Haeckel's Embryos & Evolution

Setting the Record Straight

Jonathan Wells

IN *The Origin of Species* Charles Darwin wrote that "the embryos of mammals, birds, fishes, and reptiles [are] closely similar, but become, when fully developed, widely dissimilar." He inferred that all vertebrates "are the modified descendants of some ancient progenitor," and that "the embryonic or larval stages show us, more or less completely, the condition of the progenitor of the whole group in its adult state" (Darwin 1859, pp. 338, 345). Darwin's contemporary Ernst Haeckel called this the "Biogenetic Law," according to which "ontogeny recapitulates phylogeny." To illustrate the law, Haeckel (1891) produced drawings of vertebrate embryos which have been widely used in biology textbooks ever since (Figure 1).

But Haeckel's Biogenetic Law was discredited by embryologists in Darwin's lifetime (Bowler 1989); recent work has shown that Haeckel's drawings misrepresent the embryos they purport to show (Richardson et al. 1997); and Haeckel entirely omitted the earliest stages of development in which the various classes of vertebrates are morphologically very different (Elinson 1987). Biology teachers should be aware that Haeckel's drawings do not fit the facts.

Haeckel's Discredited Biogenetic Law

Haeckel's Biogenetic Law maintains that vertebrate embryos pass through stages in which they exhibit adult features of their evolutionary ancestors. In its most famous example, the law teaches that "gill slits" in vertebrate embryos reveal their common aquatic ancestry. But human embryos do not really have gills or gill slits: like all vertebrate embryos at one stage in their development, they possess a series of "pharyngeal pouches," or tiny ridges in the neck region. In fish embryos these actually go on to form gills, but in other vertebrates they develop into unrelated structures such as the inner ear and parathyroid gland. The embryos of reptiles, birds and mammals never possess gills (Rager 1986).

The notion that vertebrate embryos transiently exhibit adult features of their evolutionary ancestors is false and was already discredited in Darwin's lifetime. Nineteenth-century embryologist Karl Ernst von Baer pointed out that although vertebrate embryos resemble each other at one point in their development, they never resemble the adult of any species, present or past (von Baer 1828; Bowler 1989, p. 129). Prominent 20th-century embryologists have also criticized the Biogenetic Law: In 1922 Walter Garstang wrote that "the basis of this law is demonstrably unsound," and in 1958 Sir Gavin de Beer called it "a mental strait-jacket which has had lamentable effects on biological progress" (Garstang 1922, p. 81; de Beer 1958, p. 172).

Although vertebrate embryos never resemble the adults of any species, it is true that they pass through an intermediate stage in which some of them superficially resemble each other (Haeckel's first stage). Looking at development from this intermediate stage onward, von Baer concluded that early embryos exhibit features common to the phylum before developing the distinguishing characteristics of classes, genera and species (von Baer 1828).

Many 20th-century biologists prefer von Baer's interpretation to Haeckel's: Early embryos may not possess ancestral *adult* structures, but their similarities are interpreted as vestiges of ancestral *embryonic* features. Since Haeckel's drawings can be used to illustrate von Baer's interpretation as well as Haeckel's, they have survived even though the latter has been discredited. Haeckel's embryos have thus become familiar to generations of biology students. Unfortunately, his drawings misrepresent the facts.

Haeckel's Distorted Drawings

The version of Haeckel's drawings that has been widely used in textbooks (Figure 1) omits two of the seven vertebrate classes (jawless fishes and cartilaginous fishes). It also uses a salamander rather than a frog to represent amphibians, and placentals rather than monotremes or marsupials to represent mammals. Thus it ignores groups that don't fit neatly into Haeckel's scheme.

