JOURNAL OF NATURAL HISTORY, 1998, **32,** 1403–1409

Caecilian viviparity and amniote origins

M. WILKINSON[†] and R. A. NUSSBAUM[‡]

[†]*School of Biological Sciences, University of Bristol, Bristol, BS8 1UG, UK and Department of Zoology, The Natural History Museum, London, SW7 5BD, UK*
[‡]*Division of Herpetology, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109-1079, USA*

(*Accepted 18 March 1998*)

A recent evaluation of alternative hypotheses for the origin of the amniotic egg, by mapping a single reproductive-mode character onto a phylogeny of tetrapods, concluded that the alternative hypotheses were equally parsimonious. However, this interpretation is dependent upon a mistaken coding of the caecilian amphibians as showing extended embryo retention. Although some caecilians are viviparous, phylogenetic analyses indicate that oviparity is ancestral for the group. With the coding of caecilians corrected, the most parsimonious inference is that the ancestral amniotes did not practice extended embryo retention. A review of the available data indicates that the widespread view that a majority of caecilians are viviparous is mistaken. Oviparity is the dominant reproductive mode in caecilians as it is in other living amphibians.

KEYWORDS: Evolution, phylogeny, parsimony, Amniota, Gymnophiona, reproductive modes.

Introduction

Explanations of major transitions in evolution are often necessarily highly speculative because the transitions happened in the distant past, and because the evidence from the fossil record is too incomplete to allow some scenarios to be ruled out. Not surprisingly then, many workers are turning to phylogenetic hypotheses and associated parsimonious interpretations of character evolution to provide frameworks for the additional testing of evolutionary scenarios. A recent, but problematic, example is provided by Laurin and Reisz's (1997) discussion of the evolution of amniotes and the origins of their key innovation, the amniotic egg.

Amniote origins

Laurin and Reisz (1997) presented a novel hypothesis of tetrapod phylogenetic relationships (figure 1) and used this as a framework to explore two alternative scenarios for the origin of the amniote egg. Carroll (1970, 1991) speculated that amniotes evolved from terrestrial anamniotes that laid their eggs on land, as do some lissamphibians (caecilians, frogs, salamanders). The characteristic extra-embryonic membranes of amniotes evolved as adaptations of terrestrial eggs. In contrast, Lombardi (1994) and Laurin and Reisz (1997) speculated that the amniotic mem-

0022-2933/98 $12.00

branes evolved in association with embryo retention and provided a pathway for foetal-maternal interaction.

Laurin and Reisz (1997) evaluated these alternative scenarios by mapping a binary character, extended embryo retention present or absent, onto their phylogeny. The optimization of their character is ambiguous, such that both the presence and absence of extended embryo retention in ancestral amniotes are equally parsimonious (figure 1). They concluded (p. 34) 'the scenario that the evolution of the amniotic condition involved the intermediate stage of anamniotic eggs being laid on land is not more parsimonious than the alternative suggested here' (that extraembryonic membranes evolved to facilitate extensive embryo retention).

However, the conclusion is dependent on the character states that they attributed to terminal taxa. In particular, it is dependent upon their erroneous coding of caecilians as showing extended egg retention. Caecilians display a number of reproductive modes including extended egg retention (in the form of viviparity). Many phylogenetic analyses based on both morphology and molecules (Nussbaum 1979; Duellman and Trueb, 1986; Hillis, 1991; Hedges *et al.*, 1993; Wilkinson and Nussbaum, 1996; Wilkinson, 1996, 1997) strongly suggest that viviparity is a derived condition that has probably arisen a number of times within caecilians (figure 2). These analyses confirm the long-held view (e.g. Dunn, 1942) that the primitive reproductive mode in caecilians is oviparity, with eggs hatching into free-living larvae that undergo metamorphosis (i.e. the characteristic amphibian bi-phasic life history with no extended embryo retention).

