

# Assembling the lophotrochozoan (=spiralian) tree of life

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The advent of numerical methods for analysing phylogenetic relationships, along with the study of morphology and molecular data, has driven our understanding of animal relationships for the past three decades. Within the protostome branch of the animal tree of life, these data have sufficed to establish its two main side branches, the moulting Ecdysozoa and the non-moulting Lophotrochozoa. In this review, I explore our current knowledge of protostome relationships and discuss progress and future perspectives and strategies to increase resolution within the main lophotrochozoan clades. Novel approaches to coding morphological characters are needed by scoring real observations on species selected as terminals. Still, methodological issues, for example, how to deal with inapplicable characters or the coding of absences, may require novel algorithmic developments. Taxon sampling is another key issue, as phyla should include enough species so as to represent their span of anatomical disparity. On the molecular side, phylogenomics is playing an increasingly important role in elucidating animal relationships, but genomic sampling is still fairly limited within the lophotrochozoan protostomes, for which only three phyla are represented in currently available phylogenies. Future work should therefore concentrate on generating novel morphological observations and on producing genomic data for the lophotrochozoan side of the animal tree of life.

**Keywords:** Metazoa; phylogeny; morphology; phylogenomics; Platyzoa; Trochozoa

## 1. INTRODUCTION

The term ‘Lophotrochozoa’ has become widely used in the modern evolutionary and developmental literature—it refers to a clade of protostome animals, sister to Ecdysozoa. These non-ecdysozoan protostomes comprise a larger number of animal phyla than any other metazoan clade. These are specifically Annelida (with a number of former phyla: Echiura; Pogonophora; Vestimentifera; and perhaps Sipuncula), Brachiopoda, Bryozoa, Chaetognatha, Cycliophora, Entoprocta, Gastrotricha, Gnathostomulida, Micrognathozoa, Mollusca, Nemertea, Phoronida, Platyhelminthes and Rotifera (Giribet 2002; Halanych 2004; figure 1). This amount of phyletic diversity adds up to about half of the extant animal phyla and includes the second largest phylum (Mollusca) and two phyla with some of the largest body plan disparity (Mollusca and Annelida). Although the relationships among these phyla are still controversial—Ecdysozoa versus Articulata issues aside (e.g. see recent reviews in Scholtz 2002; Giribet 2003)—most analyses tend to agree with two views: (i) ‘lophotrochozoans’ may be divided into two main clades and (ii) resolution within these clades is tentative at most. The goals of this article are to review the relationships of the lophotrochozoan<sup>1</sup> phyla succinctly, to establish a current working framework for the main divisions within the clade and to provide insights into how future studies of protostome

phylogeny may be able to advance our understanding of animal relationships.

### (a) *Protostome groups and affinities*

Protostomes are often considered a paraphyletic assemblage of worm-like animals characterized by the presence of a dorsal (or circumoesophageal) brain connected to a ventral longitudinal nerve cord often paired. Developmental characters such as the fate of the blastopore—which often becomes at least the adult mouth—and the mode of mesoderm formation are typical but not enough for diagnosing the clade (Nielsen 2001). The proposal of acoels and nemertodermatids as basal bilaterian members (Ruiz-Trillo *et al.* 1999, 2002; Jondelius *et al.* 2002; but see Philippe *et al.* 2007), preceding the split of protostomes and deuterostomes, renders protostomes paraphyletic. However, neither nemertodermatids nor acoels have a ventral nerve cord (e.g. Raikova *et al.* 2004a,b). The mode of mesoderm formation known in acoels (e.g. Henry *et al.* 2000; not known in nemertodermatids) differs from that of other bilaterians. Finally, the fate of the blastopore has not been described in either acoels (Boyer 1971; Henry *et al.* 2000) or nemertodermatids (Jondelius *et al.* 2004). Under this evidence and the current phylogenetic framework for metazoans, acoels and nemertodermatids are not considered as part of the clade Protostomia for the following discussion. It is true, nonetheless, that many sessile lophotrochozoans have radically altered the structure of their ventral nerve cord along with a modification of the gut, which tends to become U-shaped (Brachiopoda, Bryozoa, Cycliophora, Entoprocta, Phoronida). The nervous

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One contribution of 17 to a Discussion Meeting Issue ‘Evolution of the animals: a Linnean tercentenary celebration’.

