



A nine-family classification of caecilians (Amphibia: Gymnophiona)

MARK WILKINSON^{1,3}, DIEGO SAN MAURO¹, EMMA SHERRATT^{1,2} & DAVID J. GOWER¹

¹Department of Zoology, The Natural History Museum, London SW7 5BD, UK

²Faculty of Life Sciences, University of Manchester, Oxford Road, Manchester M13 9PT, UK

³Corresponding author. E-mail: m.wilkinson@nhm.ac.uk

Abstract

We propose a new family-level classification of caecilians that is based on current understanding of phylogenetic relationships and diversity. The 34 currently recognised genera of caecilians are diagnosed and partitioned into nine family-level taxa. Each family is an hypothesised monophylum, that, subject to limitations of taxon sampling, is well-supported by phylogenetic analyses and is of ancient (Mesozoic) origin. Each family is diagnosed and also defined phylogenetically. The proposed classification provides an alternative to an exclusive reliance upon synonymy in solving the longstanding problem of paraphyly of the Caeciliidae.

Key words: amphibians, herpetology, phylogeny, systematics, taxonomy

Introduction

Until 1968, all caecilian amphibians (Gymnophiona) were included, by default, in a single family, the Caeciliidae. Since 1968, classifications of between three and ten families (e.g., Table 1) have been proposed by different authors (Taylor, 1968, 1969; Nussbaum, 1977, 1979; Wake & Campbell, 1983; Duellman & Trueb, 1986; Laurent, 1984, 1986; Lescure *et al.*, 1986; Nussbaum & Wilkinson, 1989; Hedges *et al.*, 1993; Frost *et al.*, 2006; Wilkinson & Nussbaum, 2006). Nussbaum & Wilkinson (1989) reviewed the several substantially different classifications proposed in the 1980s (Wake & Campbell, 1983; Duellman & Trueb, 1986; Lescure *et al.*, 1986; Laurent 1986) and advocated adoption of a 'conservative' six-family system to stabilise caecilian classification.

A major problem with Nussbaum & Wilkinson's (1989) conservative classification was that the Caeciliidae, essentially what is left when the other proposed families are differentiated, was paraphyletic with respect to the Typhlonectidae (Nussbaum, 1979). Nussbaum & Wilkinson (1989) argued that this paraphyly should be accepted until understanding of phylogeny had progressed sufficiently to enable a more meaningful and useful revised classification based only upon monophyla. Subsequent phylogenetic studies, morphological and molecular (Hedges *et al.*, 1993; Wilkinson & Nussbaum, 1995; Wilkinson, 1997; Wilkinson *et al.*, 2002, 2003; San Mauro *et al.*, 2004, 2009; Frost *et al.*, 2006; Roelants *et al.*, 2007; Loader *et al.*, 2007; Zhang & Wake, 2009), have confirmed the paraphyly of the Caeciliidae with respect to the Typhlonectidae, and raised the possibility that the Caeciliidae is paraphyletic also with respect to the Scolecomorphidae (Wilkinson, 1997; Wilkinson *et al.*, 2003; Frost *et al.*, 2006; Loader *et al.*, 2007). Whereas most subsequent workers adopted Nussbaum & Wilkinson's (1989) classification, some proposed to resolve the paraphyly of the Caeciliidae solely through synonymy. Thus, Hedges *et al.* (1993) proposed synonymy of Typhlonectidae with Caeciliidae, and Frost *et al.* (2006) treated both Scolecomorphidae and Typhlonectidae as synonyms of Caeciliidae.

Molecular phylogenetic studies (Gower *et al.*, 2002; Frost *et al.*, 2006; Roelants *et al.*, 2007; Zhang & Wake, 2009) have also revealed that the Ichthyophiidae (*sensu* Nussbaum & Wilkinson, 1989) is paraphyletic with respect to the Uraeotyphlidae. Frost *et al.* (2006) removed this paraphyly by placing the Uraeotyphlidae in the synonymy of the Ichthyophiidae. Frost *et al.* (2006) succeeded in producing a family-level classification based only on monophyla but recognised just three families. In contrast, Wilkinson & Nussbaum (2006) persisted with the six-family

TABLE 1. Some previous family-level classifications of caecilian amphibians. For simplicity only currently recognised genera are included. * Lescure *et al.* (1986) employed the family name Epicriidae in place of Ichthyophiidae and their classification did not include five then nominal genera (*Idiocranium*, *Microcaecilia*, *Nectocaecilia*, *Praslinia*, *Parvicaecilia*).

	Taylor (1969)	Lescure <i>et al.</i> (1986)*	Nussbaum & Wilkinson, (1989)	Frost <i>et al.</i> (2006)
Caeciliidae	<i>Boulengerula</i> , <i>Brasilotyphlus</i> , <i>Caecilia</i> , <i>Dermophis</i> , <i>Gegeneophis</i> , <i>Geotrypetes</i> , <i>Grandisonia</i> , <i>Gymnopsis</i> , <i>Herpele</i> , <i>Hypogeophis</i> , <i>Idiocranium</i> , <i>Indotyphlus</i> , <i>Luetkenotyphlus</i> , <i>Microcaecilia</i> , <i>Mimosiphonops</i> , <i>Oscacecilia</i> , <i>Parvicaecilia</i> , <i>Praslinia</i> , <i>Schistometopum</i> , <i>Siphonops</i> , <i>Uraeotyphlus</i>	<i>Caecilia</i> , <i>Gymnopsis</i>	<i>Boulengerula</i> , <i>Brasilotyphlus</i> , <i>Caecilia</i> , <i>Dermophis</i> , <i>Gegeneophis</i> , <i>Geotrypetes</i> , <i>Grandisonia</i> , <i>Gymnopsis</i> , <i>Herpele</i> , <i>Hypogeophis</i> , <i>Idiocranium</i> , <i>Indotyphlus</i> , <i>Luetkenotyphlus</i> , <i>Microcaecilia</i> , <i>Mimosiphonops</i> , <i>Oscacecilia</i> , <i>Parvicaecilia</i> , <i>Praslinia</i> , <i>Schistometopum</i> , <i>Siphonops</i> , <i>Sylvacaecilia</i>	<i>Atratochoana</i> , <i>Boulengerula</i> , <i>Brasilotyphlus</i> , <i>Caecilia</i> , <i>Chthonerpeton</i> , <i>Crotaphatrema</i> , <i>Dermophis</i> , <i>Gegeneophis</i> , <i>Geotrypetes</i> , <i>Grandisonia</i> , <i>Gymnopsis</i> , <i>Herpele</i> , <i>Hypogeophis</i> , <i>Idiocranium</i> , <i>Indotyphlus</i> , <i>Luetkenotyphlus</i> , <i>Microcaecilia</i> , <i>Mimosiphonops</i> , <i>Nectocaecilia</i> , <i>Oscacecilia</i> , <i>Parvicaecilia</i> , <i>Potomotyphlus</i> , <i>Praslinia</i> , <i>Schistometopum</i> , <i>Scolecormorphus</i> , <i>Siphonops</i> , <i>Sylvacaecilia</i> , <i>Typhlonectes</i>
Geotrypetidae		<i>Geotrypetes</i> , <i>Hypogeophis</i>		
Ichthyophiidae	<i>Caudacaecilia</i> , <i>Epicriomops</i> , <i>Ichthyophis</i> , <i>Rhinatrema</i>	<i>Caudacaecilia</i> , <i>Ichthyophis</i>	<i>Caudacaecilia</i> , <i>Ichthyophis</i>	<i>Caudacaecilia</i> , <i>Ichthyophis</i> , <i>Uraeotyphlus</i>
Oscaciliidae		<i>Oscacecilia</i>		
Potamotyphliidae		<i>Potomotyphlus</i>		
Rhinatrematidae		<i>Epicriomops</i> , <i>Rhinatrema</i>	<i>Epicriomops</i> , <i>Rhinatrema</i>	<i>Epicriomops</i> , <i>Rhinatrema</i>
Scolecormorphidae	<i>Scolecormorphus</i>	<i>Scolecormorphus</i>	<i>Crotaphatrema</i> , <i>Scolecormorphus</i>	
Siphonopidae		<i>Boulengerula</i> , <i>Brasilotyphlus</i> , <i>Dermophis</i> , <i>Gegeneophis</i> , <i>Indotyphlus</i> , <i>Grandisonia</i> , <i>Herpele</i> , <i>Luetkenotyphlus</i> , <i>Mimosiphonops</i> , <i>Schistometopum</i> , <i>Siphonops</i>		
Typhlonectidae	<i>Chthonerpeton</i> , <i>Nectocaecilia</i> , <i>Potomotyphlus</i> , <i>Typhlonectes</i>	<i>Chthonerpeton</i> , <i>Typhlonectes</i>	<i>Chthonerpeton</i> , <i>Nectocaecilia</i> , <i>Potomotyphlus</i> , <i>Typhlonectes</i>	
Uraeotyphliidae		<i>Uraeotyphlus</i>	<i>Uraeotyphlus</i>	

classification of Nussbaum & Wilkinson (1989) in which both Caeciliidae and Ichthyophiidae are paraphyletic. This conservatism was not the result of any aversion to monophyla. Rather, it reflected the belief that stability would best be served by continued recognition of distinctive taxa such as the Scolecomorphidae and Typhlonectidae at the family level, and the expectation that the problems of paraphyly of other families would be better resolved based on improved knowledge of phylogenetic relationships, perhaps by further partitioning of paraphyletic families, especially the Caeciliidae, into less inclusive and more homogenous monophyla rather than through synonymy alone. Although knowledge of phylogenetic relationships and diversity of caecilians is far from perfect, it has advanced substantially and, we believe, sufficiently enough to enable the elimination of paraphyletic family-level taxa from caecilian classification while simultaneously refining caecilian family-level classification to distinguish more of the distinctive monophyla within the group. That is our aim here.

