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).

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 novelities. 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
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 recon-
struct this animal. First is to attribute to Urbilateria
the shared characteristics of the protostomes (Lophotro-
chozoa 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 acoe flat-
worms, 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 acoe. 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.
Philipe and collaborators have previously published
large-scale phylogenomic analyses of the position of the
acoels (Philipe 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 systema-
tics 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 paraplethic
with the earliest branch of the Bilateria, dividing the
chordates from all other bilaterians.

3. THE EVOLUTION OF THE DEUTEROSTOMES
Considering the morphological synapomorphies link-
ing the two principle branches of the deuterostomes
(Chordata and Xenambulacraria) and the low statisti-
cal support for paraplethic deuterostomes in Lartillot
and Philippe’s analysis, a paraplethic 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 calcichord-
dates (stem echinoderms) and veluticolians (arthro-
pods 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 conserva-
tion is strongest along the anteroposterior axis, yet the
patterning of the nervous system around the circum-
ference 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 acoeals 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, Platyneris
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 there-
fore 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 palaontology, Raff argues that many
larval features arose independently, often evolving
convergently, and frequently with new features emer-
ging 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 Platyhel-
minth only (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 trochoophore larva
found in both the annelids and the molluscs.

5. THE LOPHOTROCHOZOA
In addition to the annelids, molluscs and platyhel-
minths, 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 data, with shared ancestry, have made the study of genomes do the phenotypic differences between animal taxa arise. Notwithstanding the paucity of taxon 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.

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REFERENCES


