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REVIEW ARTICLE

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# There is no highly conserved embryonic stage in the vertebrates: implications for current theories of evolution and development

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**Abstract** Embryos of different species of vertebrate share a common organisation and often look similar. Adult differences among species become more apparent through divergence at later stages. Some authors have suggested that members of most or all vertebrate clades pass through a virtually identical, conserved stage. This idea was promoted by Haeckel, and has recently been revived in the context of claims regarding the universality of developmental mechanisms. Thus embryonic resemblance at the tailbud stage has been linked with a conserved pattern of developmental gene expression – the zootype. Haeckel's drawings of the external morphology of various vertebrates remain the most comprehensive comparative data purporting to show a conserved stage. However, their accuracy has been questioned and only a narrow range of species was illustrated. In view of the current widespread interest in evolutionary developmental biology, and especially in the conservation of developmental mechanisms, re-examination of the extent of variation in vertebrate embryos is long overdue. We present here the first review of the external morphology of tailbud embryos, illustrated with original specimens from a wide range of vertebrate groups. We find that embryos at the tailbud stage – thought to correspond to a conserved stage – show variations in form due to allometry, heterochrony, and differences in body plan and somite number. These variations foreshadow important differences in adult body form. Contrary to recent claims that all vertebrate embryos pass through a stage when they are the same size, we find a greater than 10-fold variation in greatest length at the tailbud stage. Our survey seriously undermines the credibility of Haeckel's drawings, which depict not a conserved stage for vertebrates, but a stylised amniote embryo. In fact, the taxonomic level of greatest resemblance among vertebrate embryos is below the subphylum. The wide variation in morphology among vertebrate embryos is difficult to reconcile with the idea of a phyogenetically-conserved tailbud stage, and suggests that at least some developmental mechanisms are not highly constrained by the zootype. Our study also highlights the dangers of drawing general conclusions about vertebrate development from studies of gene expression in a small number of laboratory species.

**Key words** Morphogenesis · Developmental biology · Comparative anatomy · Comparative study · Embryology

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## Introduction

There is no stage of development in which the unaided eye would fail to distinguish between them (vertebrate embryos) … a blind man could distinguish between them. (Sedgwick 1894).
Embryos of different species (of vertebrate) pass through identical embryonic stages before acquiring their specific features. (Butler and Juurlink 1987).

Raff (1992) has pointed out that developmental biologists tend to emphasise the similarities among species,

whereas evolutionary biologists emphasise the differences. The result is a long history of disagreement over the extent to which embryonic development is conserved during evolution (reviewed by McKinney and McNamara 1991; Hall 1992; Raff 1992, 1996; McNamara 1995; Richardson 1995). This is partly because, with a few exceptions (e.g. Slack et al. 1993; Burke et al. 1995), many of our current ideas about the molecular basis of vertebrate development and evoltuion come from studies of a small number of laboratory species. The assumption that these findings are generally applicable to all vertebrates is not necessarily a valid one (Raff 1996).

A prevalent idea in developmental evolution is that intermediate embryonic stages are resistant to evolutionary change, and that differences among species arise through divergence at later stages of development. As a consequence, all vertebrates are often said to pass through a common stage when they look virtually identical (Haeckel 1874; Butler and Juurlink 1987; Wolpert 1991; Alberts et al. 1994; Collins 1995). The conserved stage is called the *phylotypic* stage because it is thought to be the point in development when there is maximum resemblance among members of a phylum or comparable higher taxon (Slack et al. 1993). Conservation of embryonic form is thought to be associated with the conservation of patterns of developmental gene expression across a wide range of animal clades (Slack et al. 1993).

One puzzling feature of the debate in this field is that while many authors have written of a conserved embryonic stage, no one has cited any comparative data in support of the idea. It is almost as though the phylotypic stage is regarded as a biological concept for which no proof is needed. This has led to many problems, not least of which is the lack of consensus on exactly which stage is conserved (Richardson 1995). The phylotypic stage in vertebrates has been defined as the *pharyngula* stage, after the series of pharyngeal pouches seen in embryos (Ballard 1981). However it is not clear precisely which stage of development this represents, since pharyngeal pouches appear over an extended period of development. Slack et al. (1993) suggest that the tailbud stage may be a time of maximum resemblance among species. Wolpert's (1991) definition of a conserved stage is much earlier and corresponds to an early somite stage, just after neurulation. Duboule (1994) takes a broader view and regards the period between the head fold and tailbud stages as a time of high morphogenetic resemblance.