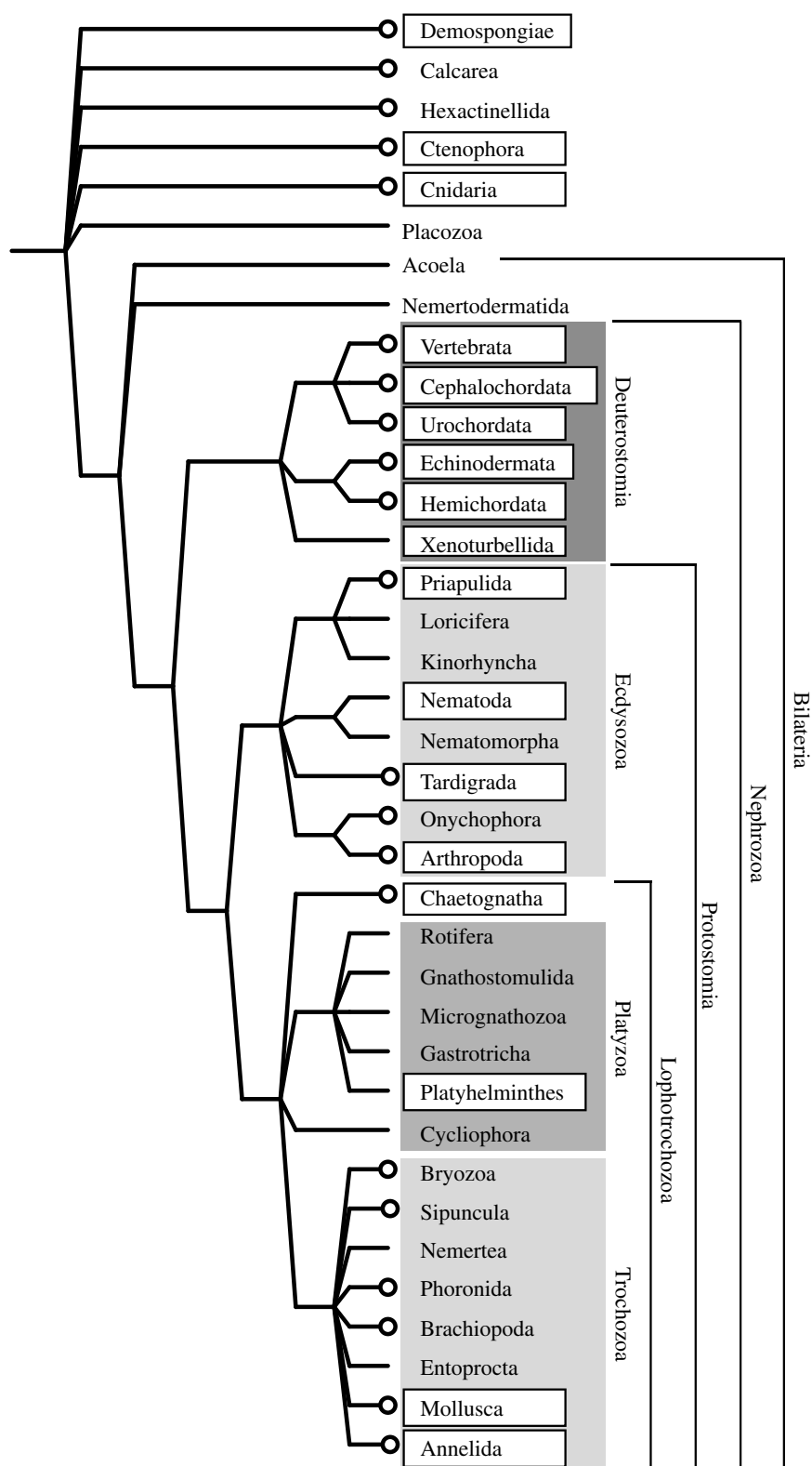


Figure 1. Hypothesis of metazoan relationships based on multiple sources of morphology and molecules. This tree has not been generated by a consensus or other numerical technique and reflects the views and biases of the author. Protostomes are divided into two sister clades, Ecdysozoa and Lophotrochozoa, the latter divided into Platyzoa and Trochozoa; affinities of Chaetognatha and Cycliophora are left unresolved. Boxed phyla are those for which genomic or EST data are publicly available (as of July 2007); note the poor representation of lophotrochozoan genomic data.

system of chaetognaths has recently been compared to that of other protostomes in having a typical circumoral arrangement of anterior CNS (Harzsch & Müller 2007).

Protostomes are the part of a larger clade of bilateral animals, most of which contain some sort of nephridial

structures for excretory purposes—this clade has been termed Nephrozoa by Jondelius *et al.* (2002). Such excretory structures are not known in any members outside the clade, although the case for homology of all nephrozoan excretory organs is contentious (Bartolomaeus & Ax 1992), and again, special excretory



Figure 2. Some extant ‘problematica’—lophotrochozoan representatives of (a) Cyclophora (*Symbion americanus*, photo courtesy of Peter Funch), (b) Chaetognatha (unidentified species from Bocas del Toro, Panama, photo courtesy of Ryan Kerney) and (c) Myzostomida (*Myzostoma cirriferum*, photo courtesy of Greg Rouse). The position of these taxa is highly controversial and awaiting new data and novel approaches to understanding their morphology and phylogenetic position.

organs are present in groups such as nematodes, tardigrades and arthropods, and several other groups lack these organs entirely.