The system of classification proposed here adopts the Frost *et al.* (2006) solution to the paraphyly of the Ichthyophiidae by treating Uraeotyphlidae as a synonym of Ichthyophiidae, but rejects synonymy of Scolecomorphidae and Typhlonectidae, and solves the paraphyly of the Caeciliidae by restricting it to the monophylum comprising only the species of *Oscacaecilia* and *Caecilia*. Other genera formerly included in the Caeciliidae are divided into additional monophyletic families based on the oldest available names known to us. We provide brief diagnoses of families and genera, emphasising one or a unique combination of a few characters without attempting to list all characters of a family (for an alternative approach to diagnoses of genera see Wilkinson & Nussbaum, 2006). We also provide phylogenetic definitions of family-level taxa based on the relationships in the summary family-level phylogeny shown in Figure 1, and for each type genus we illustrate the skull of the type species with figures produced from CT scans (for methods see Gower *et al.*, 2010). According to estimates of divergence times based on molecular sequence data (San Mauro *et al.*, 2005; Roelants *et al.*, 2007; Gower & Wilkinson, 2009; Zhang & Wake, 2009; San Mauro, 2010), each of the distinct families we recognise is an ancient lineage that originated prior to the end of the Cretaceous (Fig. 1).

We do not include fossil taxa in this classification. Following Wilkinson & Nussbaum (2006), we do not consider the putative stem-group fossils *Eocaecilia* (Jenkins & Walsh, 1993; Jenkins *et al.*, 2007) and *Rubricacaecilia* (Evans & Sigogneau-Russell, 2001) to be members of the Gymnophiona, which we restrict to the last common ancestor of all extant caecilians and its descendants. True gymnophionan fossils are few and comprise mostly isolated vertebrae that, given current knowledge of caecilian vertebral diversity, cannot be confidently assigned to families. With the exception of transferring a single species from *Grandisonia* to *Hypogeophis*, we have not modified the content of any genera. In most cases, stable revisions of seemingly or potentially paraphyletic genera will depend, we believe, on more dense sampling of species and/or of comparative (morphological and molecular) data that will also enable further tests of putative monophyletic genera or species groups, very few of which have been comprehensively sampled in any phylogenetic studies.

We have not attempted to provide complete synonymies, and the few that are given are listed in small font. Henceforth, we use "Caeciliidae" to refer to Caeciliidae *sensu* Nussbaum & Wilkinson (1989), and "caeciliids" to refer to taxa included in this paraphyletic assemblage. The new classification is summarised in Table 2.

TABLE 2. Summary of the nine-family classification proposed herein.

Family	Generic content
Caeciliidae	<i>Caecilia</i> , <i>Oscacaecilia</i> ,
Dermophiidae	<i>Dermophis</i> , <i>Geotrypetes</i> , <i>Gymnopsis</i> , <i>Schistometopum</i>
Herpelidae	<i>Boulengerula</i> , <i>Herpele</i>
Ichthyophiidae	<i>Caudacaecilia</i> , <i>Ichthyophis</i> , <i>Uraeotyphlus</i>
Indotyphlidae	<i>Gegeneophis</i> , <i>Grandisonia</i> , <i>Hypogeophis</i> , <i>Idiocranium</i> , <i>Indotyphlus</i> , <i>Praslinia</i> , <i>Sylvacaecilia</i>
Rhinatreumatidae	<i>Epicrionops</i> , <i>Rhinatrema</i>
Scolecomorphidae	<i>Crotaphatrema</i> , <i>Scolecomorphus</i>
Siphonopidae	<i>Brasilotyphlus</i> , <i>Caecilita</i> , <i>Luetkenotyphlus</i> , <i>Microcaecilia</i> , <i>Mimosiphonops</i> , <i>Parvicaecilia</i> , <i>Siphonops</i>
Typhlonectidae	<i>Atretochoana</i> , <i>Chthonerpeton</i> , <i>Nectocaecilia</i> , <i>Potomotyphlus</i> , <i>Typhlonectes</i>

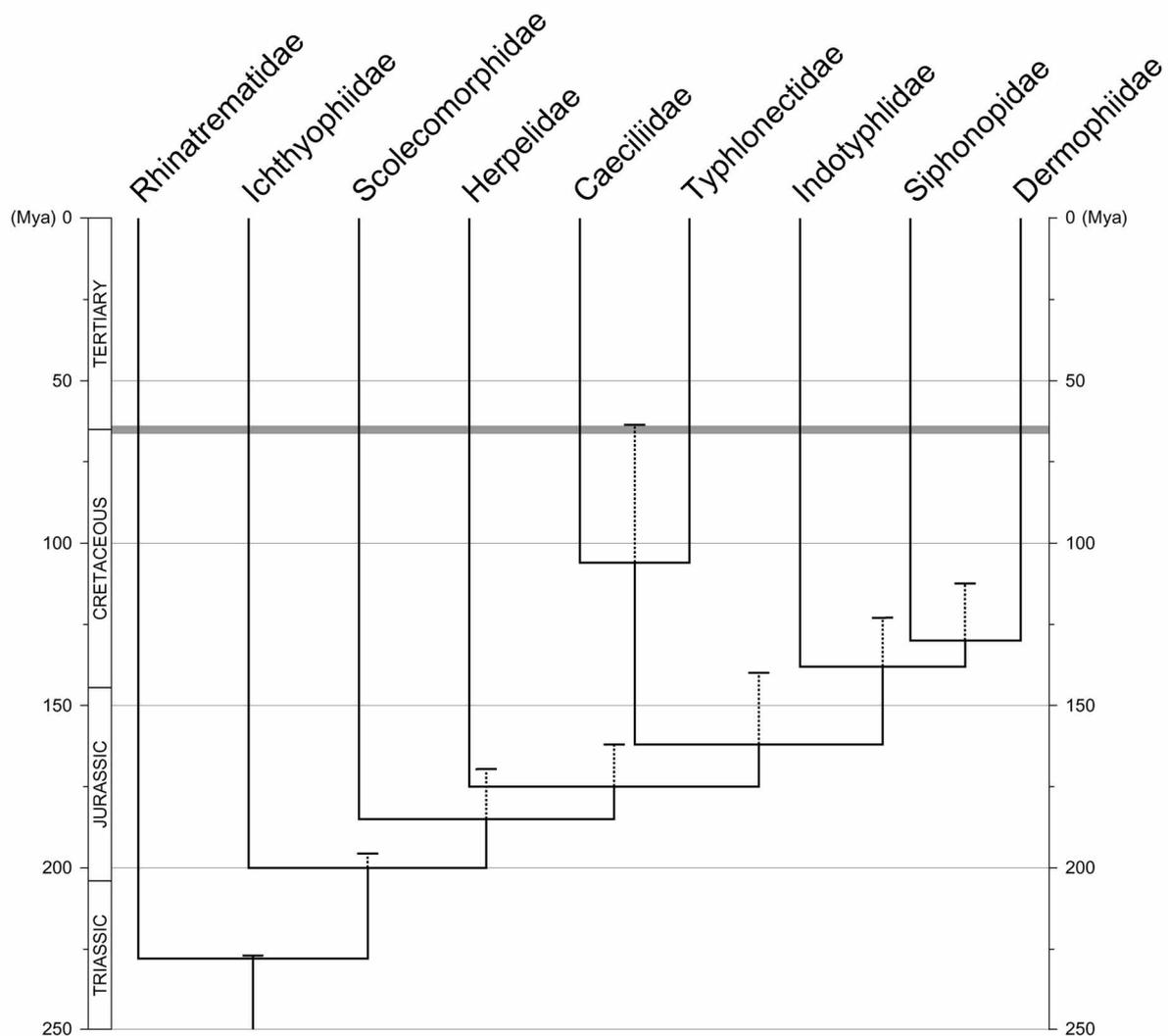


FIGURE 1. Phylogenetic relationships of the nine caecilian families recognised herein, based on recent molecular evidence (see text). Times of divergence are based on mean age estimates from Zhang & Wake (2009; main chronogram) and Roelants *et al.* (2007; dotted lines arising from each node). Grey horizontal line indicates the K/T boundary.

ORDER *Gymnophiona* Müller, 1832

Lissamphibians with elongate annulate bodies, lacking limbs and girdles. Based on current understanding of phylogeny, the extant *Gymnophiona* comprise all descendants of the last common ancestor of, for example, *Rhinatrema bivittatum* and *Caecilia tentaculata*.

I. FAMILY *Caeciliidae* Rafinesque, 1814

Osaeciliidae Lescure, Renous & Gasc, 1986

Type genus: *Caecilia* Linnaeus, 1758.

Diagnosis: The only caecilians with imperforate stapes, inner mandibular teeth, eyes surrounded or covered by the maxillopalatine, and all teeth monocusped.

Phylogenetic definition: All caecilians more closely related to *Caecilia tentaculata* than to *Typhlonectes compressicauda*.

Distribution: South and Central America.

Content: Two genera, 42 species.

Remarks: Notwithstanding the variation within the family, species of the two genera *Caecilia* and *Oscacecilia* are, as far as is known, very similar in cranial osteology and myology, and although not many unambiguous synapomorphies of the group are known, there can be little doubt that together they are monophyletic. Sampling in molecular phylogenetic studies (e.g., Roelants *et al.*, 2007; Zhang & Wake, 2009) has been very limited, but these provide nothing but additional support for monophyly. In our opinion, restricting the content of Caeciliidae to *Caecilia* and *Oscacecilia* is preferable to resolving "caeciliid" paraphyly through synonymies alone because it yields a far more morphologically homogenous and yet still substantial (more than one fifth of all caecilian species) and old monophyletic group. Monophyly of the constituent genera, which are distinguished on the basis of a single imperfect character (orbit open or closed), is far from certain. One species of *Caecilia* (*C. gracilis*) is reported to sometimes have eyes covered by bone (e.g., Nussbaum & Wilkinson, 1989). Diversity and relationships within the group is in need of substantial further study.



FIGURE 2. Volume reconstruction of high-resolution x-ray computed tomography (HRXCT) data showing skull of *Caecilia tentaculata* (MW 5138, field series of Natural History Museum, London [BMNH]). Left side from top to bottom: cranium in dorsal and palatal view. Right side from top to bottom: cranium in lateral view, mandible in lateral and dorsal view. Scale bar = 1mm. Scan parameters: a molybdenum target set at 110kV and 160 μ A; scan data were collected at 2.8 frames per second over 3142 projections in 360°; reconstructed voxel size of 19 μ m. Abbreviations as in Appendix.