If caecilians are recoded so as to correctly reflect this ancestral condition, the optimization of extended embryo retention on Laurin and Reisz's phylogeny changes, and it becomes more parsimonious to conclude that the ancestral amniotes did not practice extended embryo retention (figure 3). Judged solely on the basis of the fit

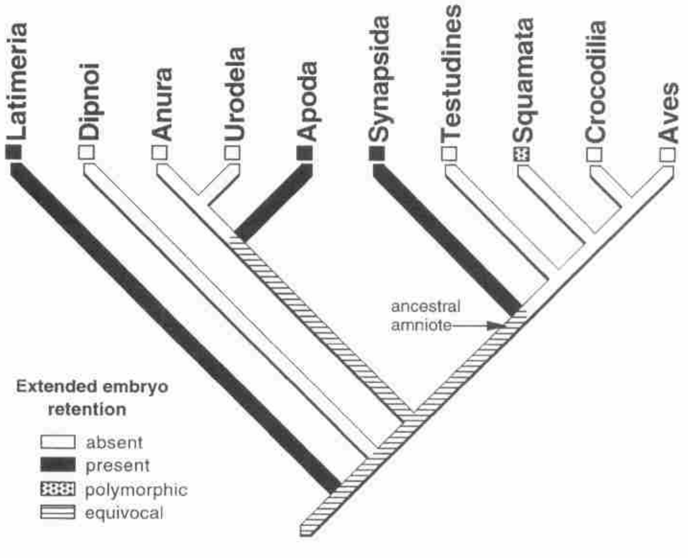

FIG. 1. Tetrapod phylogeny with the binary character, extended egg retention present or absent, mapped onto the tree by MacClade (Maddison and Maddison, 1992). After Laurin and Reisz (1977). The condition of ancestral amniotes with respect to this character is ambiguous.

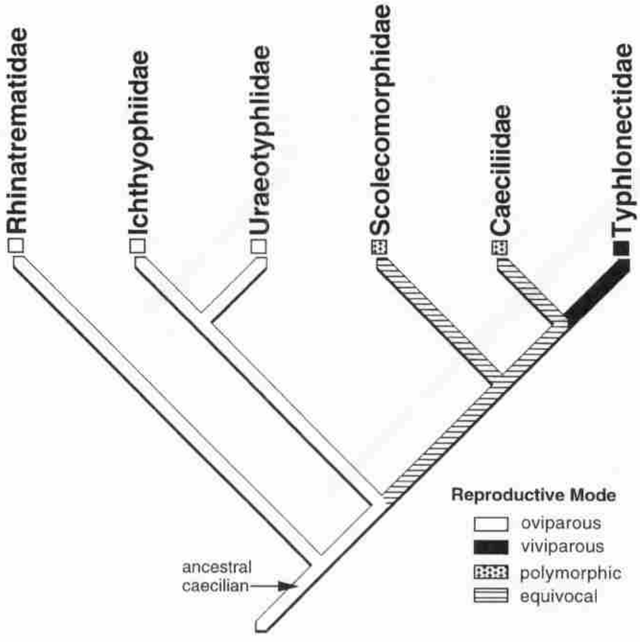

FIG. 2. Caecilian phylogeny with the binary character, viviparity (=extended egg retention) or oviparity, mapped onto the tree by MacClade (Maddison and Maddison, 1992). Caecilians are inferred to have been oviparous ancestrally. This phylogeny is based on that of Wilkinson and Nussbaum (1996) and Wilkinson (1997) and differs from other workers only in the position of the Uraeotyphlidae. Alternative phylogenies (e.g. Duellman and Trueb, 1986; Hillis, 1991) place Uraeotyphlidae as the sister group of the scolecomorphid–caeciliid–typhlonectid clade and do not affect the inferred ancestral reproductive mode.

to the phylogeny, the extended embryo retention hypothesis for the origin of the amniote egg is not as well supported as Carroll's hypothesis. This result provides some support for Carroll's scenario, although its significance depends upon the reliability of the phylogeny, the plausibility of less parsimonious schemes of character evolution, and the import of whatever other evidence can be brought to bear on the alternative scenarios. Thus, we echo Laurin and Reisz's (1997: 34) view that 'this aspect of the origin of amniotes needs further study'.

Caecilian viviparity

Laurin and Reisz (1997) did not explain their coding of caecilians with respect to extended embryo retention, but their misinterpretation of caecilian reproduction presumably stems from the widespread, but mistaken, view that viviparity is the dominant reproductive mode in caecilians, combined with the assumption that common equals primitive. The latter commonality principle is far from perfect, and the phylogenetic considerations that suggest that viviparity is not primitive for caecilians (figure 2) illustrate why. Furthermore, the many assertions that the majority of caecilian species are, or probably are, viviparous (e.g. Wake, 1977, 1986, 1992, 1993; Duellman and Trueb, 1986; Pough *et al.*, 1989; Stebbins and Cohen, 1995) are not supported by the available evidence.