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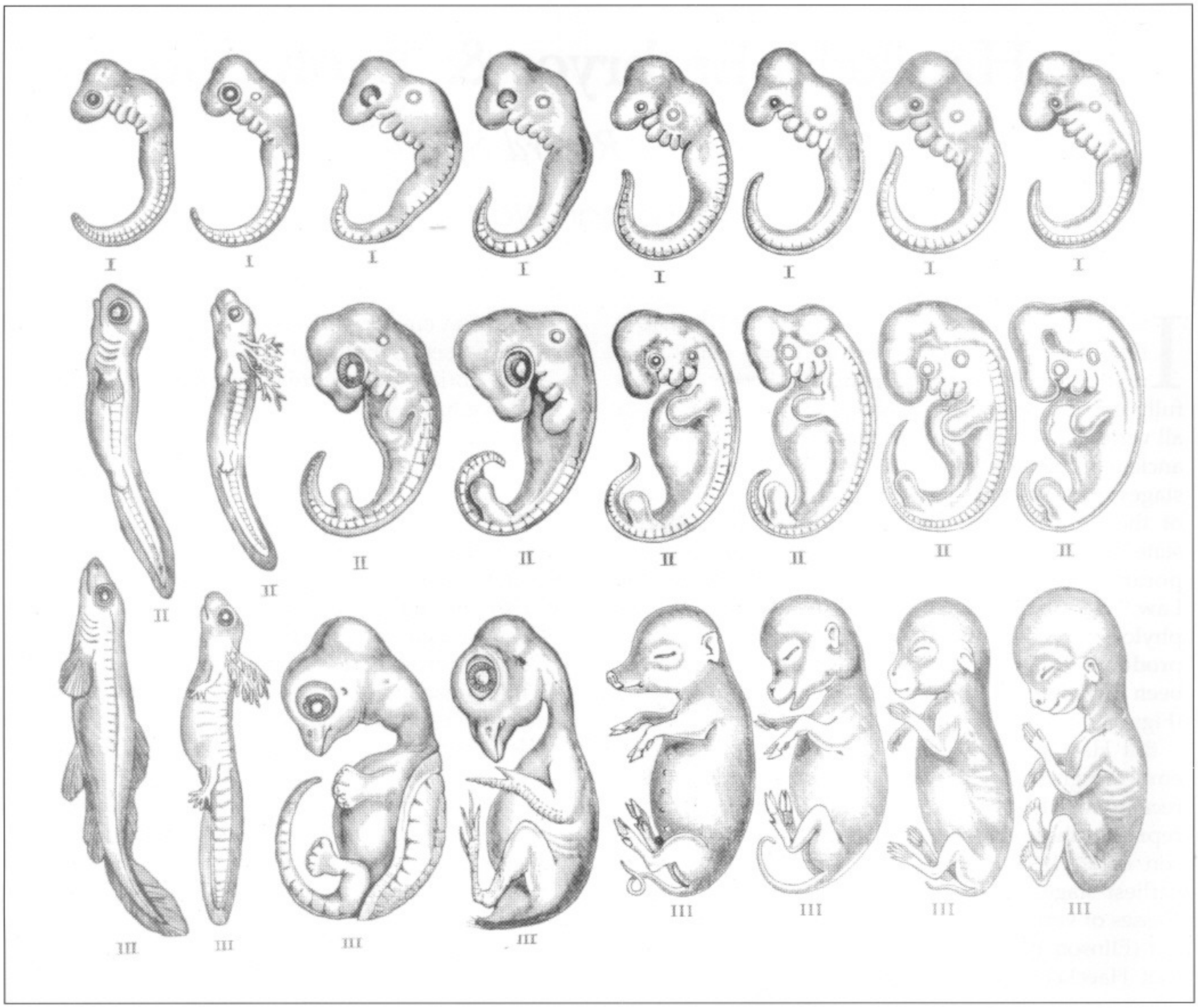

Figure 1. Haeckel's drawings, as reproduced by Romanes (1892). The embryos are (left to right) fish, salamander, tortoise, chick, hog, calf, rabbit and human. Note that only five of the seven vertebrate classes are represented and that half the embryos are mammals.

