

# Editorial overview: Developmental mechanisms, patterning and evolution: New models for genetics and development — diversity at last

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Detlev Arendt studied biology at the University of Freiburg in Germany, where he also obtained his doctorate in natural sciences. Since 2003, his laboratory in the Developmental Biology Unit at the European Molecular Biology Laboratory has established the marine annelid *Platynereis dumerilii* as a molecular model for evolutionary, developmental and neurobiological research. His major interest is the evolution of animal body plans and nervous systems. He has also studied the evolution of photoreceptor cells and in recent years pioneered the new field of cell type evolution and development. He holds a honorary professorship at the Centre for Organismal Studies at Heidelberg University.

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Cassandra Extavour received her BSc at the University of Toronto and obtained her PhD at the Autonomous University of Madrid. In 2007 she established her independent laboratory in the Department of Organismic and Evolutionary Biology at Harvard University. She became a full professor in 2014. Her lab is interested in understanding early embryonic development, the genes that control this development, the evolutionary origins of these genes and how their functions have changed over evolutionary time.

It no longer seems heretical to assert that our long-lasting and prevailing focus on a handful of animal model systems has been too reductionist. We will not understand life if we keep ignoring most of the existing diversity — there is more to learn about molecular biology, cell biology, neurobiology and developmental biology than the mouse, *Drosophila* or nematode worm can tell us. From an evolutionary viewpoint, flies are highly modified crustaceans, so why not study a ‘real’ crustacean to start with? If insects are preferred, there are water striders, cockroaches and midges that can tell us more about this incredibly diverse group. Insects make up at least 90% of all the species of animals on earth. No other group of animals has colonized terrestrial, aquatic and aerial habitats more efficiently, has members three times heavier than a mouse (the giant Weta from New Zealand, and the Goliath beetles of equatorial Africa) or that weigh as little as 0.005 mg (some species of parasitic wasp). Insects hold the record for strongest animal compared to body weight (dung beetles can pull over 1100 times their own weight), heat tolerance (desert ants of the Sahara have an upper critical temperature of 53 °C) or loudest penis (stridulation of a European water strider creates a noise of nearly 100 decibels). To understand these remarkable feats of evolution, *Drosophila* alone cannot suffice.

Or take the stupendous Lophotrochozoans, representing the wealth of animal life that lives in the world’s oceans, which are the greatest reservoir of the unknown. If you ever saw an octopus elsewhere than on your plate, you would want to know about this seemingly alien form of intelligence, what it is curious about, and how its impressive brain works. With almost the same level of nervous system complexity, but so different in morphology, behavior and life history, studying it should teach us a lot about our own brains. Alternatively, why not fall in love with flatworms — the true masters of regeneration? Some can be cut into literally hundreds of pieces, and each piece will still recover and form a fully functioning flatworm. And don’t forget that you can always pursue something completely off track, such as the marine worm *Bonellia viridis* with its giant, meter-long proboscis and dwarf males.

It is a truism that the study of evolution requires a comparative approach. If we want to reconstruct and learn about extinct common ancestors, the study of one extant relative is not nearly enough. Evolutionary principles emerge only when we look at a plethora of forms in phylogenetic context. Among these, so-called living fossils are especially important, as they did not change

much relative to a last common ancestor, or at least less than others species. It is equally rewarding to study animals that branched off early in the animal tree, including the beautiful sponges or comb jellies. Whatever we share with our most distant relatives is really old and truly fundamental.

More than ever before in the history of the biological sciences, we have the power to not only describe diversity but also to understand mechanistically its genetic, cellular and developmental origins at an unprecedented level of resolution. CRISPR/Cas9-mediated genome editing technology allows us to study the function of almost any gene of interest, so that we can finally take advantage of the sheer flood of genomic and transcriptomic data that have been accumulating since the advent of high-throughput sequencing over a decade ago. All forms of functional genomics, epigenomics, proteomics, etc. approaches should work in your organism of choice, as long as you can collect/breed/obtain specimens in sufficient numbers. Single cell sequencing techniques only require good dissociation, transcriptome library preparation and sequencing protocols and, voila, a first glimpse into cellular diversity and the evolution of cell types is within reach. For these reasons, this issue highlights the increasing diversity of animal model systems now available to probe genetics and development. We have asked all contributing authors to report on the state of the art in their model of choice, the specialties and mysteries it has on offer, and on its experimental amenability.