The most direct inferences of caecilian reproductive modes come from observa-

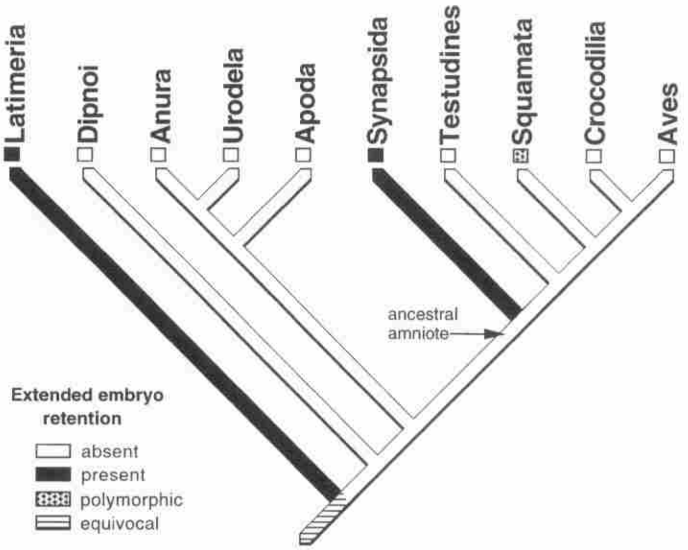

FIG. 3. Tetrapod phylogeny with the binary character, extended egg retention present or absent, mapped onto the tree by MacClade (Maddison and Maddison, 1992) after correction of the coding of caecilians (Apoda) from present to absent. The parsimonious interpretation is unambiguous and indicates the absence of extended embryo retention in the ancestral amniote.

tions 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. More indirect inferences, that make use of several lines of evidence, are possible. Chief among these are:

1. Oviductal egg size. Large eggs are associated with oviparous species, small eggs with viviparity (Wake, 1977; Nussbaum, 1985).
2. Morphological features of young specimens that may betray a larval or foetal existence. No caecilian species are known that have both viviparity and a free living larval stage. Premetamorphic larvae or juveniles with larval features, such as lateral line organs, labial folds and spiracles, thus provide evidence for the absence of viviparity (Wilkinson, 1992). Foetal caecilians possess a characteristic 'foetal' dentition that is thought to be used in feeding from the hypertrophied maternal oviduct lining (Parker, 1956), and 'foetal' teeth in young specimens have been taken as evidence of recent parturition and viviparity in the genus *Caecilia*. However, the young of some caecilians, such as *Siphonops annulatus* (Mikan) and *S. paulensis* Boettger, that are known to be oviparous (Goeldi, 1899; Gans, 1961; C. Jared, pers. comm.) also have the apparently misnamed 'foetal' dentition (M. Wilkinson, pers. obs., e.g. *S. annulatus* Museu Nacional, Rio de Janeiro – Nos. 18633–18637; *S. paulensis* Museu de Zoologia, Universidade de São Paulo – No. 36724). Furthermore, at least some *Caecilia* are definitely oviparous, having laid eggs in captivity (R. A. Nussbaum, pers. obs.). These observations indicate that viviparity cannot be reliably inferred from observations of 'foetal' teeth in young specimens.

3. Extrapolation from other inferences based on the assumption that species of the same genus or family or other closely related group have the same reproductive mode (i.e. parsimony).

Inferences of the taxonomic distribution of reproductive modes in caecilians are summarised in table 1. On the basis of the most direct observations, combined with

Table 1. Distribution of reproductive modes across caecilian genera. O = oviparity; V = viviparity; ? = uncertain. Letters in parentheses indicate more indirect inferences.