1. *Caecilia* Linnaeus, 1758

Type species: *Caecilia tentaculata* Linnaeus, 1758 (Fig. 2) by subsequent designation of Dunn (1942).

Diagnosis: The only caeciliids with eyes not covered by bone.

Distribution: Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, Venezuela.

Content: 33 species (*abitaguae*, *albiventris*, *antioquiensis*, *armata*, *attenuata*, *bockermani*, *caribea*, *corpulenta*, *crassiquama*, *degenerata*, *disossea*, *dunni*, *flavopunctata*, *gracilis*, *guntheri*, *leucocephala*, *inca*, *isthmica*, *marcusi*, *mertensi*, *nigricans*, *occidentalis*, *orientalis*, *pachynema*, *perdita*, *pressula*, *subdermalis*, *subnigricans*, *subterminalis*, *tentaculata*, *tenuissima*, *thompsoni*, *volcani*).

2. *Osaecilia* Taylor, 1968

Type species: *Caecilia ochrocephala* Cope, 1866 by original designation.

Diagnosis: The only caeciliids with the eyes covered by bone.

Distribution: Colombia, Costa Rica, Ecuador, French Guiana, Guyana, Panama, Peru.

Content: Nine species (*bassleri*, *elongata*, *equatorialis*, *hypereumeces*, *koepckeorum*, *ochrocephala*, *osae*, *polyzona*, *zwiefeli*).

II. FAMILY Dermophiidae Taylor, 1969

Geotrypetidae Lescure, Renous & Gasc, 1986

Type genus: *Dermophis* Peters, 1879.

Diagnosis: The only viviparous caecilians with secondary annuli and annular scales.

Phylogenetic definition: All caecilians more closely related to *Dermophis mexicanus* than to *Siphonops annulatus* and/or to *Hypogeophis rostratus*.

Remarks: This clade has been recovered or uncontradicted by all relevant molecular phylogenetic studies (Hedges *et al.*, 1993; Frost *et al.*, 2006; Loader *et al.*, 2007; Roelants *et al.*, 2007; Zhang & Wake, 2009). The phylogenetic definition reflects the fact that the interrelationships of the Dermophiidae, Indotyphlidae and Siphonopidae are currently the least certain of the higher-level phylogenetic relationships of caecilians. Taylor (1969) introduced Dermophiinae for the paraphyletic grouping of all "caeciliids" except *Caecilia* and *Osaecilia*, and first use of Dermophiidae at the family level denoted the same group (Laurent, 1984), whereas Wake & Campbell (1983) employed the name only at subfamilial level and refined the content by transferring *Microcaecilia*, *Parvicaecilia* and their new genus *Minascaecilia* to the "Caeciliinae". *Minascaecilia* is a junior synonym of the dermophiid *Gymnopsis* (Nussbaum, 1988), and we consider *Microcaecilia* and *Parvicaecilia* to be members of the Siphonopidae. Dermophiidae appears to be the oldest available family-group name for the four genera included in this clade, although its current content and meaning is quite different from earlier uses.

Distribution: Africa, Central America, South America.

Content: Four genera, 13 species.

1. *Dermophis* Peters, 1879

Type species: *Siphonops mexicanus* Duméril & Bibron, 1841 (Fig. 3) by subsequent designation of Noble (1924).

Diagnosis: The only dermophiids without inner mandibular teeth.

Distribution: Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama.

Content: Seven species (*costaricense*, *glandulosus*, *gracilior*, *mexicanus*, *oaxacae*, *occidentalis*, *parviceps*).

2. *Geotrypetes* Peters, 1880

Type species: *Caecilia seraphini* Duméril, 1859 by original monotypy.

Diagnosis: The only dermophiids with the tentacle far forward, below the nostril.

Distribution: Benin, Cameroon, Congo, Democratic Republic of Congo, Ivory Coast, Equatorial Guinea, Ghana, Guinea, Liberia, Nigeria, Sierra Leone, Togo.

Content: Three species (*angeli*, *pseudoangeli*, *seraphini*).



FIGURE 3. Volume reconstruction of HRXCT data showing skull of *Dermophis mexicanus* (BMNH 64.1.26.397). Views as in Fig.2. Scale bar = 1mm. Scan parameters: a molybdenum target set at 100kV and 200 μ A; scan data were collected at 2.0 frames per second over 3142 projections in 360 $^{\circ}$; reconstructed voxel size of 17 μ m. Abbreviations as in Appendix.

3. *Gymnopsis* Peters, 1874

Type species: *Gymnopsis multiplicata* Peters, 1874 by original monotypy.

Diagnosis: The only dermophiids with eyes covered by bone.

Distribution: Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama.

Content: Two species (*multiplicata*, *syntrema*).

4. *Schistometopum* Parker, 1941.

Type species: *Dermophis gregorii* Boulenger, 1894 by original designation.

Diagnosis: The only dermophiids with eyes not covered with bone, tentacular apertures closer to the eyes than to the nares, and inner mandibular teeth.

Distribution: Democratic Republic of Congo, Kenya, São Tomé, Tanzania.

Content: Two species (*gregorii*, *thomense*).

III. FAMILY Herpelidae Laurent, 1984

Type genus: *Herpele* Peters, 1879.

Diagnosis: The only caecilians with perforate stapes, no separate septomaxillae or prefrontals, and multiple small antotic foramina on each side (see Fig. 11).

Phylogenetic definition: All caecilians more closely related to *Herpele squalostoma* than to *Caecilia tentaculata*.

Remarks: Phylogenetic analyses of molecular data (Wilkinson *et al.*, 2003; Frost *et al.*, 2006; Roelants *et al.*, 2007) have revealed this lineage to be the sister group of all other sampled "caeciliids". A perforate stapes is a plesiomorphic condition that further supports the hypothesis that this lineage lies outside the other "caeciliids". The content of the family is quite different from that of Laurent's (1984) Herpelinae, which included all old world "caeciliids".

Distribution: Africa.

Content: Two genera, nine species.

1. *Boulengerula* Tornier, 1896

Type species: *Boulengerula boulengeri* Tornier, 1896 by original monotypy.

Diagnosis: The only herpelids with fused nasopremaxillae (lacking separate nasals and premaxillae).

Distribution: Kenya, Malawi, Rwanda, Tanzania.

Content: Seven species (*boulengeri*, *changamwensis*, *denhardti*, *fischeri*, *niedeni*, *taitanus*, *uluguruensis*).

2. *Herpele* Peters, 1879

Type species: *Caecilia squalostoma* Stutchbury, 1834 (Fig. 4) by original monotypy.

Diagnosis: The only herpelids with separate nasals and premaxillae.

Distribution: Cameroon, Gabon, Equatorial Guinea, Nigeria.

Content: Two species (*multiplicata*, *squalostoma*).

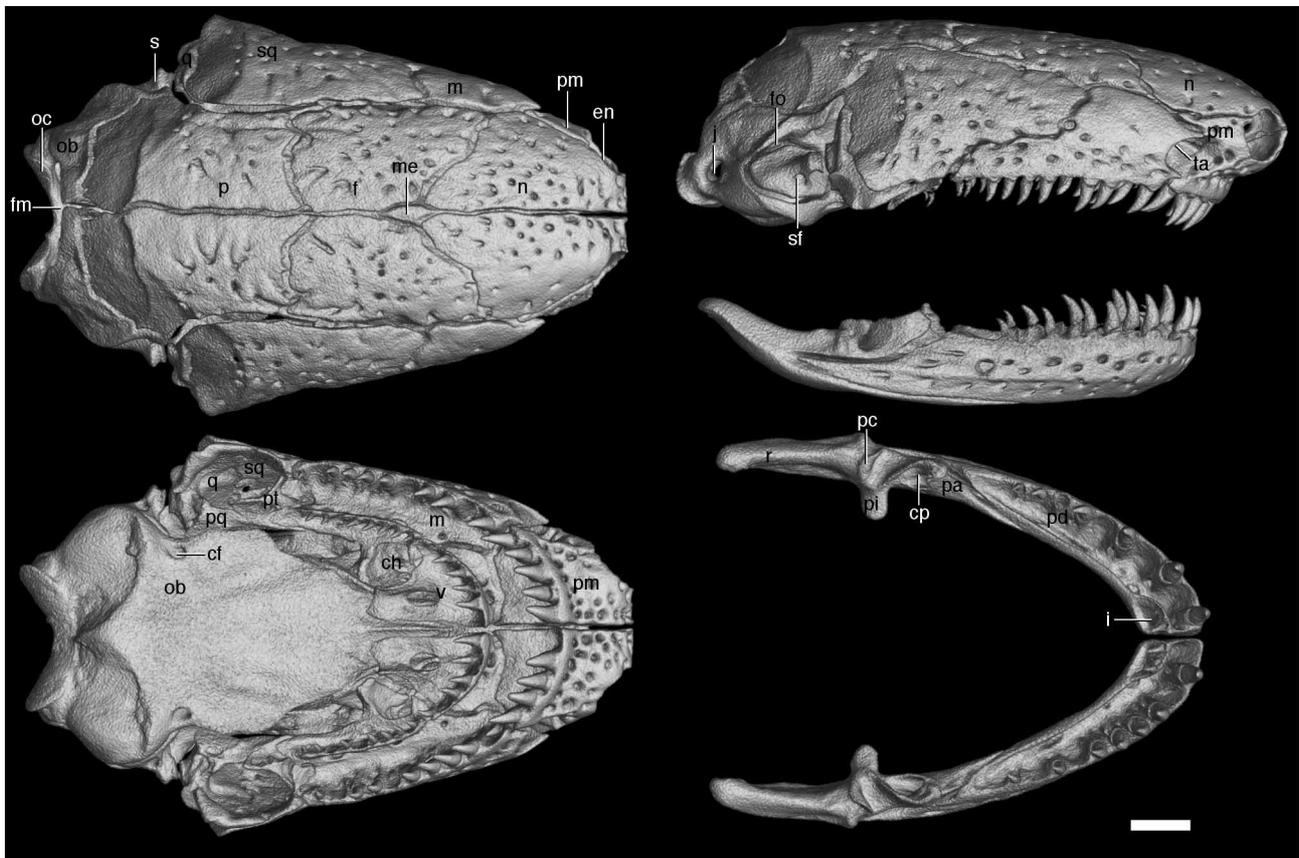


FIGURE 4. Volume reconstruction of HRXCT data showing skull of *Herpele squalostoma* (MW 4532). Views as in Fig.2. Scale bar = 1mm. Scan parameters: a molybdenum target set at 100kV and 155 μ A; scan data were collected at 2.8 frames per second over 3142 projections in 360°; reconstructed voxel size of 11 μ m. Abbreviations as in Appendix

IV. FAMILY Ichthyophiidae Taylor, 1968

Epicriidae Fitzinger, 1843 (Lescure et al., 1986)

Uraeotyphlidae Nussbaum, 1979 (e.g. Duellman & Trueb, 1986; Hillis, 1991; Laurent, 1986; Lescure *et al.*, 1986; Nussbaum & Wilkinson, 1989; Pillai & Ravichandran, 1999; Wilkinson & Nussbaum, 1996, 1997, 2006)

Type genus: *Ichthyophis* Fitzinger, 1826.

