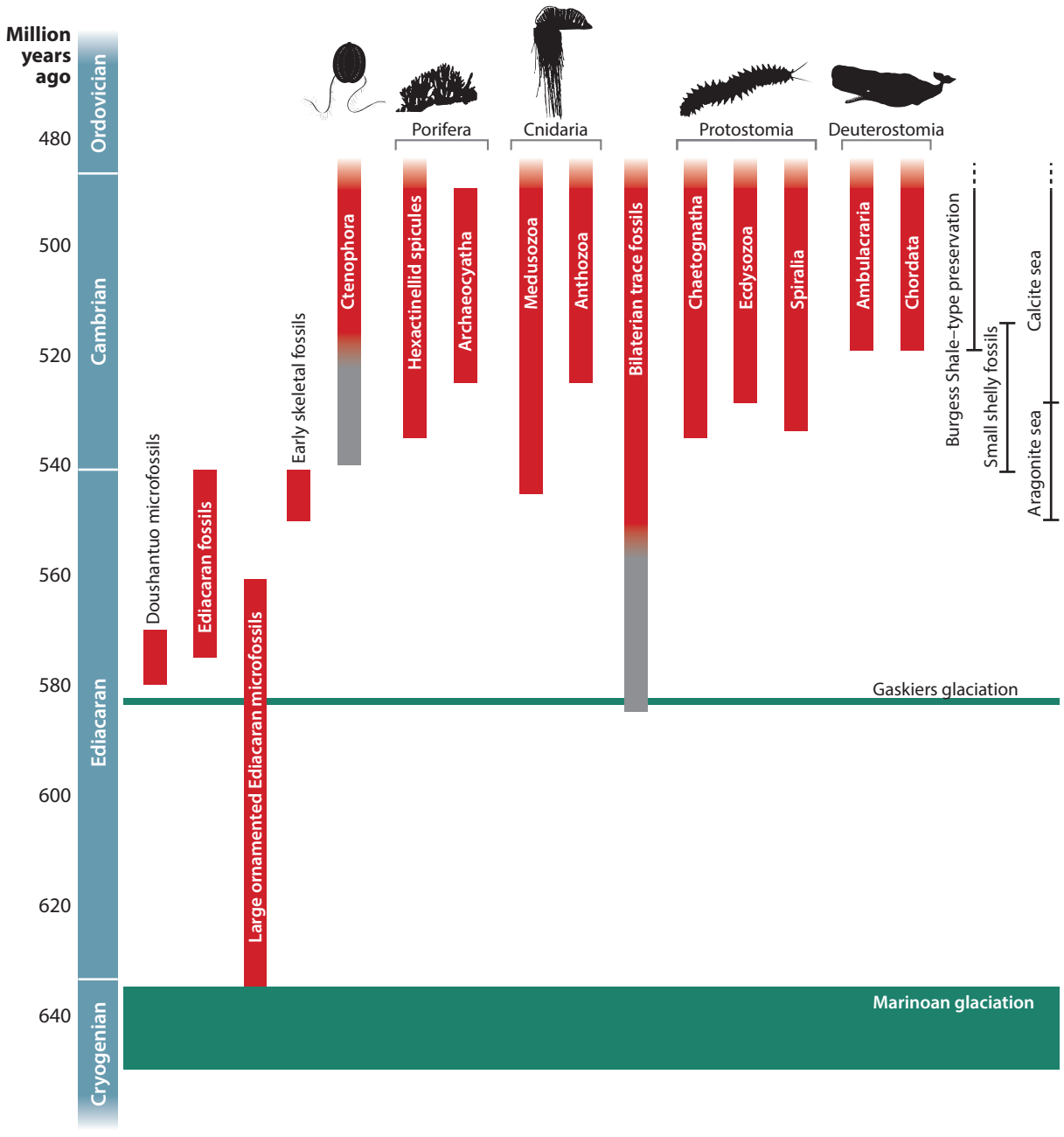

Figure 5

Chronogram for the Late Cryogenian through the Cambrian, showing reliable first appearances of major animal groups (*red bars*), styles of fossil preservation, and relationships to key events in Earth's history. Gray shaded bars indicate date ranges established by fossils of uncertain affiliation. The animal images are a subset of those shown in **Figure 1**, which were illustrated by Noah Schlottman and submitted to PhyloPic (**www.phylopic.org**). They are available for reuse under the Creative Commons Attribution-ShareAlike 3.0 Unported license.

