<Further Development 1_5>

Important Transitions in Animal Evolution

“Community of embryonic structure reveals community of descent,” Charles Darwin concluded in On the Origin of Species in 1859. This statement is based on Darwin’s evolutionary interpretation of Karl Ernst von Baer’s laws—namely, that relationships between groups can be established by finding common embryonic or larval forms. In 1828, just a few years before Darwin’s voyage on the HMS Beagle, von Baer reported a curious observation. “I have two small embryos preserved in alcohol, that I forgot to label. At present I am unable to determine the genus to which they belong. They may be lizards, small birds, or even mammals.” Drawings of such early-stage embryos allow us to appreciate his quandary (Figure 1).

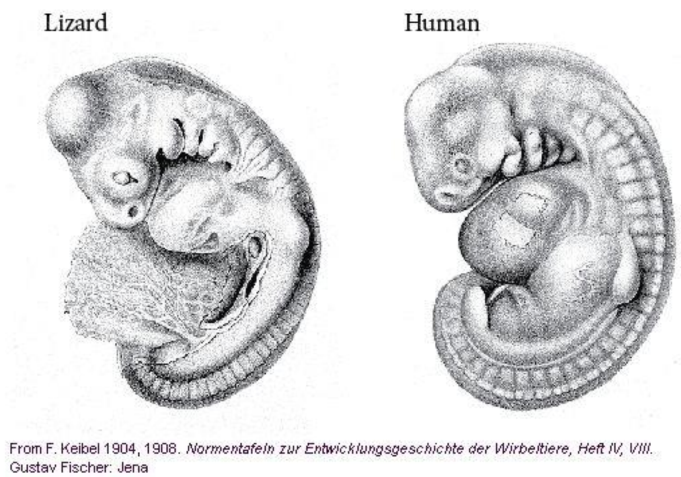


Figure 1 The vertebrates—fish, amphibians, reptiles, birds, and mammals—all start development very differently because of the enormous differences in the sizes of their eggs. By the beginning of neurulation, however, all vertebrate embryos have converged on a common structure. Here, a lizard embryo is shown next to a human embryo at a similar stage. As they develop beyond the neurula stage, the embryos of the different vertebrate groups become less and less like each other. (From Keibel 1904, 1908; see Galis and Sinervo 2002.)

From his detailed study of chick development and his comparison of chick embryos with the embryos of other vertebrates, von Baer derived four generalizations known as “von Baer’s laws” (Table 1). von Baer’s laws can be summarized as describing how all animals begin as simple embryos that share common characteristics, traits of which become progressively specialized in species-specific ways. For instance, human embryos initially share characteristics in common with fish and avian embryos but diverge in form later in development, and never pass through the adult stages of lower vertebrate species. Recent research has confirmed von Baer’s view that there is a phylotypic stage at which the embryos of the different phyla of vertebrates all have a similar physical structure, such as the stage depicted in Figure 1. At this same stage there appears to be the least amount of difference among the genes expressed by the different groups within the same vertebrate phylum (Irie and Kuratani 2011).[i]

TABLE 1	von Baer's laws of vertebrate embryology
1. The general features of a large group of animals appear earlier in development than do the specialized features of a smaller group.	
All developing vertebrates appear very similar right after gastrulation. All vertebrate embryos have gill arches, a notochord, a spinal cord, and primitive kidneys. It is only later in development that the distinctive features of class, order, and finally species emerge.	
2. Less general characters develop from the more general, until finally the most specialized appear.	
All vertebrates initially have the same type of skin. Only later does the skin develop fish scales, reptilian scales, bird feathers, or the hair, claws, and nails of mammals. Similarly, the early development of limbs is essentially the same in all vertebrates. Only later do the differences between legs, wings, and arms become apparent.	
3. The embryo of a given species, instead of passing through the adult stages of lower animals, departs more and more from them.	
For example, as seen in Figure 1.12, the pharyngeal arches start off the same in all vertebrates. But the arch that becomes the jaw support in fish becomes part of the skull of reptiles and becomes part of the middle ear bones of mammals. Mammals never go through a fishlike stage (Riechert 1837; Rieppel 2011).	
4. Therefore, the early embryo of a higher animal is never like a lower animal, but only like its early embryo.	
Human embryos never pass through a stage equivalent to an adult fish or bird. Rather, human embryos initially share characteristics in common with fish and avian embryos. Later in development, the mammalian and other embryos diverge, none of them passing through the stages of the others.	

After reading Johannes Müller's summary of von Baer's laws in 1842, Darwin saw that embryonic resemblances would be a strong argument in favor of the genetic connectedness of different animal groups. Even before Darwin, larval forms were used in taxonomic classification. In the 1830s, for instance, J. V. Thompson demonstrated that larval barnacles were almost identical to larval shrimp, and therefore he (correctly) counted barnacles as arthropods rather than mollusks (Figure 2; Winsor 1969). Darwin, himself an expert on barnacle taxonomy, celebrated this finding: "Even the illustrious Cuvier did not perceive that a barnacle is a crustacean, but a glance at the larva shows this in an unmistakable manner." Alexander Kowalevsky (1871) made the similar discovery that larvae of the sedentary tunicate (sea squirt) had the defining chordate structure called the notochord,[ii] and that it originates from the same early embryonic tissues as the notochord does in fish and chicks. Thus, Kowalevsky reasoned, the invertebrate tunicate is related to the vertebrates, and the two great domains of the animal kingdom—invertebrates and vertebrates—are thereby united through larval structures. Darwin applauded Kowalevsky's finding, writing in The Descent of Man (1874) that "if we may rely on embryology, ever the safest guide in classification, it seems that we have at last gained a clue to the source whence the Vertebrata were derived." Darwin further noted that embryonic organisms sometimes form structures that are inappropriate for their adult form, but demonstrate their relatedness to other animals. He pointed out the existence of eyes in embryonic moles, pelvic bone rudiments in embryonic snakes, and teeth in baleen whale embryos.

