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A modern look at the Animal Tree of Life*

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Abstract

The phylogenetic interrelationships of animals (Metazoa) have been elucidated by refined systematic methods and by new techniques, notably from molecular biology. In parallel with the strong molecular focus of contemporary metazoan phylogenetics, morphology has advanced with the introduction of new approaches, such as confocal laser scanning microscopy and cell-labelling in the study of embryology. The discovery of new animal diversity (previously unknown groups like Cycliophora and Micrognathozoa) has invigorated the field as well. At present, broad consensus exists for the monophyly of bilaterian animals, a split of Bilateria into Deuterostomia and Protostomia, a division of protostomes into a clade of mostly spiral cleavers (Lophotrochozoa) and a moulting clade (Ecdysozoa), a 'restricted' deuterostome hypothesis that excludes the lophophorate phyla, and a basal position of acoel and nemertodermatid flatworms within Bilateria. However, the position of several protostome phyla, especially Bryozoa and Chaetognatha, remains intractable. Phylogenomic approaches such as Expressed Sequence Tags are showing much promise for resolving ongoing controversies at the base of the animal tree, especially the branching pattern among ctenophores, sponges and cnidarians.

Key words: Animals, Ecdysozoa, Expressed Sequence Tags, metazoa, phylogeny, Spiralia, systematics

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> The great tree of life which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications.
>
> C.R. Darwin (1859)

The setting

The great tree of life, which shows the evolutionary relationships among all organisms, is one of the most powerful metaphors for biologists. One of the first and, remarkably, most explicit of such trees was presented by German zoologist Ernst Haeckel (1866), but the exact shape of the tree of life has remained elusive. The relationships of some groups of organisms have been well resolved and uncontroversial since the dawn of Evolutionary Biology, while the placement of other groups has remained entirely enigmatic or even subject to strongly supported but conflicting results across studies. Our focus here is on a large branch that has been particularly problematic, but is of central interest—the relationships among the major groups of animals, a group of multicellular eukaryotes also known as Metazoa (Haeckel 1874). Specifically, we explore the implications of recent phylogenetic findings based on large datasets for the evolution of key developmental and morphological characters across the group. We also briefly discuss the application of previously defined node-based name for the metazoan clade Lophotrochozoa in light of remaining phylogenetic uncertainty.

Modern zoology has come a long way in providing evidence for our current understanding of animals and the way they function in their environments. A series of disciplines, including embryology and anatomy, as well as techniques, including light and transmission electron microscopy, have played key roles in the development of 19th and 20th Century zoology, well after Swedish biologist Carl von Linné established his taxonomic system (Linnaeus 1758). Linné recognized six ranks (kingdom, class, order, genus, species and variety—he did not propose the rank of phylum), and one of his three kingdoms, Animalia, consisted of 6 classes: Amphibia, Aves, Mammalia, Pisces, Reptilia, Insecta, and Vermes, the latter divided into Intestina, Mollusca, Testacea, Lithophyta and Zoophyta. It is this classification of animals that has been under revision ever since.

Two ancillary scientific disciplines in particular, both developed in the second half of the 19th Century, have provided a framework and rich set of tools for the integration of all other findings in an evolutionary context. The first is *cladistics* (understood in a broad sense), a way of evaluating and comparing phylogenetic hypotheses formulated on the basis of shared evolutionary novelties. Cladistics allowed an examination of diverse sets of characters (morphological, behavioral, or others) by taking their evidence into simultaneous consideration when evaluating competing phylogenetic trees. The second is *molecular biology*, which enables the examination of organisms at the level of genes and gene products and provides the opportunity to collect many more character data relevant to discerning among competing phylogenetic hypotheses than have ever been available. Molecular sequence data allow for what we could term *naïve* phylogenetic assessment, while dramatically increasing the amount of phylogenetic information available to study animal relationships. It is in this latter respect and the role that molecular data are playing in reconstructing the Animal Tree of life that we will concentrate on for this review.

The Animal Tree of Life—molecules and history

It was barely two decades ago that the first molecular biologists used sequence data from ribosomal RNAs to produce phylogenetic trees of selected animals (Field *et al.* 1988; Lake 1989; 1990). These were by no means the first animal phylogenies proposed, but the first cladistic hypotheses for all major animal lineages based on parsimony analysis of a morphological character matrix were actually subsequent to the publication of the molecular trees (Meglitsch and Schram 1991; Schram 1991; Eernisse *et al.* 1992). Nonetheless, morphology-based hypotheses had dominated our views of animal phylogeny for decades, but were plagued by a major lack of consensus on the one hand (see a summary of earlier hypotheses in Eesnisse *et al.* 1992), and by using groundplans as terminals on the other hand (see Prendini 2001 for a thorough discussion on this topic), which often resulted in strong disagreement among the position of certain key taxa. Several more refined cladistic hypotheses were published based on new morphological matrices in the following years (e.g., Nielsen *et al.* 1996; Zrzavý *et al.* 1998, 2001; Sørensen *et al.* 2000; Nielsen 2001; Zrzavý 2003; Jenner and Scholtz 2005), or on a combination of these morphological matrices with subsets of molecular characters (e.g., Zrzavý *et al.* 1998, 2001; Giribet *et al.* 2000; Peterson and Eernisse 2001; Zrzavý 2003; Glenner *et al.* 2004). These sets of characters and publications constitute, undoubtedly, key references to be considered in the study of modern zoology, but they are substantially outnumbered by a vast literature examining relationships of animals based solely on molecular data.

Why are molecular papers examining animal relationships so abundant in the modern literature? On the one hand, molecular data are now—and have been for a while—much easier (and nowadays also less expensive) to obtain than morphological data. In addition, molecular data can be collected by individuals without previous experience or detailed knowledge on a given group of organisms. This has advantages, such as lowering the barrier for new investigators to make novel contributions to the field and allowing for economies of scale across taxa. But it also has disadvantages, such as reducing the time available that a scholar can dedicate to building expertise in biological details unique to their organisms because mastering molecular skills that, while valuable for inferring relationships, reveal little else about the organisms' biology. Regardless, it is also clear that the amount of molecular information continues to grow at a much faster rate than the amount of morphological information, this being driven largely by technological developments in DNA sequencing and other molecular methods. For example, the phylogeny of the genus *Drosophila* can now be estimated from 12 complete genomes (Clark *et al.* 2007—12 *Drosophila* Genome Consortium).

