Caecilian viviparity and amniote origins: a reply to Wilkinson and Nussbaum

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An evaluation of the evolution of reproduction in amniotes by the authors has been recently criticized. This criticism is shown to be based on a misrepresentation of our work. The ancestral amniote was certainly oviparous, but this does not necessarily imply that eggs were laid at an early stage of development. The presence of a significant amount of intrauterine development in the earliest amniotes remains as parsimonious as the alternative, despite recent claims to the contrary. The relative rarity of amniote groups that laid heavily mineralized egg membranes in the Palaeozoic may explain why no amniote fossil egg has been found in the Palaeozoic.

KEYWORDS: Evolution, phylogeny, parsimony, Amniota, Gymnophiona, eggs, fossil record.

Introduction

The evolution of the amniotic egg has fascinated many biologists, but its origin is still inadequately understood. We know that the amniotic egg must have existed at least 310 million years ago because amniotes had appeared at that time, and all extant amniotes possess an amniotic egg (although it may be somewhat modified in viviparous groups). In the absence of the necessary information from the fossil record (no Palaeozoic tetrapod egg is known), the evolution of the amniotic egg must be studied by comparing extant taxa in the context of amniote phylogeny.
Origin of the amniotic egg

The amniotic egg is usually interpreted as an adaptation for life on land (Carroll, 1988). However, Lombardi (1994) and Laurin and Reisz (1997) recently raised the possibility that some of the extra-embryonic membranes evolved in an embryo-retaining form, in which they facilitated embryo–mother interactions. Laurin and Reisz (1997: figure 6) argued that an optimization of a binary character (absence or presence of extended embryo retention) on a sarcopterygian phylogeny showed that two hypotheses were equally parsimonious; extended embryo retention may or may not have been present in the first amniote.

All amniote eggs, as well as the eggs of all caecilians, some other lissamphibians, and various other vertebrates (the coelacanth, chondrichthysans, etc.) are internally fertilized. Internal fertilization allows the development of interactions between the embryo and the mother, which could lead to viviparity (but not always, as shown by monotremes and many squamates, for example). The ubiquitous presence of internal fertilization in amniote eggs raises the possibility that the first amniote already retained embryos in utero for a significant portion of their development, and that the extra-embryonic membranes of the amniotic egg developed to facilitate embryo–mother interactions.

This proposition was recently attacked by Wilkinson and Nussbaum (1998), who misrepresented this issue by equating the state ‘extended embryo retention present’ with ‘viviparity’. Having thus reformulated the problem, Wilkinson and Nussbaum then proceeded to show that the ancestral amniote would have been oviparous. We concur with that view, and we have never argued the contrary.

When viviparity is observed in an organism, it is quite valid to argue that it represents embryo retention. This is an obvious result of this particular reproductive strategy, and we used this to argue for embryo retention in caecilians. However, oviparity does not by itself show evidence to the contrary, i.e. absence of embryo retention. Egg retention in tetrapods exhibits continuous variation, and viviparity is only its extreme form. For example, in monotremes, there is an intrauterine phase of development followed by oviposition and a short period of incubation (about 10 days) of the egg within a pouch. During intrauterine development, the volume of the egg increases dramatically through absorption of uterine secretions (Stewart, 1997). Therefore, monotremes possess extended embryo retention while being oviparous. Similarly, a substantial amount of egg development precedes oviposition in typical squamates (Blackburn, 1993: 418). More precisely, numerous squamates retain eggs in utero for about one-half of the total period of embryonic development (Shine, 1985). Stewart (1993: 445) even suggested that in squamates, ‘Functionally, the early stages of extraembryonic membrane formation may be equivalent in oviparous and viviparous species, at least for viviparous species with telolecithal eggs’.