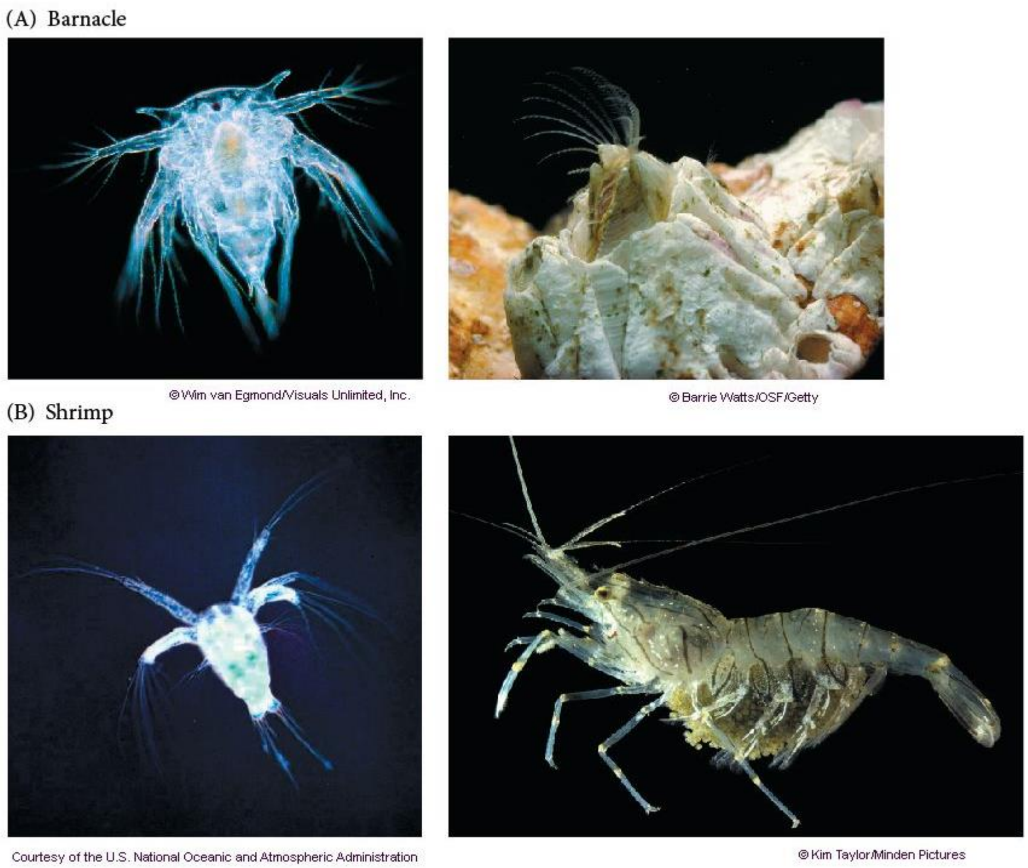


Figure 2 Larval stages reveal the common ancestry of two crustacean arthropods, barnacles (A) and shrimp (B). Barnacles and shrimp both exhibit a distinctive larval stage (the nauplius) that underscores their common ancestry as crustacean arthropods, even though adult barnacles—once classified as mollusks—are sedentary, differing in body form and lifestyle from the free-swimming adult shrimp. A larva is shown on the left in each pair of images, an adult on the right.

Darwin also argued that adaptations that depart from the "type" and allow an organism to survive in its particular environment develop late in the embryo.[iii] He noted that the differences among species within genera become greater as development persists, as predicted by von Baer's laws. Thus, Darwin recognized two ways of looking at "descent with modification." One could emphasize common descent by pointing out embryonic similarities between two or more groups of animals, or one could emphasize the modifications to show how development has been altered to produce structures that enable animals and plants to adapt to particular conditions.

Understanding the tree of life to see our developmental relatedness

Earth is estimated to have formed 4.56 billion years ago (bya), with evidence of the first signs of life occurring about 3.8 bya. The theory of evolution is fundamentally based on all life on Earth originating from a common ancient ancestor, so named LUCA, the last universal common ancestor. This is important because it means all forms of life are related to one another—from you to the elephant, to the oyster toadfish,[iv] to the honeybee, to the horseshoe crab, to the horrible parasitic Ascaris roundworm, to the beautiful brain coral, to the brain puffball mushroom, to the nearly 400,000 species of flowering plants, to the 200,000 species of protists, and even to the bacteria living in your gut. If we are all related, then the mechanisms governing how a Homo sapiens develops are fundamentally derived from the common ancestors that connect all life along the tree—the tree of life (Figure 3).