Molecular phylogenetic analyses of metazoan relationships have come a long way since the seminal article of Field *et al.* (1988). Since then, major advances have been the addition of numerous unsampled phyla (e.g., Halanych *et al.* 1995; Winnepenninckx *et al.* 1995, 1998; Bourlat *et al.* 2003; Giribet *et al.* 2004; Park *et al.* 2006), and molecular data are now available for at least one species of each animal phylum. Other developments include the analysis of multiple loci per taxon obtained through Polymerase Chain Reaction (PCR) (e.g., Giribet 2003; Peterson *et al.* 2004; Rokas *et al.* 2005) to the more sophisticated *phylogenomic analyses* (Blair *et al.* 2002; Dopazo *et al.* 2004; Wolf *et al.* 2004; Philip *et al.* 2005) and Expressed Sequence Tags (EST)-based phylogenies (Philippe *et al.* 2005, 2007; Bourlat *et al.* 2006; Marlétaz *et al.* 2006; Matus *et al.* 2006a; Webster *et al.* 2006). Some of these analyses have considered absence/presence of more than 3,000 genes (Dopazo *et al.* 2004).

Another area where molecular phylogenetics has been instrumental is in the attention focused on the phylogenetic relationships within each of the major animal phyla. Naming all these studies for each phylum would go beyond the number of pages allocated to this review. The reader could easily be referred to the pages of journals such as *Cladistics*, *Journal of Molecular Evolution, Molecular Biology and Evolution, Molecular Phylogenetics and Evolution, Nature, PNAS, Science, Systematic Biology,* and *Zoologica Scripta*, among others. Several of these studies have recently been reviewed by Giribet (in press).

The Animal Tree of Life—morphology and new developments

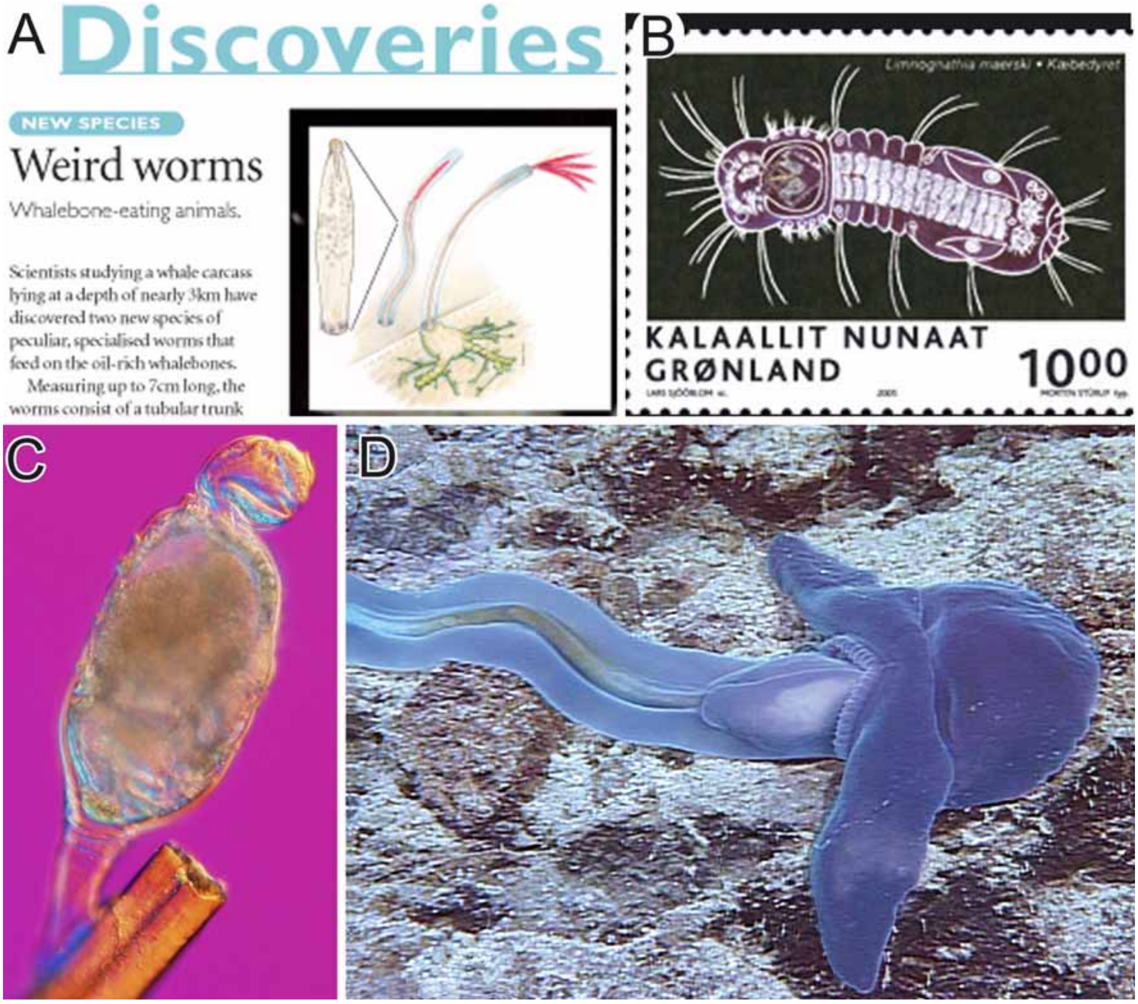
While molecular phylogenetics first, and phylogenomics more recently, have revamped the scientific attention paid to animal phylogenies in a way perhaps not seen since the introduction of the transmission electron microscope, novel techniques for studying the anatomy of animals and their development have also flourished in the past decade or so. This has led to large advances in our understanding of phylogenetically informative character data, which are a great asset when evaluating new hypotheses suggested by molecular data. One such developments is confocal laser scanning microscopy and its application to the study of the development of musculature (e.g., Wanninger and Haszprunar 2002a; b; Müller and Schmidt-Rhaesa 2003; Müller *et al.* 2004; Müller and Sterrer 2004; Worsaae and Müller 2004; Leasi *et al.* 2006) and nervous systems (e.g., Hessling *et al.* 1999; Hessling and Purschke 2000; Müller and Westheide 2000, 2002; Wanninger and Haszprunar 2003; Maxmen *et al.* 2005; Wanninger *et al.* 2007; Zantke *et al.* 2007) with the aid of specific antibodies. These studies have helped towards postulating novel hypotheses of relationships while adding a new dimension to our understanding of fundamental organ systems and their evolution in animals. For example, Hessling and Westheide (2002) provided the first evidence for a serially repeated nervous system in Echiura, an indication that they are derived from segmented ancestors.