Starting at the base of the animal tree, [Maja Adamska](#) discusses the implications of sponge studies on our understanding of early animal evolution. She surveys existing data at different scales of biological organization — genomes, cell types, and body plans — and relates those features that link sponges with their single-celled relatives, the choanoflagellates. [Jager and Manuel](#) write about comb jellies, another early branch in the animal tree. They provide a balanced view on several recent ‘hot’ topics such as their phylogenetic position and the possible independent evolution of neurons and the nervous system. Next, [Rentzsch and Technau](#) fuel our interest in cnidarian biology. Concentrating on sea anemones, they review the content and organization of sequenced genomes, microRNAs and their mode of action, patterning of body axes and nervous system development in this incredibly diverse group of animals. Adding to this, [Leclère and colleagues](#) describe new models in another cnidarian branch, the hydrozoans. Their emphasis is on life cycle complexity with polyps and medusae, gametogenesis, the organization of the primary body axis and, finally, hydrozoan stem cell systems. [Hejnol and Pang](#) explore how the enigmatic acoel worms, that seem to populate the very root of the bilaterian tree, are informative about bilaterian ancestors. The stunning diversity within this small clade

helps us to move from a naïve linear view of evolution to a more realistic picture of frequent loss and gain of features.

[Henry and Lyons](#) set the stage for the Lophotrochozoans, with a first spotlight on molluscs. The slipper snail *Crepidula* is presented as a new model for development, evolution and ecology and, last but not least, as a food source. The authors outline the cellular and molecular basis of development, the study of sex change, the ecological impact of invasive snails, and recent cell lineage studies. [Goulding and Lambert](#) provide an interesting review on a related model, the snail *Ilyanassa*. Their focus is on its unique amenability to embryological manipulations, which enable the study of cytoplasmic determinants inherited by individual blastomeres, and of signaling events. Staying within the Lophotrochozoans, [Elaine Seaver](#) introduces the annelid *Capitella telata* as a model for development and regeneration; and finally, [Williams and Jékely](#) report on another annelid, the nereidid *Platyneris dumerilii* that, due to its ‘big bang’ mode of reproduction, is uniquely amenable to comparative studies in molecular development and evolution, but also to ecology, neurobiology, connectomics, and, most recently, single cell biology.

[Stamatakis and Pavlopoulos](#) move to the other major protostome branch, the Ecdysozoa. Their review on crustacean model systems focuses on the amphipod *Parhyale*. The multiple appendages of this fascinating animal are reminiscent of a Swiss army knife, with each appendage specialized for a different task. A rich toolbox of transgenic techniques should enable us to understand the molecular mechanisms that control this rich morphological diversity. To examine the major terrestrial divergence of crustaceans, namely the insects, [Lynch and Schmidt-Ott](#) discuss recent advances in a wide range of holometabolous insects. The Holometabola are the monophyletic clade of insects that undergo complete metamorphosis, and include *Drosophila*. Beyond fruit flies, however, there are a large number of other fly, mosquito, butterfly, moth, wasp, bee and ant model organisms that are used to shed light on fundamental developmental problems such as long-range organizing signals, and potential control mechanisms for insect vectors of human disease, many of which fall into this group. The basally branching groups of insects, or Hemimetabola, are discussed by [Khila](#), who highlights members of the Hemiptera as incredibly versatile models for investigating the evolution of extremely exaggerated morphologies, such as the long, oar-like legs displayed by water striders, and the potential fitness impact of such traits. To complete the arthropods by considering their most basally branching groups, [Leite and McGregor](#) discuss advantages of the most popular myriapod and chelicerate model systems, which have recently received a massive boost by the sequencing and public release of the first myriapod genome, and by the forthcoming genome of the common

house spider. Rounding out the consideration of ecdysozoan protostomes is the contribution of [Pires-daSilva](#), presenting nematode systems outside of the well-known *Caenorhabditis elegans* model. Studies of multiple nematode species, both in the laboratory and collected from their natural environments, are enabling us to understand the genetic basis not just of heritable morphological change, but also of phenotypic plasticity in morphology and behavior.