Taxa	Number of species	Reproductive mode
Rhinatrematidae		
Epicrionops	8	O
Rhinatrema	1	?(O)[a]
Ichthyophiidae		
Caudacaecilia	5	O
Ichthyophis	32	O
Uraeotyphlidae		
Uraeotyphlus	4	O
Scolecomorphidae		
Crotaphatrema	2	?(O)[b]
Scolecomorphus	3	V
Typhlonectidae		
Atretochoana	1	?(V)[c]
Chthonerpeton	7	V
Nectocaecilia	1	V
Potomotyphlus	1	?(V)[c]
Typhlonectes	3	V
Caeciliidae		
Boulengerula	5	O
Brasilotyphlus	1	?
Caecilia	32	O
Dermophis	3	V
Gegeneophis	3	O
Geotrypetes	3	V
Grandisonia	4	O
Gymnopis	2	V
Herpele	2	?
Hypogeophis	1	O
Idiocranium	1	O
Indotyphlus	1	?
Lutkenotyphlus	1	?
Microcaecilia	5	?
Mimosiphonops	2	?
Oscaecilia	9	?(O)[d]
Parvicaecilia	2	?
Praslinia	1	O
Schistometopum	2	V
Siphonops	5	O
Sylvacaecilia	1	O

[a] inference based on close phylogenetic relationship to *Epicrionops* (Nussbaum, 1977).

[b] inference based on size of ova (Nussbaum, 1985).

[c] inference based on close phylogenetic relationship to other typhlonectids (Wilkinson and Nussbaum, 1997).

[d] inference based on close phylogenetic relationship to *Caecilia* (Nussbaum and Wilkinson, 1989; Wilkinson, 1997).

the assumption that all species of a genus have the same reproductive mode, 13 genera and 102 species are oviparous, whereas only eight genera and 24 species are viviparous, and for 12 genera and 28 species the reproductive mode is unknown. Incorporating hypothesised reproductive modes based upon additional indirect inferences reduces the extent of ignorance to seven genera and 14 species, produces a slight increase in the extent of viviparity to ten genera and 26 species, and a slightly more substantial increase in oviparity to 16 genera and 114 species.

The above estimates indicate that the predominant caecilian reproductive mode is oviparity, with viviparity occurring in only 24 to 30% of genera and 15 to 17% of species for which inference of reproductive mode is possible. Oviparity occurs in 39 to 48% of genera and a clear majority (66–74%) of species. If our estimates and inferences are correct, then, in terms of numbers of species, oviparity would remain the predominant caecilian reproductive mode even in the unlikely event of all species for which reproductive mode cannot be inferred proving to be viviparous.

Discussion

The view that viviparity is the predominant reproductive mode in caecilians appears to have originated with Wake (1977: 83) who stated that '50% of the species having a known reproductive mode are live-bearers' and 'I suspect that further data will demonstrate that the majority of caecilian species are live-bearers'. However, in Wake's (1977) review, which focused on the available reproductive data for individual caecilian species, and did not employ indirect inferences based on extrapolations to genera or other presumed phylogenetic groups, the number of species listed as oviparous (24) actually slightly exceeds the number known to be viviparous (17).

This persistent error has influenced understanding of caecilian evolution and the relation of caecilians to other Amphibia. For example, caecilian viviparity has been identified as one of the key adaptations in the evolution of the lineage that sets the group apart from other Amphibia, in which viviparity is rare (Wake, 1986). More surprising is its potential significance, as seen here, for interpretation of the origins of the Amniota.

Acknowledgements

This work was supported in part by NERC grants GST/02/832 and GR9/02881. We are grateful to C. Jared for sharing his field observations on *Siphonops annulatus* and Dave Gower, John Measey, Peter Miller and Joe Thorley for discussions and comments on the manuscript. MW thanks Miguel Trefaut Rodrigues and Paulo Vanzolini (Museu de Zoologia, Universidade le São Paulo), and Ulisees Caramaschi and Jose Pombal Jr. (Museu Nacional, Rio de Janeiro) for facilitating his studies of the caecilian collections in their care.

References

Carroll, R. L., 1970, Quantitative aspects of the amphibian-reptilian transition, *Forma et Functio*, **3**, 165–178.

Carroll, R. L., 1991, The origin of reptiles, in H.-P. Schultze and L. Trueb (eds), *Origins of the higher groups of tetrapods – controversy and consensus* (Ithaca: Comstock Publishing Associates), pp. 331–335.

Duellman, W. E. and Trueb, L., 1986, *Biology of Amphibians* (New York: McGraw-Hill), 670 pp.

Dunn, E. R., 1942, The American caecilians, *Bulletin of the Museum of Comparative Zoology, Harvard*, **91**, 439–540.

