



OXFORD  
BIOLOGY



*the* **TIMETREE** *of* **LIFE**

*edited by* **S. BLAIR HEDGES** *and* **SUDHIR KUMAR**  
*foreword by* James D. Watson

# Caecilians (Gymnophiona)

David J. Gower\* and Mark Wilkinson

Department of Zoology, The Natural History Museum, London SW7 5BD, UK

\*To whom correspondence should be addressed (d.gower@nhm.ac.uk)

## Abstract

The ~170 species of caecilians (Gymnophiona) are grouped into three to six families. Analyses of molecular data since 1993 have largely consolidated earlier hypotheses of family relationships inferred from morphology, although Uraeotyphlidae nests within a paraphyletic Ichthyophiidae rather than being Teresomata's closest relative. Dating analyses conducted thus far broadly agree. Most families diversified by the end of the Jurassic, 146 million years ago (Ma), with Uraeotyphlidae and Typhlonectidae originating from their ichthyophiid and caeciliid ancestors, respectively, by about 100–40 Ma. The Asian Ichthyophiidae and Uraeotyphlidae diverged after the breakup of Gondwana, probably on the Indian subcontinent before its collision with Asia.

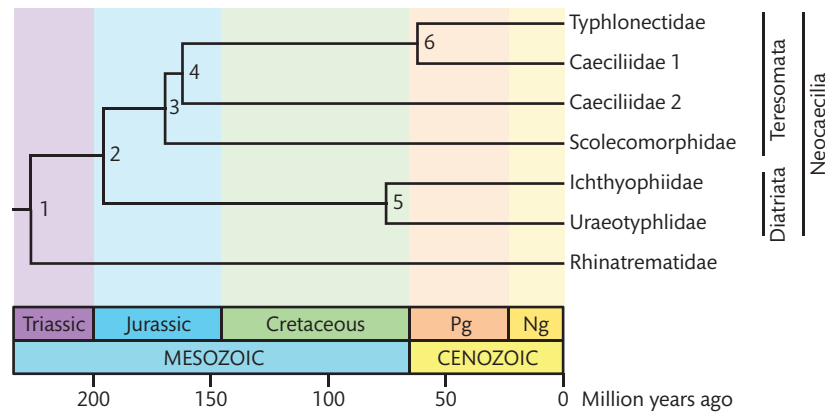
Caecilians are a monophyletic group of elongate, snake- or wormlike amphibians lacking all trace of limbs and girdles, and with tails reduced or absent (Fig. 1). They are one of the three orders of the extant Lissamphibia, the Gymnophiona (~naked snakes), and are most likely the closest relatives of the more familiar frogs and salamanders (1, 2). All caecilians possess a distinctive cranial sensory organ, the tentacle, and have a unique dual jaw closing mechanism (3). Males have an eversible cloaca used in copulation, and fertilization is internal (4). Some groups retain the ancestral trait of an aquatic larval stage, but direct development and viviparity are common (5). The skin is externally segmented, with scales present in dermal pockets in many species. Most of the ~170 known species, grouped into three to six families (1, 6), inhabit soils as adults and, associated with burrowing, have reduced visual systems and heavily ossified skulls. The group has a primarily tropical (Gondwanan) distribution. Here we review the inferred phylogenetic relationships and estimated divergence times of the major lineages of caecilians. The classification used here follows the most recent review (6).

Until 1968 only a single family of caecilians was recognized. Taylor (7, 8) provided a four family classification that has been variously modified and extended by subsequent authors to accommodate new information on morphology, alternative hypotheses of phylogeny and differing perspectives on how best to deal with demonstrably paraphyletic taxa (1, 3, 6, 9–11). The first numerical phylogenetic analysis of caecilians (9) investigated intergeneric relationships using morphological (and life history) data. This and other family-level studies based on these initial data (12, 13) yielded a view of the phylogenetic relationships of the major lineages that has, in the main, been corroborated by subsequent molecular and morphological studies. The major exception has been a change in the placement of the Uraeotyphlidae, an Indian endemic that despite many similarities to the Teresomata (scolecomorphids, caeciliids, and typhlonectids) is now placed in the closest relative of the Teresomata, the Diatriata (Uraeotyphlidae + Ichthyophiidae), based on both morphological (9) and molecular (1, 2, 14–16) data (Fig. 2).

The first molecular phylogenetic studies used only partial mitochondrial ribosomal genes. Taxonomic



Fig. 1 A caeciliid caecilian amphibian (*Herpele squalostoma*) from Cameroon. Credit: © 1999 Natural History Museum, London.