According to recent models, not only is the putative conserved stage followed by divergence, but it is preceded by variation at earlier stages, including gastrulation and neurulation. This is seen for example in squamata, where variations in patterns of gastrulation and neurulation may be followed by a rather similar somite stage (Hubert 1985). Thus the relationship between evolution and development has come to be modelled as an "evolutionary hourglass" (Fig. 1; Elinson 1987; Duboule 1994; Collins 1995).

The idea of a conserved embryonic stage arose in the nineteenth century. Pioneers in the field of embryology

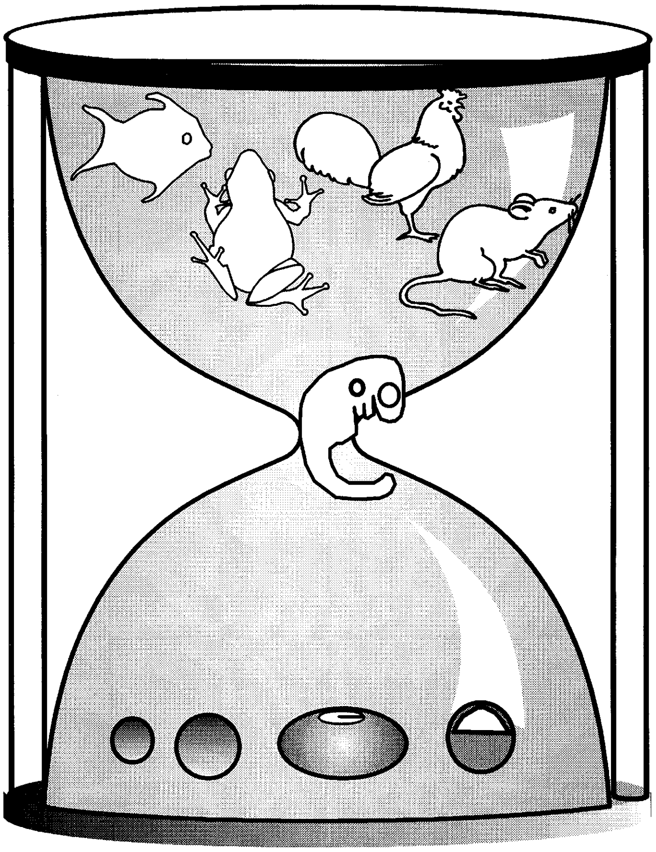

**Fig. 1** The hourglass model of the relationship between evolution and development. This model implies divergence at earlier and later stages from a conserved intermediate stage. Horizontal distance represents morphological divergence during evolution, and vertical distance represents developmental stage. Based on Elinson (1987), Duboule (1994), and Collins (1995)

in particular stressed the similarities among the embryos of different vertebrates. For example, von Baer (1828) argued that the embryos of different amniotes often appear strikingly similar, and that many differences among the adults of different species arise at later stages of development. The gradual appearance during development of differences among embryos is known as divergence or deviation (de Beer 1951). Haeckel took this idea further and suggested that essentially *all* differences among species arise at late stages, and that embryos are therefore virtually identical. This was famously depicted in his drawings (Fig. 2) which purport to show different species arising from a conserved embryonic stage (Haeckel 1874). The drawings were intended to demonstrate Haeckel's recapitulation theory or biogenetic law. A conserved stage was a necessary part of this theory because evolution was claimed to progress principally by the terminal addition of new adult stages to the end of ancestral developmental sequences.

Haeckel's ideas soon came in for strong criticism. His drawings are also highly inaccurate, exaggerating the similarities among embryos, while failing to show the differences (Sedgwick 1894; Richardson 1995; Raff