Developmental biology, combined with molecular techniques for gene expression patterns, has also provided important insights into basic concepts such as homology of body parts, symmetry, and others (Panganiban *et al.* 1994; Panganiban *et al.* 1995; Panganiban *et al.* 1997; Seaver *et al.* 2001; Wanninger and Haszprunar 2001; Lee *et al.* 2003; Kusserow *et al.* 2005; Martindale 2005; Seaver *et al.* 2005; Matus *et al.* 2006b; Matus *et al.* 2007a; Matus *et al.* 2007b). Classical embryology has also benefited from new techniques for marking specific cells, allowing high-resolution fate-maps (e.g., Boyer *et al.* 1996; 1998; Henry and Martindale 1998; Henry *et al.* 2004; Maslakova *et al.* 2004b; Hejnol *et al.* 2007). 4D-microscopy has allowed following the fate maps for species where injection techniques are not feasible (Schnabel *et al.* 1997; Hejnol and Schnabel 2005, 2007; Hejnol *et al.* 2006).

Another area of growth is the study of embryogenesis and larval development in animals of special interest—this being due to their potential phylogenetic implications or their novel morphologies and habitats. Some examples come from the recent interest in the development of aplacophoran molluscs (Okusu 2002; Nielsen *et al.* 2007) as a source of data to address questions about putative segmentation in molluscs (Giribet *et al.* 2006), or the homology of ciliary bands among spiralian larvae (Rouse 1999; Maslakova *et al.* 2004a; b).

Although studied for more than a century, after the pioneering work of Gustaf Retzius (see Afzelius 1995) and Franzén (1955), sperm ultrastructure has continued to provide phylogenetically-informative characters due to the large amount of data amassed for virtually all metazoan groups (see for example Jamieson *et al.* 1995). Some classic sperm-based groupings have been corroborated by new sources of character data, e.g., DNA sequence data (Abele *et al.* 1989) and mitochondrial gene order (Lavrov *et al*. 2004) in the case of pentastomids and fish lice (Wingstrand 1972).

Finally, the discovery of new forms of animal life in the past decades (Funch and Kristensen 1995; Kristensen and Funch 2000; Klass *et al.* 2002; Rouse *et al.* 2004; Holland *et al.* 2005; Voight 2005) has also contributed to broadening general interest in zoology. These discoveries, in addition to their broad impact on the field, have often had broad media coverage, helping to make scientific discovery available to the public (Figure 1).


Discoveries

NEW SPECIES

Weird worms

Whalebone-eating animals.

Scientists studying a whale carcass lying at a depth of nearly 3km have discovered two new species of peculiar, specialised worms that feed on the oil-rich whalebones.

Measuring up to 7cm long, the worms consist of a tubular trunk

FIGURE 1. Recently discovered and unusual animals. (A) Press coverage of the discovery of the bone-eating worm *Osedax* (for details see Rouse and Pleijel, this volume). (B) Greenland stamp after the discovery of Micrognathozoa. (C) Detail of the cycliophoran *Symbion pandora* (photograph courtesy of Peter Funch). (D) An undescribed deep-sea lophenteropneust (photograph courtesy of Nick Holland [see Holland *et al.* 2005]).

Recent consensus on the Animal Tree of Life

Although several questions regarding the branching pattern of the Animal Tree of Life remain unanswered, agreement has been reached for several nodes that receive support from a variety of sources of data and analyses. One such hypothesis is presented in Figure 2.

Although the traditional hypotheses radial/bilateral symmetry, axis polarity, and diploblasty/triploblasty have been called into question (Martindale *et al.* 2002; Martindale *et al.* 2004; Martindale 2005; Dunn 2005), the Animal Tree of Life shows strong evidence for the monophyly of Bilateria (= Triploblastica) (Figs. 4, 5), leaving the phyla Porifera (Fig. 3A), Cnidaria (Figs. 3B, C), Ctenophora (Fig. 3D) and Placozoa outside of this clade, and with uncertain affinities.

Current views of the relationships among Bilateria have benefited greatly from molecular data that have resolved some relationships that appeared intractable from a morphological perspective. Several recent reviews have attempted to summarize what we know, and what we have yet to solve, with respect to animal phylogeny (Cavalier Smith 1998; Giribet 2002; 2003; Halanych 2004). While these reviews were molecular-centred, and differed considerably from equally modern morphologically-oriented views (Nielsen 2001; but see Jenner and Scholtz 2005 for less-resolved hypotheses based on morphology), they were based on analyses of single or few genes, often the same genes being used in different studies. Most of these studies agree on (a) the monophyly of Bilateria, (b) the presence of a clade of mostly spiralian protostomes often referred to as

Lophotrochozoa (Halanych *et al.* 1995), (c) the existence of a clade of moulting animals, or Ecdysozoa (Aguinaldo *et al.* 1997), which unites panarthropods with the bulk of 'Aschelminthes', (d) a 'restricted' deuterostome hypothesis containing *Xenoturbella* (Fig. 4A), the chordate phyla, and with hemichordates (Fig. 4B) as sister to echinoderms (Fig. 4C) as Ambulacraria (Bourlat *et al.* 2003), but excluding the lophophorate phyla

