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Haeckel and the Vertebrate Archetype

A recent paper by Michael Richardson and his colleagues (1997) has corrected a major misunderstanding among developmental biologists and evolutionary biologists which can be traced back to Ernst Haeckel. Haeckel (1874) had claimed that members of all vertebrate classes pass through an identical evolutionarily conserved "phylotypic" stage. Until this new paper appeared, it was assumed that Haeckel was correct and that there was a particular stage of development that was identical in all vertebrates. Only later in development would specific differences appear. Interestingly, there was some discussion as to what exactly this stage was (Richardson 1995). This conserved stage was sometimes considered the neurula stage (Wolpert 1991), the "pharyngula" stage (characterized by the branchial arches; Ballard 1981), the tailbud stage (Slack et al. 1993), or the stages between those of headfold and tailbud (Duboule 1994). Figure 1 shows one of Haeckel's representation of vertebrate embryology. The top row shows that all the vertebrate embryos (no matter what path they took to reach this stage) have a stage where they appear almost identical.

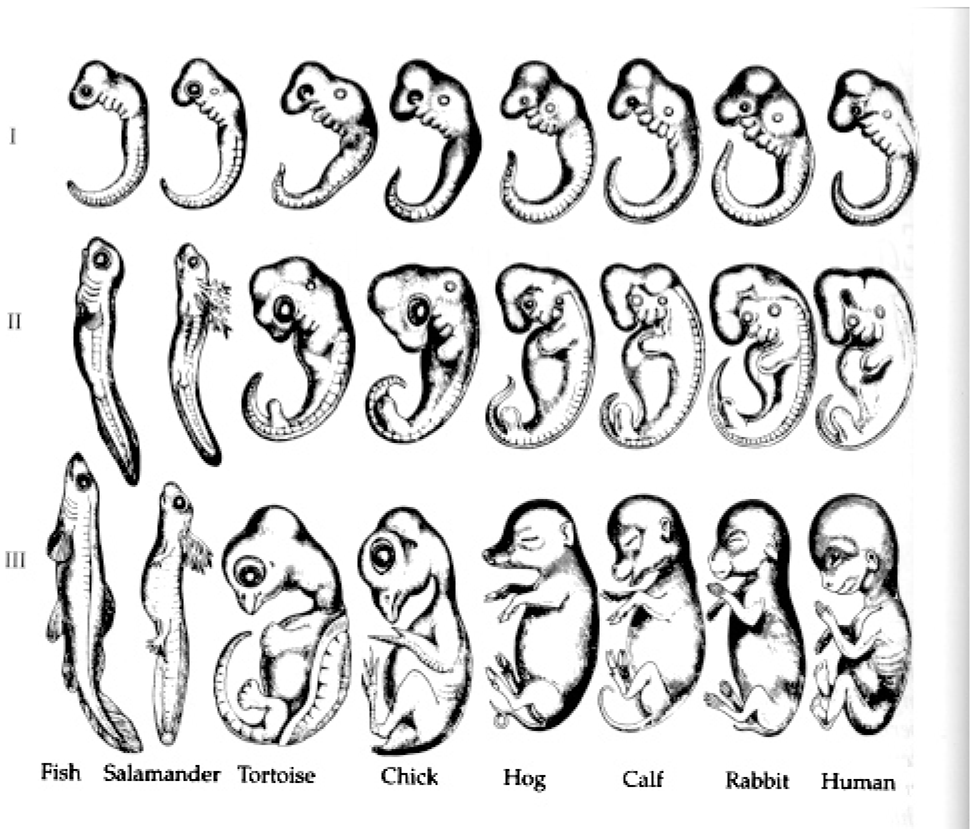

Figure 1 Haeckel's 1874 version of vertebrate embryonic development. The top row shows an early stage common to all groups, the second row shows a middle stage of development, and the bottom row shows a late stage embryo. Groups from left to right are: fish, salamander, turtle, chicken, pig, cow, rabbit, and human. (Adapted from Gilbert 1997.)