Relationships among the nephrozoan clades have received considerable attention in the recent metazoan literature, although the placement of the nephrozoan root is still a matter of contention and often results in paraphyly of one of its two constituent groups, Protostomia and Deuterostomia (e.g. Giribet *et al.* 2000; Peterson *et al.* 2004). More recently, a few multilocus phylogenetic analyses of metazoan relationships based on ESTs seem to be able to resolve the two nephrozoan clades (Philippe *et al.* 2005, 2007; Delsuc *et al.* 2006; Matus *et al.* 2006), although support for Deuterostomia is more elusive than that for Protostomia. Most recent analyses—at least those based on molecular sequence data—largely agree in the composition of both protostomes and deuterostomes, including the protostomian affinities of chaetognaths (Ball & Miller 2006; Marlétaz *et al.* 2006; Matus *et al.* 2006; figure 1).

Within Nephrozoa, protostomes are now widely recognized to be composed of two large clades, the moulting Ecdysozoa and its sister clade, Lophotrochozoa, also called Spiralia (Giribet 2002) owing to the stereotypical spiral development that occurs only within this clade (Nielsen 2001; Maslakova *et al.* 2004a). Ecdysozoa is currently recognized as monophyletic in most analyses, although some recent genome-wide analyses have questioned the validity of the clade (Blair *et al.* 2002; Dopazo *et al.* 2004; Wolf *et al.* 2004; Philip *et al.* 2005; Rogozin *et al.* 2007)—without doubt, a bias derived, among other aspects, from poor taxon sampling (Philippe *et al.* 2005). Ecdysozoa is discussed in detail in this volume by Telford *et al.* (2008), and therefore will not be dealt with in this paper.

