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Patterns In Palaeontology: Development in the Fossil Record

by Jo Wolfe*¹

Introduction:

Development, the process by which a single egg cell transforms into a complex adult organism, has fascinated biologists for more than 200 years. In the mid-nineteenth century, before and during the time when Charles Darwin was uncovering the principles of natural selection, a number of biologists who wondered what caused evolutionary relationships among organisms looked to development for answers. The German zoologist Ernst Haeckel popularized the phrase “Ontogeny recapitulates phylogeny” — where ontogeny is an organism’s development and phylogeny is its evolutionary relationships. You may have seen a version of his famous diagram in biology textbooks (Fig. 1). Haeckel suggested that, during each successive stage of development, an animal would pass through a stage from its evolutionary history (for example, in the fourth week of development, human embryos have structures called pharyngeal arches, which look similar to gill slits in fishes). In the 1920s, marine biologist Walter Garstang contributed to discrediting Haeckel’s theory, instead proposing that ontogeny creates phylogeny. Garstang suggested that natural selection is able to modify the form of each larval stage independently, leading to complex life cycles in many marine organisms.

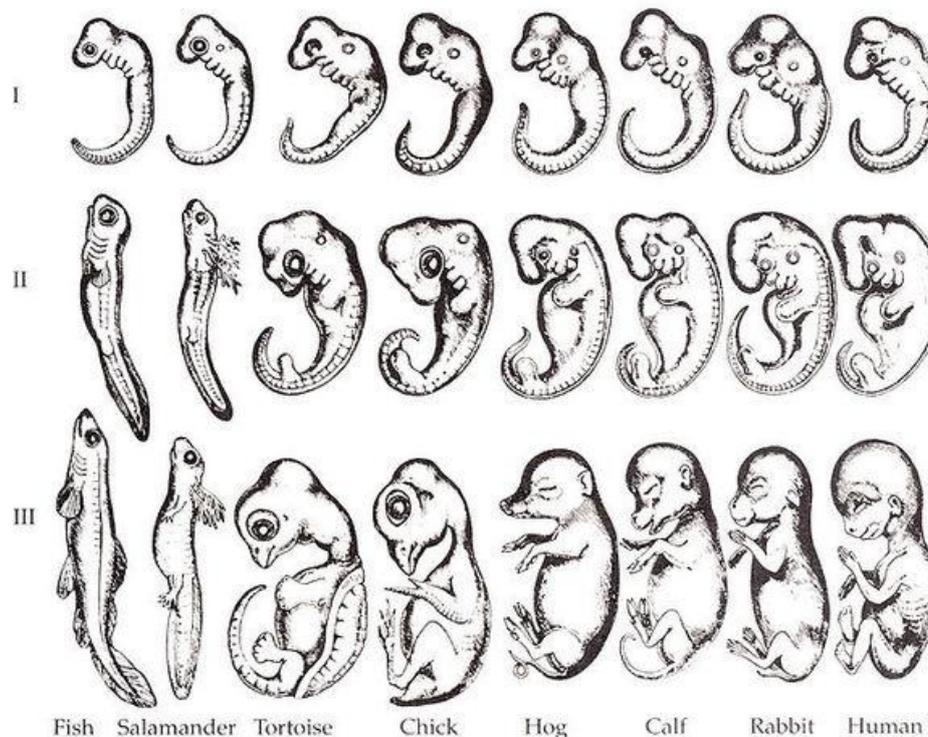


FIGURE 1 — A REPRESENTATION OF HAECKEL’S RECAPITULATION THEORY, ILLUSTRATING SIMILARITIES IN VERTEBRATE EMBRYOS. SOURCE: http://en.wikipedia.org/wiki/Recapitulation_theory.