Gans, C., 1961, The first record of egg laying in the caecilian *Siphonops paulensis* Boettger, *Copeia*, **1961**, 490–491.

Goeldi, E. A., 1899, Über die entwicklung von *Siphonops annulatus*, *Zoologish Jahrbuecher Abteilung fuer Systematik Oekologie und Geographie der Tiere*, **12**, 170–173.

Hedges, S. B., Nussbaum, R. A. and Maxson, L., 1993, Caecilian phylogeny and biogeography inferred from mitochondrial DNA sequences of the 12S and 16S rRNA genes (Amphibia: Gymnophiona), *Herpetological Monographs*, **7**, 64–76.

Hillis, D. M., 1991, The phylogeny of amphibians: current knowledge and the role of cytogenetics, in S. K. Sessions and D. M. Green (eds), *Amphibian cytogenetics and evolution* (San Diego: Academic Press), pp. 7–31.

Laurin, M. and Reisz, R. R., 1997, A new perspective on tetrapod phylogeny, in S. Sumida and K. L. M. Martin (eds), *Amniote origins: completing the transition to land* (San Diego: Academic Press), pp. 9–59.

Lombardi, J., 1994, Embryo retention and the origin of the amniote condition, *Journal of Morphology*, **220,** 368.

Maddison, W. P. and Maddison, D. R., 1992, *MacClade version 3.01* (Sunderland: Massachusetts).

Nussbaum, R. A., 1977, Rhinatrematidae: a new family of caecilians (Amphibia: Gymnophiona), *Occasional Papers of the Museum of Zoology University of Michigan*, **682**, 1–30.

Nussbaum, R. A., 1979, The taxonomic status of the caecilian genus *Uraeotyphlus* Peters, *Occasional Papers of the Museum of Zoology University of Michigan*, **687**, 1–20.

Nussbaum, R. A., 1985, Systematics of the caecilians (Amphibia: Gymnophiona) of the family Scolecomorphidae, *Occasional Papers of the Museum of Zoology University of Michigan*, **713**, 1–49.

Nussbaum, R. A. and Wilkinson, M., 1989, On the classification and phylogeny of caecilians (Amphibia: Gymnophiona), a critical review, *Herpetological Monographs*, **3**, 1–42.

Parker, H. W., 1956, Viviparous caecilians and amphibians. *Nature*, **178**, 250–252.

Pough, F. H., Heiser, J. B. and MacFarland, W. N., 1989, *Vertebrate Life* (New York: MacMillan), 904 pp.

Stebbins, R. and Cohen, N., 1995, *A Natural History of Amphibians* (Princeton University Press), 305 pp.

Wake, M. H., 1977, The reproductive biology of caecilians: an evolutionary perspective, in D. G. Taylor and S. I. Guttman (eds), *The Reproductive Biology of Amphibians* (New York: Plenum), pp. 73–101.

Wake, M. H., 1986, A perspective on the systematics and morphology of the Gymnophiona (Amphibia), *Mêmoires de la Societe Zoologique de France*, **43**, 21–37.

Wake, M. H., 1992, Reproduction in caecilians, in W. C. Hamlett (ed.), *Reproductive Biology of South American Vertebrates* (New York: Springer-Verlag), pp. 112–120.

Wake, M. H., 1993, Evolution of oviductal gestation in amphibians, *Journal of Experimental Biology*, **266**, 394–413.

Wilkinson, M., 1992, On the life history of the caecilian genus *Uraeotyphlus* (Amphibia: Gymnophiona), *Herpetological Journal*, **2**, 121–124.

Wilkinson, M., 1996, Majority-ruled reduced consensus trees and their use in bootstrapping, *Molecular Biology and Evolution*, **13**, 437–444.

Wilkinson, M., 1997, Characters, congruence and quality: a study of neuroanatomical and traditional data in caecilian phylogeny, *Biological Reviews*, **17**, 423–470.

Wilkinson, M. and Nussbaum, R. A., 1996, On the phylogenetic position of the Uraeotyphlidae (Amphibia: Gymnophiona), *Copeia*, **1996**, 550–562.

Wilkinson, M. and Nussbaum, R. A., 1997, Comparative morphology and evolution of the lungless caecilian *Atretochoana eiselti* (Amphibia: Gymnophiona), *Biological Journal of the Linnean Society*, **62**, 39–109.