Lophotrochozoa has been suggested to comprise two putative clades, Platyzoa (Cavalier Smith 1998) and Trochozoa (Giribet *et al.* 2000), and the latter a possible extension of Eutrochozoa (Ghiselin 1988; Eernisse *et al.* 1992; Valentine 2004). Admittedly, support for Platyzoa is ambiguous (e.g. Zrzavý 2003; Glenner *et al.* 2004; Todaro *et al.* 2006), as many analyses provide low support for the exact position of the ‘platyzoan phyla’, but most tend to group them in a clade or in a grade. Both major putative clades contain members where the type of development is typically

spiralian (e.g. annelids, molluscs, nemertean and entoprocts within Trochozoa; polyclad flatworms and possibly gnathostomulids (Riedl 1969) within Platyzoa), although this character, as with most other characters within Metazoa, shows homoplasy in the form of secondary reduction—but never as convergence outside the clade. This indicates that any animal with spiral development is an unambiguous member of the clade Lophotrochozoa, although the absence of this type of development does not discriminate against its membership.

Platyzoans are hard to define morphologically. The putative clade contains a series of acoelomate or pseudocoelomate animals—no coelomate belongs to this group—some with a special type of jaws formed of cuticularized rods, or Gnathifera—Gnathostomulida, Micrognathozoa and Rotifera (Kristensen & Funch 2000; Sørensen 2003). Platyzoa also includes other types of flat worms, including Platyhelminthes and Gastrotricha (but see Zrzavý 2003 for an alternative position of gastrotrichs as sister to Ecdysozoa). With the exception of polyclad flatworms, and the parasitic acanthocephalans, platyzoans are strict direct developers. The membership of Cyclophora (figure 2a) within Platyzoa remains a contentious issue (see Giribet *et al.* 2004).

Trochozoa contains those groups with a typical trochophore larva (Annelida *sensu lato*, Mollusca, Entoprocta) and the lophophorate phyla. Recently, some nemertean larvae have been interpreted as modified trochophores, with a vestigial prototroch (Maslakova *et al.* 2004b). As in the case of spiral development, this type of larva does not occur outside the clade, but several ingroup members do not develop through a trochophore. Such is the case of the lophophorate phyla Brachiopoda, Phoronida and Bryozoa.

The position of the chaetognaths, or arrow worms (figure 2b), has been debated for a long time, but current studies based on their nervous system (Harzsch & Müller 2007) and phylogenomics (Ball & Miller 2006; Marlétaz *et al.* 2006; Matus *et al.* 2006) suggest that they are protostomes. Within protostomes they are often considered members of Trochozoa (or its sister group), although some authors place them at the base of the protostome radiation (e.g. Philippe *et al.* 2007).

Cyclophoran affinities to entoprocts are still under consideration (Giribet *et al.* 2004), and one of the

cycliophoran larval forms, the chordoid larva, has been interpreted as a modified trochophore (Funch 1996). Trochozoa includes, in general, larger protostomes than Platyzoa. Many trochozoans are coelomates with large body cavities and metanephridial excretory organs in the adult phase. Some are functionally acoelomates, with protonephridial excretory systems as adults (Nemertea), or even acoelomates (Entoprocta), also with protonephridia as excretory organs.

### (b) *Problematica*

Some of the most problematic protostomes, not only in terms of their phylogenetic placement, are the members of the parasitic group Myzostomida (Eeckhaut & Lanterbecq 2005; figure 2c). From its original description, *Myzostoma cirriferum* was considered a trematode platyhelminth (Leuckart 1827). Since then, myzostomids have been associated to crustaceans, tardigrades, pentastomids and finally to polychaetes. Jägersten (1940) grouped Myzostomida and Annelida (as two separate classes) into a protostome group called Chaetophora. Based on the unusual sperm ultrastructure of myzostomids and acanthocephalans, with a pulling (instead of pushing) flagellum, both groups were classified into the phylum Procoelomata (Mattei & Marchand 1987). However, due to the presence of parapodia-like structures with chaetae and aciculae, and a trochophore larva, most modern authors consider myzostomids as polychaete annelids (e.g. Nielsen 2001; Rouse & Pleijel 2001; Brusca & Brusca 2003; but see Haszprunar 1996). Molecular phylogenetic studies of myzostomids have suggested rather contradictory hypotheses, with some analyses suggesting a relationship to rotifers, acanthocephalans and cycliophorans (Zrzavý *et al.* 2001)—an expanded 'Procoelomata' of Mattei & Marchand (1987)—or to Platyhelminthes (Eeckhaut *et al.* 2000). Both cases presuppose a platyzoan affinity of myzostomids, as opposed to their more traditional trochozoan kinship. However, a more recent molecular analysis using mitochondrial genome data and multiple nuclear genes suggests that myzostomids should be placed back within polychaetes (Bleidorn *et al.* 2007). This debate is probably not yet settled, as multiple research groups have embarked on generating cDNA libraries and EST (expressed sequence tags) data for at least two species of myzostomids (Dunn *et al.* 2007, unpublished results; C. Bleidorn 2007, personal communication).