Even now, nobody knows the exact relationship between ontogeny and phylogeny. But modern biologists have made startling discoveries. The genetic ingredients used to build the bodies of all animals, from human limbs to fruit fly wings, are remarkably similar. These areas of research make up the emerging field of biology called evolutionary developmental biology, or evo-devo. This includes, but is not limited to: analyses of how embryonic development evolved; the origin and modification of anatomical features; the origin and modification of life-history stages; and the interaction of genetics (genotype) and observable characteristics (phenotype) throughout the life cycle. Ultimately, evo-devo seeks to answer the questions: why do organisms look the way they do and how did they get that way? Evo-devo has also been combined with palaeontology for increasingly powerful studies of evolution. Here I will introduce what fossils can tell us about development, as well as what development can tell us about the fossil record.

What can fossils tell us about development?

Fossil embryos have been described for a variety of animal groups from the [Cambrian period](#) (542 million to 488 million years ago). Some palaeontologists say that they have even found fossil embryos from the [Ediacaran period](#) (635 million to 542 million years ago), but [these have mostly been discredited](#). The Cambrian embryos that have been assigned to groups that still have some living species — such as the [cnidarians](#), which include jellyfish — demonstrate that development has been conserved in some animals for more than 500 million years. Larval stages (which come in development after the embryo and are usually free-swimming) have also been preserved from a variety of animals, including vertebrates and [arthropods](#). Fossil arthropod larvae are frequently preserved, because arthropods must completely shed their exoskeletons repeatedly during growth, a process known as moulting. Each moult has the opportunity to become fossilized, whether the animal is still living inside it or not. Some of the best-known fossil larvae come from [trilobites](#). Thanks to preserved larvae, the patterns of segment addition in many trilobite species are well understood.

Lots of larval fossils are exceptionally preserved — that is, anatomical features that would normally decay and not be preserved are visible. Exceptional preservation can occur only under specific environmental conditions, and deposits that provide such conditions are rare but of tremendous scientific value. One group of deposits that bear fossil larvae, found worldwide and dating from about 525 million to 480 million years ago (in the Cambrian period and the [Ordovician period](#)), are known as Orsten. They include tiny fossils embedded in round limestone nodules, which can be revealed only by dissolving the rock in acid, and then painstakingly sorting through the remaining debris under a microscope. The resulting fossils are truly spectacular (Fig. 2).

Fossils are important for discovering evolutionary relationships, because scientists cannot always tell what anatomical features evolved from the same common ancestor, especially if those groups evolved a very long time ago. Fossils are closer in age to the time when particular groups split apart, and often have a mishmash of characters shared by each of the living related groups. Consider, for example, the famous fossil *Archaeopteryx lithographica*, which had both birdlike characters (feathers, wings, a wishbone) and reptilian characters (teeth, a long tail), and became key evidence for the discovery that birds evolved from dinosaurs.

Focusing on larvae, Orsten fossils are very important for understanding evolutionary relationships among arthropods, because they are some of the oldest members of living groups. My research