Diagnosis: The only caecilians with partial external division of the atrium and a long anterior pericardial space.

Phylogenetic definition: All caecilians more closely related to *Ichthyophis glutinosus* than to *Caecilia tentaculata*.

Remarks: Uraeotyphlinae was established by Nussbaum (1979) as a sub-family of the Ichthyophiidae. Subsequent elevation to family rank (Duellman & Trueb, 1986) was based on the hypothesis that *Uraeotyphlus* is more closely related to "higher caecilians" than to other ichthyophiids. This hypothesis has been overturned by subsequent morphological (Wilkinson & Nussbaum, 1996) and molecular (Wilkinson *et al.*, 2002; San Mauro *et al.*, 2004, 2005, 2009; Frost *et al.*, 2006; Roelants *et al.*, 2007; Zhang & Wake, 2009) phylogenetic analyses. Molecular phylogenetic studies (Gower *et al.*, 2002; Frost *et al.*, 2006; Roelants *et al.*, 2007) also show that continued recognition of the Uraeotyphlidae renders the Ichthyophiidae paraphyletic by virtue of *Ichthyophis bombayensis* being more closely related to sampled *Uraeotyphlus* than to other sampled *Ichthyophis*. We adopt Frost *et al.*'s (2006) solution to this paraphyly at the family level by accepting Uraeotyphlidae as a junior synonym of Ichthyophiidae. The problem of paraphyly remains at the genus level and is not addressed here. Additionally, whereas we have no reason to suspect that *Uraeotyphlus* is not monophyletic, *Caudacaecilia* and *Ichthyophis* are distinguished only on the basis of the absence or presence of inner mandibular teeth, and *Ichthyophis* was found to be paraphyletic with

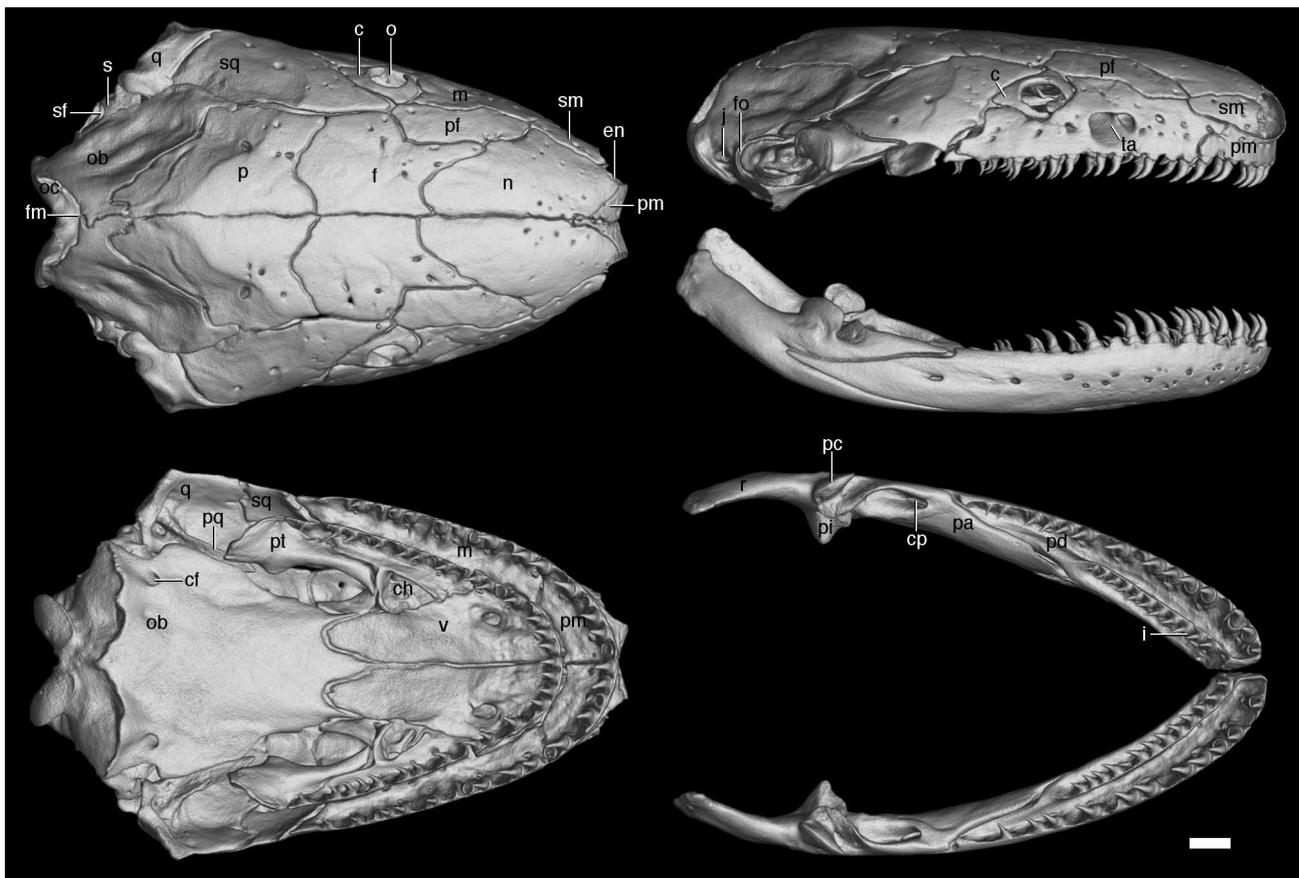


FIGURE 5. Volume reconstruction of HRXCT data showing skull of *Ichthyophis glutinosus* (MW 1773). Views as in Fig.2. Scale bar = 1mm. Scan parameters: a molybdenum target set at 95kV and 190 μ A; scan data were collected at 2.0 frames per second over 3142 projections in 360 $^{\circ}$; reconstructed voxel size of 13 μ m. Abbreviations as in Appendix.

respect to *Caudacaecilia* by Roelants *et al.* (2007). We consider both genera to be in need of revision. Wilkinson & Nussbaum (2006) coined the term Diatriata for "ichthyophiids" + "uraeotyphlids" = Ichthyophiidae, which can now be abandoned as a clade name.

Distribution: South and Southeast Asia.

Content: Three genera and 50 species.

1. *Caudacaecilia* Taylor, 1968

Type species: *Ichthyophis nigroflavus* Taylor, 1960b by original designation.

Diagnosis: The only ichthyophiids lacking inner mandibular teeth.

Distribution: Brunei, Indonesia, Malaysia, Philippines.

Content: five species (*asplenia*, *larutensis*, *nigroflava*, *paucidentula*, *weberi*).

2. *Ichthyophis* Fitzinger, 1826

Type species: *Caecilia glutinosa* Linnaeus, 1758 (Fig. 5) by original monotypy.

Diagnosis: The only ichthyophiids with inner mandibular teeth and tentacular apertures below and intermediate between the eyes and nares.

Distribution: Bangladesh, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Philippines, Sri Lanka, Thailand, Vietnam.

Content: 38 species (*acuminatus*, *alfredii*, *atricollaris*, *bannanicus*, *beddomei*, *bernisi*, *biangularis*, *billitonensis*, *bombayensis*, *daribokensis*, *dulitensis*, *elongatus*, *garoensis*, *glandulosus*, *glutinosus*, *humphreyi*, *husaini*, *hypocyaneus*, *javanicus*, *khumhzi*, *kodaguensis*, *kohtaoensis*, *laosensis*, *longicephalus*, *mindanaoensis*, *monochrous*, *moustakius*, *nokrekensis*, *orthoplicatus*, *paucisulcus*, *pseudangularis*, *sendenyu*, *sikkimensis*, *singaporensis*, *sumatranus*, *supachaii*, *tricolor*, *youngorum*).

3. *Uraeotyphlus* Peters, 1879

Type species: *Coecilia oxyura* Duméril & Bibron, 1841 by subsequent designation of Noble (1924).

Diagnosis: The only ichthyophiids with tentacular apertures far forward, below the nares.

Distribution: India.

Content: Seven species (*malabaricus*, *oxyurus*, *narayani*, *menoni*, *interruptus*, *gansi*, *oommeni*).

V. FAMILY Indotyphlidae Lescure, Renous & Gasc, 1986

Type genus: *Indotyphlus* Taylor, 1960.

Diagnosis: The only caecilians with imperforate stapes, inner mandibular teeth, some teeth bicusped, eye at the border of the squamosal and maxillopalatines, and either viviparity with neither scales nor secondary annuli, or oviparity.

Phylogenetic definition: All caecilians more closely related to *Hypogeophis rostratus* than to *Siphonops annulatus* and/or *Dermophis mexicanus*.