Molecular evidence that early animal lineages diverged long before they appeared in the fossil record (Erwin et al. 2011) bears fundamentally on rates of evolution in the Cambrian explosion. It has been supposed that condensing the basal animal radiation into the relatively narrow Ediacaran–early Cambrian window suggested by the fossil record (i.e., accepting the Cambrian explosion as broadly accurate rather than an artifact of fossils failing to preserve the diagnostic characters of more ancient lineages) would require prohibitively fast rates of morphological and molecular evolution. On the contrary, relaxed clock analyses of arthropods suggest that accelerating molecular and morphological character evolution in the latest Ediacaran through middle Cambrian by a few times faster than background rates over the past 500 million years is sufficient to account for observed branch lengths (Lee et al. 2013) without having to infer a lengthy extent of time in the Neoproterozoic for which fossil data are entirely lacking.

The generally endorsed framework for animal diversification predicts Neoproterozoic divergences and Cambrian radiation (Erwin et al. 2011). This temporal interval corresponds to a time of profound changes in ocean and atmospheric chemistry, in climate, and in paleogeography (reviewed by Erwin & Valentine 2013). For example, hypotheses involving animal origins in the Cryogenian, as predicted by many molecular dates, require these lineages to have persisted through geographically widespread Neoproterozoic glaciations (**Figure 5**). Ediacaran sediments also record massive fluctuations in carbon isotopes, including some long-lasting anomalies (Grotzinger et al. 2011), and the organic carbon curve remained volatile through the early Cambrian. Calcium concentrations in the oceans display another important geochemical trend through the main burst of the Cambrian explosion, one that has a clear consequence for animal skeletons. The early Cambrian witnessed a severalfold increase in oceanic calcium, which coincided with a proliferation of skeletonized animals (Kouchinsky et al. 2012). A shift in magnesium-to-calcium ratios in seawater in the early Cambrian has come to be known as a transition from an aragonite sea to a calcite sea (Porter 2007). This transition is reflected in the polymorph of calcium carbonate that animals used to biomineralize and is marked by a shift from small shelly fossils in Cambrian Stages 1 and 2 having principally aragonitic skeletons to the largely coincident appearances of groups having calcitic exoskeletons (echinoderms, calcareous brachiopods, and calcareous sponges) at the base of Cambrian Stage 3 (**Figure 5**).

AN INTEGRATED VIEW OF ANIMAL EVOLUTION

The open questions in animal phylogeny are now well defined thanks to progress made in many other regions of the tree, and there are clear ways forward to attempt to resolve them. Further advances will come from the efficient utilization of new data acquisition approaches, improved taxonomic sampling (perhaps including the discovery of previously unknown animal lineages), and analytical methods designed specifically to address the challenges posed by the data now available. Greatly expanded genome sequencing and analysis will likely play a central role in addressing open questions in deep animal phylogeny (GIGA Community of Scientists 2014). In addition to resolving how animal species are related to each other, answering such questions will provide a much more nuanced view of genome evolution. The minimal gene set of the most recent common ancestor of animals is already much larger than had been anticipated. In some cases, genes that were thought to first arise well within animals (associated with specific clades and characters) actually precede the radiation of animals.

Broad sampling of genomic, morphological, and functional data across animals is critical to understanding animal evolution because, along with a well-resolved animal phylogeny, it allows us to reconstruct the series of evolutionary changes that led to the diversity of animals. The extensive homoplasy that is now apparent in the animal tree indicates that many animals that are simple in

some respects, such as nervous system structure or cell number, are complex in other respects, such as genome composition. The entirely artificial construct of higher and lower animals is long past its useful sell-by date.

As this review shows, many traits once thought to be highly conserved are quite variable across different body plans in the animal tree. This realization should not come as too much of a surprise. Most early attempts to resolve animal phylogeny presumed that it was difficult to gain or lose characters such as segmentation, nervous systems, and coelomic cavities and constructed trees that attempted to minimize changes in these characters. This endeavor was guaranteed to lead to the simplest possible evolutionary history for these traits but was not really an independent test of the history of these characters. As additional data and analyses have come to robustly support trees that contradict aspects of these simple scenarios, it is now increasingly apparent that the evolutionary histories of complex characters can themselves be quite complex.

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