THE PHYLOTYPIC EGG TIMER

by

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ABSTRACT

Von Baer and Haeckel provided the basis of what came to be known as the phylotypic egg timer: during their development vertebrate embryos pass through a period in which they show the archetype of the vertebrate body plan. During this period vertebrate embryos are similar, in both form and morphogenic processes taking place. The phylotypic egg timer has been explained using phylogenetic constraints on the mechanism of body plan formation. Physical laws also pose constraints on embryonic variability. Fathoming these physical and phylogenetic constraints gives us insight in the measure of freedom for variation at a specific stage of vertebrate embryonic development.

KEY WORDS: vertebrates, phylotypic period, phylotypic egg timer, phylogenetic constraints, physical constraints.

INTRODUCTION

In his Entwicklungsgeschichte der Thiere, VON BAER (1828) published four empirical laws of embryology: 1) common characters of a taxon develop earlier in ontogeny than specialised ones, 2) specialised forms develop from more general ones, 3) every embryo of a certain taxon diverges more and more from other taxa instead of going through those other forms, 4) an embryo of a higher taxon never resembles (the adult of) another taxon, but only its embryo. Von Baer argued that during ontogeny all animals diverge from one of the four embranchements (radiates, molluscs, articulates and vertebrates), defined in 1812 by Georges Cuvier. Although von Baer saw the similarity among vertebrate embryos, he never accepted the concept of evolution, not even after the publication of Darwin’s Origin of Species in 1859 (RAFF, 1996). It was HAECKEL (1866) who combined the concept of evolution and the similarity among early vertebrate embryos, which culminated in his recapitulation theory or biogenetic law (HALL, 1992; RAFF, 1996). With his four laws, von Baer already rejected the concept of recapitulation, which can be traced back

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until Aristotle’s (384-322 BC) Great Chain of Being (RAFF, 1996). In his Anthropogenie, HAECKEL (1877) published a series of comparative drawings which show different vertebrates to develop from a nearly identical ‘frühes Stadium mit Kiemenspalten, ohne Beine.’ A citation from his Natürliche Schöpfungs-Geschichte (HAECKEL, 1902) might serve to illustrate the implications on society of Haeckel’s theory and drawings: “Was sollen diese Edelleute noch von dem Vollblut, das in ihren privilegirten Adern rollt, denken, wenn sie erfahren, dass alle menschlichen Embryonen, adelige ebenso wie bürgerliche, während der ersten beiden Monate der Entwicklung von den geschwänzten Embryonen des Hundes und anderer Säugethiere kaum zu unterscheiden sind?”

The developmental stage at which all vertebrates look rather similar is commonly called the pharyngula stage (BALLARD, 1976) or phylotypic stage (SLACK et al., 1993). It is the stage at which all vertebrates express the archetype of the vertebrate body plan (DUBOULE, 1994a).

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Haeckel’s recapitulation theory has largely been rejected and it is nowadays believed that phylogenetic divergence finds its origin in ontogenetic divergence. Early ontogenetic divergence is usually coupled to early common ancestors, while late ontogenetic divergence points to the close phylogenetic relationship of the species compared.

The phylotypic stage of vertebrate development is not the earliest stage. In fact, stages prior to the pharyngula stage show quite some variation among vertebrates (RAFF, 1996), of which Haeckel was well aware (Table II and III in HAECKEL, 1877; fig. 1). This variation consists of, for example, differences in fertilisation (ELINSON, 1987), differences in the origin of cells constituting the extraembryonic membranes (resulting from cleavage or not), the existence of holoblastic and meroblastic cleavage in different groups of fish (SLACK et al., 1993) and differences in migration patterns and temporary structures among vertebrate classes (BALLARD, 1976). This very early divergence followed by a more or less common stage is very interesting since we would expect a common early ontogeny followed by (relatively late) divergence.

Apparently, stages prior to and after the phylotypic stage are more variable in an evolutionary sense than the phylotypic stage itself. This idea has been metaphorised as ‘the phylotypic egg-timer’ (DUBOULE, 1994a), ‘the developmental hourglass’ (RAFF, 1996) or ‘the evolutionary hourglass’ (RICHARDSON et al., 1997).

Recently, RICHARDSON (1995) showed that heterochrony has shifted the developmental timing of structures in different vertebrates and that