

# The evolution of the animals: introduction to a Linnean tercentenary celebration

Celebrating 300 years since the birth of Carl Linnaeus (1707–1778), a meeting was held in June 2007 to review recent progress made in understanding the origins and evolutionary radiation of the animals. The year 2008 celebrates the 250th anniversary of the publication of the 10th edition of Linnaeus' *Systema Naturae*, generally considered to be the starting point of zoological nomenclature. With subsequent advances in comparative taxonomic and systematic studies, Darwin's discovery of evolution by natural selection, the birth of phylogenetic systematics, and the wider interest in biodiversity, it is salutary to consider that many of the major advances in our understanding of animal evolution have been made in recent years. Phylogenetic systematics, drawing from evidence provided by genotype, phenotype and an understanding of the link between them through comparative embryological and evolutionary developmental studies, has provided a wide consensus of the major branching patterns of the tree of life. More importantly, the integrated approaches discussed in the 16 contributions to this volume highlight the identity and nature of problematic taxa, the missing data, errors in existing analytical procedures and the promise of a wealth of additional characters from genomes that need to be accumulated and assessed in providing a definitive *Systema Naturae*.

**Keywords:** Linnaeus; animal evolution; evo–devo; phylogenetics

## 1. INTRODUCTION

As part of the celebrations of the 300th birthday of Carl Linnaeus (1707–1778), the Swedish 'father of modern plant and animal classification', a Royal Society discussion meeting was held in June 2007 to consider recent advances in understanding animal evolution. Linnaeus, perhaps best known for his introduction of a system of binomial nomenclature that is still used today to name and systematize life on Earth, produced global inventories of more than 7700 species of plants and more than 4400 species of animals, which provided a secure foundation for modern taxonomy. Although Linnaeus appears to have spent considerably more time working on plants, his 10th edition of *Systema Naturae*, volume 1 (Linnaeus 1758), celebrating its own significant anniversary in 2008, is widely accepted to be the official starting point for zoological nomenclature (Blunt 2004; see also [www.linnean.org](http://www.linnean.org)).

The diversity of animal phyla has always been a test to biologists' abilities to reveal interrelationships (Valentine 2004). The tree of life, a definitive phylogeny that links all living forms (and incorporates many extinct (fossil) forms too) is widely considered to be a tractable problem for systematists (see Cracraft & Donoghue (2004) and papers therein). Nevertheless, it is clear that there is considerable conflict arising from our ignorance of how to differentiate signal from noise, how to reconcile mutually incompatible signals and how to take into account all available evidence without favouring one or other source. We are also coming to recognize a number of more or less subtle traps set by the nature of the data. The central questions of how animals originated and how they diverged and radiated to become the diverse forms they are today are of

sufficient interest to engage a varied group of scientists using an equally broad variety of approaches. More importantly, in spite of the problems so far encountered, recent history suggests that much can be revealed about animal evolution and that the resolution of key branching points in the tree of life is indeed achievable.

In this volume, we chose to promote dialogue between systematists and evolutionary developmental biologists, reflecting our own interests but also, we believe, an area where collaboration is driving a greater understanding of animal evolution. In some cases the dialogue resulted in direct collaborations between the two camps (e.g. Swalla & Smith 2008). In others, we hoped to demonstrate the progress being made by each field as applied to the same branches of the metazoan tree of life.

## 2. ROOTS AND FRUITS FROM THE PAST

Perhaps it is axiomatic, but the oldest discipline in revealing the evolution of animal life is palaeontology. Fossils are in a unique position to provide additional characters for resolution of phylogenies, polarization and ordering of character transformations, and provide the time and ecological background for the evolution of key novelties. Budd (2008) explores the nature and beginnings of the animal fossil record and considers in particular the recent findings of fossil embryos and other key forms, the incongruence between molecular and palaeontological estimates of the time of origin of major clades, and the nature and significance of events around the Cambrian. Employing the latest Bayesian methods of estimating divergence times from molecular data, Peterson *et al.* (2008) also consider the vagaries of estimating divergence times from the fossil record alone. They conclude that available data satisfy the notions of a Cambrian explosion of metazoans but

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

indicate that the ecological and evolutionary fuses were set with the emergence of the Bilateria in the Ediacaran.

The characteristics of the last common ancestor of the Bilateria, the so-called 'Urbilateria', are of great current interest and, in addition to the study of fossils, there are two approaches being employed to reconstruct this animal. First is to attribute to Urbilateria the shared characteristics of the protostomes (Lophotrochozoa and Ecdysozoa) and the deuterostomes. However, as [Baguña \*et al.\* \(2008\)](#) point out, this node on the tree may more correctly be termed the protostome/deuterostome ancestor and it is possible that an additional group of animals, the acoel flatworms, represent a bilaterian group branching earlier than this node. The second approach, therefore, is to look directly at the extant members of this earlier branch. [Hejnol & Martindale \(2008\)](#) take recent evidence from gene expression studies of an acoel. By comparison with recent evidence from the Cnidaria, they consider ontogeny at its animal roots, so to speak, with a review of what happens at gastrulation. With the patterns of gene expression of numerous genes to hand, they provide an even clearer picture of how the stem species of Bilateria might have looked, at least in terms of describing a detailed set of plesiomorphic features from development to adult morphology.