### (c) *Working framework for lophotrochozoan relationships*

All the previous work, although contradictory for certain aspects, has yielded an important advance in our understanding of metazoan relationships. Focusing on the lophotrochozoans—the topic of this paper—previous work has served for delimiting two putative main clades and their core membership. The affinities of bryozoans, chaetognaths, cycliophorans and myzostomids may still be debatable, but it seems that the remaining protostome phyla (following the definition provided above) either belong to Platyzoa (Gastrotricha, Gnathostomulida, Platyhelminthes, Rotifera) or Trochozoa (Annelida, Brachiopoda, Entoprocta, Mollusca, Nemertea,

Phoronida, Sipuncula; figure 1). Interestingly, only Trochozoa includes members with chaetae (Annelida, Brachiopoda; Lüter 2000; Hausen 2005). Other chaetae-like structures in chitons (Leise & Cloney 1982), juvenile octopods (Brocco *et al.* 1974) and the gizzard teeth of a bryozoan (Gordon 1975) are often considered to be convergent (Hausen 2005), but could instead be plesiomorphic for trochozoans. More detailed study is needed in chaetae-like structures across protostomes.

Relationships among the phyla that constitute Platyzoa is not well established (e.g. Giribet *et al.* 2004), although good synapomorphies exist for Gnathifera (Kristensen & Funch 2000; Sørensen 2001, 2003). Interestingly, no members of Platyzoa are known from the Palaeozoic fossil record (see discussion on fossils below), most certainly due to their small size and lack of hard parts—with the exception of the gnathiferan jaws (Sørensen 2001). The internal phylogenies of several of these phyla are well understood as total evidence and multilocus analyses have been published for Gnathostomulida (Sørensen *et al.* 2006), Platyhelminthes (Littlewood *et al.* 1999), Rotifera (Sørensen & Giribet 2006) and Gastrotricha (Zrzavý 2003).

Trochozoan internal relationships remain uncertain. Monophyly of annelids and its membership is still not well corroborated. There seems to be a consensus now about the affinities of the former phyla Echiura and Pogonophora/Vestimentifera as highly modified polychaete families (McHugh 1997; Hessling & Westheide 2002; Struck *et al.* 2007). This could also be the case of Sipuncula (Struck *et al.* 2007). But resolution within Annelida is far from agreed upon. Molecular analyses (e.g. Bleidorn *et al.* 2003; Rousset *et al.* 2004, 2007; Colgan *et al.* 2006; Struck *et al.* 2007) radically contrast with the most comprehensive morphological analyses of annelid relationships based on morphology (Rouse & Fauchald 1995, 1997; Rouse & Pleijel 2001). Without doubt, an important leap is needed in the amount of data to be incorporated into annelid phylogenetic studies.

The other large trochozoan phylum, Mollusca, does not have much brighter prospects at present. Relationships based on morphology (e.g. Salvini-Plawen & Steiner 1996; Haszprunar 2000) and molecules (e.g. Passamanek *et al.* 2004; Giribet *et al.* 2006) are still at odds, and molecular analyses have traditionally had trouble recovering their monophyly. Only a recent multilocus analysis of molluscan relationships was able to recover monophyly, although with low clade support (Giribet *et al.* 2006), and the internal relationships among the molluscan classes were not supported, with the exception of the controversial relationship of Polyplacophora and Monoplacophora (e.g. see Nielsen *et al.* 2007).