But Haeckel's drawings are wrong. Photographing actual embryos at these stages, Richardson and colleagues show that Haeckel's drawings are oversimplified to the point of obscuring important differences between classes of vertebrates. The Richardson et al. paper does not dispute that there is a highly conserved embryonic stage among the vertebrate classes. Indeed, at the late tailbud stage, vertebrate embryos of most all classes possess "somites, neural tube, optic anlagen, notochord, and pharyngeal pouches." However, these authors do criticise the notion that this stage is nearly identical in all species and that differences between the classes can be resolved only after subsequent development. Rather, they discover significant differences between groups. Size is one distinctive marker. The scorpion fish embryo is 700 microns long at the tailbud stage, while the mudpuppy salamander measures some 9 millimeters. Heterochrony is another problem. In some species of direct developing frogs, and in monotreme mammals, limb buds are already present at the tailbud stage, whereas in other species, these are not seen until significantly later. Birds are characterized by their prominent mesencephalon. Whereas most amniote embryos have a heart by this stage, the zebrafish does not. (Teleosts such as zebrafish are even the exception to the rule mentioned above. They eventually possess a notochord, somites, pharyngeal pouches, etc., but they do not have the pharyngeal pouches until *after* the tailbud stage). Some of these differences are depicted in Figure 2.

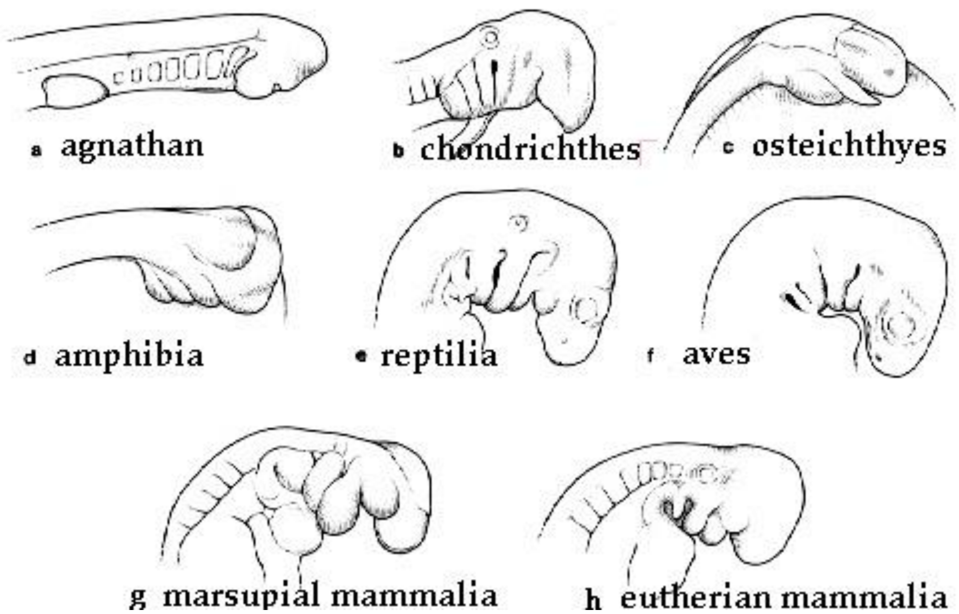

Figure 2 Selected embryos shown at the "phylotypic" stage. (A) Sea lamprey (jawless cyclostome fish, *Petromyzon*) with nearly identical pharyngeal pouches and heart that is caudal to the pharynx; (B) electric ray (cartilagenous chondrichthes fish, *Torpedo*) with nearly identical pharyngeal pouches and a pronounced hindbrain/midbrain flexure; (C) sterlet (bony Osteichthyes fish, *Acipenser*) where the pharyngeal pouches have not yet formed; (D) frog (direct-developing anuran amphibian *Eleutherodactylus*) which has hindlimb buds at the tailbud stage and only two pairs of aortic arches; (E) pond turtle (chelonian reptile, *Emys*) where there is no craniocaudal rotation (torsion) to the embryo, whereas the same stage of the chick (avian) embryo (F) shows pronounced torsion; (G) brush-tailed possum (marsupial mammal, *Trichosurus*) where there is (in contrast to the cartilagenous fishes) large maxillary and mandibular processes. In the cat (eutherian mammal, *Felis*) there is a similar size difference between the anterior and posterior pouches, although their appearance differs from that of the marsupials. (After Richardson 1997.)