Even worse, Haeckel's drawings distort the embryos he selected. Embryologist Michael Richardson and his colleagues recently surveyed all seven classes of vertebrates, and made drawings of actual embryos at the stage in which Haeckel claimed they were most similar. Their drawings, unlike Haeckel's, show significant differences among the various classes, and even between marsupial and placental mammals (Figure 2). Richardson and his coworkers conclude that their survey "seriously undermines the credibility of Haeckel's drawings" (Richardson et al. 1997, p. 91).

Even if Haeckel's drawings were accurate, however, they would not justify the claim that vertebrate embryos are most similar in their earliest stages. This is because Haeckel omitted the earliest stages entirely.

Early Vertebrate Embryos Are Morphologically Dissimilar

After fertilization, an animal embryo first undergoes a process called "cleavage," during which the fertilized egg subdivides into hundreds or thousands of separate cells. At the end of cleavage, those cells begin to rearrange themselves in a process known as "gastrulation." During cleavage and gastrulation, the embryo establishes the general body plan (e.g. shellfish, insect or vertebrate) and generates basic tissue types and organ systems (e.g. skin, muscles and gut). Only after cleavage and gastrulation does a vertebrate embryo reach the stage that Haeckel treated as the first step in development.

If it were true (as von Baer, Darwin and Haeckel thought) that all vertebrates are most similar during