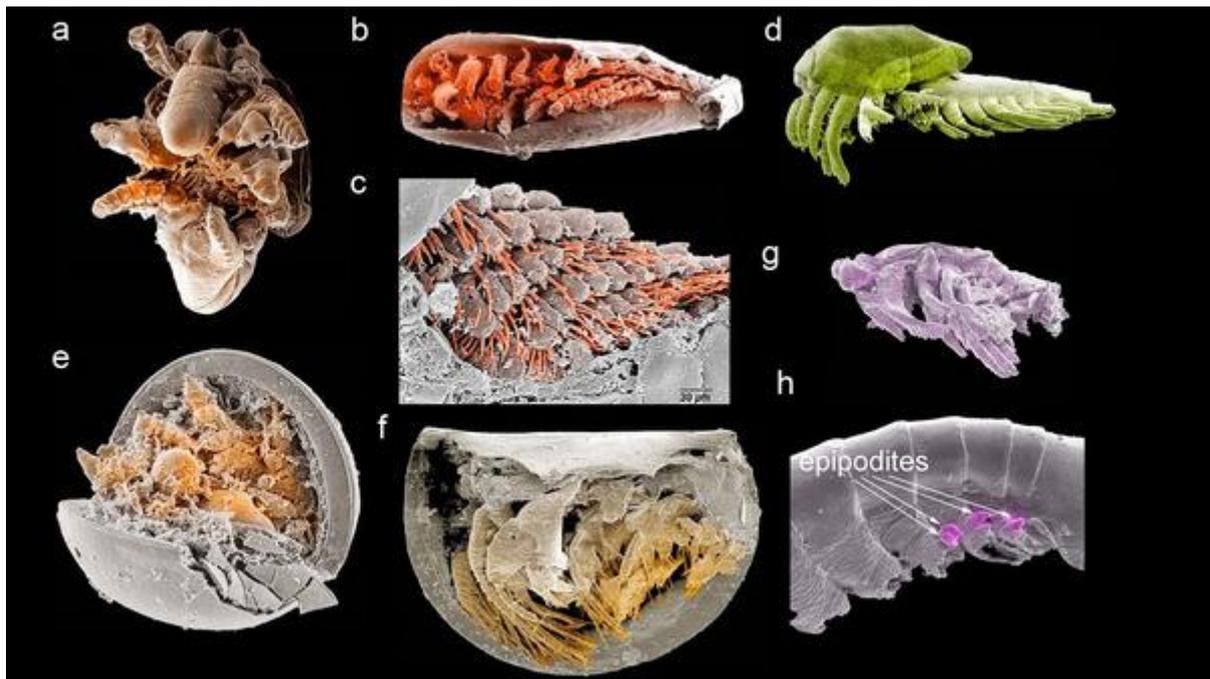


FIGURE 2 — REPRESENTATIVE ORSTEN FOSSIL ARTHROPOD LARVAE. (A–C) REHBACHIELLA KINNEKULLENSIS, A POSSIBLE RELATIVE OF CRUSTACEANS SUCH AS SEA MONKEYS. IMAGE (C) IS A MAGNIFICATION OF THE LIMBS OF THE FOSSIL IN (B), ILLUSTRATING EXQUISITELY PRESERVED SENSORY HAIRS IN ORANGE (THE SCALE BAR IS 30 MICROMETRES, OR A LITTLE SMALLER THAN THE DIAMETER OF A HUMAN HAIR!). (D) BREDOCARIS ADMIRABILIS (DISCUSSED BELOW). (E–F) THE PHOSPHATOCOPINES KLAUSMUELLERIA SALOPENSIS AND HESSLANDONA ANGSTATA, WITH THEIR PROTECTIVE CARAPACES SPLIT OPEN TO REVEAL DETAILS OF THE LIMBS. WHAT ANIMAL GROUPS THEY BELONG TO REMAINS A SOURCE OF CONTROVERSY. (G–H) YICARIS DIANENSIS, WITH A POSSIBLE CRUSTACEAN STRUCTURE MAGNIFIED IN IMAGE (H) IN PURPLE. SOURCES: <http://www.core-orsten-research.de/>.

looks at how larval stages affect the methods used to reconstruct phylogeny, and the Orsten fossils have been fundamental in my work. I have found that these larvae can make a difference in analyses of relationships between animals, and can extend the geological time range of living groups. For example, the Orsten fossil *Bredocaris admirabilis* is an early relative of barnacles, but it shows similarities to only larvae of living barnacles, rather than adults. The oldest adult barnacle fossil is from the [Silurian period](#), and dates to about 425 million years ago, but *B. admirabilis* tells us that barnacles split from their common ancestor at least 75 million years earlier than was previously known — that’s a longer time than between the extinction of the dinosaurs and now!

Fossilized embryos may also provide information about the creature’s mode of life and behaviour. For example, embryos of ichthyosaurs and mosasaurs (marine reptiles from the Mesozoic era, 251 million to 65 million years ago) have been preserved. Certain specimens of these fossil embryos have been discovered lying in place in their mother’s womb, demonstrating that these animals gave birth to live young. Furthermore, a specimen of an armoured fish from the [Devonian period](#) of Australia preserved an embryo in place with its umbilical cord (Fig. 3), showing that many vertebrates gave live birth as far back as 380 million years ago!