**Fig. 2** A timetree of caecilians (Gymnophiona). Divergence times are shown in Table 1. The single species (26) of *Ichthyophis* that is the closest relative of *Uraeotyphlus* (thus making Ichthyophiidae paraphyletic) has not yet been included in dating analyses, and is ignored here. Codes for paraphyletic and/or

polyphyletic groups are as follows: Caeciliidae-1 (*Caecilia* + *Oscacaecilia*, *Chthonerpeton*, and *Typhlonectes*) and Caeciliidae-2 (*Boulengerula* and *Herpele*). Abbreviations: Ng (Neogene) and Pg (Paleogene).

sampling has been increased steadily so as to improve the coverage of families from four to six, and to begin testing their monophyly as well as their interrelationships (11, 14, 17). Substantial expansions of the available molecular data have seen combined analyses of complete mitochondrial genomes and the *RAG-1* nuclear gene of representatives of all six families (15) and of concatenations of multiple nuclear and mitochondrial markers as part of large-scale analyses of amphibian interrelationships (1, 2). Sampling at the generic level is not yet complete.

We present a consensus view of the phylogenetic relationships of the major lineages of caecilians emerging from morphological and molecular studies (Fig. 2). Monophyly of four (of six families)—Rhinatrematidae, Uraeotyphlidae, Scolecomorphidae, and Typhlonectidae—is well supported by analyses of morphological and/or molecular data. The large and heterogeneous Caeciliidae, and the relatively more uniform Ichthyophiidae, have been convincingly demonstrated to be paraphyletic to Typhlonectidae and Uraeotyphlidae, respectively (1, 2, 9, 10, 16). Interfamilial relationships are generally well-supported by both morphology and molecules, except for the position of the Scolecomorphidae. While some molecular analyses have placed scolecomorphids within the Caeciliidae (1, 17), analyses of morphological data, of complete mitochondrial genomes and *RAG-1*, and of the most recent concatenated mitochondrial and nuclear markers indicate that Scolecomorphidae is the closest relative of the group containing Caeciliidae and Typhlonectidae (2, 10, 15).

Only a few studies have used molecular data to estimate the age of divergences among caecilian families (2, 14, 18, 19). Only Roelants *et al.* (2) have estimated dates of divergence for all six nodes in the inter-family tree, and so we focus on that study here (Fig. 2). This study dated a phylogeny of 171 amphibians (24 caecilians) based on ca. 3750 kb of sequences for one mitochondrial and four nuclear genes by using 22 calibrations from both (caecilian and noncaecilian) paleobiogeographic and (noncaecilian) fossil data. Use of two different statistical methods produced similar results (2).

Divergences among most caecilian families are estimated to have occurred in the early Mesozoic (251–146 Ma), at least by the end of the Jurassic (146 Ma). The two exceptions are later Mesozoic/early Cenozoic (100–40 Ma) divergences associated with the paraphyly of Ichthyophiidae and Caeciliidae (Fig. 2). Depth of divergence might profitably be employed to determine rank in future revisions of caecilian classification (20).

Other molecular dating estimates for divergences of some caecilian families based on smaller taxon and character samplings and using a variety of methods (14, 18, 19) are generally a little older, but they overlap with those from Roelants *et al.* (2). The main difference is an estimate of 250 Ma for the divergence between Diatriata and Teresomata (19), which is based on a single non-amphibian fossil calibration. Reanalysis of that data set with improved, multiple calibrations generally resulted in substantially younger dates throughout amphibians, although a revised estimate for the Diatriata–Teresomata divergence was not reported (21). Two other studies have

**Table 1.** Divergence times (Ma) and their 95% confidence/credibility intervals (CI) among caecilians (Gymnophiona).

Timetree		Estimates									
Node	Time	Ref. (2)(a)		Ref. (2)(b)		Ref. (14)		Ref. (18)		Ref. (19)	
		Time	CI	Time	CI	Time	Interval	Time	CI	Time	CI
1	226.4	226.4	254–197	217.8	242–192	–	–	214.3	256–177	–	–
2	195.8	195.8	223–168	188.2	214–167	178	278–126	192.4	233–160	250	274–224
3	169.3	169.3	193–146	162.8	185–145	–	–	177.1	218–148	–	–
4	161.8	161.8	185–140	156.5	175–139	–	–	155.2	193–134	–	–
5	75.3	75.3	100–54	74.6	99–55	94	123–72	104.3	151–65	–	–
6	62.0	62.0	83–46	59.6	77–42	–	–	–	–	–	–

Note: Node times in the timetree are from Thorne–Kishino analysis (a) of one mitochondrial and four nuclear genes (~3750 basepairs) for 24 caecilian species as reported in ref. (2), in which results were also reported for penalized likelihood analysis (b) of the same data.

used molecular dating analyses to interpret caecilian evolution. Published substitution rates for amphibian mitochondrial DNA were used to estimate the divergence between Indian and the monophyletic Sri Lankan ichthyophiids at between 9.25 and 26 Ma (22), and relative dating was used to demonstrate that the divergences of three pairs of disjunctly distributed East–West African caeciliids and scolecomorphids were not contemporaneous (23).

Currently, the poverty of the “caecilian” fossil record (24) renders it irrelevant to the issue of dating divergences within Gymnophiona, because it comprises only two (ca. 190 and 140 Ma) fossil taxa not assignable to living lineages (= Gymnophiona) and three kinds of fossil vertebrae that may or may not belong to living lineages. Thus, it is not possible to use any currently known “caecilian” fossil to estimate the minimum age of Gymnophiona. As a result, molecular dating estimates have relied on paleogeographic data and noncaecilian fossils for calibration (2, 14, 18, 19).