Remarks: With the exception of Frost *et al.* (2006), a clade comprising the "caeciliids" of the Seychelles and India has been found repeatedly in molecular phylogenetic analyses (Wilkinson *et al.*, 2002, 2003; Loader *et al.*, 2007; Roelants *et al.*, 2007; Zhang & Wake, 2009). The phylogenetic definition reflects the fact that the interrelationships of the Dermophiidae, Indotyphlidae and Siphonopidae are currently the least certain of the higher-level phylogenetic relationships of caecilians. The group has no known unambiguous synapomorphies but is readily diagnosed by combinations of characters. We are much less certain of the phylogenetic relationships of the two African genera (*Idiocranium* and *Sylvacaecilia*). These are the only Old World genera of caecilians that have yet to



FIGURE 6. Volume reconstruction of HRXCT data showing skull of *Indotyphlus battersbyi* (AMNH [American Museum of Natural History] 89788). Views as in Fig.2. Scale bar = 1mm. Scan parameters: a molybdenum target set at 70kV and 175 μ A; scan data were collected at 1.0 frames per second over 3142 projections in 360°; reconstructed voxel size of 5 μ m. Abbreviations as in Appendix.

be represented in any molecular phylogenetic study, and we include them within the Indotyphlidae on the basis of their morphological similarity to the Indo-Seychellean species and because it is not easy to produce as simple a diagnosis for only the Indo-Seychelles species (excluding the African taxa). Lescure *et al.* (1986) did not include *Idiocranium*, *Praslinia* or *Sylvacaecilia* in their classification. They placed the included Seychelles genera (*Hypogeophis* and *Grandisonia*) in different Epifamilies, and *Grandisonia* and the Indian genera (*Gegeneophis*, *Indotyphlus*) in separate Infrafamilies, proposing the Tribe Indotyphlini for the Indian genera and the Infrafamily Grandisoniilae for only the genus *Grandisonia*. These are the oldest available family-group names of which we are aware, and we prefer to use the former.

Subsequent workers have followed Taylor (1968) in including the Seychelles caecilian *Hypogeophis brevis* Boulenger, 1911 in *Grandisonia*. Molecular data (Hedges *et al.*, 1993; Zhang & Wake, 2009, Gower *et al.*, 2011) do not convincingly resolve the relationships of *Hypogeophis rostratus* and the species of *Grandisonia*, but do suggest that *Grandisonia sensu* Wilkinson & Nussbaum (2006) is paraphyletic with respect to *Hypogeophis*. Morphological data suggest that *brevis* is the sister species of *Hypogeophis rostratus* (they are the only Seychelles caecilians with strongly projecting snouts, tentacles placed far anterior and tentacular grooves covered with bone) and on that basis we herein return this species to *Hypogeophis*, which facilitates much simpler diagnoses of the genera and might contribute also to resolving the problem of the paraphyly of *Grandisonia*.

We have employed the presence or absence of a bony *eminentia olfactoria* in generic diagnoses within this family. Where present, this process projects from the floor of a nasal cavity and divides partially divides it into medial and longitudinal cavities. The structure is illustrated in, for example, Ramaswamii (1941).

Distribution: Seychelles, India, Africa.

Content: Seven genera, 21 species.

1. *Gegeneophis* Peters, 1879

Type species: *Epicrium carnosum* Beddome, 1870 by original monotypy.

Diagnosis: The only indotyphlids with the eyes covered by bone.

Distribution: India.

Content: 11 species (*carnosus*, *danieli*, *fulleri*, *goensis*, *krishni*, *madhavai*, *mhadeiensis*, *nadkarnii*, *pareshi*, *ramaswamii*, *seshachari*).

2. *Grandisonia* Taylor, 1968

Type species: *Hypogeophis alternans* Stejneger, 1893 by original designation.

Diagnosis: The only indotyphlids with eyes and tentacular grooves not covered by bone, tentacular apertures not adjacent to or above level of eyes, and olfactory chambers partially divided by bony *eminentia olfactoria*.

Distribution: Seychelles.

Content: Three species (*alternans*, *larvata*, *sechellensis*).

3. *Hypogeophis* Peters, 1879

Type species: *Coecilia rostrata* Cuvier, 1829 by subsequent designation of Parker (1958).

Diagnosis: The only indotyphlids with eyes not covered by bone, tentacular grooves covered by bone, and mesethmoid not massively exposed between frontals.

Distribution: Seychelles.

Content: Two species (*brevis*, *rostratus*).

4. *Idiocranium* Parker, 1936

Type species: *Idiocranium russeli* Parker, 1936 by original designation and monotypy.

Diagnosis: The only caecilians with massive exposure of the mesethmoid between the nasals.

Distribution: Cameroon.

Content: One species (*russeli*).

5. *Indotyphlus* Taylor, 1960

Type species: *Indotyphlus battersbyi* Taylor, 1960a (Fig. 6) by original designation and monotypy.

Diagnosis: The only indotyphlids with tentacular apertures close to and slightly above the level of the eye.

Distribution: Seychelles.

Content: Two species (*battersbyi*, *maharashtraensis*).

6. *Praslinia* Boulenger, 1909

Type species: *Praslinia cooperi* Boulenger, 1909 by monotypy.

Diagnosis: The only indotyphlids with the tentacular apertures adjacent to the eyes.

Distribution: Seychelles.

Content: One species (*cooperi*).

7. *Sylvacaecilia* Wake, 1987

Type species: *Geotrypetes grandisonae* Taylor, 1970 by original designation and monotypy.

Diagnosis: The only indotyphlids with eyes and tentacular grooves not covered by bone, tentacular apertures not adjacent to or above the level of the eyes, and olfactory chambers lacking bony *eminentia olfactoria*.

Distribution: Ethiopia.

Content: One species (*grandisonae*).

VI. FAMILY Rhinatrematidae Nussbaum, 1977

Type genus: *Rhinatrema* Duméril & Bibron, 1841.

Diagnosis: The only caecilians with the paired *m. adductores mandibulae externi* extending through the upper temporal fenestra to the mid-dorsum of the cranium.

Phylogenetic definition: All caecilians more closely related to *Rhinatrema bivittatum* than to *Caecilia tentaculata*.

Remarks: The monophyly and distinctiveness of the Rhinatrematidae, and its special status as sister group to all other caecilians, has not been seriously doubted since Nussbaum (1977) reported the substantial differences between the South American and Asian forms that Taylor (1968) had included in his Ichthyophiidae, and partitioned that family. There has been little taxonomic work on *Epicrionops* and no new taxa or synonyms established since Taylor's (1968) monograph. Most of the species are very poorly known and there are no known synapomorphies of the genus. These facts suggest that directed fieldwork and a thorough taxonomic review are merited. Although all three species of *Rhinatrema* share the derived condition of having short tails, monophyly of the genus is uncertain given that the recently described *R. ron* shares some features (large size, plicate palatal mucosa, somewhat longitudinal vent) with some species of *Epicrionops* (Wilkinson & Gower, 2010).

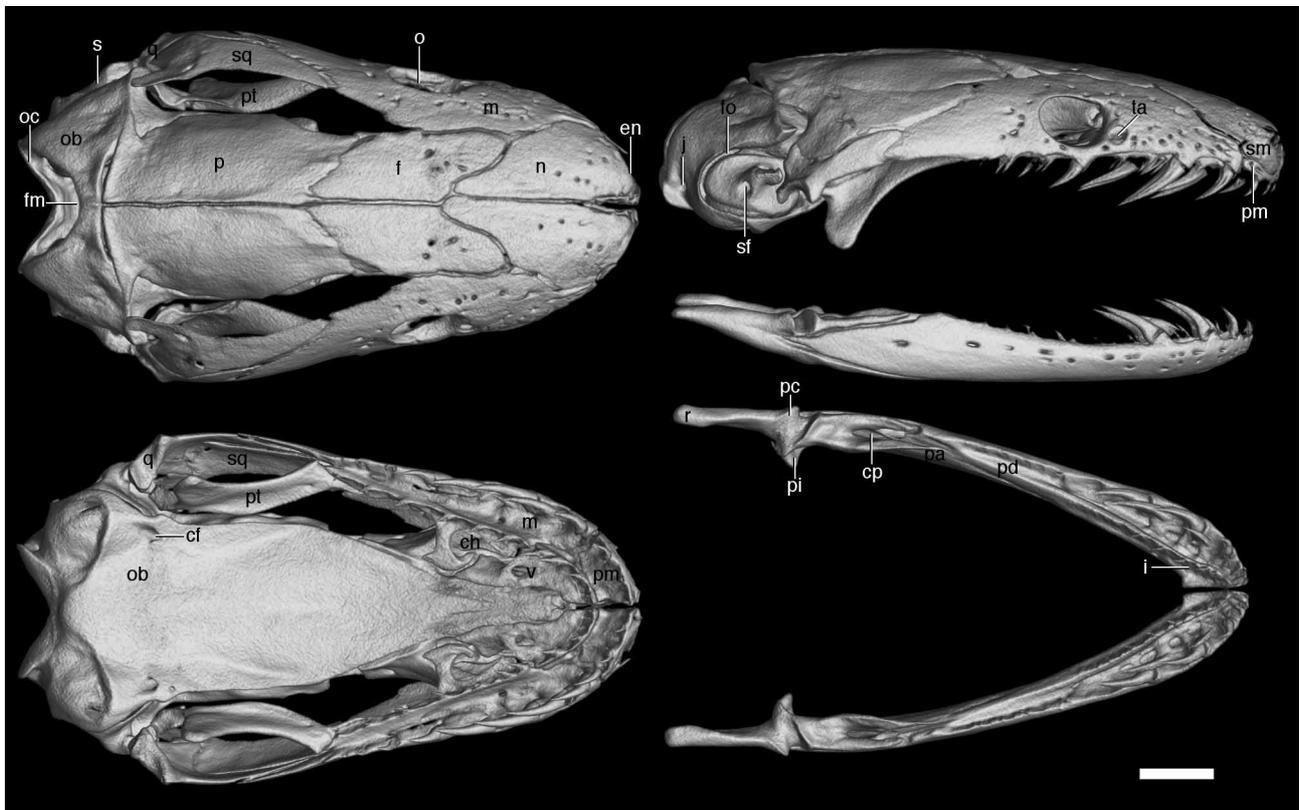


FIGURE 7. Volume reconstruction of HRXCT data showing skull of *Rhinatrema bivittatum* (MW 2051). Views as in Fig.2. Scale bar = 1mm. Scan parameters: a molybdenum target set at 95kV and 190 μ A; scan data were collected at 2.0 frames per second over 3142 projections in 360°; reconstructed voxel size of 10 μ m. Abbreviations as in Appendix.