THE ARMoured FISH *MATERPISCUS ATTENBOROUGHI* (NAMED AFTER SIR DAVID ATTENBOROUGH). ON THE LEFT IS A RECONSTRUCTION OF THE MOTHER AND ITS BABY ATTACHED BY AN UMBILICAL CORD; ON THE RIGHT IS THE FOSSIL ITSELF. SOURCE:

http://species.asu.edu/2009_species08

What can development tell us about fossils?

Unfortunately, the cloning of dinosaurs in *Jurassic Park* is pure fantasy: DNA sequences degrade after only hundreds of thousands of years. We cannot extract genetic information from the vast majority of fossils (although we can from the remains of more recently extinct species such as Neanderthals and mammoths!). The major body plans of animals evolved in the Cambrian, so what can the developmental biology of living animals tell us about extinct species? The answer is that we can study the genes that direct the processes of development, and make inferences about their evolutionary origins.

The overwhelming majority of knowledge about development in living animals comes from only a few species: the fruit fly (*Drosophila melanogaster*), the nematode or roundworm (*Caenorhabditis elegans*), the sea urchin (*Strongylocentrotus purpuratus*), the zebrafish (*Danio rerio*), the African clawed frog (*Xenopus laevis*), the chicken (*Gallus gallus*) and the mouse (*Mus musculus*). Four out of seven of these species are vertebrates, but vertebrates represent only 3% of described species diversity (Fig. 4). A significant goal of evo-devo is to expand this knowledge to other groups. It can be difficult to do experiments with many animals, either because there are problems with collecting them (for example, coelacanth fish live only in deep waters of the Indian Ocean) or with getting them to reproduce in the laboratory. An alternative approach is to use rapidly improving genomic technology. As recently as three years ago, it was difficult and very expensive to sequence a full genome. Now technology has become so efficient that we can sequence a full genome in a matter of days, for as little as US\$8,000! Genomic information is incredibly useful for evolutionary study because scientists can mine the databases already created for other organisms to see how many genes are related, and what their function is (if it is known).

Perhaps the most intriguing genomic data come from what is known as the developmental toolkit: the subset of genes required for development of the adult body plan. A large number of genes function solely to send signals to other genes, telling them to turn on or off (gene expression). Then those genes send signals to more genes, and on and on in a cascade of gene regulation, so the body is able to respond by, for example, creating proteins to build more cells to increase the size of the growing leg or heart or eye (see Video 1: <http://www.youtube.com/watch?v=LFG-aLidT8s>). The DNA sequences of the genes responsible for these signals are common across deep evolutionary time.