As we have hinted, however, the position of the acoels at the base of the Bilateria is not set in stone. Philippe and collaborators have previously published large-scale phylogenomic analyses of the position of the acoels ([Philippe \*et al.\* 2007](#)) and have evidence to link them to the deuterostomes, perhaps with the worm *Xenoturbella*, a similarly simply organized animal. Taking a dense sampling of bilaterian taxa and sequences available from expressed sequence tag (EST) and genome studies, [Lartillot & Philippe \(2008\)](#) demonstrate that a greater understanding of molecular evolution helps to reveal problems (such as the phenomenon of long-branch attraction) and they provide pertinent solutions (greater taxon sampling and better suited models of evolution implemented in phylogenetic analyses). Phylogenomics, like systematics in general, proceeds iteratively with denser taxon and character sampling providing the pulses of change or the reassurance of stability and consensus. So far, consensus prevails in many parts of the tree, but with the advent of many more genomes being completed soon ([Boore & Fuerstenberg 2008](#)), estimates of the interrelationships of animal phyla will be tested severely. The analyses of [Lartillot & Philippe \(2008\)](#) are typically provocative, raising the extraordinary possibility that the deuterostomes are paraphyletic with the earliest branch of the Bilateria, dividing the chordates from all other bilaterians.

### 3. THE EVOLUTION OF THE DEUTEROSTOMES

Considering the morphological synapomorphies linking the two principle branches of the deuterostomes (Chordata and Xenambulacraria) and the low statistical support for paraphyletic deuterostomes in Lartillot and Philippe's analysis, a paraphyletic Deuterostomia will not be readily accepted. [Swalla & Smith \(2008\)](#) consider the evolution of the deuterostomes as

generally accepted, including consideration of more or less contentious fossil members such as the calcichordates (stem echinoderms) and vetulicolians (arthropods or chordates?). [Lowe \(2008\)](#) describes studies comparing development in the chordates with those of xenambulacrarian hemichordates. Despite significant differences in morphology, the degree of conservation of gene expression patterns is striking. The conservation is strongest along the anteroposterior axis, yet the patterning of the nervous system around the circumference of the animals differs in a way that reflects the difference between the central nervous system (CNS) of the chordates when compared with the diffuse nervous system of the hemichordates. The lack of a single nerve chord in the supposedly basal acoels is one indication that this diffuse nervous system might be a primitive character retained in the hemichordates.

[Arendt \*et al.\* \(2008\)](#) on the other hand reveal complex similarities between the patterning of the CNS of a protostome (the annelid worm, *Platynereis dumerilii*) and that of the chordates. They conclude that the protostome/deuterostome ancestor already had a centralized rather than diffuse nervous system patterned in this common manner and suggest that the diffuse nervous system in hemichordates is therefore a derived rather than a primitive characteristic.

### 4. ONTOGENY REVITALIZES PHYLOGENY

As [Raff \(2008\)](#) reminds us, bilaterian animal body plan origins are not only about adult forms. Understanding animal evolution must also result in an explanation of embryology and larval evolution. What, for instance, are the origins of larval forms? Reviewing evidence from expression of patterning genes, phylogeny, morphology and palaeontology, Raff argues that many larval features arose independently, often evolving convergently, and frequently with new features emerging as adult bilaterian-expressed genes were co-opted. Gene expression pattern studies give powerful insights into evolution, yet require a rigorous understanding of homology as it is applied variously from gene to genome to phenotype and ontogeny. The question of the homology of larvae is also confronted by a second surprising result from the phylogenetic analysis of [Lartillot & Philippe \(2008\)](#) which places Platyhelminthes (of which the polyclad turbellarians uniquely have a spirally cleaving larval stage) as the sister group of the annelids to the exclusion of the molluscs. This position suggests that the polyclad larva might be homologous to the spirally cleaving trochophore larva found in both the annelids and the molluscs.

### 5. THE LOPHOTROCHOZOA

In addition to the annelids, molluscs and platyhelminths, membership of the Lophotrochozoa is not so contentious these days, but interrelationships change wildly, highlighting the need for considerable taxon and character sampling. Once again phylogenomics has been applied to what many have seen to be a persistent problem, but this time coupled with a new look at morphology and development across the group. [Giribet \(2008\)](#) provides us with a glimpse of where some stability might finally prevail from these

coordinated efforts, while pragmatically and helpfully highlighting the numerous homeless lophotrochozoans that still need attention. In taking perhaps the least studied and most difficult group of the three major bilaterian divisions, these studies on the Lophotrochozoa will not only provide much needed insight into their interrelationships and comparative biology, but also highlight the benefits for a combined evidence approach that involves active researchers across many disciplines.