Distribution: South America.

Content: Two genera, 11 species.

1. *Epicrionops* Boulenger, 1883a.

Type species: *Epicrionops bicolor* Boulenger, 1883a by original monotypy.

Diagnosis: The only rhinatrematids with long tails (more than 10 postcloacal annuli).

Distribution: Colombia, Ecuador, Guyana, Peru, Venezuela.

Content: eight species: (*bicolor*, *colombianus*, *lativittatus*, *marmoratus*, *niger*, *parkeri*, *peruvianus*, *petersi*).

2. *Rhinatrema* Duméril & Bibron, 1841.

Type species: *Caecilia bivittata* Guérin-Méneville, 1838 (Fig. 7) by original monotypy.

Diagnosis: The only rhinatrematids with short tails (fewer than 10 postcloacal annuli).

Distribution: Brazil, French Guiana, Guyana, Suriname.

Content: Three species (*bivittatum*, *shiv*, *ron*).

VII. FAMILY *Scolecophoridae* Taylor, 1969

Type genus: *Scolecophorus* Boulenger, 1883b.

Diagnosis: The only caecilians that lack stapes and *fenestrae ovaes* as adults.

Phylogenetic definition: All caecilians that are more closely related to *Scolecophorus vittatus* than to *Caecilia tentaculata*.

Remarks: In Wilkinson *et al.*'s (2003), Frost *et al.*'s (2006), and Loader *et al.*'s (2007) molecular phylogenetic analyses, and in some trees in Wilkinson's (1997) morphological phylogenetic study (those that included seemingly low quality neuroanatomical data), scolecophorids were nested, without strong support, within the "Caeciliidae" of earlier authors, further adding to the paraphyly of the latter. Other molecular phylogenetic analyses (San Mauro *et al.*, 2004, 2005, 2009; Roelants *et al.* 2007; Zhang & Wake, 2009) have agreed with Nussbaum's (1979) and Wilkinson & Nussbaum's (1995) studies of more traditional morphological data in placing scolecophorids outside "Caeciliidae". We find the latter hypothesis sufficiently compelling to justify removing *Scolecophoridae* from the synonymy of *Caeciliidae*. Monophyly of the family and of its two genera has never been seriously questioned and is supported by available morphological (Nussbaum, 1985) and molecular (Loader *et al.*, 2007; Doherty-Bone *et al.*, 2011) data.

Distribution: Africa.

Content: Two genera, six species.

1. *Crotaphatrema* Nussbaum, 1985

Type species: *Herpele bornmuelleri* Werner, 1899 by original designation.

Diagnosis: The only stegokrotaphic scolecophorids.

Distribution: Cameroon.

Content: Three species (*bornmuelleri*, *lamottei*, *tchabalmbaboensis*).



FIGURE 8. Volume reconstructions of HRXCT data showing cranium of holotype of *Scolecomorphus kirkii* (BMNH 1946.9.5.58) in dorsal, palatal and lateral view and mandible of *Scolecomorphus* cf. *kirkii* (BMNH 2005.1388) in lateral and dorsal view. Scale bar = 1mm. Scan parameters: a molybdenum target set at 120kV and 100 μ A; scan data were collected at 1.4 frames per second over 3142 projections in 360°; reconstructed voxel size of 8 and 9 μ m respectively. Abbreviations as in Appendix.

2. *Scolecomorphus* Boulenger, 1883b

Type species: *Scolecomorphus kirkii* Boulenger, 1883b (Fig. 8) by original monotypy.

Diagnosis: The only zygokrotaphic scolecomorphids.

Distribution: Malawi, Mozambique, Tanzania.

Content: Three species (*kirkii*, *uluguruensis*, *vittatus*).

VIII. FAMILY Siphonopidae Bonaparte, 1850

Type genus: *Siphonops* Wagler, 1828.

Diagnosis: The only oviparous caecilians with imperforate stapes and no inner mandibular teeth.

Phylogenetic definition: All caecilians more closely related to *Siphonops annulatus* than to *Dermophis mexicanus* and/or *Hypogeophis rostratus*.

Remarks: The phylogenetic definition reflects the fact that the interrelationships of the Dermophiidae, Indotyphlidae and Siphonopidae are currently the least certain of the higher-level phylogenetic relationships of caecilians. Compared to Old World taxa, very few of the genera included in this Neotropical family have been included in any phylogenetic analyses. Wilkinson & Nussbaum (1992) used the informal term siphonoforms for the group comprising *Siphonops*, *Mimosiphonops* and *Luetkenotyphlus* which they supposed to be monophyletic based on their substantial overall similarity, including several clearly derived traits such as lack of secondary annular grooves and scales and absence of inner mandibular teeth. Molecular data (San Mauro *et al.*, 2006; Roelants *et al.*, 2007) support the association of *Luetkenotyphlus* and *Siphonops* (*Mimosiphonops* is as yet unsampled), and indi-

cate that *Microcaecilia* is more closely related to *Siphonops* than to any sampled member of any other family recognised here (Roelants *et al.*, 2007; Zhang & Wake, 2009). *Parvicaecilia* and *Brasilotyphlus* and the recently described *Caecilita* remain unsampled in any molecular phylogenetic analyses, and are included here because they appear to resemble *Microcaecilia* more closely than any other genus. Lescure *et al.* (1986) used Siphonopidae for a non-monophyletic subset of "caeciliids" (see Table 1) and attributed the family-group name to Bonaparte (1850), who employed the name Siphonopina for two unspecified American species, probably *Siphonops annulatus* (Mikan, 1820) and *Dermophis mexicanus* (Duméril & Bibron 1841) both of which were included in *Siphonops* at that time.

Distribution: South America.

Content: Seven genera, 19 species.

1. *Brasilotyphlus* Taylor, 1968

Type species: *Gymnopsis braziliensis* Dunn, 1945 by original designation and monotypy.

Diagnosis: The only siphonopids with a diastema between the vomerine and palatine teeth and eyes covered by bone.

Distribution: Brazil.

Content: Two species (*braziliensis*, *guarantanus*).

2. *Caecilita* Wake & Donnelly, 2010

Type species: *Caecilita iwokrama* Wake & Donnelly, 2010 by original designation and monotypy.

Diagnosis: The only caecilians with sealed external nares.

Distribution: Guyana.

Content: One species (*iwokrama*).

3. *Luetkenotyphlus* Taylor, 1968

Type species: *Siphonops brasiliensis* Lütken, 1852 by original designation and monotypy.

Diagnosis: The only siphonopids with short premaxillary-maxillary tooth series (not extending posterior to the choanae), no secondary annuli or scales, and eyes not covered by bone.

Distribution: Brazil.

Content: One species (*brasiliensis*).

4. *Microcaecilia* Taylor, 1968.

Type species: *Dermophis albiceps* Boulenger, 1882 by original designation.

Diagnosis: The only siphonopids with eyes under bone, tentacular apertures closer to the eyes than the nares, and no diastemata between vomerine and palatine teeth.

Distribution: Brazil, Ecuador, French Guiana, Guyana, Suriname, Venezuela.

Content: Seven species (*albiceps*, *grandis*, *iyob*, *rabei*, *supernumeraria*, *taylori*, *unicolor*).

5. *Mimosiphonops* Taylor, 1968

Type species: *Mimosiphonops vermiculatus* Taylor, 1968 by original designation and monotypy.

Diagnosis: The only siphonopids with the tentacular apertures closer to the nares than to the eyes.

Distribution: Brazil.

Content: Two species (*reinhardti*, *vermiculatus*).

6. *Parvicaecilia* Taylor, 1968

Type species: *Gymnopsis nicefori* Barbour, 1924 by original designation.

Diagnosis: The only siphonopids with secondary annuli and scales, eyes not covered by bone, and open external nares.

Distribution: Colombia.

Content: Two species (*nicefori*, *pricei*).

7. *Siphonops* Wagler, 1828

Type species: *Caecilia annulata* Mikán, 1820 (Fig. 9) by original monotypy.

Diagnosis: The only siphonopids with the tentacles closer to the eyes than to the nares, no secondary annuli or scales, no diastemata between vomerine and palatine teeth series, and eyes not under bone.

Distribution: Argentina, Brazil, Colombia, Ecuador, Guyana, Peru, Paraguay, Venezuela.

Content: Five species (*annulatus*, *hardyi*, *insulanus*, *leucoderus*, *paulensis*).