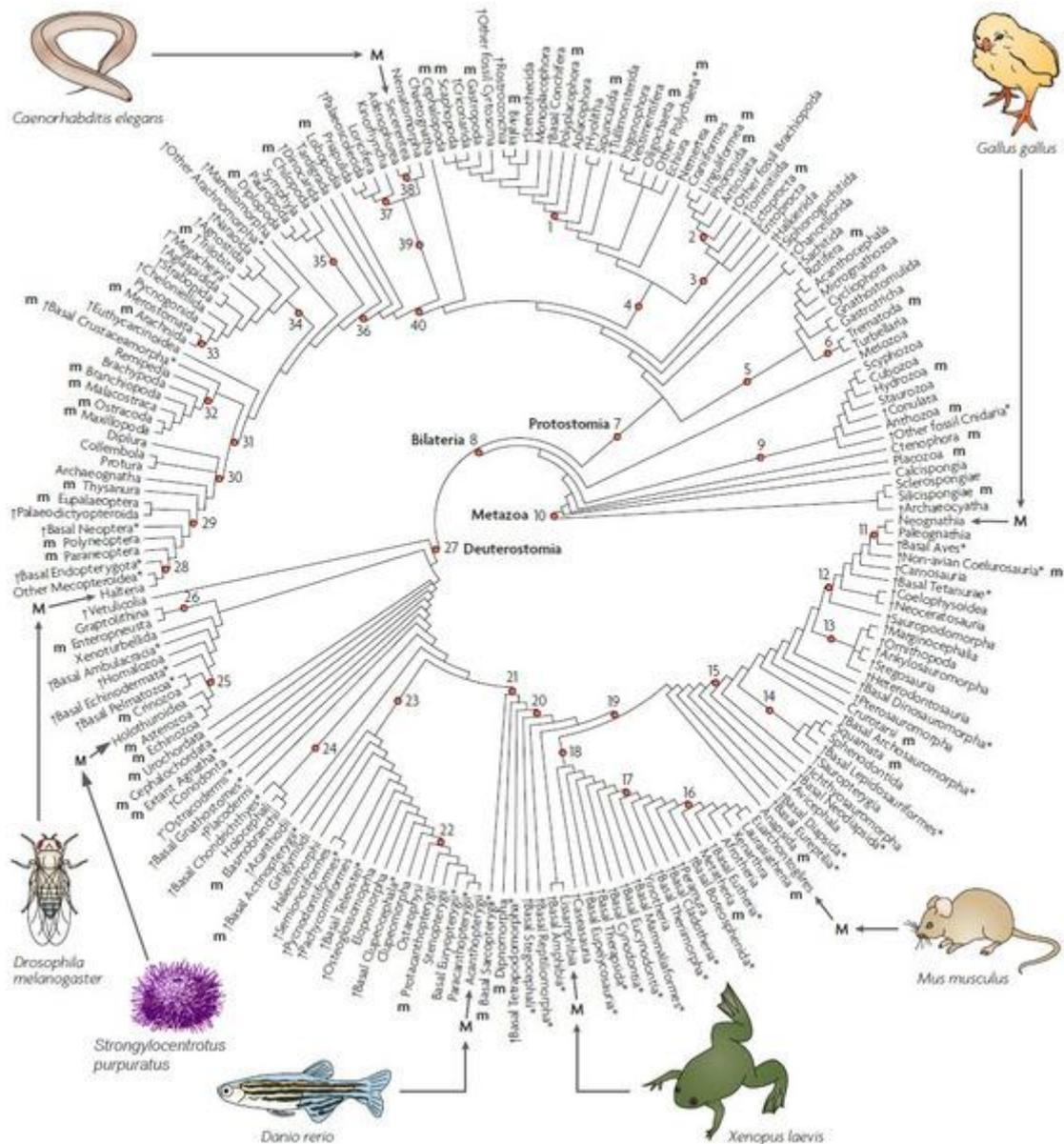
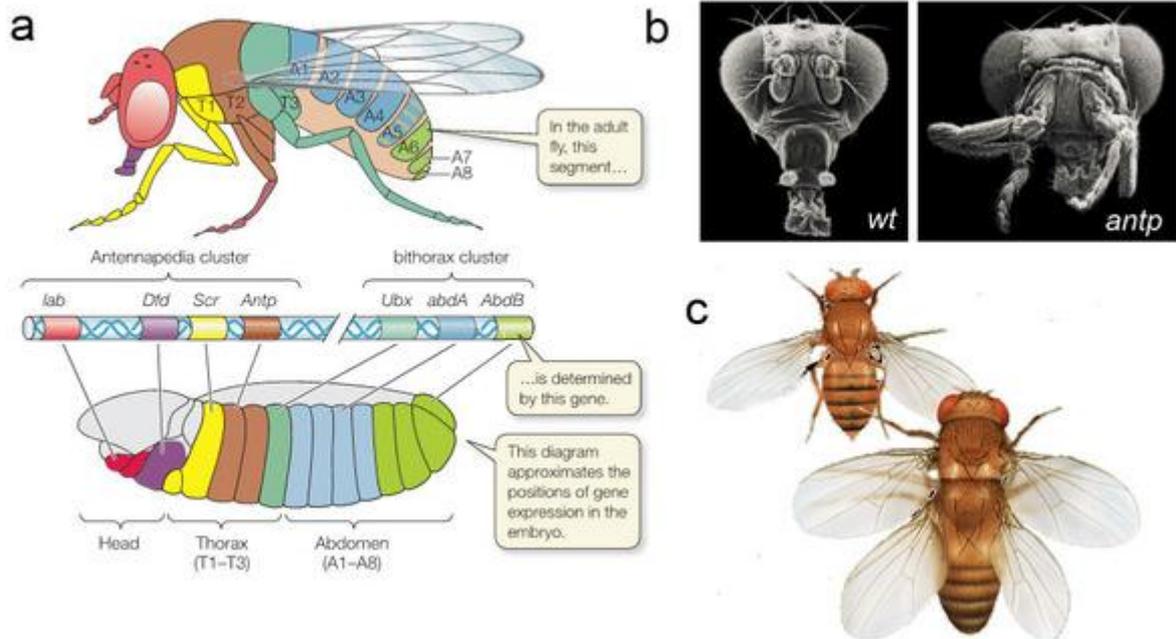