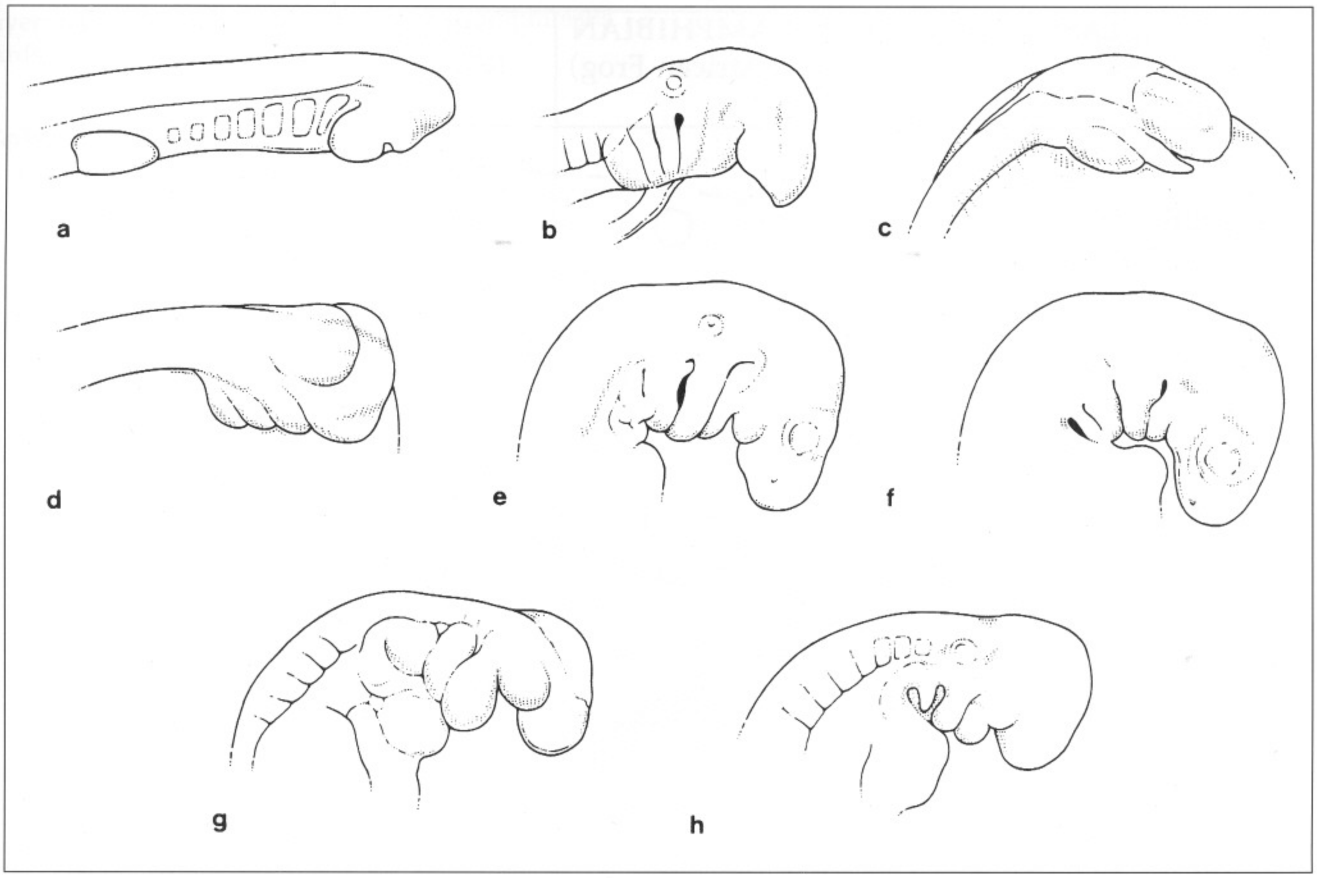

Figure 2. Drawings of actual embryos at the first stage represented in Haeckel's drawings. All seven vertebrate classes are shown; for mammals, both a marsupial and a placental are included to show that differences exist even within a class. The embryos are: (a) a jawless fish (sea lamprey); (b) a cartilaginous fish (electric ray); (c) a bony fish (sterlet); (d) an amphibian (Puerto Rican tree frog); (e) a reptile (European pond terrapin); (f) a bird (chicken); (g) a marsupial mammal (brush-tailed possum); and (h) a placental mammal (domestic cat) (from Richardson et al. 1997, p. 104; © Springer-Verlag, used by permission).

the earliest stages of their development, then the various classes would be most similar during cleavage and gastrulation. Yet a survey of only four classes (bony fish, amphibian, bird and mammal) reveals that this is not the case (Figure 3).

Differences among the four classes are evident even in the fertilized eggs: zebrafish and frog eggs are approximately the same size (about a millimeter in diameter); the chick embryo is a disk 3 to 4 millimeters in diameter which sits on top of a large yolk; while the human embryo is only about 0.05 millimeters in diameter (Figure 3, top row). The earliest cell divisions in zebrafish, frog and chick embryos are similar except for the fact that they are unable to penetrate the yolk in fish and bird eggs; but the earliest cell divisions in humans (and all other mammals) are completely different from the other three, since one of the second cleavage planes is rotated 90° relative to the other (Figure 3, second row).

At the end of cleavage, the cells of the zebrafish embryo form a large cap on top of the yolk; in the frog they form a ball with a cavity in one hemisphere; in the chick they form a thin, two-layered disk on top of the yolk; and in humans they form a disk within a ball (Figure 3, third row). Cell movements during gastrulation also differ among the four classes: in zebrafish the cells migrate down the outside of the yolk; in frogs they migrate through a pore into the inner cavity; and in chicks and humans they move through a furrow into the hollow interior of the embryonic disk (Figure 3, fourth row).

Although cleavage is somewhat similar in zebrafish and chick embryos, and gastrulation somewhat similar in chick and human embryos, it is clearly not the case that vertebrate embryos are most similar in their earliest stages and diverge as they develop. This fact is well known to modern embryologists, many of whom have noted that it is inconsistent with the notions of von Baer, Darwin and Haeckel. In 1976, William Ballard wrote that it is "only by semantic tricks and subjective selection of evidence" and by "bending the facts of nature" that one can argue that the cleavage and gastrulation stages of vertebrates "are more alike than their adults" (Ballard 1976, p. 38). In 1991, Rudolf Raff and his colleagues confirmed that "eggs, cleavage, gastrulation and germ