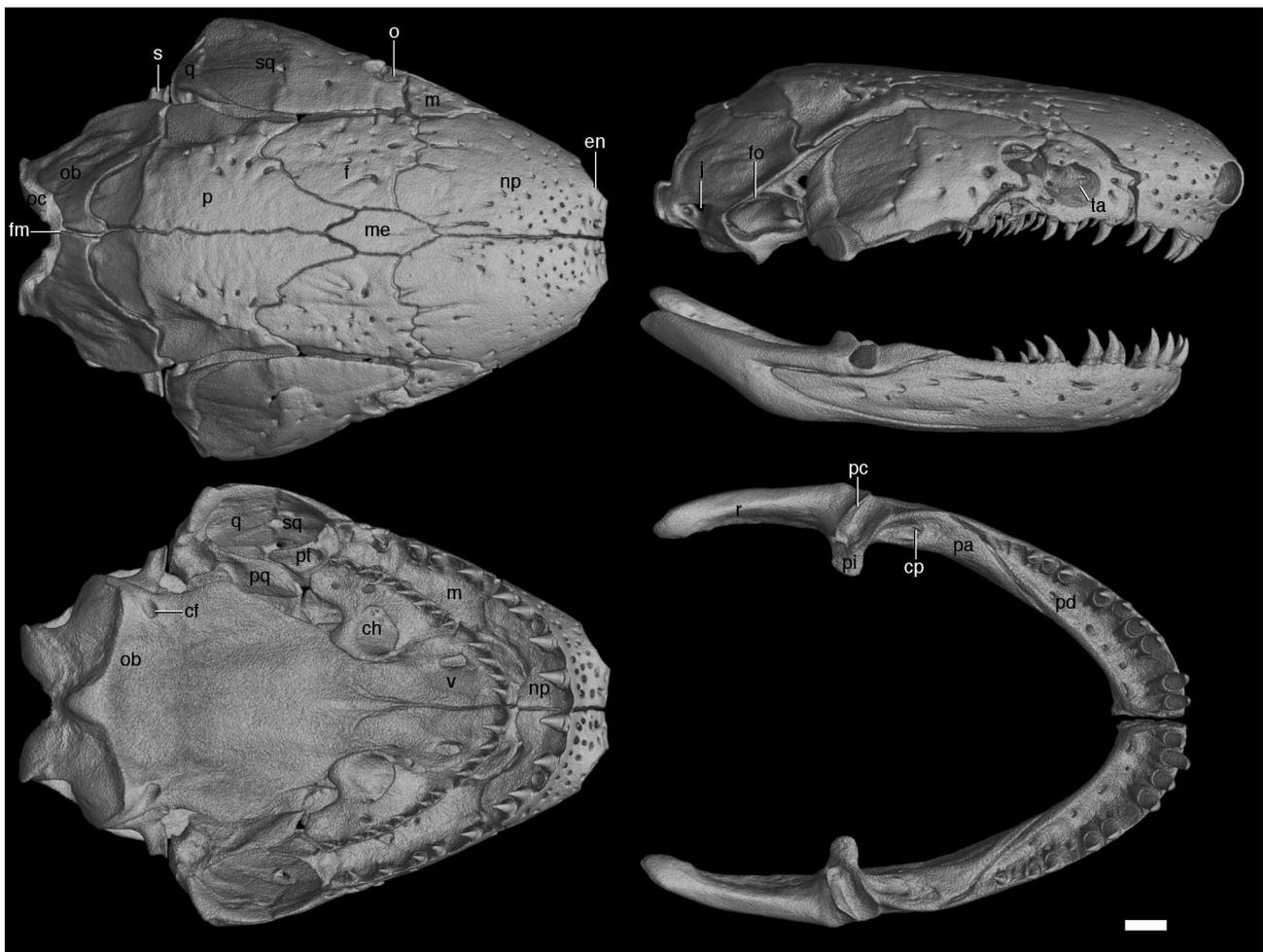


FIGURE 9. Volume reconstruction of HRXCT data showing skull of *Siphonops annulatus* (BMNH 2005.9). Views as in Fig.2. Scale bar = 1mm. Scan parameters: a molybdenum target set at 110kV and 160 μ A; scan data were collected at 2.8 frames per second over 3142 projections in 360°; reconstructed voxel size of 11 μ m. Abbreviations as in Appendix.

IX. FAMILY Typhlonectidae Taylor, 1968

Potamotyphlidae Lescure, Renous & Gasc, 1986

Type genus: *Typhlonectes* Peters, 1879.

Diagnosis: The only caecilians with fused, sheet- or sac-like embryonic gills.

Phylogenetic definition: All caecilians more closely related to *Typhlonectes compressicauda* than to *Caecilia tentaculata*.

Remarks: The Typhlonectidae is one of the better-studied families of caecilians, at least in terms of morphological diversity (Wilkinson, 1989; Wilkinson & Nussbaum, 1997, 1999). Monophyly has never been seriously questioned and is supported by the only relevant molecular phylogenetic study (Roelants *et al.*, 2007) and by many synapomorphies (Wilkinson & Nussbaum, 1999). However, Taylor's (1968) erection of the Typhlonectidae was problematic because it led to "caeciliid" paraphyly, with subsequent workers divided over whether the Typhlonectidae should be synonymised with the Caeciliidae to remove the paraphyly, and used as a subfamilial rank if at all. We prefer to emphasise the distinctiveness of typhlonectids from their closest relatives (*Oscacaecilia* + *Caecilia*) while simultaneously resolving "caeciliid" paraphyly by recognising both sister taxa at the family level.

Distribution: South America.

Content: Five genera, 13 species.

1. *Atretochoana* Nussbaum & Wilkinson, 1995

Type species: *Typhlonectes eiselti* Taylor, 1968 by original designation and monotypy.

Diagnosis: The only typhlonectids without lungs.

Distribution: "South America", probably Brazil.

Content: one species (*eiselti*).

2. *Chthonerpeton* Peters, 1879

Type species: *Siphonops indistinctus* Reinhardt & Lütken, 1861 by original monotypy.

Diagnosis: The only typhlonectids with ovate external nares.

Distribution: Argentina, Brazil, Ecuador, Uruguay.

Content: Eight species (*arii*, *braestrupi*, *exile*, *indistinctum*, *noctinectes*, *onorei*, *perissodus*, *viviparum*).

3. *Nectocaecilia* Taylor, 1968

Type species: *Chthonerpeton petersii* Boulenger, 1882 by original designation.

Diagnosis: The only typhlonectids with subtriangular nares, and lacking fins.

Distribution: Brazil, Venezuela.

Content: One species (*petersii*).

4. *Potomotyphlus* Taylor, 1968

Type species: *Caecilia kaupii* Berthold, 1859 by original designation.

Diagnosis: The only typhlonectids with an anteriorly expanded anal (cloacal) disc.

Distribution: Brazil, Ecuador, French Guiana, Peru, Venezuela.

Content: One species (*kaupii*).

5. *Typhlonectes* Peters, 1879

Type species: *Caecilia compressicauda* Duméril & Bibron, 1841 (Fig. 10) by subsequent designation of Dunn (1942).

Diagnosis: The only typhlonectids with a subcircular anal disc, lungs and fins.

Distribution: Brazil, Colombia, French Guiana, Guyana, Peru, Venezuela.

Content: Two species (*compressicauda*, *natans*).

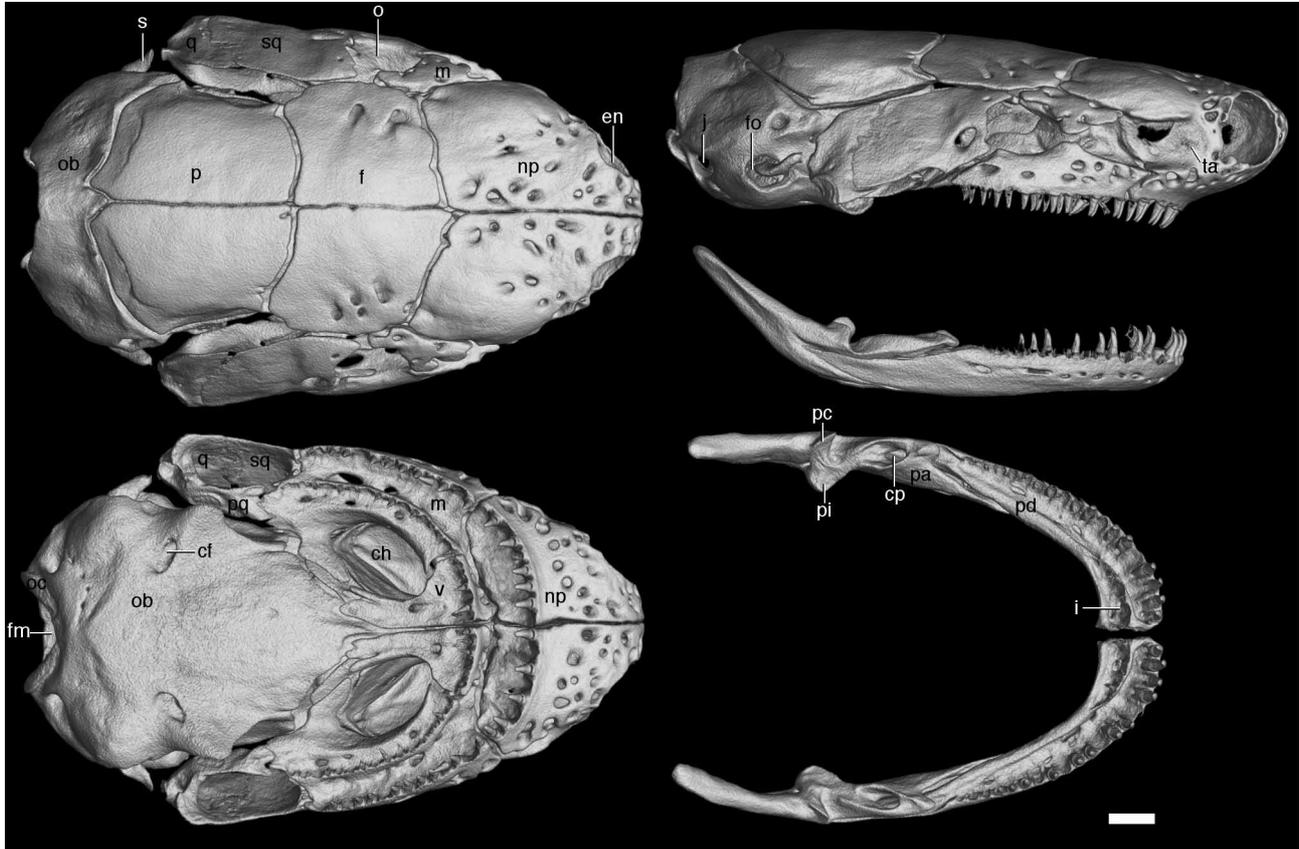


FIGURE 10. Volume reconstruction of HRXCT data showing skull of *Typhlonectes compressicauda* (MW 5820). Views as in Fig.2. Scale bar = 1mm. Scan parameters: a molybdenum target set at 100kV and 155 μ A; scan data were collected at 2.8 frames per second over 3142 projections in 360°; reconstructed voxel size of 12 μ m. Abbreviations as in Appendix.