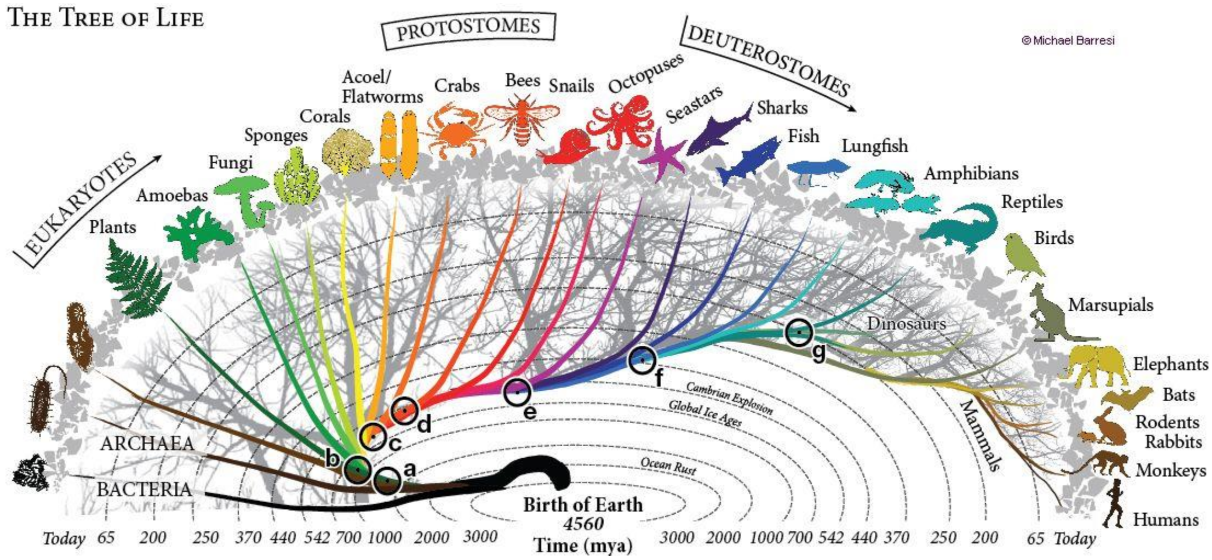


Figure 3 The tree of life—an illustration of the major branches of life. A geological timescale moves radially from the bottom to the top of the diagram. All life on Earth is related. To better comprehend this reality, some of the major organismal groups are illustrated with colored branches for simplicity. The underlying layer of gray branches implies a more realistic and chaotic interconnectedness of life's lineage. The letters a–g denote the locations of common ancestors, including those of plants (b) and of multicellular organisms (a). Many of the common ancestors of aceols and flatworms, insects, vertebrates, and land animals (annelids, arthropods, mollusks, echinoderms, and vertebrates) (c–f) can be traced to the Cambrian explosion of diversity.

One of the most important distinctions made by evolutionary embryologists was the difference between analogy and homology. Both terms refer to structures that appear to be similar. Homologous structures are those whose underlying similarity arises from their being derived from a common ancestral structure. For example, the wing of a bird and the arm of a human are homologous, both having evolved from the forelimb bones of a common ancestor. Moreover, their respective parts are homologous (Figure 4).

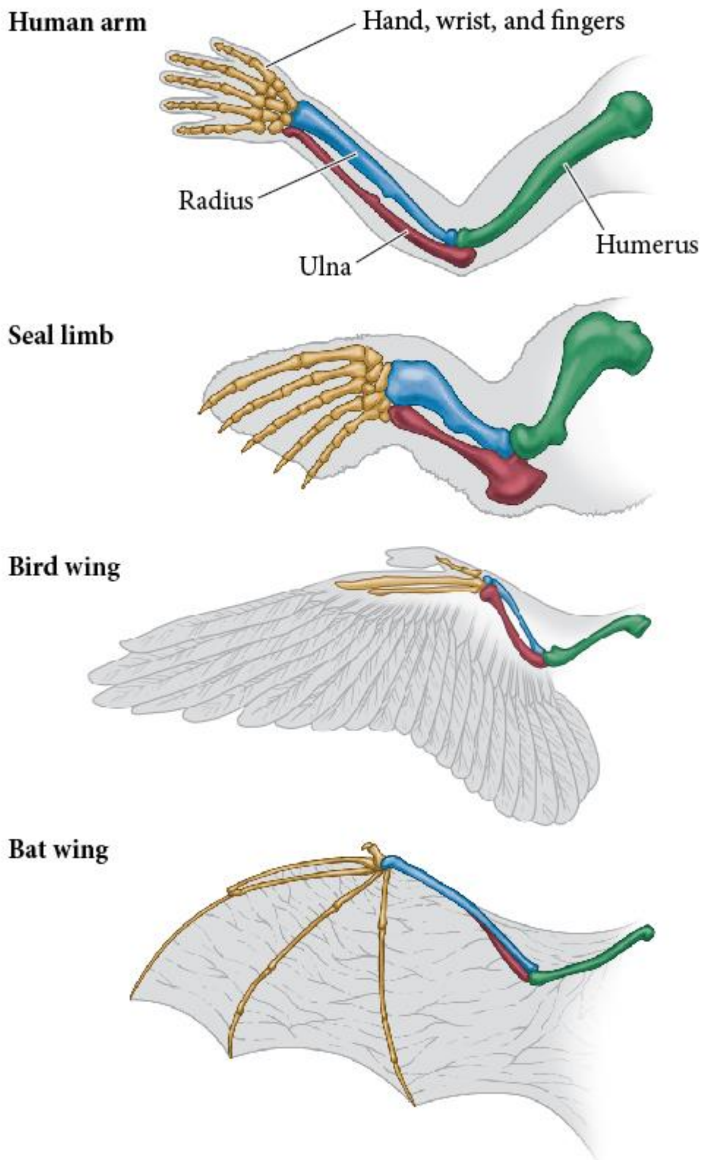
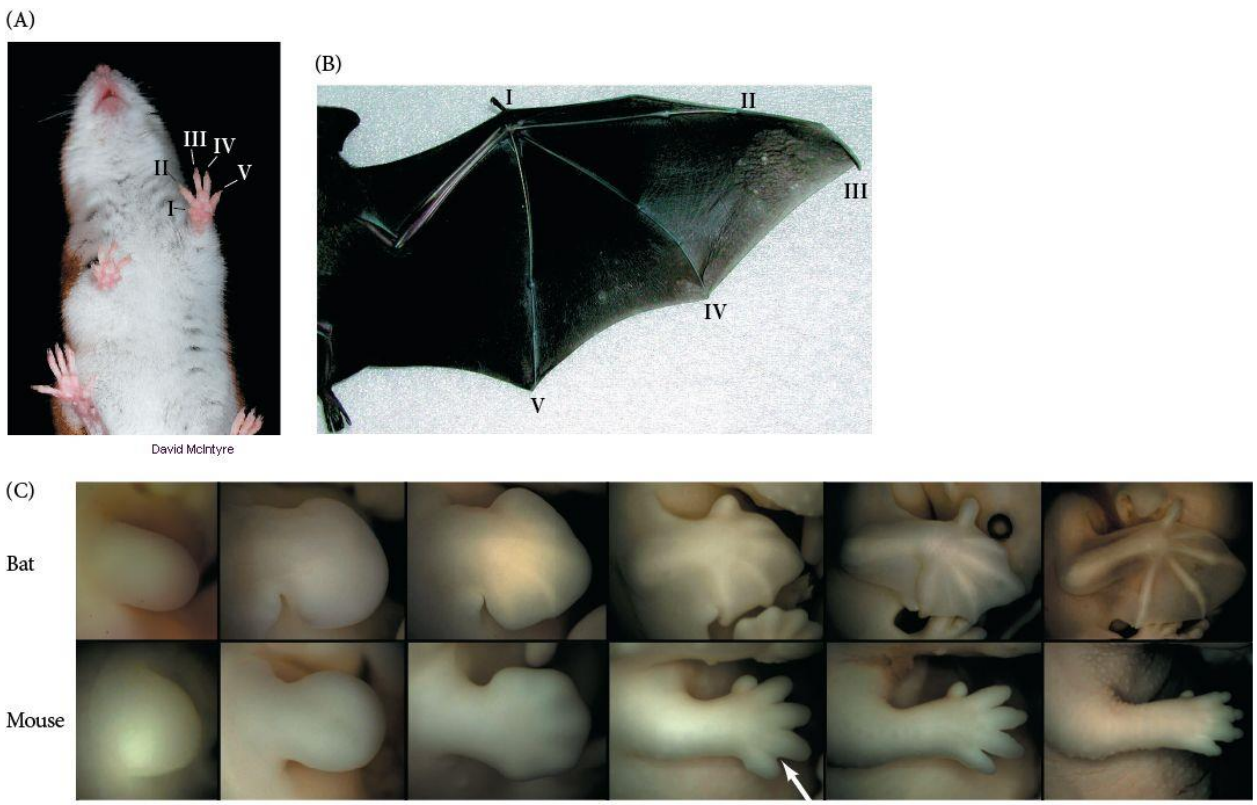