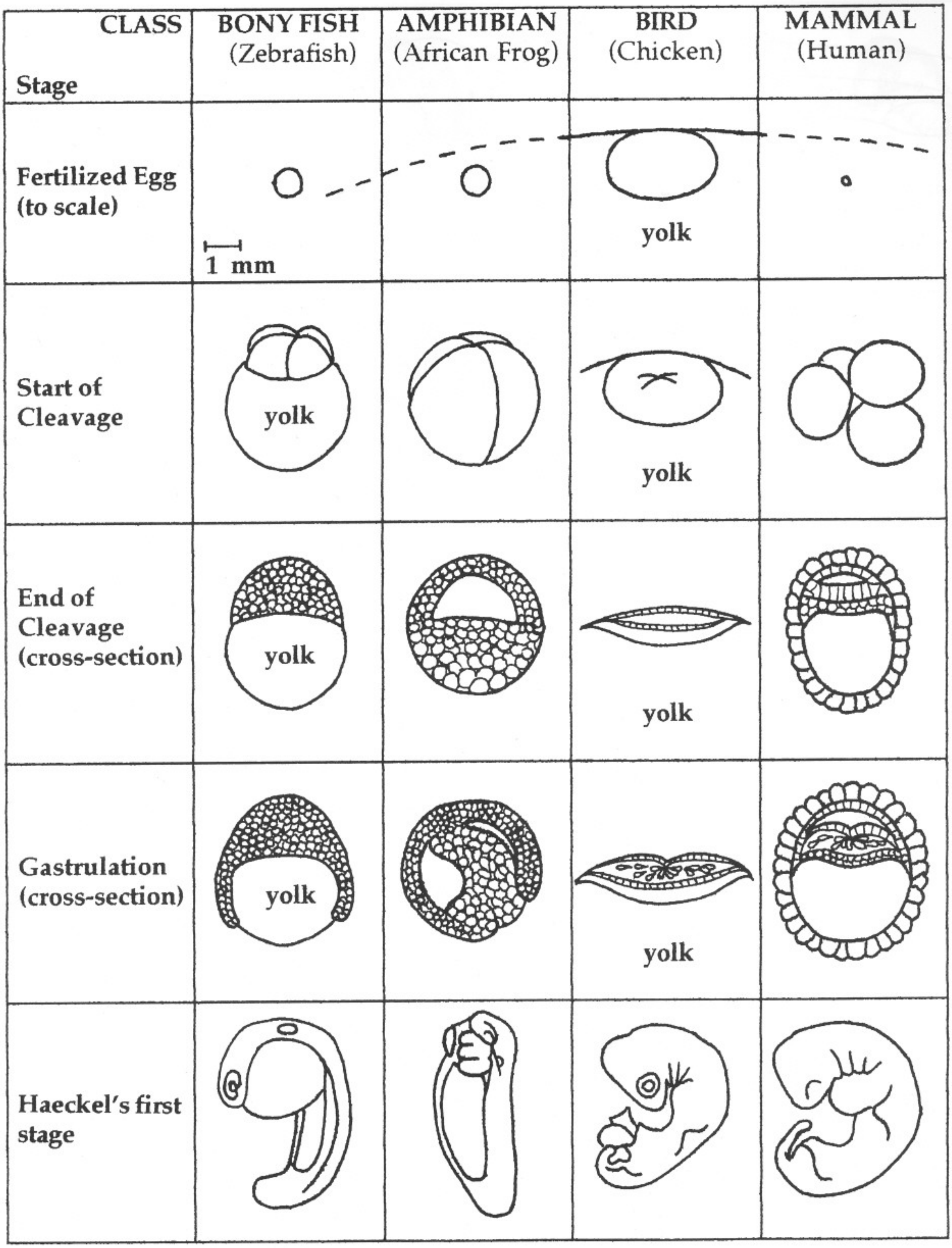

Figure 3. Drawings of embryos from four classes of vertebrates showing that their earliest stages are morphologically very different. The stages are (top to bottom): fertilized egg; early cleavage; late cleavage; gastrulation; and Haeckel's first stage. The fertilized eggs are drawn to scale relative to each other, while the scales of the succeeding stages are normalized to facilitate comparisons. The embryos are (left to right): a bony fish (zebrafish); an amphibian (South African clawed frog); a bird (chicken); and a placental mammal (human). The dashed line extending through all four top panels represents the outline of the large, yolk-filled chick egg (based on an idea in Elinson 1987).

layer formation are very different in amphibians, birds, and mammals" (Raff et al. 1991).