Wilkinson and Nussbaum (1998) based their contribution on a demonstration that caecilians are primitively oviparous and did not provide any information or references about the early embryology of egg-laying caecilians. A thorough literature search revealed that information on this topic is scanty (Duellman and Trueb, 1986). Sarasin and Sarasin (1887–1890) described embryos of Ichthyophis glutinosus of various stages, but we could not, after careful reading, find the mention of when the eggs were laid. A few other embryos of Ichthyophis have been described (Breckenridge and Jayasinghe, 1979; Balakrishna et al., 1983), but only from accidentally found eggs that had been laid for an unknown period of time. Only Brauer
(1897) gives some information on the developmental stage at oviposition for another caecilian species, *Hypogeophis rostratus*, that appears to lay its eggs in the blastula stage. Unfortunately, no other study has confirmed this observation, or provided similar data for other caecilian species. In any other report (and any other caecilian), the smallest observed caecilian embryos in laid eggs measured 6 mm and possessed at least 21 somites (Breckenridge and Jayasinghe, 1979; Balakrishna *et al.*, 1983). Therefore, the literature does not appear to provide decisive evidence regarding the amount of intra-uterine development in most oviparous caecilians. Wilkinson and Nussbaum themselves emphasized that the reproductive biology of caecilians is poorly known, even though they were only interested in determining whether various caecilian clades were oviparous or viviparous: ‘The most direct inferences on caecilian reproductive modes come from observations of parturition, clutches of eggs, larvae, and oviductal foetuses. Unfortunately, because caecilian amphibians are mostly secretive, burrowing, tropical forms, such observations are unavailable for the great majority of the approximately 160 caecilian species’. If evidence about the early development of all but one species of oviparous caecilians is lacking in the scientific literature, the arguments presented by Wilkinson and Nussbaum are not valid, and they have not falsified our hypothesis. Indeed, whereas the viviparous caecilians possess an extended embryo retention, the vast majority of oviparous caecilians for which no data on early development are available may or may not share this condition. The simultaneous occurrence of oviparity and viviparity within two caecilian clades (scolecomorphids, caeciliids) suggests that the reproductive mode of caecilians has evolved several times independently, and that the information about the stage of embryonic development at oviposition for a single caecilid species (*Hypogeophis rostratus*; see Brauer, 1897) does not provide a safe basis to infer the primitive reproductive pattern for caecilians. Therefore, until more data about the early development of oviparous caecilians become available, it is still justifiable to consider that caecilians could perform extended embryo retention.

**Amniotic eggs in the fossil record**

For vertebrate palaeontologists working on the early history of amniote evolution, the absence of fossil evidence of nests and eggs in the Palaeozoic is perplexing, especially in light of the extensive fossil record of such things in the Mesozoic (Mikhailov, 1991; Norell *et al.*, 1994). It is clear that amniotes were present and diversifying explosively during this time (Laurin and Reisz, 1995), but nests and fossilized eggs only appear in the Triassic (Bonaparte and Vince, 1979), at least 80–90 million years after the appearance of the oldest known amniotes (Carroll, 1964). Therefore, the fossil record is not inconsistent with the hypothesis that the earliest amniotic eggs were poorly mineralized.

The distribution of various types of egg membranes in amniotes corroborates the thesis that early amniotic eggs had an unmineralized shell membrane. Stewart (1997: 308–309) concluded that the ancestral amniote eggshell was flexible and unmineralized, and that a mineralized eggshell membrane is a synapomorphy of Reptilia (the last common ancestor of turtles and diapsids, and all its descendants). Finally, a heavily mineralized, rigid eggshell (the only kind that would have a reasonably good fossilization potential) seems to have appeared independently among archosaurs, some gekkonid lizards, and at least five times among turtles (Stewart, 1997).
The vast majority of the amniote diversification in the Palaeozoic is represented by synapsids, whereas reptiles were relatively rare members of the fossil record in the Palaeozoic (the only exception being the pareiasaurs, presumed to be extinct relatives of turtles that were fairly common in parts of the Upper Permian). The evolution of the mineralization in the amniote eggshell outlined by Stewart (1997) suggests that stem-anapsids (such as pareiasaurs) and most Palaeozoic diapsids would have laid poorly mineralized eggs with a low preservation potential.

These conclusions about the evolution of the amniotic egg are compatible with the hypothesis that the earliest amniotes performed embryonic retention, although they do not prove it. Furthermore, they provide a compelling hypothesis for the absence of fossil eggs for the first 80 or 90 million years of the history of amniotes.

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References