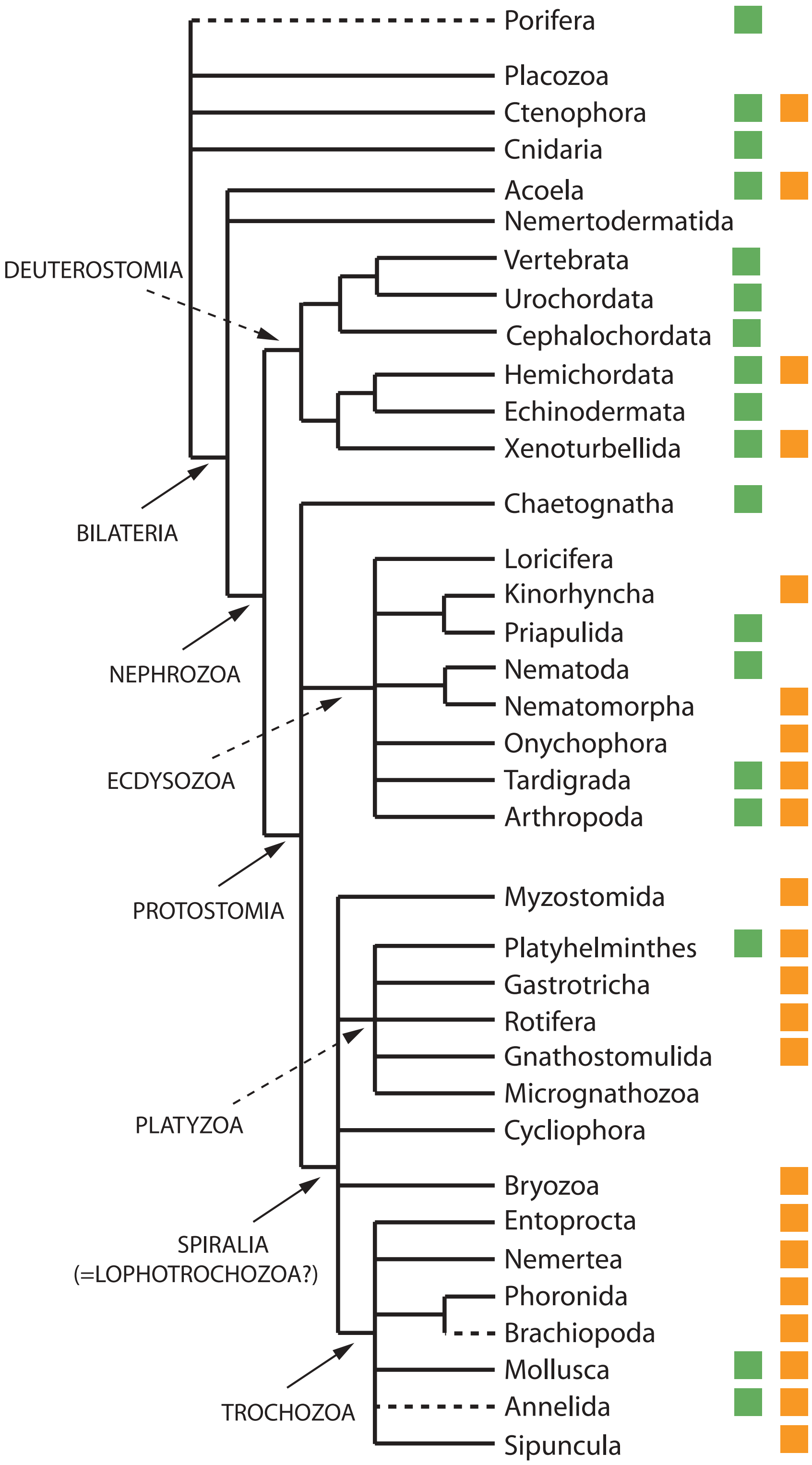


FIGURE 2. Conservative hypothesis of metazoan relationships summarizing findings up to 2007. Green squares indicate genomic/EST data available. Orange squares indicate ESTs generated by the authors and other participants in the NSF-funded Assembling the Protostome Tree of Life project (Dunn *et al.* submitted).

(Fig. 5C), and (e) the basal position of acoels and nemertodermatids as sister to all other bilaterians or Nephrozoa (Ruiz-Trillo *et al.* 1999; Jondelius *et al.* 2002). Another clade of non-ecdysozoan protostomes that groups diverse mostly acoelomate phyla (platyhelminths [Fig. 5A], gastrotrichs, gnathostomulids, rotifers, micrognathozoans), named Platyzoa (Fig. 2) (Cavalier Smith 1998; Giribet *et al.* 2000), has not found uniform support across different studies. Also, the internal relationships within major recognized clades has remained contentious. For example, the sister-group relationship of the largest phylum, Arthropoda, is still debatable (e.g., Telford *et al.* 2005; but see Mallatt and Giribet 2006 for a tree providing strong support for Panarthropoda (= arthropods, onychophorans [Fig. 5I] and tardigrades) but not for the precise sister group of arthropods). Likewise, the composition, phylogeny and sister-group relationships of annelids (Fig. 5G) are still fiercely debated (Eeckhaut *et al.* 2000; Zrzavý *et al.* 2001; Bleidorn *et al.* 2007; Rousset *et al.* 2007; Struck *et al.* 2007; Rouse and Pleijel this volume). The monophyly and sister-group relationship of molluscs (Fig. 5F)—to provide just another example of a large phylum—and the relationships among its eight classes, remain among the most challenging phylogenetic problems that molecular phylogeneticists have faced (Winnepenninckx *et al.* 1996; Passamaneck *et al.* 2004; Giribet *et al.* 2006). Broader (deep) relationships among protostome phyla remained even more intractable (Winnepenninckx *et al.* 1995; Giribet *et al.* 2004; Peterson and Butterfield 2005; Rokas *et al.* 2005; Telford *et al.* 2005; Mallatt and Giribet 2006; Park *et al.* 2006; Passamaneck and Halanych 2006) despite considerable efforts in increasing sampled diversity and number of loci. A few exceptions are several recognized pairs of sister phyla, based on morphology, that also receive strong molecular support, such as Kinorhyncha + Priapulida (Fig. 5H), Nematoda + Nematomorpha, paraphyly of Rotifera with respect to Acanthocephala, and the relationship of Phoronida (Fig. 5C) with Brachiopoda—with the former sometimes nested within the latter.

This panorama looks even worse when several ‘minor’ phyla are considered, such as Bryozoa (=Ectoprocta), Chaetognatha (Fig. 5J), Cycliophora (Fig. 1C), Entoprocta (Fig. 5D), and Myzostomida (Fig. 5E). Their membership to even the larger clades is uncertain. Two of these phyla, Bryozoa and Chaetognatha have received special attention. Although chaetognaths were traditionally placed within Deuterostomia, it is now clear that they are more closely related to protostomes, although whether they are the protostome sister group or part of the ingroup is still unsolved (Ghirardelli 1995; Giribet *et al.* 2000; Kapp 2000; Shimotori and Goto 2001; Helfenbein *et al.* 2004; Papillon *et al.* 2004; Ball and Miller 2006; Marlétaz *et al.* 2006; Matus *et al.* 2006a; Harzsch and Müller 2007). Even more problematic is the case of Bryozoa, because they were used to define the node-based clade Lophotrochozoa (Halanych *et al.* 1995) and their uncertain position makes this name a synonym of Protostomia, Spiralia, or Trochozoa, depending on whether they are sister to all other protostomes (Giribet *et al.* 2000; Passamaneck and Halanych 2006), spiralians (Passamaneck and Halanych 2006), or trochozoans (Peterson and Eernisse 2001). More recent analyses of bryozoan relationships cannot discern among the latter two hypotheses, as they did not include Platyhelminthes or other putative platyzoans (Waeschenbach *et al.* 2006).