Figure 4 Homologies of structure among a human arm, a seal forelimb, a bird wing, and a bat wing; homologous supporting structures are shown in the same color. All four limbs were derived from a common tetrapod ancestor and thus are homologous as forelimbs. The adaptations of bird and bat forelimbs to flight, however, evolved independently of each other, long after the two lineages diverged from their common ancestor. Therefore, as wings they are not homologous, but analogous.

Analogous structures are those whose similarity comes from their performing a similar function rather than their arising from a common ancestor. For example, the wing of a butterfly and the wing of a bird are analogous; the two share a common function (and thus both are called wings), but the bird wing and insect wing did not arise from a common ancestral structure that became modified through evolution into bird wings and butterfly wings. Homologies must always refer to the level of organization being compared. For instance, bird and bat wings are homologous as forelimbs but not as wings. In other words, they share an underlying structure of forelimb bones because birds and mammals share a common ancestor that possessed such bones. Bats, however, descended from a long line of non-winged mammals, whereas bird wings evolved independently, from the forelimbs of ancestral reptiles (follow the tree branches in Figure 3).

As we discuss in Chapter 26, evolutionary change is based on developmental change. The bat wing, for example, is made in part by (1) maintaining a rapid growth rate in the cartilage that forms the fingers and (2) preventing the cell death that normally occurs in the webbing between the fingers. As seen in Figure 5, mice start off with webbing between their digits (as do humans and most other mammals). This webbing is important for creating the anatomical distinctions between the fingers. Once the webbing has served that function, genetic signals cause its cells to die, leaving free digits that can grasp and manipulate. Bats, however, use their fingers for flight, a feat accomplished by changing the expression of those genes in the cells of the webbing. The genes activated in embryonic bat webbing encode proteins that prevent cell death, as well as proteins that accelerate finger elongation (Cretekos et al. 2005; Sears et al. 2006; Weatherbee et al. 2006). Thus, homologous anatomical structures can differentiate by altering development, and such changes in development provide the variation needed for evolutionary change.



David McIntyre

B and C: From C. J. Cretekos et al. 2008. *Genes Dev* 22: 141-151, courtesy of C. J. Cretekos. © Cold Spring Harbor Laboratory Press

Figure 5 Development of bat and mouse forelimbs. Mouse (A) and bat (B) torsos, showing the mouse forelimb and the elongated fingers and prominent webbing in the bat wing. The digits are numbered on both animals (I, thumb; V, "pinky"). (C) Comparison of mouse and bat forelimb morphogenesis. Both limbs start as webbed appendages, but the webbing between the mouse's digits dies at embryonic day 14 (arrow). The webbing in the bat forelimb does not die and is sustained as the fingers grow.

Charles Darwin observed artificial selection in pigeon and dog breeds, and these examples remain valuable resources for studying selectable variation. For instance, the short legs of dachshunds were selected by breeders who wanted to use these dogs to hunt badgers (German Dachs, "badger" + Hund, "dog") in their underground burrows. The mutation that causes the dachshund's short legs involves an extra copy of the Fgf4 gene, which makes a protein that informs the cartilage precursor cells that they have divided enough and can start differentiating. With this extra copy of Fgf4, cartilage cells are told that they should stop dividing earlier than in most other dogs, so the legs stop growing (Parker et al. 2009). Similarly, long-haired dachshunds differ from their short-haired relatives in having a mutation in the Fgf5 gene (Cadieu et al. 2009). This gene is involved in hair production and allows each follicle to make a longer hair shaft (Ota et al. 2002; see Chapter 16). Thus, mutations in genes controlling developmental processes can generate selectable variation.

Key morphological transitions in animals over evolutionary history

How do we know that one animal form actually preceded the evolution of another form? It's not like we can literally see a lizard suddenly sprout feathers on its forelimbs and fly off into the sky. However, there are examples of some creatures showing traits of two closely related species, a so-called transitional morphological state. By examining such transitional organisms over the evolutionary history of metazoans (all animals), we can illuminate some of the most important aspects of embryonic development that were altered to drive the morphological diversity we see today (Figure 6 supports this entire section; see also the review by Stefan Rensing 2016).

From water to tetrapod to flight: Let's begin our climb down the tree of life (see Figure 3) by starting with a group of animals we are all familiar with, the birds. We now know that birds are derived from reptiles. Fossils of Archaeopteryx that date back to the late Jurassic (~150 million years ago [mya]) show the combined distinctive features of both a reptilian skeleton and avian feathered wings (Figure 7A). This transitional-state fossil highlights the morphological transition from dinosaur to bird and their evolutionary relatedness. Before the reptile could fly, however, it needed to walk, and that is what Tiktaalik roseae did as it emerged from the water some 375 mya. The skeletal structure of Tiktaalik's forelimb shows aspects of both a fish's fin rays and the organization and articulation of an amphibian's shoulder, and therefore represents the oldest example of a fish-to-tetrapod or fin-to-limb transition (Figure 7B; Shubin et al. 2006, 2014).