Sipunculan phylogeny has been addressed in recent times, based on both morphology and molecular analyses (e.g. Maxmen *et al.* 2003; Schulze *et al.* 2005, 2007), as is the case for the Brachiopoda/Phoronida clade (Carlson 1995; Cohen *et al.* 1998), renamed Phoroniformea by Cohen (2000). Although several higher-level morphological and molecular analyses exist within the phylum Nemertea (e.g. Sundberg *et al.* 2001; Tholleson & Norenburg 2003), results are still dependent on few



markers, and none have been integrated with morphological analyses. Only little or no synthetic phylogenetic work has been published on the phylogeny of entoprocts or bryozoans.

#### (d) *The 'missing' lophotrochozoan Palaeozoic fossil record*

The Palaeozoic fossil record is rich in members belonging to protostome phyla (Valentine *et al.* 1999; Budd & Jensen 2000; Valentine 2004), and in general it is thought that most metazoan phyla were already present in the Cambrian. Recent discoveries of Cambrian sipunculans (Huang *et al.* 2004) and chaetognaths (Szaniawski 2005; Vannier *et al.* 2007) reduce the number of animal phyla missing from the Palaeozoic record. Among the large animal phyla, none are now missing from this period. However, no member of Platyzoa has yet been found in the Palaeozoic record—a major phylogenetic gap (see figure 1). This obviously may be due to the small size and lack of conspicuous hard parts and cuticles in these animals, but there is also the (unlikely) possibility that the clade originated later than the other animals. One could also argue that larger polyclad flatworms could have left a record, but no verified records of flatworm body fossils exist, despite the general belief that some of the trails found in Late Neoproterozoic rocks are from the activities of flatworms or of organisms of the same grade (Valentine 2004). Another interesting missing Palaeozoic taxon is the ecdysozoan phylum Kinorhyncha, whose segmented cuticles have great potential for fossilization, although their small size may play a role in the lack of evident fossils.

## 2. NOVEL APPROACHES IN MORPHOLOGY

Morphology and development, including early cleavage patterns, have played fundamental roles in shaping our understanding of animal relationships. A major shift within the past two decades, towards using molecular evidence, has proposed some major rearrangements. Still, morphological analysis maintains its role in deciphering animal relationships and interpreting the results derived from molecular studies. Animal morphological analyses underwent an initial revolution with the advent of cladistic techniques, which led to the proposal of numerous phylogenetic hypotheses based on numerical (parsimony-based or Bayesian) analyses of explicit data matrices (e.g. Eernisse *et al.* 1992; Nielsen *et al.* 1996; Zrzavý *et al.* 1998; Sørensen *et al.* 2000; Peterson & Eernisse 2001; Jenner & Scholtz 2005). Morphological matrices are not exempt from arbitrary decisions in inclusion of characters, along with their definition and the identification of character states. Common problems of these previous approaches to metazoan morphological data matrices are the uncritical recycling of characters (see Jenner 2001), the assignment of homology to absences of a given character state (Jenner 2002) and others (see Jenner 2004a for a general discussion). Another major problem is the decision of what character state is assigned to higher (supraspecific) taxa, as all morphological metazoan phylogenies published so far rely on 'groundplan' coding. This could lead to the arbitrary

choice of character states—often in a hypothesis-driven manner (Jenner 2001). An alternative to some of these problems is to code real observations for a selected number of species instead of supraspecific taxa (Prendini 2001), in the same fashion that species are used for molecular analyses. This solution is not only appealing from an operational perspective, but also philosophically, since it allows for a stricter test of monophyly than previous strategies.