This ongoing lack of consensus has led some authors to legitimately question whether there is enough information in molecular data to resolve animal relationships (Rokas *et al.* 2005), allegedly due to the temporally compressed radiation of animals postulated to have occurred during the Cambrian explosion. This view has nonetheless been openly criticized as a taxon sampling bias, among other possible factors (Baurain *et al.* 2007).

Phylogenomic data have begun to offer responses to some long-standing phylogenetic questions where other approaches appear to have failed. Early phylogenomic studies corroborated nodes such as Bilateria, Protostomia, or Ecdysozoa despite limited taxon sampling (Philippe *et al.* 2005). The addition of further taxa has stabilized other nodes, such as Deuterostomia and Trochozoa, although ‘suspicious’ results were also reported for the relationships of cephalochordates and echinoderms (Delsuc *et al.* 2006; see Gee 2006), until the deuterostome tree was largely settled by the inclusion of hemichordates (Fig. 4B) and *Xenoturbella* (Fig. 4A) (Bourlat *et al.* 2006). Subsequent analyses added diversity mostly within Ecdysozoa (Webster *et al.*

2006), or for the phyla Chaetognatha (Fig. 5J) (Marlétaz *et al.* 2006; Matus *et al.* 2006a), and Acoela (Philippe *et al.* 2007), although support for the position of the two latter phyla was not strong. By the time the study of Philippe *et al.* (2007) appeared, genomic or EST data were available for Porifera (Fig. 3A) and Cnidaria (Figs. 3B, 3C), among the non-bilaterians, for all the deuterostome phyla (Fig. 4), chaetognaths (Fig. 5J), and six of the ca. 22 protostome (Fig. 4) phyla: three ecdysozoans (arthropods, nematodes, tardigrades) and three spiralians (annelids, molluscs, platyhelminths) (see Fig. 2). The most intensively sampled analyses to date demonstrate that some earlier phylogenomic findings, notably support for a monophyletic group of coelomate animals, Coeolomata (Blair *et al.* 2002; Dopazo *et al.* 2004; Wolf *et al.* 2004; Philip *et al.* 2005), are artifacts of inadequate sampling. Current phylogenies based on EST data corroborate the Ecdysozoa-Lophotrochozoa split within Protostomia (Philippe *et al.* 2005; Marlétaz *et al.* 2006; Matus *et al.* 2006; Longhorn *et al.* 2007; Philippe *et al.* 2007).

Fossil data, especially from Cambrian sites of exceptional preservation, have been integrated into the "New animal phylogeny" and present some important insights into the course of morphological character evolution. In Protostomia, for example, the arthropod stem group has been reinterpreted in terms of segmentation evolving within Ecdysozoa (Budd 2003), Cambrian embryos show developmental mode in the cycloneuralian ecdysozoans (Dong *et al.* 2005; Donoghue *et al.* 2006), and Cambrian scleritome-bearing taxa present unique character combinations within the Lophotrochozoa that bear on the stem-groups of Mollusca and a clade that includes annelids and brachiopods (Caron *et al.* 2006; Conway Morris and Caron 2007).

The base of the animal tree

Most studies have shown or assumed that sponges (Fig. 3A), whether monophyletic or paraphyletic, are the earliest diverging metazoans. The early appearance of sponges in the fossil record, confidently dating back to the Cambrian (Botting and Butterfield 2005) and most probably to the Late Proterozoic (Gehling and Rigby 1996; Li *et al.* 1998; Xiao *et al.* 2000), places them among the oldest of the modern metazoans. In addition to their antiquity, there are several reasons that sponges have been thought to be the earliest diverging lineage of metazoans. For one, the relatively simple organization (i.e., indefinite symmetry, few cell types, highly regulative growth) of the adults of extant sponges is often presented as being representative of the primitive organization of the first multicellular animals. In this view, which is consistent with molecular analyses that resolve sponges as a grade at the base of Metazoa (Peterson and Butterfield 2005), sponges are presented as having diverged prior to the origin of developmental mechanisms that allowed for the more complex morphology of other organisms, and as being living relicts of some of the earliest animals (Sperling *et al.* 2006).

Other unique features of sponges are the lack of intestinal epithelium, digestive parenchyma or any cell population specialized in digestion (Ereskovsky and Dondua 2006). However, many of the developmental mechanisms once thought to be unique to more 'complex' animals, including key signaling and adhesion genes, are known to have been in place prior to the divergence of sponge and eumetazoan lineages (Nichols *et al.* 2006).

The similarities of sponge choanocytes to choanoflagellates, the closest unicellular relatives to metazoans, is also often presented as evidence that sponges are the earliest diverging metazoans (Medina *et al.* 2001; Nielsen 2001; Müller 2003). Both have a collar of microvilli surrounding a flagellum, and the motion of the flagellum creates a current that traps food particles in the microvilli. In traditional treatments of early animal evolution it is presumed that these complex structures are homologous, and were therefore also present in the most recent common ancestor of Metazoa, but subsequently lost along the stem of all non-sponge metazoans. Recent ultrastructural studies of sponge choanocytes and choanoflagellates have, however, indicated that these cells may not be as similar as previously thought, and that collar cells are found in a wider diversity of animals than previously appreciated (reviewed by King 2004). This raises the possibility that they have been independently derived multiple times and do not on their own support the divergence of sponges prior to other metazoans.