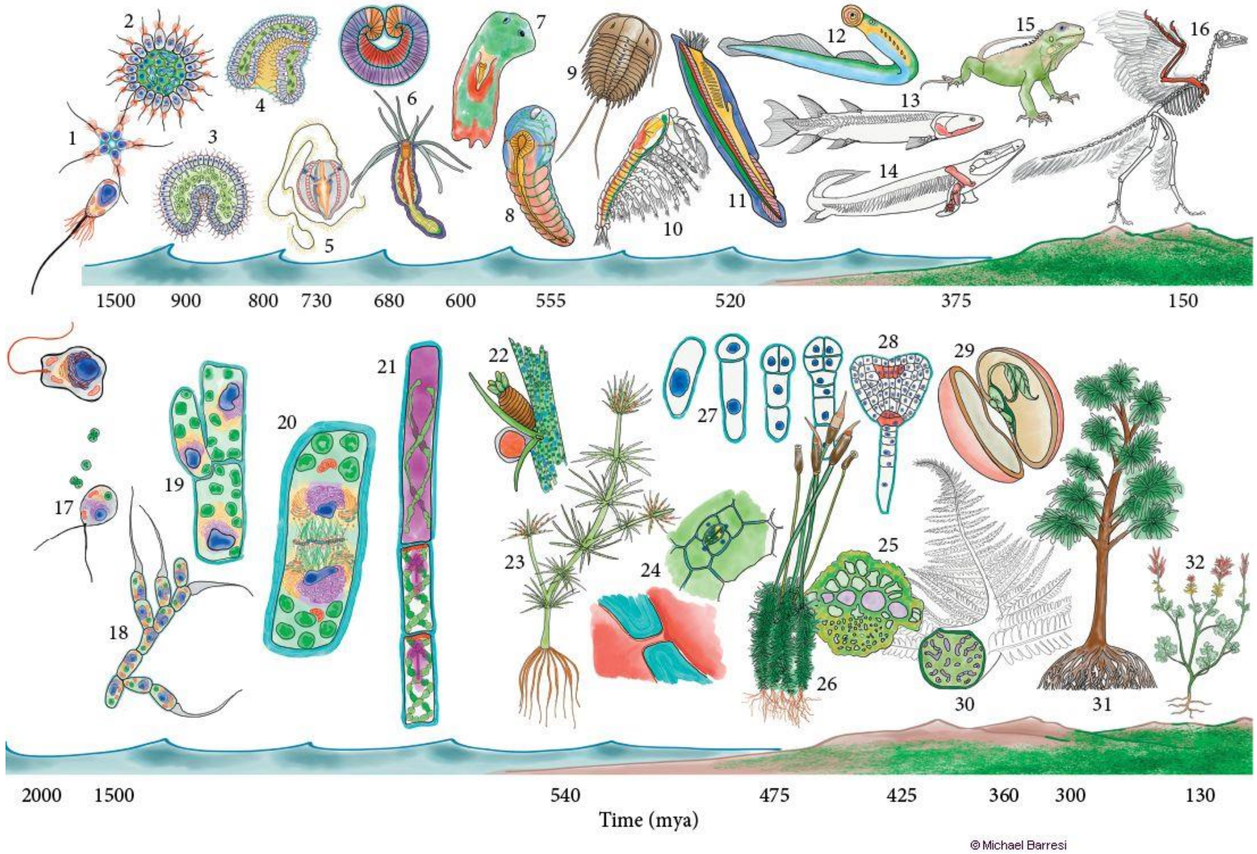


Figure 6 The developmental evolution of life. This illustration depicts key developmental adaptations that occurred over the course of evolutionary history in animals (top) and plants (bottom). The last eukaryotic common ancestor (LECA) gave rise to both plants and animals 2000 million years ago (mya). (Top) (1) Colonization of choanoflagellate cells. (2) Development of a two-layered organism with a proliferative inner layer and an epithelial filter-feeding outer layer. (3) Digestive architectures emerge with the evolution of tighter junctions and extracellular matrix (neon blue). (4) A primitive gut with aboral and oral openings appears, as in the sponge. (5) Ctenophores, such as this comb jelly, exhibit the first interconnected system of nerve-like cells. (6) Cnidarians such as the sea anemone show the first signs of gastrulation. (7) Bilateral symmetry evolves (aceols) and (8) segmentation emerges, generating (9,10) a diversity of arthropod lineages. (11) Adaptation of mesoderm produces the first axial derivative—the notochord (red)—giving rise to chordates. (12–14) From jawless fish (12, lamprey) to jawed fish (13, teleost) and from paired fins to articulating forelimbs (14, *Tiktaalik*), metazoans walk out of the water. (15,16) Among the terrestrial tetrapods, reptiles (15) further adapt their forelimbs into wings, giving rise to avian species (16). (Bottom) (17) Endosymbiosis of a cyanobacterium sets the stage for a path of photosynthesis-driven evolution. (18,19) Fixed modifications of collagen-based extracellular matrix genes foster the formation of filamentous colonies of algae (18) and a more protective cell wall (19, neon blue). (19) Integration of plastid DNA guides the biogenesis of multiplastid cells. (20) The phragmoplast builds the cell wall during cytokinesis. (21) Expansion of the phytohormone machinery opens communication across the entire plant for cell growth and morphogenesis. (22, 23) Alternation of generations is evident in the sporophytic and gametophytic phases displayed by the rhizoid-bearing charophytic algae, the common ancestor of all embryophytes. (24) Stomata and plasmodesmata provide the basis for a vascular future. (25) Hydroid cells (light purple) for nutrient transport are present in the first land plants: bryophytes (26, moss). (27) Embryonic development defines the embryophytes. (28) Pluripotent shoot and root apical meristems fuel indeterminate growth (red). (29) Seed adaptations protect and disperse embryos. (30, 31) Lignin further strengthens the cell wall for increased efficiencies of water and nutrient transport from the first vascular plants (30, ferns) to the tallest trees (31, conifers). (32) Coevolution with metazoan life helps promote an enormous diversity of angiosperms (flowering plants).