Among Deuterostomia, [Arnone and co-workers](#) provide an overview of studies on comparative developmental gene regulatory networks in different echinoderms, with coverage of all currently explored models. They examine not only axis determination and neural specification, but also the larval skeleton, an evolutionary novelty of our pentaradial deuterostome relatives. [Tagawa](#) continues this story with his account of hemichordate animal models, a group of animals regarded as half chordate and half oddball. He describes possible chordate-like features, such as the stomochord, dorsal and ventral nerve cords and pharyngeal gills. [Yong and Yu](#) draw our attention to the study of our closest invertebrate relative, the lancelet amphioxus, and on the exciting search for possible equivalents of vertebrate skeletal tissue in the amphioxus gill slits, oral cirri, and notochord. [De Tomaso's](#) account of colonial ascidians draws our attention to members of the next most basally branching clade to amphioxus. With a completely different life history to that of the relatively well-known solitary ascidians *Ciona intestinalis* and *Haliynthia roretzi*, colonial ascidians display incredible regenerative abilities, have an unusually sophisticated self-non-self recognition system that regulates interactions between members of the colony, and shed light on the evolution of complex vascular systems. Finally, in the vertebrates, rodents represent more than 40% of mammalian diversity; yet, developmental genetic research almost exclusively studies mouse. Overcoming this, [Manceau and co-workers](#) focus on newly emerging rodent models that allow us, for the first time, to study and compare development of diverse traits in a wide range of rodent species.

Finally, a discussion of some of the most promising novel genetic model systems in flowering plants, through the lens of the evolution of morphological diversity, is offered within two articles in this issue. Focusing on the bitter

herb *Cardamine hirsuta*, [Hay](#) explains how we have come to realize that diversification of leaf shape is mediated by mechanisms that include pleiotropy, heterochrony, and gene loss. [Walcher-Chevillet and Kramer](#) consider work on columbines, grapevines, and monkey flowers, and show how each of these models have led us to understand the developmental and cellular processes that characterize different types of lateral organs (leaves, petals, stamens and carpels), and the evolutionary relationships between these organs.

We know that animals and plants are but two of many instances of the evolution of multicellularity among eukaryotes. To put these findings into context, we include studies on non-animal eukaryotic systems. [Schaap](#) brings us up to speed on the latest results concerning the slime mold *Dictyostelium discoideum*. This fascinating organism uses a complex signaling system to transition between unicellular and multicellular life forms in response to changes in the environment. A profound mechanistic understanding of the pathways that control this transition has been achieved through the use of the many sophisticated genetic tools available. [Hoffmeyer and Burkhardt](#) discuss two species of choanoflagellates, in which some types of multicellular behaviors can be observed, albeit transiently. One of the opportunities that these organisms offer is the chance to understand the heritable and environmental factors that underlie formation of true cell–cell junctions, similar to those seen in animal epithelia. For a view from an independent evolution of obligate eukaryotic multicellularity, [Olson and Nedelcu](#) enlighten us on recent progress in the study of volvocine green algae, within which, as has happened across eukaryotes, multicellularity has evolved multiple times convergently.

In conclusion, times have never been more favourable for expanding the application of molecular and genetic mechanistic approaches to a broader diversity of multicellular life, enabled by the ease of transfer of exciting new techniques. The concept of a 'model system', as so well demonstrated by these reviews, appears to be less and less relevant, or more and more flexible, as an ever-increasing number of species with their own distinctive and sometimes peculiar attributes are now accessible for exploring the genetic logic underlying development and adaptation.