FIGURE 4 — THE EVOLUTIONARY RELATIONSHIPS OF DEVELOPMENTAL MODEL SPECIES, SHOWING THE EMPHASIS ON VERTEBRATES. M INDICATES COMMON MODEL SPECIES; m INDICATES SPECIES THAT HAVE BEEN STUDIED (SOMETIMES FOR ONLY ONE OR A FEW GENES). MODIFIED FROM: JENNER AND WILLS 2007.

A particularly important and famous group of toolkit genes are known as homeotic (Hox) genes. These genes — whose sequences are similar between most animals, from humans to fruit flies — lay down the pattern of building blocks from the anterior (head) to posterior (rear) of the body (Fig. 5). These genes signal that a particular body segment should be made in that location — for example, in the fruit fly, they might signal that the second segment of the thorax (body) has wings whereas the third segment has a structure called halteres (used in flight).

Mutations of these toolkit genes (natural or experimentally induced) provide clues as to their function (Fig. 5b, c). In this way, living embryos can be experimentally changed to develop features that look similar to those found only in fossils. For example, mutant chicken embryos have been given teeth, a characteristic lacking in modern birds, but found in crocodiles and dinosaurs. Homeotic shifts have also been induced in chicken wings so that they resemble [morphologies](#) found in



HOX GENES IN THE FRUIT FLY. (A) THE SET OF HOX GENES ARE FOUND IN THE SAME ORDER ON A CHROMOSOME AS THE ORDER IN WHICH THEY ARE EXPRESSED FROM ANTERIOR TO POSTERIOR IN THE EMBRYONIC AND ADULT FLY. (B) THE EFFECTS OF EXPRESSING THE ANTENNAPEDIA GENE IN A SEGMENT ANTERIOR TO ITS NATURAL POSITION: WT IS A NORMAL FLY, AND ANTP IS THE MUTANT, WITH LEGS (FOUND IN THE NATURAL ANTENNAPEDIA SEGMENT) GROWING FROM THE HEAD. (C) EXPRESSION OF ULTRABITHORAX POSTERIOR TO ITS NORMAL POSITION PRODUCES AN EXTRA PAIR OF WINGS ON THE FLY. SOURCES:

<http://www.nature.com/scitable/content/hox-genes-in-drosophila-33246>,

<http://www.ucl.ac.uk/~ucbzwdr/teaching/b250-99/homeotic.htm>,

<http://www.snv.jussieu.fr/bmedia/homeotique/homeo2.html>.