Chordates and the chord that connects us: Whether we are talking about an eagle, dinosaur, frog, or clownfish, they all have the common feature of being a vertebrate. The notochord is the most basal structure that defines an organism as a vertebrate, or chordate. The notochord is a flexible rodlike structure that runs down the middle of an embryo’s trunk and plays a pivotal role in organizing all surrounding tissues of the embryo. A critical moment in the transition from invertebrate to vertebrate developmental evolution is seen in amphioxus, or the lancelet, a benthic, filter-feeding animal that resembles a cross between a worm and a tiny razorlike fish (Figure 7C). Although amphioxus has no bones or even a brain of significance, it is related to the common ancestor of all chordates because it has a rudimentary notochord and nerve cord structures (Garcia-Fernàndez and Benito-Gutiérrez 2009).

A left and right, and a head and a tail: Continuing down the tree of life to the huge and marvelous diversity of invertebrate animals, we encounter the arthropods, which include spiders, centipedes, crustaceans (e.g., crabs), and insects. Despite a mass extinction at the end of the Permian (~xxx mya), trilobite fossils from that era reveal some of the most minimal features of arthropods, such as compound eyes, an exoskeleton that molted for growth, and segmented bodies and legs (Figure 7D). An abundance of these fossils has identified the trilobite as one of the earliest common ancestors of all segmented arthropods (Hughes 2003; Fusco et al. 2012). More important, the trait of segmentation actually provides a further clue to the next lower branch on the tree of life. It is suspected that some 600 mya a soft-bodied, bilaterally symmetrical worm served as the common ancestor of protostomes, which include the arthropods as well as the annelids and mollusks (e.g., snails) (Figure 7E; Parry et al. 2016). All of the species mentioned above have one major feature in common: bilateral symmetry. Although no fossils have been discovered to confirm the last common ancestor of all bilaterians (bilaterally symmetrical animals: acoelomorphs, protostomes, and deuterostomes), a hypothetical urbilaterian (German ur, “original”) is presumed to have been a small, bilaterally symmetrical, soft-bodied, wormlike organism that lacked segments[v] (Cameron et al. 2000; Engel 2015). Kimberella, a bilaterally symmetrical mollusk-like organism known from fossils dating back to 555 mya, has been suggested to be the closest relative of the Urbilateria (Figure 7F; Martin et al. 2000; Erwin and Davidson 2002).
So far, we have traveled back in time from complex appendages (wings) to the simplicity of bilateral symmetry. At each transition point it is important to reflect on the question of how?

How is bilateral symmetry created, with a head and tail positioned correctly? How could an elongated organism become organized into repeated segments, with some regions producing unique appendages such as antennae, fins, or wings? Once we learn about the mechanisms of developmental biology driving these different forms, it becomes feasible to understand how selection for certain genetic and molecular changes can tweak these morphologies over the course of evolution to create the diversity around us today. But wait, our journey down the tree is not over yet.

The basic layers of us

Bilateral symmetry is thought to have evolved from organisms possessing simpler radial and spherical geometric morphologies. The radially symmetrical cnidarians (jellyfishes, corals, and their relatives) already had nervous systems, guts, and even muscles (Figure 7G). In bilaterians, these three tissue types are derived from three separate embryonic germ layers: ectoderm, endoderm, and mesoderm. Cnidarian anatomy visibly shows only two layers, which originally were deemed to be ectoderm and endoderm; however, due to the presence of muscle and the expression of mesoderm-specific genes, cnidarians have been thought to possess a transitional mesendodermal embryonic layer (Holland 2000). Interestingly, it has recently been suggested that the two layers of cnidarian construction may actually have more discrete regions of not only ectoderm but also endoderm and mesoderm—a finding that spurs speculation about the origins of germ layer development before the emergence of bilaterians (Steinmetz et al. 2017).

I think, therefore I am

The fact that you are able to read this textbook demonstrates the irrefutable importance that development of the nervous system has had on animal evolution. The highly interconnected central nervous systems of mammals, birds, reptiles, and fish represent a significant developmental change

from the nerve cord and sensory ganglia of arthropods. It is currently debated whether cnidarians and ctenophores (comb jellies) possess homologous nervous systems, but both have epithelial nervous systems with a mesogleal nerve net (Figure 7H; Marlow et al. 2009; Jékely et al. 2015). They represent the oldest phylogenic system of nerves, but one that could still offer the most critical of functions, movement. For some derived species, the nervous system was an essential adaptation to enable movement toward food and even to use the tentacles to capture prey, as well as contract the muscles of the gut for controlled digestion. Further illuminating are the sessile sponges (poriferans), which are widely considered to hold the most basal location of all metazoan phyla (said another way, “they sit at the base of the tree of animal life”) (Figure 7I and 7J). In terms of the evolution of the nervous system, it is important to know that neither an adult sponge nor its larvae have a nervous system or even an epithelial gut. Nevertheless, sponges do have synapse-like machinery—cells that communicate through connected channels and signaling proteins that are conserved across animals. Therefore, it appears that our nervous systems have evolved from cells and tissues originating from a sponge (Nielsen 2008)! Now try to use your brain to soak up that fact.
The origins of gastrulation: Some controversy surrounds the notion of whether the sponge embryo undergoes the quintessential embryonic process of gastrulation—those cell movements in the embryo that produce the bilaterian germ layers and primitive gut. Adult sponges form channels with chambers covered with choanocytes, ciliated cells that power the unidirectional flow of water through the organism (see Figure 7I). In most cases the adult sponge is created indirectly through the metamorphosis of a free-floating larva—a physical change from a spherical embryonic and larval body type to the adult, ground-attached, filter-feeding chamber (see Figure 7J). It is irrefutable, however, that the sponge embryo and larvae have a well-delineated anterior-posterior axis with both inner and outer tissues. This is suggestive of the early origins of cell types exhibiting characteristics of epithelia (a tightly bound, nonmigratory tissue) with differential patterning across an axis—a developmental phenotype essential for complex tissue-layer construction and with the potential for primitive gut morphogenesis (the cell and tissue movements that create more complex forms, in this case a primitive gut) (Maldonado et al. 2006; Nakanishi et al. 2014). It has been proposed that the larvae of some ancient sponges (homoscleromorphs) underwent sexually maturity prior to metamorphosing into the juvenile sponge. This would have freed the homoscleromorphs from maturation into the adult form, which may have opened a new door for the natural selection of tighter epithelial cell connections capable of supporting the movements of gastrulation, and ultimately the evolution of diploblastic (two-layered) metazoans such as the aforementioned cnidarians (Nielsen 2008).