## 6. RECOGNIZING, CONTAINING AND SOLVING PROBLEM TAXA

Palaeontologists have long understood the difficulties in handling poorly preserved fossils or those with a beguiling mix of characters. Some reach the status of Problematica, as accommodating them in satisfactory classification systems or phylogenies is all but impossible, and using them to infer historical events is equivocal. Arguably, many extant taxa have achieved the same status and Jenner & Littlewood (2008) consider what defines a member of the Problematica in the light of current efforts to find a place for each branch and leaf on the tree of life, whether fossil or living. With each problem, there is at least one attempt to find a solution and Jenner & Littlewood (2008) suggest ways in which Problematica can be recognized and, in time, dealt with. It is the problematic taxa that indicate the priorities in finding novel solutions to phylogenetic problems.

As molecular data have increasingly dominated systematics, and as more and more complex molecular features have been described for various taxa, there has been a move away from analysis strictly at the nucleotide level. Instead, shared complex features of genes and genomes, with shared ancestry, have made the study of molecular data more like a study of morphological characters. Boore & Fuerstenberg (2008) review the nature and power of these novel genomic apomorphies (sometimes referred to as rare genetic changes, RGCs), and argue that with the flood of whole genome sequencing in progress, we need to be ready to find new ways of recognizing evolutionary signatures.

## 7. THE ECDYSOZOA

One such RGC is the derived version of the mitochondrial NAD5 gene found uniquely in the protostomes. Telford *et al.* (2008) discuss this synapomorphy and point out that a monophyletic Protostomia is incompatible with numerous whole genome studies that have claimed evidence for a closer relationship between arthropods and vertebrates (Coelomata) than between arthropods and nematodes (Ecdysozoa).

Establishing the validity of the Ecdysozoa has set the trend in modern animal (at least protostome) systematics, and Telford *et al.* (2008) review the evidence that has provided this level of stability since Aguinaldo *et al.* (1997) first suggested the clade. Once again, tracking the growth and accumulation of disparate, predominantly molecular markers, the story of the Ecdysozoa provides a satisfying sense of progress but a persistent need to sort out each of the major divisions. Such is the disparity of form, the wealth of comparative

information afforded by fossil forms, and the overwhelming species richness of the group, full phylogenetic resolution over many taxonomic scales within the clade is a problem well worth solving.

## 8. LINKING PHENOTYPE WITH GENOTYPE

The phylogeny of the Ecdysozoa is of particular interest, thanks to the communities of comparative developmental biologists who work on members of the group, most notably *Caenorhabditis elegans* and *Drosophila melanogaster*. However, the diversity of non-model ecdysozoan systems is steadily increasing. Saenko *et al.* (2008) describe one such system, the butterfly *Bicyclus anynana*, and their novel approach to study one striking aspect of these butterflies, their wing eyespots. As fruitflies do not have anything homologous to these features, novel approaches are needed to understand the genetics behind the evolution of these structures. The finding that such novelties have involved the redeployment of genes from well-understood genes and pathways involved in diverse aspects of patterning in fruitflies has provided one way to address this question.

Peel (2008) also addresses questions of the evolution of novelty in the insects, looking at the evolution of long- versus short-germ development in the holometabolous insects. One major conclusion is that developmental modes are not fixed in stone and have evolved both divergently and convergently in the insects. Morphology and developmental genetic networks can effectively become decoupled; one result of which is that attributing homology to developmental features based on common gene expression can be misleading. The source of morphological diversity is a fundamental obsession of the evo-devo field and is particularly puzzling considering little of the apparent differences in complexity correlate with numbers of genes. Humans, for instance, have a similar gene count to that of the humble nematode. Copley (2008) asks where in the genomes do the phenotypic differences between animal taxa arise. Notwithstanding the paucity of taxon sampling that requires us to consider current model laboratory organisms as exemplars of metazoan diversity, it seems clear that the more we know about comparative genomics the more we can reveal about function across the genome. Copley argues that to understand fully the differences and similarities between genomes, it is necessary to go well beyond catalogues of shared genes. Instead, it is an understanding of the interactive components that link genotype with phenotype that will allow genomic studies to contribute to what might be construed as a return to organismal biology in its modern sense, where entire animals are viewed in a comparative evolutionary context, integrating all available evidence. Linnaeus' legacy lives on, albeit considerably updated.

We thank the Royal Society for their generous support in organizing this meeting, and to the Linnean Society of London and the Systematics Association for further financial and logistical support. We thank the speakers and participants for making the meeting so enjoyable. We are also grateful to the Novartis Foundation for providing an extra day where speakers and guests could discuss topics in greater depth and with candour; a very comfortable, soundproofed setting was ideal. Finally, we thank the authors who have contributed

manuscripts, the many referees and the editorial team of the Royal Society for their assistance in helping to bring this volume to press.

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April 2008

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