Karl Ernst von Baer's Laws of Embryology [1]

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In 1828, while working at the University of Königsberg in Königsberg, Germany, Karl Ernst von Baer [4] proposed four laws of animal development, which came to be called von Baer's laws [5] of embryology [6]. With these laws, von Baer described the development (ontogeny [7]) of animal embryos while also critiquing popular theories of animal development at the time. Von Baer's laws of embryology [6] provided a framework to research the relationships and patterns between the development of different classes of organisms, and the patterns between ontogeny [7] and the diversification of species on Earth (phylogeny [8]).

Von Baer's laws, published in 1828, responded to Johann Friedrich Meckel [9]'s recapitulation theory [10]. Meckel worked at the University of Halle [11] in Halle, Germany. In 1808, Meckel published his recapitulation theory [10] in Beiträge zur vergleichenden Anatomie [Contributions to Comparative Anatomy]. In this text, Meckel claimed that throughout ontogeny [7], embryos pass through successive stages that represent the adult forms of less complex organisms. He said that more complex organisms went through developmental stages [12] that chronologically replayed the scala naturae, a hierarchical system of classification that places the least complex organisms on the bottom of the classification and the more complex organisms on the top. Later, Meckel's theory was termed the Meckel-Serres law, because Antoine Étienne Reynaud Augustin Serres, a physician in France, independently published a similar theory in 1821. Von Baer aimed to discredit Meckel and Serres's theory because he argued that this theory of development was too linear. Von Baer believed that instead of passing through the linear stages of the scala naturae, animal embryos started from one, or a few, shared basic forms and then developed in a branching pattern into increasingly different looking organisms.

Von Baer described his laws of embryology [6] in both editions of his book Über Entwickelungsgeschichte der Thiere [On the Development of Animals], published in 1828 and 1837. In this work, von Baer reviewed existing information on the development of vertebrates. He used the information in this review to extrapolate his laws. These laws, translated by Thomas Henry Huxley [13] in Scientific Memoirs are verbatim as follows:

1. [...] the more general characters of a large group appear earlier in the embryo than the more special characters.  
2. From the most general forms the less general are developed, and so on, until finally the most special arises.  
3. Every embryo of a given animal form, instead of passing through the other forms, rather becomes separated from them.  
4. Fundamentally, therefore, the embryo of a higher form never resembles any other form, but only its embryo.

Von Baer's first two laws explained how animal embryos develop and whether or not they progress from preformed structures. During the seventeenth and eighteenth centuries, there had been a debate between two groups of researchers in embryology [6]. One group, the epigenists, argued that organisms start from unformed material and slowly progress to become more complex organisms. The other group, the preformationists, argued that a fully formed organism exists from the beginning of ontogeny [7], and then merely grows as ontogeny [7] proceeds. Von Baer's first law states that the general characters of an animal group appear earlier in the embryo than the specialized characters do, which contradicted preformationist theories.

Von Baer's second law states that embryos develop from a uniform and noncomplex structure into an increasingly complicated and diverse organism. For example, a defining and general characteristic of vertebrates is the vertebral column [14]. This feature appears early in the embryonic development of vertebrates. However, other features that are more specific to groups within vertebrates, such as fur on mammals or scales on reptiles, form in a later developmental stage. Von Baer argued that this evidence supporting epigenetic development rather than development from preformed structures. He concluded from the first two laws that development occurs through epigenesis [15], when the complex form of an animal arises gradually from unformed material during development.

Von Baer used the third and fourth laws to counter the recapitulation theories of Meckel and Serres, which became increasingly popular in Europe throughout the eighteenth and nineteenth centuries. As mentioned, these theories posit that as the ontogeny [7] of an animal embryo progresses, the embryo's different stages of development represent lower animals' adult forms. For example, according to the recapitulation theory [10], the early human embryos have structures similar to gill slits, and thus that early stage represents the form of adult fish [16], which also have gill slits.

Von Baer's third law states that animals from different species start out similar and become more dissimilar from one another as ontogeny [7] proceeds. As an example, von Baer discusses the embryos of humans [17], fish [16], and chicks, all of which look
similar to each other in the early stages of their development. As they grow, however, they look increasingly different from one another. The embryo of one species never resembles the adult of another species. Instead of recapitulating other animals' adult forms, von Baer's third law theorized that animal embryos diverge from one or a few shared embryonic forms. The fourth law states that the stages of development in more complex animals never represent the adult stages of less complex animals; they resemble only the embryos of less complex animals.

By 1866, von Baer's laws [5] competed with the theory of a professor at the University of Jena [18] in Jena, Germany. Ernst Haeckel [19] proposed a theory of recapitulation called the biogenetic law [20], which states that ontogeny [7] recapitulates phylogeny [6]. Unlike the Meckel Serres interpretation of recapitulation, Haeckel's form of recapitulation proposed that embryos pass through the chronological stages of their species' evolutionary ancestry rather than through the scala naturae. Haeckel said that stages during the ontogeny [7] of organisms replay that organism's evolutionary ancestry. He popularized this theory when he synthesized theories of ontogeny [7] with Charles Darwin's [21] 1859 theory of the evolution [22] of species via natural selection [23], more than thirty years after von Baer had proposed his laws of embryology [6]. Given that Haeckel's theory was of linear development, similar to Meckel's, von Baer was no more convinced by Haeckel's theory than he was by Meckel's. Furthermore, von Baer did not accept that all species shared a common ancestor. Despite von Baer's objections to Haeckel's biogenetic law [20] and recapitulation in general, the biogenetic law [20] persisted in biology until the turn of the twentieth century when new experimental and comparative evidence rendered it untenable.

Although von Baer was skeptical of common ancestry and natural selection [23], Charles Darwin's [21]'s portrayal of development in The Origin of Species was the same as von Baer's: branching and epigenetic. Darwin also provided the same critiques of recapitulation as had von Baer; Darwin said that adult forms of one animal do not show themselves in other animal's development, and that only the embryos look similar to one another. Darwin also wrote that embryology [6] provided the strongest class of facts in support of his theory of evolution [22].

Twentieth century historians such as Jane Oppenheimer and Stephen Jay Gould [24] later said that von Baer's laws [5] made possible twentieth century developmental biology. They note that von Baer described developmental processes as epigenetic and as progressing in a branching manner in relation to different organisms as did twentieth century developmental biologists.

Sources

13. Serres, Étienne Renaud Augustin. Anatomie comparée du cerveau dans les quatre classes des animaux vertébrés appliquée à la physiologie & à la pathologie du système nerveux [Comparative Anatomy of Brain in the Four Classes of
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