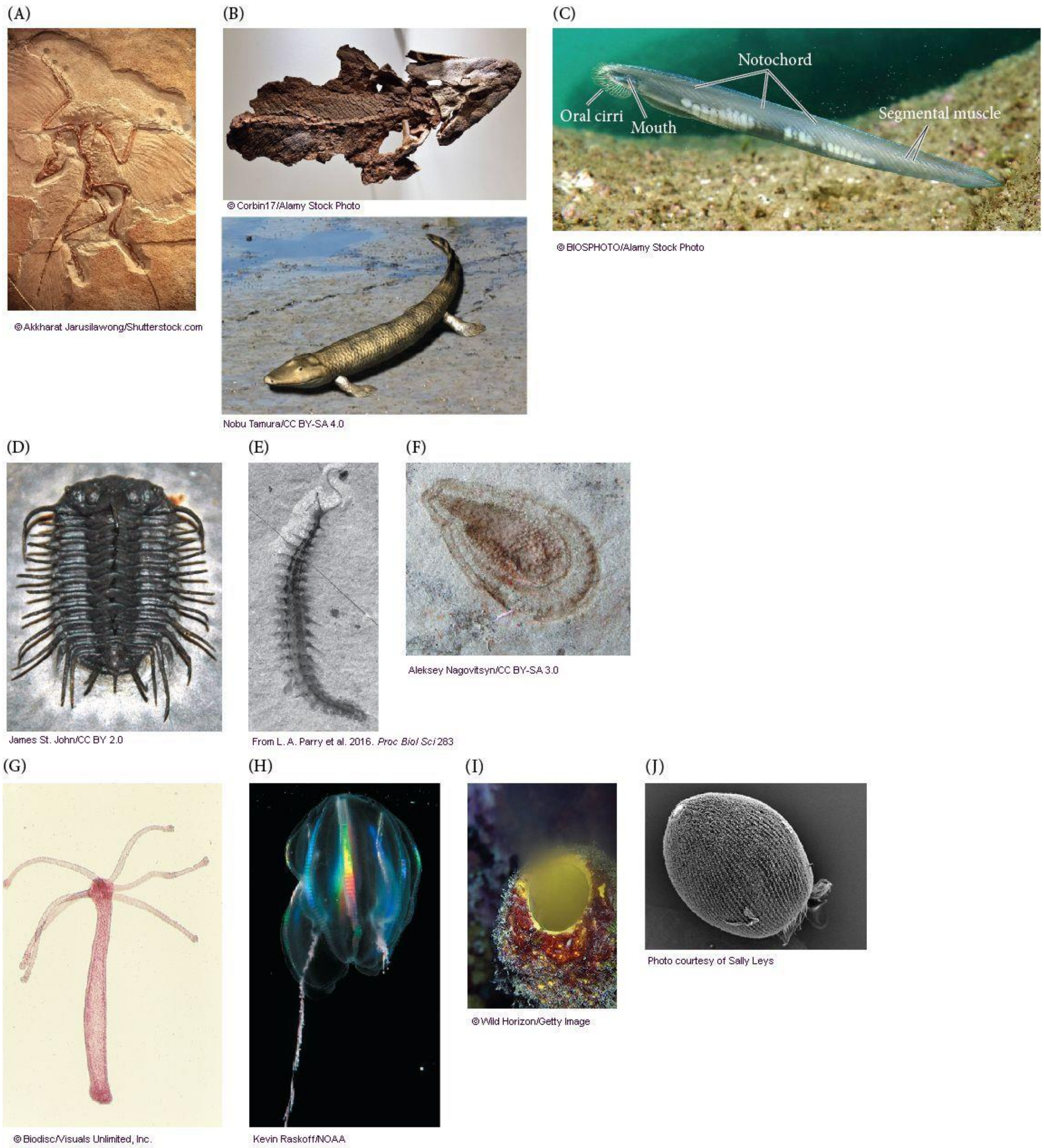


Figure 7 Transitional states over the course of animal evolution. (A) A late Jurassic (~150 mya) fossil of *Archaeopteryx* showing its distinctive features of both a reptilian skeleton and avian feathered wings. (B) *Tiktaalik roseae* emerged 375 mya from the water to be the first animal hypothesized to walk on land. This fossil (upper) and reconstruction (lower) revealed characteristics of both fish fins and amphibian forelimbs, among other characteristics. (C) Amphioxus, or the lancelet, has a rudimentary notochord and nerve cord structures and thus is related to the common ancestor of all vertebrates. (D) Despite their Permian era mass extinction, an abundance of Trilobite fossils identified them as one of the earliest common ancestors to all arthropods. (E) Fossil annelid. (F) Kimberella quadrata (G) Scanning electron micrograph of the cnidarian, hydra. (H) Arctic comb jelly or sea nut *Mertensia ovum*. (I) A tube sponge. Dye placed at the base of the sponge is then squirted out the top, showing the pumping action of the sponge. (J) A motile larva of a sponge.

From one to many: Of course, the most fundamental evolutionary step required to build an animal was that of multicellularity—going from one cell to many different cells. Imagine a single eukaryotic cell in the water. Something like a protist perhaps. Is it moving? Is it interacting with other cells? How do you imagine it becoming multicellular? Maybe it grabs hold of neighboring cells, tightly, and never lets go. Conceivably, this ancient single cell could have just divided, with the daughter cells failing to separate. Alternatively, instead of initially dividing, the cell could have replicated its DNA and duplicated its nucleus but failed to separate the nuclei into new cells—creating what is known as a syncytium (many nuclei within one cell membrane, like your skeletal muscle cells). Then at some point new membranes were generated around each nucleus to turn this hypothetical protist into a multicellular organism. Perhaps you can think of yet another method for the evolution of multicellularity, because it is estimated to have occurred independently 25–50 times over Earth's history. Nevertheless, today we have only six groups of multicellular organisms: the brown, green, and red algae, land plants, fungi, and animals.