The timetree indicates that multiple lineages of Gymnophiona coexisted with the two fossil (possibly stem-) taxa that do not belong to Gymnophiona, *Eocaecilia* and *Rubricacaecilia*. The stegokrotaphic (closed roofed) skull of *Eocaecilia* has been used to argue that, unlike the frogs and salamanders, and rhinatrematid caecilians (which have open roofed skulls), the ancestral caecilian was stegokrotaphic and therefore had a separate ancestry from the other amphibians (25). However, the long independent histories of *Eocaecilia* and Gymnophiona, the plausibility of their convergent adaptation to burrowing and independent evolution of stegokrotaphy, and the morphology of rhinatrematids caution against

accepting *Eocaecilia* as an accurate model for the ancestral caecilian.

The timetree is consistent with the hypothesis, based on present-day geographical distributions, that Gymnophiona is primarily a radiation of Gondwana (and the Gondwanan part of Pangea) and that the divergence of the exclusively Asian Ichthyophiidae and Uraeotyphlidae occurred on the Indian plate subsequent to the breakup of Gondwana and before its collision with Laurasian Asia (14).

One of the most interesting aspects of caecilian biology is the diversity of reproductive modes within the group. Some caecilians have been recently discovered to have extended parental care in which altricial young feed on a modified, lipid-rich epidermis of their attending mothers (5). Consideration of phylogenetic relationships suggests that this maternal dematophagy may be fairly widespread within Neocaecilia (27). Molecular dates indicate that this highly unusual form of parental care has persisted in multiple lineages for perhaps more than 138 million years.

## Acknowledgment

H. Taylor photographed the caecilian used in Fig. 1.

## References

1. D. R. Frost *et al.*, *Bull. Am. Mus. Nat. Hist.* **297**, 1 (2006).
2. K. Roelants *et al.*, *PNAS* **104**, 887 (2007).
3. R. A. Nussbaum, *Occ. Pap. Univ. Mich. Mus. Zool.* **683**, 1 (1977).
4. D. J. Gower, M. Wilkinson, *Bull. Nat. Hist. Mus. (Zool.)* **68**, 143 (2002).
5. A. Kupfer *et al.*, *Nature* **13**, 440 (2006).

6. M. Wilkinson, R. A. Nussbaum, in *Reproductive Biology and Phylogeny of Gymnophiona*, J.-M. Exbrayat, Eds. (Science Publishers, Enfield, NH, 2006), pp. 39–78.
7. E. H. Taylor, *The Caecilians of the World* (University of Kansas Press, 1968).
8. E. H. Taylor, *Univ. Kansas Sci. Bull.* **10**, 297 (1969).
9. R. A. Nussbaum, *Occ. Pap. Univ. Mich. Mus. Zool.* **687**, 1 (1979).
10. M. Wilkinson, R. A. Nussbaum, *Copeia* **1996**, 550 (1996).
11. S. B. Hedges, R. A. Nussbaum, L. R. Maxson, *Herpetol. Monogr.* **7**, 64 (1993).
12. W. E. Duellman, L. Trueb, *Biology of Amphibians* (John Hopkins University Press, Baltimore, 1994), pp. 696.
13. D. M. Hillis, in *Amphibian Cytogenetics and Evolution*, D. M. Green, S. K. Sessions, Eds. (Academic Press, San Diego, 1991), pp. 7–31.
14. M. Wilkinson *et al.*, *Mol. Phylogenet. Evol.* **23**, 401 (2002).
15. D. San Mauro *et al.*, *Mol. Phylogenet. Evol.* **33**, 413 (2004).
16. D. J. Gower *et al.*, *Proc. Roy. Soc. Lond. B* **269**, 1563 (2002).
17. M. Wilkinson *et al.*, *Afr. J. Herpetol.* **52**, 83 (2003).
18. D. San Mauro *et al.*, *Am. Nat.* **165**, 590 (2005).
19. P. Zhang *et al.*, *Syst. Biol.* **54**, 391 (2005).
20. J. C. Avise, G. C. Johns, *PNAS* **96**, 7358 (1999).
21. D. Marjanovic, M. Laurin, *Syst. Biol.* **56**, 369 (2007).
22. F. Bossuyt *et al.*, *Science* **306**, 479 (2004).
23. S. P. Loader *et al.*, *Biol. Lett.* **3**, 505 (2007).
24. S. E. Evans, D. Sigogneau-Russell, *Palaeontology* **44**, 259 (2001).
25. R. L. Carroll, *Zool. J. Linn. Soc.* **150** (s1), 1 (2007).
26. D. J. Gower *et al.*, *J. Zool.* **272**, 266 (2007).
27. M. Wilkinson *et al.*, *Biol. Lett.* **4**, 358 (2008).