Interestingly, this knowledge appears to be "old hat" among German biologists. Yet, the idea that early vertebrate embryos are essentially identical has survived. I think there were two reasons for the survival. First, Haeckel's illustration was reproduced in Romane's (1901) *Darwin and After Darwin*. From here, the illustration entered Anglophone biology, "sanitized" from Haeckel. Second, the picture can be used (as it has been in several developmental biology books) to illustrate von Baer's principles rather than Haeckel's biogenetic law. K. E. von Baer had noted that the general features of a large group of animals appear earlier in the embryo than do the specialized features. Indeed, von Baer wrote, “The embryo of the mammal, bird, lizard, and snake and probably also the turtle, are in their early stages so uncommonly similar to one another that one can distinguish them only according to their size" (translated in Stephen Jay Gould's 1977 *Ontogeny and Phylogeny*).

Darwin quoted this (it was Thomas Huxley's translation) although he misattributed the story to Agassiz rather than to von Baer (see Richards 1992 for an analysis). The notion of development proposed by von Baer is still used as a general approximation of certain developmental phenomena. Certainly, the early embryos of certain vertebrate classes are very similar (for instance, the chick and mouse twenty-somite embryos), and the processes of somitogenesis, limb formation, axis generation, etc. are probably conserved throughout the vertebrate groups).

Similarities and Differences

What the Richardson et al. paper tells us is that we have to be attentive to the differences as well as to the similarities. A bird embryo is not the same as a mammalian embryo. We should not assume identity, even at a stage where all vertebrate embryos seem to pass. The Richardson et al. paper can be read as a critique of the recent priority of similarities over differences.

The concept of homology enables one to celebrate the differences or the similarities between two structures. Whether one emphasizes the similarities between our forelimb and a bird's wing or the differences between them depends on what you are describing. Comparative anatomy—with its Aristotelian and Cuverian interest in relating structure to function—usually emphasizes the differences. Morphology—with its Platonic and Geoffroyan interest in the underlying unities of structure—usually focuses on the similarities.

As Joseph Needham noted, embryology has swung between these two poles during different stages of its morphogenesis. In the late 1800s, the morphological tradition prevailed, and the similarities between developmental stages in different organisms constituted some of the best evidence for classification (see Nyhart 1995; Bowler 1996). Thus, the discovery of the Nauplius stage of the barnacle showed that it was a modified crustacean, and the notochord-containing tadpole of the tunicate demonstrated its affinities with the chordates. However, after the 1920s, embryology was no longer a major support for evolutionary biology, and the comparative anatomy tradition came to predominate. Until the 1980s, embryology was extremely descriptive. Each organ was seen to develop differently from any other organ, and each species was seen to develop differently from any other species. Indeed, embryology was defined (by one of its practitioners, E. G. Conklin) as a "lawless science," because generalities could not be made from the observations of animal development. When embryology underwent its anagenic transition to become developmental biology, the similarities among organisms were again emphasized. The similarities were now posited on the molecular rather than the morphological or cell lineage level. The 1990s has seen a remarkable celebration of the similarity of molecular processes throughout the animal kingdom. Homologous genes abound (the Hox genes, *fringe*, *tinman*, and *Pax6* being seen to specify the anterior-posterior axis, the limb, the heart, and the eye, respectively, of organisms as diverse as insects and flies). Even signalling pathways are seen as being homologous both within a developing organism and between organisms. Thus, the neural tube in vertebrates and insects are seen as being formed through the same interactions of the "same" proteins, even though one neural tube is dorsal and the other ventral. The Richardson et al. paper reminds us that despite these similarities, differences are also important, especially if one is thinking in terms of the relationships between development and evolution.

The Richardson et al. paper is also a plea for comparative anatomy and less reliance on "model systems." This critique of model systems echoes a recent plea from Leo Buss, Rudy Raff, Jessica Bolker, and James Hanken, who observe that model systems converge on several factors (see Bolker and Raff 1997; Hanken 1993): they all can develop in the laboratory and are thus relatively free of environmental factors effecting their morphogenesis; they are all organisms which segregate their germ line extremely early; they develop rapidly, are small as adults, and they have short generation times.

The Richardson et al. paper does a great service to developmental biology. As they mention, there is renewed interest in evolutionary developmental biology, and in view of the conservation of developmental mechanisms, we need to re-examine the extent of variation in vertebrate embryos. There is more variation than had been assumed, and these variations foreshadow important differences in the adult bodies. This is important because we need to know how conservative the early embryonic stages actually are.

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