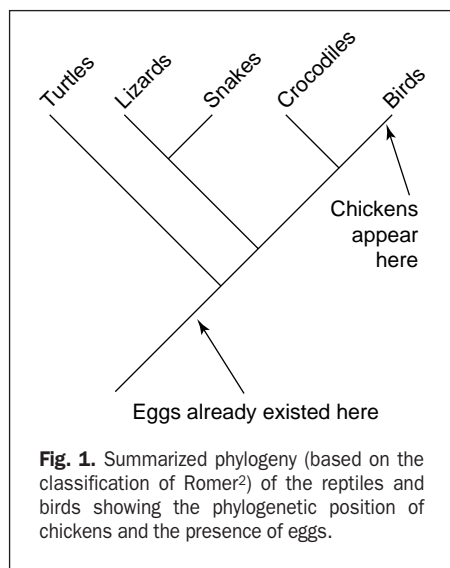


Eggs first

It has come to our attention that the well known question 'Which came first, the chicken or the egg?' remains unanswered despite recent developments in comparative biology that provide the methodology for solving this problem. One approach taken in modern comparative biology involves examining trait distributions across groups of similar taxonomic level to determine, among other things, if a trait arose *de novo* in a particular group or was already present in that group's ancestors (see Ref. 1 for a thorough discussion of the comparative method and its applications). This method, then, is ideally suited for investigating whether eggs or chickens came first.



To employ the comparative method a trustworthy phylogeny for the groups of interest is necessary. It has been accepted at least since the 1960s that birds and other reptiles form a monophyletic group, with birds and crocodilians representing the most recently derived clade within that group². Oviparity is the most common and broadly distributed reproductive mode found in the reptiles and birds, and must therefore be considered the ancestral character state for the entire group (see Fig. 1). Eggs, therefore, clearly came before chickens.

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References

- 1 Harvey, P.H. and Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*, Oxford University Press
- 2 Romer, A.S. (1966) *Vertebrate Paleontology*, University of Chicago Press

Phylotypic stage theory

Brian Hall¹ provides a thought-provoking and scholarly review of the phylotypic stage theory, and its relation to patterns of development in different phyla. He discusses a recent paper on this subject by MKR, JH and colleagues². His assessment contributes to current debate concerning the validity of the phylotypic stage as applied to the vertebrates.

We regard the phylotypic stage as an archetype and not a real entity. Like Owen's archetype, the vertebrate phylotype applies to all vertebrates in general, but to no one species in detail. Other authors have equated the phylotypic stage with the ancestral condition. We do not support this view because, although primitive patterns of morphogenesis and gene expression are inherited from common ancestors³, these patterns can be modified during evolution. In some vertebrate clades (e.g. eutherian mammals) relatively little evidence of embryonic variation is apparent². In these cases a phylotypic stage can be recognized insofar as it represents a set of synapomorphic character states (i.e. a cluster of taxic homologies). But in other groups (e.g. anurans and caecilians), embryonic variation – some of it related to divergence in adult body plan rather than to larval adaptations – makes a common stage problematic^{2,4}.

The identity of the vertebrate phylotypic stage as an archetype is confirmed when one tries to match it to primary data on morphogenesis^{5,6}. For example, Ballard's pharyngula and the phylotype (tailbud stage) of Slack *et al.*³ represent different stages; a tailbud zebrafish lacks pharyngeal arches and is not therefore a pharyngula⁷. There is a real problem here: as argued by many biologists (reviewed in Gould⁵), the pervasive effects of heterochrony make the precise definition of common vertebrate developmental stages impossible. And recent analyses of primary data support this view, suggesting instead the recognition of a phylotypic period within which variations in the timing, sequence and diversity of character appearance may be included⁵.

Thinking in terms of types, either as developmental stages or as putative ancestors, can be helpful in searching for order in the diversity of animal life. However we need to be aware of the limitations of typologism.

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References

- 1 Hall, B.K. (1997) *Trends Ecol. Evol.* 12, 461–463
- 2 Richardson, M.K. *et al.* (1997) *Anat. Embryol.* 196, 91–106
- 3 Slack, J.M., Holland, P.W. and Graham, C.F. (1993) *Nature* 361, 490–492
- 4 Richardson, M.K. *et al.* (1998) *Development* 125, 151–160
- 5 Gould, S.J. (1977) *Ontogeny and Phylogeny*, Belknap Press
- 6 Richardson, M.K. (1995) *Dev. Biol.* 172, 412–421
- 7 Kimmel, C.B. *et al.* (1995) *Dev. Dynam.* 203, 253–310

Analysing diversification through time

In a recent perspective in *TREE*, Benton¹ examined hypotheses and data concerning the diversification of life through geologic time. He argued that most patterns in the history of life can be interpreted as exponential expansion, free of the constraints of limited resources and interspecific competition. However, the scale at which he evaluated these patterns was hundreds of millions of years, and he applied no quantitative tests to evaluate his assertions. At shorter timescales, on the order of five million years, other patterns of diversification are evident that can be assessed quantitatively.

Mass extinctions have been viewed as either annoying perturbations of diversity² or external factors that reset patterns of diversification³. Both views ignore the evolutionary response of the biota after mass extinction, which can tell much about how it and its components are diversifying. Miller and Sepkoski⁴ recognized this with respect to the diversification of bivalve molluscs. The history of bivalves from the Ordovician (490 million years ago) to the present would probably be interpreted by Benton as an unfettered, exponential increase, as would be expected for a group with no competitors. But how does one explain that bivalves experienced accelerated diversification during the Ordovician radiations and after the end Permian and Cretaceous mass extinctions? And how does one rationalize that these accelerated rates were all equal and well above the long-term rate of exponential diversification? Miller and Sepkoski argued that the accelerated radiations of bivalves occurred when global diversity was low because of a dearth of competitors. This occurred early in their history, when global diversity had not yet reached Paleozoic equilibrium levels, as well as immediately following mass extinctions, when global diversity had become suddenly depressed.

This analysis was not qualitative. Miller and Sepkoski⁴ presented a quantitative model of how bivalves could appear to have exponential diversification on time scales of hundreds of millions of years and yet exhibit 'hyperexponential' diversification on time scales of fives of millions of years when global diversity was depressed. The model assumed some sort of interaction with other, unspecified groups of marine organisms.