Setting the Record Straight

If evolution is central to understanding biology, as many writers have argued, then it is important that we give our students reliable information about it. Clearly, Haeckel's drawings are *not* reliable. Students who are taught that teachers constitute evidence for evolution, and later learn that teachers misrepresent the facts, may feel betrayed by their former biology teachers and develop a distrust of science in general. Yet Haeckel's drawings are still featured prominently in some biology textbooks.

Of course, it would be illogical to conclude that Haeckel's distortions invalidate Darwin's theory. Although Darwin considered the embryological evidence "second to none in importance" (Darwin 1859, p. 346), he did not base his theory on that evidence alone. Given the complexities of early vertebrate development, it might be better to look elsewhere for evidence of evolution, at least in an introductory course.

This does not mean that students interested in evolution should be discouraged from studying embryology. On the contrary, the interface between evolution and development is one of the most exciting research areas in biology today. According to evolutionary development biologist Rudolf Raff, "We are in a position to add to Darwin's synthesis by being able to probe more deeply into what were for him impenetrable laws of growth, reproduction, and inheritance" (Raff 1996, p. 29). Cell and developmental biologists John Gerhart and Marc Kirschner are equally optimistic: "Further study of the nature and modifiability of cellular and embryonic processes will help complete the explanation offered by Darwin for evolution as a process of descent with modification" (Gerhart & Kirschner 1997, p. 614).

The field of evolutionary developmental biology may provide us with many new insights. But these will surely come from facing the facts of nature, not from bending them to prop up old misconceptions.

References

Ballard, W.W. (1976). Problems of gastrulation: Real and verbal. *BioScience, 26,* 36–39.

Bowler, P.J. (1989). *Evolution: The History of an Idea* (Revised ed.). Berkeley: University of California Press.

Darwin, C. (1859). *The Origin of Species.* Reprint 1936. New York: Modern Library.

de Beer, G. (1958). *Embryos and Ancestors* (3rd ed.). Oxford: Clarendon Press.

Elinson, R.P. (1987). Change in developmental patterns: Embryos of amphibians with large eggs. In R.A. Raff & E.C. Raff (Eds.), *Development as an Evolutionary Process, volume 8* (pp. 1–21). New York: Alan R. Liss.

Garstang, W. (1922). The theory of recapitulation: A critical restatement of the biogenetic law. *Journal of the Linnean Society (Zoology), 35,* 81–101.

Gerhart, J.C. & Kirschner, M. (1997). *Cells, Embryos, and Evolution.* Malden, MA: Blackwell Science.

Haeckel, E. (1891). *Anthropogenie, oder Entwicklungsgeschichte des Menschen.* Leipzig: Verlag von Wilhelm Engelmann.

Raff, R.A. (1996). *The Shape of Life: Genes, Development, and the Evolution of Animal Form.* Chicago: The University of Chicago Press.

Raff, R.A., Wray, G. & Henry, J.J. (1991). Implications of radical evolutionary changes in early development for concepts of developmental constraint. In L. Warren & H. Koprowski (Eds.), *New Perspectives in Evolution* (pp. 189–207). New York: Wiley-Liss.

Rager, G. (1986). Human embryology and the law of biogenesis. *Rivista di Biologia, 79*(4), 449–465.

Richardson, M.K., Hanken, J., Gooneratne, M.L., Pieau, C., Raynaud, A., Selwood, L. & Wright, G.M. (1997). There is no highly conserved embryonic stage in the vertebrates: Implications for current theories of evolution and development. *Anatomy & Embryology, 196,* 91–106.

Romanes, G.J. (1892). *Darwinism Illustrated.* Chicago: Open Court.

von Baer, K.E. (1828). *Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion.* Konigsberg: Bornträger.