The relationships among sponges and the other three non-bilaterian phyla (Placozoa, Cnidaria and Ctenophora) remains enigmatic, although cnidarians (Figs 3B, 3C) and not ctenophores (Fig. 3D) appear as a likely sister group to bilaterians (Medina *et al*. 2001). Others have suggested that *Trichoplax*, rather than Porifera, is the earliest diverging metazoan (Dellaporta *et al*. 2006; Signorovitch *et al*. 2007), with sponges as the sister group to cnidarians, although these studies do not consider ctenophores. Others have considered that the apparent simplicity of *Trichoplax* could be secondarily derived (Miller and Ball 2005). Although frond-like fossils from the Lower Cambrian that are similar to Ediacaran "vendobiont" fronds have been allied to ctenophores (Shu *et al*. 2006), palaeontological data have not clarified the cnidarian-ctenophore-bilaterian question.

At present, then, there is even less certainty regarding the earliest nodes in the metazoan tree of life than there was even a decade ago. Phylogenomic approaches may be able to resolve these relationships. Additional data from sponges and ctenophores are especially critical now that genomes have been released for two cnidarians and *Trichoplax*.

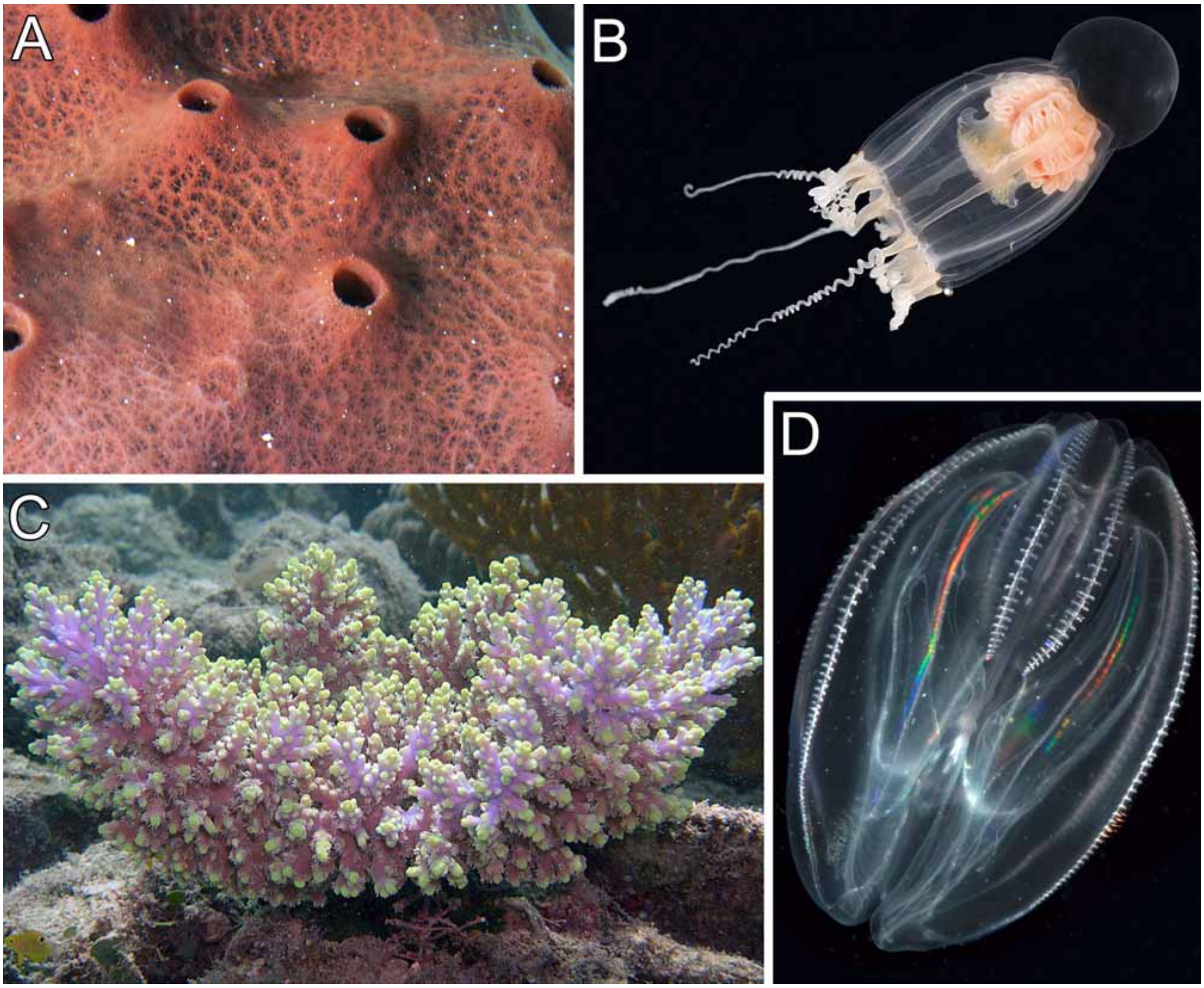


FIGURE 3. Examples of basal metazoans. (A) A species of the sponge genus *Diplastrella* (photograph by G. Giribet). (B) The hydrozoan cnidarian *Leuckartiara octona* (photograph by F. Pleijel). (c) An Indopacific coral *Acropora* sp. (photograph by G.W. Rouse). (d) An invasive ctenophore, *Mnemiopsis leidyi* (photograph by F. Pleijel).