No metazoan matrix has yet been produced using species as terminals, although we are currently working on such a matrix (G. D. Edgecombe, G. Giribet, A. Hejnol, G. W. Rouse, M. V. Sørensen & K. Worsaae 2007, unpublished data). This strategy is not without difficulties. It requires two principal conditions, incorporating multiple species per phylum—ideally a collection of species that represents the phyletic morphological disparity, and requiring careful species choice—and coding observations for many species. Certain characters, especially those of development and ultrastructure, are unobserved (or not described) for many terminals and filling the matrix requires a considerable amount of work. Filling all cells with observations for a metazoan matrix of hundreds of taxa and hundreds of characters requires substantial effort by a much larger group of researchers than the team assembled. It is therefore necessary to perfect collaborative software that allows data matrices to be updated by a group of authors over the web (see, e.g. [www.mesquiteproject.org](http://www.mesquiteproject.org)) and requires what we call 'coding parties', where experts in taxa or characters meet periodically to discuss characters, character states and specific coding of taxa.

Defining the characters and their states remains difficult (e.g. Jenner 2004a,b). Hence some researchers believe that such efforts should be done explicitly and discussed by the scientific community at large, developing specific ontologies (e.g. Ramírez *et al.* 2007; see also [www.morphdbase.de](http://www.morphdbase.de)). For example, characters that have played fundamental roles in shaping animal relationships through time, such as the fate of the blastopore, segmentation, or the origins of body cavities, are still poorly understood and their states need further research and discussion. Problems with assigning a homologous state to the lack of a feature have received little attention in the literature. The same is true for inapplicable characters and their specific treatment by computer algorithms (e.g. Lee & Bryant 1999; Strong & Lipscomb 1999). One possible solution to these issues is the addition of as many states as there are non-homologous absences, although this would incur the necessity of adding complex Sankoff characters with more than the 10 states allowed by some software implementations. Another solution would be the use of a dynamic approach to morphology (Schulmeister & Wheeler 2004; Ramírez 2007), analogous to the direct optimization of molecular characters. Although this option is still in its infancy, it could deal with the problem of absences and inapplicable character states in a completely different way.

## 3. NOVEL MOLECULAR APPROACHES: THE ERA OF PHYLOGENOMICS

Since the publication of the earliest metazoan analyses based on molecular data (Field *et al.* 1988; Lake 1990),

molecular phylogenetics has advanced our understanding of metazoan relationships. Novel concepts, now widely accepted by the community, such as Ecdysozoa (Aguinaldo *et al.* 1997), Lophotrochozoa (Halanych *et al.* 1995) and the more controversial Platyzoa (Giribet *et al.* 2000) are rooted on molecular analyses of ribosomal sequence data. The specific position of many odd taxa have also benefited from molecular techniques. Salient examples are those of acoels (Ruiz-Trillo *et al.* 1999), nemertodermatids (Jondelius *et al.* 2002), xenoturbellids (Bourlat *et al.* 2003), nemerteans (Turbeville *et al.* 1992) or gnathostomulids (Giribet *et al.* 2000). However, the positions of other phyla such as loriciferans, micrognathozoans or cycliophorans are not well resolved in molecular analyses (Giribet *et al.* 2004; Park *et al.* 2006). Most of these early studies were based on one or at most a few molecular markers.

New phylogenetic trends have emerged within the past few years though, following the sequencing of complete metazoan genomes—the so-called phylogenomics approach (Delsuc *et al.* 2005). A first set of analyses took advantage of a few complete eukaryotic genomes to tackle metazoan relationships and test hypotheses such as Ecdysozoa or Coelomata (Blair *et al.* 2002; Dopazo *et al.* 2004; Wolf *et al.* 2004; Philip *et al.* 2005). These studies, although broad in the amount of genetic data included, suffer from one of the most crucial phylogenetic biases—deficient taxon sampling. Not surprisingly, analyses including a broader taxon sampling followed immediately, focusing not only on whole genome approaches, but also taking advantage of EST projects (Philippe & Telford 2006). Such studies have provided insights into the relationships of several animal phyla (Philippe *et al.* 2005), including *Xenoturbella* (Bourlat *et al.* 2006), cephalochordates (Delsuc *et al.* 2006), chaetognaths (Marlétaz *et al.* 2006; Matus *et al.* 2006) and acoels (Philippe *et al.* 2007). These studies are exemplary in including approximately 150 genes for a large number of taxa. For example, they comprise all the deuterostome phyla (Chordata, Urochordata, Cephalochordata, Hemichordata, Echinodermata, Xenoturbellida) as well as representatives of the major protostome phyla, including multiple Ecdysozoa (Priapulida, Nematoda, Tardigrada, Arthropoda). However, taxon sampling for the other protostome clades is extremely deficient. Of the 14 lophotrochozoan phyla, only Annelida, Chaetognatha, Mollusca and Platyhelminthes have been represented in these earlier studies (figure 1). Clearly, phylogenomics has still to make a dent into resolving the protostome relationships.