dinosaur fingers. Of course, we cannot prove that these particular genes were responsible for patterning dinosaur teeth or fingers, but experiments do provide insight into potential pathways, especially in cases that we can also compare to the living sister group, such as crocodiles with birds and dinosaurs. Similarly, we cannot measure patterns of Hox gene expression in fossil arthropods and their relatives, but with some knowledge of the phylogenetic distribution of body patterning in living groups, and the relationship of fossils to those living species, it is possible to infer, for example, how the body is divided into different types of segments. Trilobites, as probable relatives of mandibulates (centipedes, millipedes, crustaceans, and insects) probably shared gene-expression patterns with those arthropods, especially centipedes and millipedes (which, like trilobites, have a series of repeated similar segments throughout the body).

Although most developmental genes were present in the common ancestor of cnidarians and [bilaterian](#) animals, the number of regulatory microRNA sequences in the genome increased dramatically as bilaterians evolved (Fig. 6). The function of microRNAs remains an active area of research, but we do know that they do not produce genes, yet they are involved in regulating when (during development) and where (in the body) other genes are expressed. It has been suggested that increases in the number and type of microRNAs contributed to the increase in complexity of animal forms during the Cambrian explosion. Note that in Fig. 6 the two largest increases are at the base of bilaterians (the first appearance of bilateral symmetry and three embryonic cell layers, as opposed to the two in cnidarians) and at the base of the vertebrates (with an internal skeleton and complex brain). Knowledge of the evolutionary distribution of developmental toolkit genes allows us to infer

when in the fossil record complex body plans might have occurred, and provides some explanation for the rapid appearance of new body plans during the Cambrian explosion.