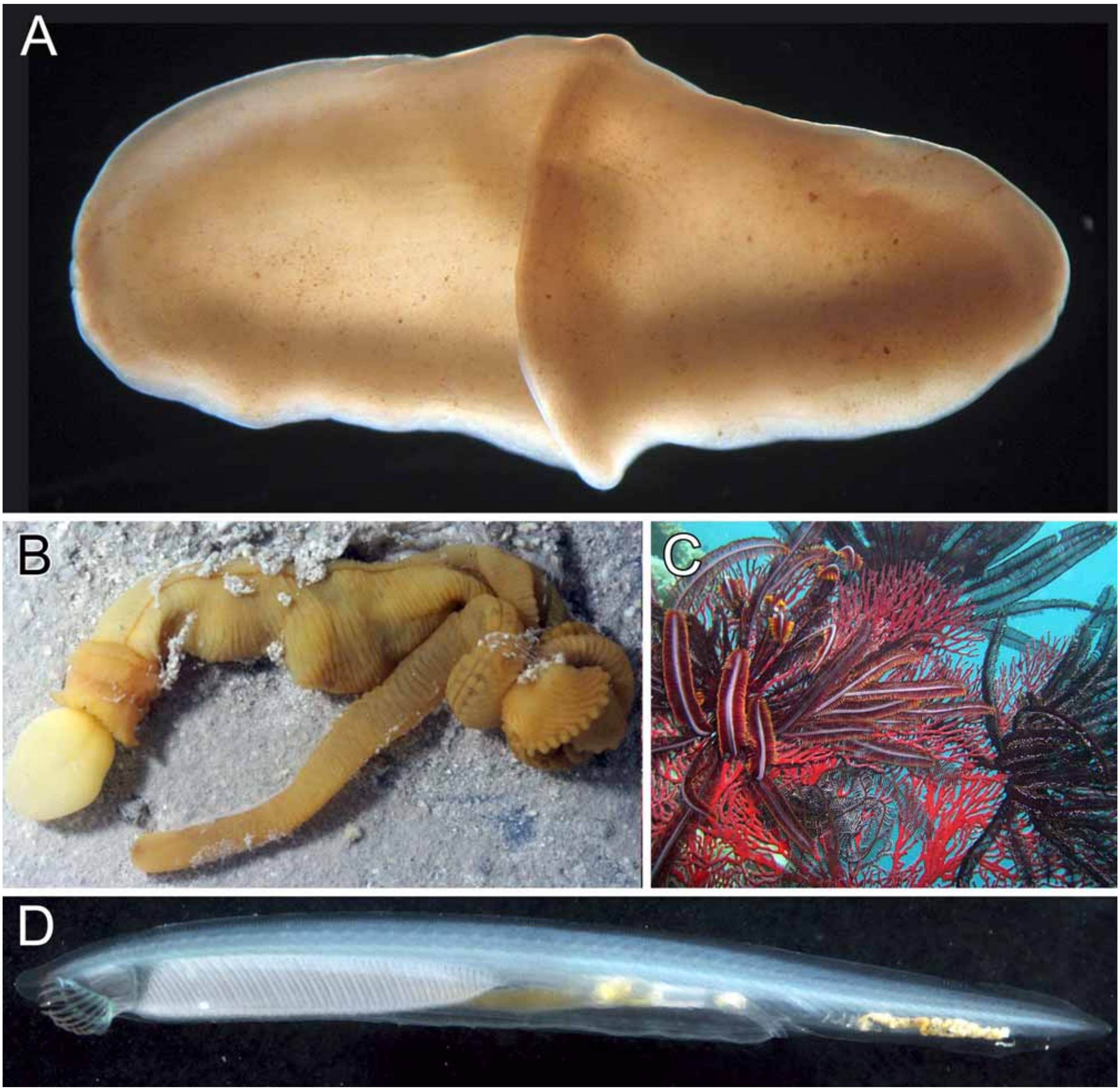
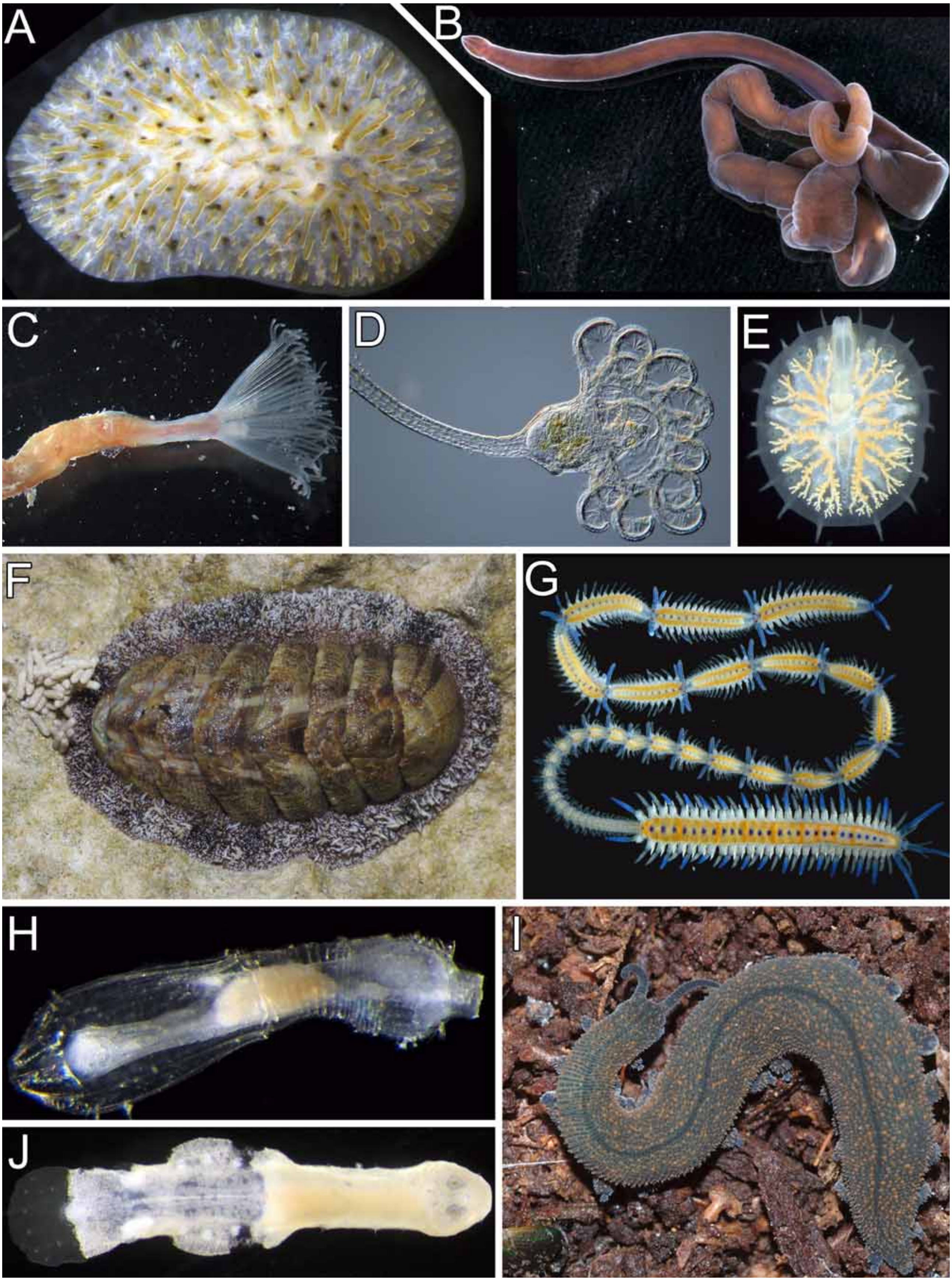


FIGURE 4. Examples of deuterostome animals. (A) The enigmatic *Xenoturbella bocki* (photograph by G.W. Rouse). (B) The hemichordate *Ptychodera bahamensis* (photograph by G. Giribet). (C) Three species of crinoid echinoderms (feather stars) on a gorgonian specimen (photograph by G.W. Rouse). (D) The lancelet *Branchiostoma caribaeum* (photograph by G.W. Rouse).