Current research groups, especially those funded under the USA NSF AToL program and the German Deep Metazoan Phylogeny program, have begun to fill in EST projects for the missing protostome diversity. These novel data will soon encompass nearly all animal phyla. The time and the technology are ready for a new vision of the protostome tree of life. For example, EST analyses are finally contributing towards vexing issues for molecular phylogenetic studies such as the monophyly of Mollusca or the kinship of Annelida (Dunn *et al.* 2007, personal communication).

#### 4. CONCLUSIONS: THE FUTURE OF LOPHOTROCHOZOAN PHYLOGENY

The probable existence of two main clades of lophotrochozoans, platyzoans and trochozoans, and the putative affinity of chaetognaths with lophotrochozoans are corroborated now by multiple sources of evidence (Dunn *et al.* 2007, unpublished data). But the relationships within each lophotrochozoan clade are still unresolved for the most part. Key questions such as the sister group of molluscs, the affinities of nemerteans, bryozoans, cycliophorans or the exact position of gastrotrichs and micrognathozoans—to mention just a few—lack a convincing answer. But two qualitative changes are taking place in the study of animal relationships, which may contribute towards a more resolved picture of the lophotrochozoan tree. First is the fresh study of animal morphology and development, translated into a data matrix where observations (instead of inferences) and species (instead of supraspecific taxa) are coded. Second is the widespread use of phylogenomic techniques, now beginning to span the lophotrochozoan diversity. Once hundreds (or thousands) of genes become available for a large array of lophotrochozoan species, relationships may be finally established with confidence. We will then be able to proceed to the even more fundamental task of attempting to explain the origins of morphological disparity and taxonomic diversity. Once the circle is closed, zoologists, palaeontologists, developmental biologists and molecular systematists will have accomplished the grandest scientific enterprise of all times—fulfilling Darwin's dream of the (animal) tree of life.

I wish to acknowledge Tim Littlewood and Max Telford for organizing the Linnean Tercentenary Symposium on Animal Evolution at the Royal Society—one of the most stimulating and well-organized symposia I have ever attended. The Royal Society and the Novartis Foundation made the symposium possible. Ron Jenner, an anonymous reviewer, and the editors provided insightful comments that improved an earlier version of this manuscript. Errors and biases remain my sole responsibility. All the collaborators on the protostome AToL project (Jessica Baker, Casey Dunn, Greg Edgecombe, Noemí Guil, Andi Hejnol, Reinhardt Møbjerg Kristensen, Mark Martindale, Dave Matus, Akiko Okusu, Joey Pakes, Greg Rouse, Elaine Seaver, Martin Sørensen, Ward Wheeler, Katrine Worsaae), without whom the research could have not been conducted, provided stimulating discussions that have led to the writing of this review. This material is based upon work supported by the National Science Foundation AToL program under grant nos. 0334932 and 0531757.

#### ENDNOTE

<sup>1</sup>Lophotrochozoans are also referred to as 'spiralian' in the recent literature (e.g. Giribet *et al.* 2000) to capture a synapomorphy that evolved in the common ancestor of all lophotrochozoans—spiral development.

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