Each of these ideas regarding the origin of metazoan multicellularity is plausible. However, the "colonial theory" seems to be the prevailing hypothesis. If we consider the most basal metazoans, the sponges, then a particular ciliated cell type comes to mind—the choanocytes we mentioned above. With their ciliated structure and their water-filtering functions, choanocytes are considered to be homologous to the single-celled and colony-forming tiny aquatic protists known as choanoflagellates (Figure 8; Nielsen 2008; Nosenko et al. 2013). Most interesting are the types of cell-to-cell connecting proteins that choanoflagellates possess, which include well-conserved genes still found in triploblastic bilaterally symmetrical animals (us), such as genes that encode cadherins involved in cell-to-cell adhesion. In fact, loss of a leptin-like gene (known to be a bifunctional signaling and adhesion receptor) in extant (living today) choanoflagellates prevents single cells from adhering and forming their characteristic rosette-shaped colonies (Levin et al. 2014).

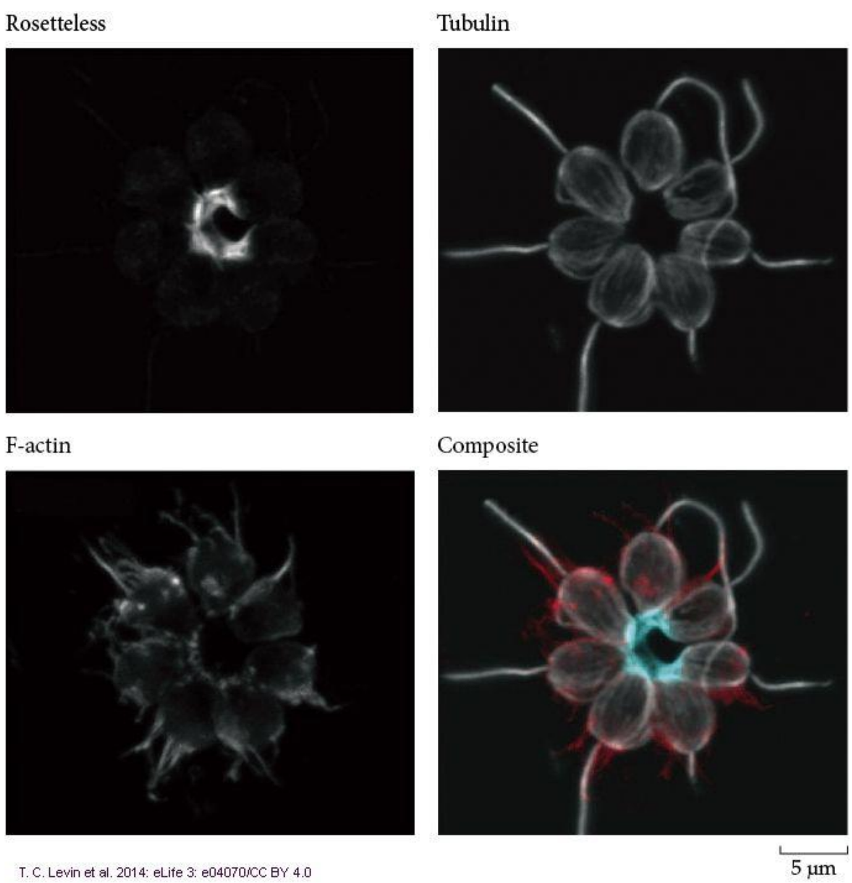


Figure 8 Choanoflagellates were the common ancestor of all animals. Shown here are extant choanoflagellates in a rosette colony formation. These cells were immunolabeled for the proteins Rosetteless (a leptin-like protein; cyan in the composite), tubulin (marking the flagella; white in the composite), and filamentous actin (F-actin, marking the microvilli that take on a "collar-like" formation; red in the composite).

So now imagine that some 3 bya, an ancient chanoflagellate started to form loosely packed colonies, just as choanoflagellates do today. Mutations in genes encoding adhesion proteins conferred tighter junctions between neighboring choanoflagellates to a degree where they could even transfer nutrients between each other, sharing the labor for mutual survival. This was the birth of the first multicellular organism, proposed to be the choanoblastaea, consisting of a single-layered, hollow sphere of choanocytes (think of a three-dimensional rosette) (Nielsen 2008). Along this metazoan branch, choanoblastaea continued to adapt its epithelium for more complex functions and tissue movements, giving rise to the ancient homoscleromorphs, a special group of sponges, and the birth of the metazoan embryo.

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[i]Indeed, one definition of a phylum is that it is a collection of species whose gene expression at the phylotypic stage is highly conserved among them, yet different from that of other species (see Levin et al. 2016). However, controversy over what constitutes a phylum persists. For instance, some authors consider cephalochordates (amphioxus), tunicates, and chordates as separate phyla, whereas others unite them in one phylum, Chordata.

[ii]The notochord is a rodlike structure that runs down the middle of an embryo's trunk (see Figure 7C) and functions as an organizing center for the neural and non-neural tissues that surround it. It is seen in every vertebrate embryo and thus is a defining feature of chordates (vertebrates).

[iii]As first noted by Weismann (1875), larvae must have their own adaptations. The adult viceroy butterfly mimics the monarch butterfly, but the viceroy caterpillar does not resemble the beautiful larva of the monarch. Rather, the viceroy larva escapes detection by resembling bird droppings (Begon et al. 1986).

[iv]The oyster toadfish is arguably the ugliest fish in the ocean (author opinion). So yes, due to this exemplified relationship, you could consider this a personal criticism. *Yes, we are making a joke here. It's okay to laugh* (*at the joke or us—both welcomed*).

[v]This hypothesis is not without significant debate as an alternative view suggests that the urbilaterian organism was originally more complex, possessing segments as well as a mouth and anus, prior to diverging (Holland 2000; Manuel 2009).