FIGURE 5. Examples of protostome animals. (A) The free-living platyhelminth *Hoploplana californica* (photograph by G.W. Rouse). (B) An undescribed species of the nemertean genus *Baseodiscus* (photograph by G. Giribet). (C) The phoronid *Phoronis hippocrepia* (photograph by G.W. Rouse). (D) The entoproct *Pedicellina* sp. (photograph by G.W. Rouse). (E) The myzostome *Myzostoma cirriferum* (photograph by G.W. Rouse). (F) The intertidal chiton *Acanthopleura granulata* (photograph by G. Giribet). (G) The polychaete annelid *Myrianida pachycera* with a chain of reproductive stolons (photograph by G.W. Rouse). (H) A juvenile of *Priapulus caudatus* (photograph by G.W. Rouse). (I) The onychophoran *Peripatoides novaezealandiae* (photograph by G. Giribet).(J) A spadellid chaetognath from Belize (photograph by G.W. Rouse).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Bilateria

An ongoing debate has centered in the nature of the so-called *Urbilateria*, the common ancestor of all Bilateria, and whether this was a segmented and complex animal, or a much simpler one without complex organ systems (Balavoine and Adoutte 2003; Baguñà and Riutort 2004). It is currently more widely accepted that the Urbilateria was indeed a simple organism, much like modern acoels or nemertodermatids (Hejnol and Martindale in press). Such an animal would have a simple blind gut and a non-ganglionated nervous system with statocyst-like sensory structures, and a compact body without cavities or excretory organs. At least three bilaterian clades match this definition, including acoels, nemertodermatids and *Xenoturbella* (Fig. 5A). From these, acoels and nemertodermatids have been placed as sister to Nephrozoa (the remainder of Bilateria) (Carranza *et al.* 1997; Ruiz-Trillo *et al.* 1999, 2002; Jondelius *et al.* 2002), although a recent phylogenomic study suggests an alternative position for acoels as a basal deuterostome (Philippe *et al.* 2007), although with low nodal support. Xenoturbellida, despite sharing the morphological attributes of the theoretical Urbilaterian, has been recently, and after a turbulent period, placed within deuterostomes, as sister to Ambulacraria (= Echinodermata + Hemichordata) (Bourlat *et al.* 2003, 2006). The fact that such animals appear at the base of Bilateria or near the base of Deuterostomia in fact reinforces that such simple morphologies may be plesimorphic for Bilateria. We cannot forget that these are the first animals able to disturb sediments three-dimensionally, and therefore we could expect that *Treptichnus pedum*, the trace-fossil that defines the Precambrian/Cambrian boundary (Valentine et al. 1999) was in fact produced by some sort of Urbilaterian with a muscular system.

Protostomia-Deuterostomia

Despite the conflict with traditional treatments of metazoans, the core composition of deuterostomes (Fig. 4) and protostomes (Fig. 5) is now well established (Fig. 2). Deuterostome relationships, as discussed earlier, are well resolved, with minor issues persisting with respect to the relative positions of urochordates and cephalochordates (Fig. 5D) relative to vertebrates (Bourlat *et al.* 2006; Philippe *et al.* 2007). But new discoveries of exquisitely preserved Cambrian fossils are leading to the reinterpretation of the ancestral deuterostome characters, such as the possibility of the possession of gill slits by the most common recent ancestor of Deuterostomia (Shu *et al.* 2001, 2003, 2004). A good understanding of protostome relationships remains more elusive, as discussed earlier. An added difficulty to understanding—and discussion of—protostome relationships is a nomenclatural issue that we aim to clarify here, referring to a clade of mostly spiralian developers often referred to as Lophotrochozoa (Halanych *et al.* 1995).

The original definition of the taxon Lophotrochozoa is quite precise and so allows for the unequivocal delineation of its membership based on a tree topology: "…the last common ancestor of the three traditional lophophorate taxa, the mollusks, and the annelids, and all of the descendents of that common ancestor" (Halanych *et al.* 1995). This was later extended to also include the phyla Platyhelminthes and Rotifera (Aguinaldo *et al.* 1997), though without redefining the name in an unequivocal way. This has resulted in the name Lophotrochozoa being applied in two different ways, a restricted one with reference to trees and the original specifiers, and one with a less precise and more inclusive membership The current widespread use of the name in the latter sense, to designate all non-ecdysozoan protostomes is therefore somewhat problematic, as others have pointed out (Garey and Schmidt-Rhaesa 1998; Giribet 2002). Because there is uncertainty in the placement of Bryozoa (one of the lophophorate specifiers for Lophotrochozoa), the original definition applied to the phylogeny presented here (Fig. 2) designates a large clade that makes Lophotrochozoa a synonym of the older name Spiralia.

The Future of the Animal Tree of Life

The investigation of deep animal evolution is now advancing at a faster pace than at any time in history, due among other factors to the technological developments and to the federal support for large-scale phylogenetic projects, such as the *US National Science Foundation* “Assembling the Tree of Life” program (atol.sdsc.edu) or the *Deutsche Forschungsgemeinschaft* “Deep Metazoan Phylogeny” initiative. But more importantly, the knowledge amassed during the past three centuries is now available to more zoologists than ever through impressive research libraries and the Internet. Two incipient initiatives may actually be good indicators of the healthy state of modern zoology, or at least of its promising future, despite also facing a noticeable biodiversity crisis. The Encyclopedia of Life aims to create a web page/portal for every one of the ca. 1.7 million described species (www.eol.org) while the Biodiversity Heritage Library (www.biodiversitylibrary.org) is currently scanning and making available all the non-copyright taxonomic literature. The possibilities for these two initiatives, currently funded through private foundations, are tremendous. The Animal Tree of Life is more alive than ever. We just need to connect its branches.

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