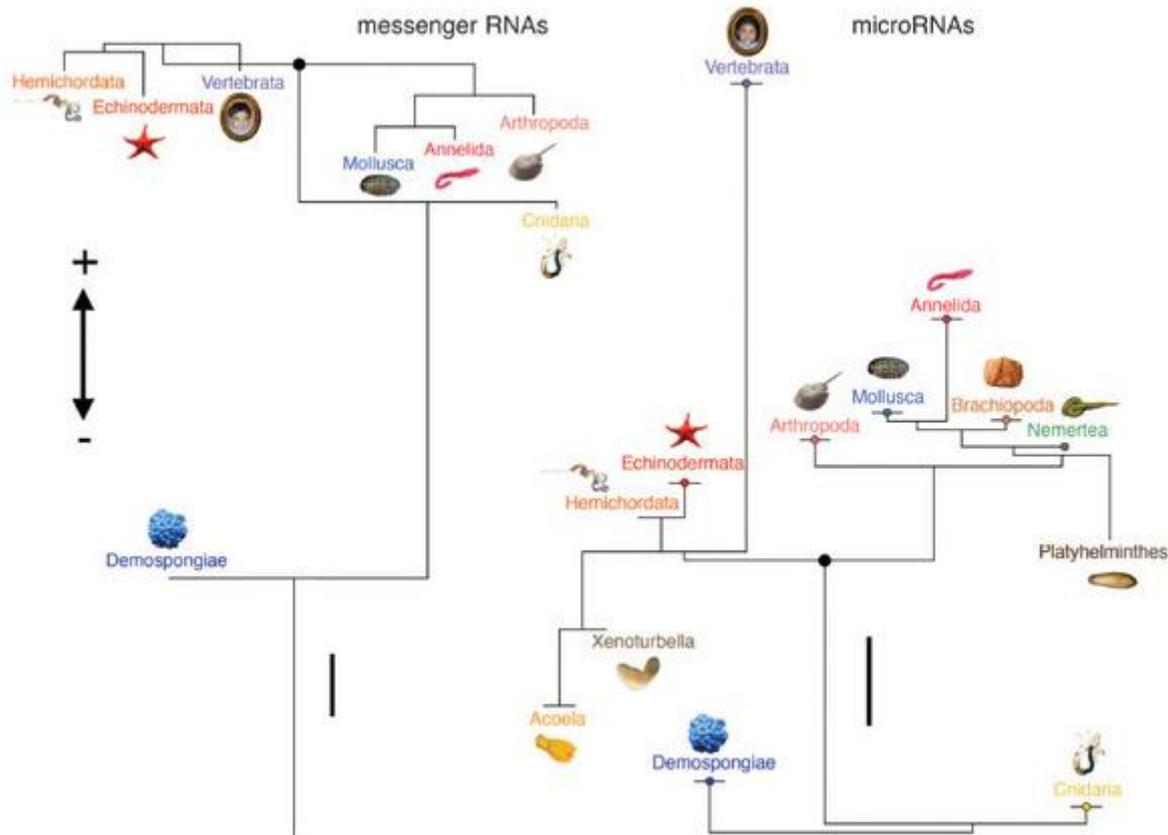


FIGURE 6 — EVOLUTIONARY ACQUISITION OF DEVELOPMENTAL TOOLKIT GENES. MOST MESSENGER RNAs (PROTEIN-CODING GENES) EVOLVED IN THE COMMON ANCESTOR OF CNIDARIANS AND BILATERIANS, BUT THE SET OF MICRORNAs HAD MASSIVE INCREASES AT THE BASE OF BILATERIANS AND AGAIN IN VERTEBRATES, INDICATING SIGNIFICANT LEAPS IN DEVELOPMENTAL COMPLEXITY IN THOSE GROUPS. SOURCE: ERWIN ET AL. 2011.

Summary:

Emerging research at the intersection of palaeontology and evo-devo is extremely exciting. As more and more fossil embryos and larvae are found, we learn about the development of extinct animals and gain new sources of data to understand their relationships with living groups. Complementary work on the genomics and functional development of living animals reveals shared aspects of body-plan organization throughout deep evolutionary time. A combination of these two approaches is needed to move towards understanding the centuries-old questions perplexing zoologists: why do organisms look the way they do and how did they get that way?

Suggestions for further reading:

Carroll, S. B. 2005. *Endless Forms Most Beautiful: The New Science of Evo Devo*. W.W. Norton. ISBN: 9780393060164. An episode of the show NOVA was partially based on this book. It can be watched [online](#), and is excerpted in Video 1.

Erwin, D. H., Laflamme, M., Tweedt, S. M., Sperling, E. A., Pisani, D. & Peterson, K. J. 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. *Science* 334, 1091–1097. [doi:10.1126/science.1206375](https://doi.org/10.1126/science.1206375)

Hall, B. K. 2012. Evolutionary developmental biology (evo-devo): past, present, and future. *Evolution: Education & Outreach* 5, 184–193. [doi:10.1007/s12052-012-0418-x](https://doi.org/10.1007/s12052-012-0418-x)

Hall, B. K. & Olson, W. M. 2003. *Keywords and Concepts in Evolutionary Developmental Biology*. Harvard University Press. [ISBN: 0674009045](https://www.isbn-international.org/product/0674009045).

Harris, M. P., Hasso, S. M., Ferguson, M. W. J. & Fallon, J. F. 2006. The development of archosaurian first-generation teeth in a chicken mutant. *Current Biology* 16, 371–377. [doi:10.1016/j.cub.2005.12.047](https://doi.org/10.1016/j.cub.2005.12.047)

Sánchez, M. R. 2012. *Embryos in Deep Time: The Rock Record of Biological Development*. University of California Press. [ISBN: 9780520271937](https://www.isbn-international.org/product/9780520271937).

Shubin, N. 2009. *Your Inner Fish: A Journey into the 3.5-Billion-Year History of the Human Body*. Vintage Books. [ISBN: 978-0-375-42447-2](https://www.isbn-international.org/product/9780375424472), The same NOVA episode was also partially based on this book.

Waloszek, D. & Maas, A. 1996–2013. [Center of 'Orsten' Research & Exploration](http://www.orsten.org/). A fantastic website with loads of information, pictures and links about Orsten fossils.

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