Discussion

Knowledge of caecilian phylogeny has outpaced caecilian classification in revealing, for example, that some traditional family taxa were not monophyletic, and yet efforts to reconcile the two (i.e., by producing a supraspecific classification of only monophyla) have been limited primarily to acts of synonymy. This, we believe, has been because of a lack of a more detailed understanding of caecilian interrelationships, limited sampling in molecular phylogenetic studies, and a comparable lack of knowledge of morphological diversity. Hedges *et al.*'s (1993) pioneering molecular phylogenetic work provided compelling evidence of "caeciliid" paraphyly with respect to the Typhlonectidae, but included representatives of so few "caeciliid" taxa as to make synonymy the only practical solution (other than temporary acceptance) of "caeciliid" paraphyly. Even here, synonymy simply shifted the problem of paraphyly from the family to the subfamily level without really resolving it, and brought with it another problem: the subfamilial affinities of the vast majority of "caeciliid" taxa that were unsampled, unstudied and/or of uncertain affinities. These problems explain Wilkinson & Nussbaum's (2006) conservative attitude to the acceptance of proposed changes of rank for the Typhlonectidae, and our desire for a more satisfactory solution to "caeciliid" paraphyly than can be achieved by synonymy alone.

Many caecilian taxa remain poorly sampled and their relationships poorly understood. However, sampling for molecular phylogenetic studies has increased, promoting studies able to address both intrageneric and intrafamilial relationships, and the monophyly of some genera. Knowledge of morphology has also advanced, and has recently been boosted by the large-scale application of CT scanning (e.g., Figs. 2–11), which has enhanced our ability to provide familial and generic diagnoses that sometimes depend upon osteology, and increased our confidence that such diagnoses can be reasonably well founded. Molecular phylogenetics has revealed well-supported phylogenetic relationships among a number of ancient caecilian lineages without yet providing a comprehensive genus-level phylogeny. We propose recognition of nine of these ancient lineages as distinct families, each of which is estimated to have originated in the Cretaceous or earlier (Fig. 1). With the exception of Caeciliidae and Typhlonectidae, the caecilian families recognised herein are at least as old as the most ancient families in the two other orders of extant amphibians (Anura and Caudata), according to recent molecular divergence studies (San Mauro *et al.*, 2005; Roelants *et al.*, 2007; San Mauro, 2010). Families Caeciliidae and Typhlonectidae are younger lineages that are at least as old as most families of neobatrachian frogs (San Mauro *et al.*, 2005; Roelants *et al.*, 2007). Given unevenness of sampling and reliance upon morphological data to assign taxa that are as yet unrepresented in any molecular phylogenetic study, the content of some of the families is more certain than others. Of course, the monophyletic status of most of the families and genera of caecilians needs further testing, and the content and diagnoses of suprageneric taxa should be expected to change with the additional sampling and study that is needed. Frost *et al.* (2006) provided a familial level classification of caecilians that relied upon only monophyla but which lumped much caecilian diversity. It has served as a stimulus to our proposal of what we hope will be a usefully more fine-grained classification that also does not depend upon any non-monophyletic groups and which, in turn, we hope will also provide a stimulus to further work.

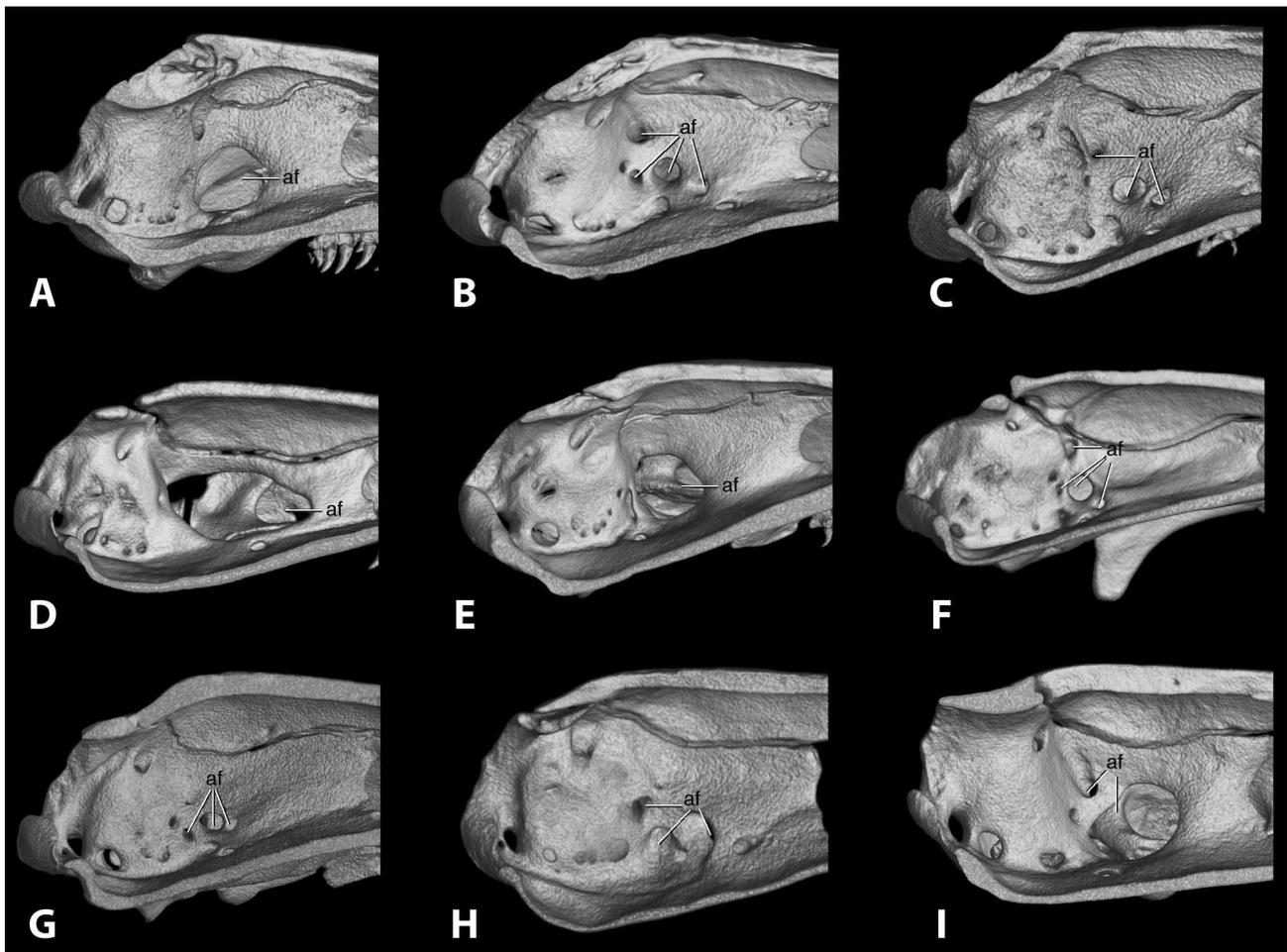


FIGURE 11. Internal views of left-side of braincase showing variation in size and number of antotic foramina of *Caecilia tentaculata* (A), *Dermophis mexicanus* (B), *Herpele squalostoma* (C), *Indotyphlus battersbyi* (D), *Ichthyophis glutinosus* (E), *Rhinatrema bivittatum* (F), *Scolecormorphus kirkii* (G), *Siphonops annulatus* (H), *Typhlonectes compressicauda* (I). Abbreviations as in Appendix.

Acknowledgements

We dedicate this work to Prof. Ronald A. Nussbaum (University of Michigan) in acknowledgement of his pioneering, detailed and scholarly osteological, myological and systematic studies of caecilians and to his training, directly or indirectly, of all of us. ES was supported by Natural Environment Research Council (UK) studentship NE/F009011/1 and thanks Richie Abel for help with HRXCT. DSM was supported by the EU Marie Curie Mobility and Training Programme (FP7, proposal PIEF-GA-2009-237658). We acknowledge the assistance of the numerous individuals who have helped with fieldwork, benchwork, access to collections and sharing of information that have contributed to this work.

References

- Barbour, T. (1924) A new *Gymnophis* [sic] from Colombia. *Proceedings of the Biological Society of Washington*, 37, 125–126.
- Beddome, R.H. (1870) Descriptions of new reptiles from the Madras Presidency. *Madras Monthly Journal of Medical Science*, 2, 169–176.
- Berthold, A.A. (1859) Einige neue Reptilien des Akademie Zoologisches Museums zu Göttingen. *Nachrichten von der Gesellschaften der Wissenschaftlichen zu Göttingen*, 1859(1–20), 179–181.
- Bonaparte, C.L.J.L. (1850) *Conspectus Systematum. Herpetologiae et Amphibiologiae. Editio altera reformata*. Lugdini Bataavorum: E. J. Brill.
- Boulenger, G.A. (1882) *Catalogue of the Batrachia Gradientia s. Caudata and Batrachia Apoda in the Collection of the British Museum* (2nd Ed.), Taylor and Francis, London.
- Boulenger, G.A. (1883a) Description of the new genus of *Coeciliae*. *Annals and Magazine of Natural History*, ser 5(11), 202–203.
- Boulenger, G.A. (1883b) Description of the new genus of *Coeciliae*. *Annals and Magazine of Natural History*, 5(11), 48.
- Boulenger, G.A. (1894) Third report on additions to the batrachian collection in the Natural-History Museum. *Proceedings of the Zoological Society of London*, 1894(4), 640–646.
- Boulenger, G.A. (1909) A list of the freshwater fishes, batrachians, and reptiles obtained by Mr. J. Stanley Gardiner's expedition to the Indian Ocean. *Transactions of the Linnaean Society of London*, 2(12), 291–300.
- Boulenger, G.A. (1911) List of batrachians and reptiles obtained by Prof. Stanley Gardiner on his second expedition to the Seychelles and Aldabra. *Transactions of the Linnaean Society of London*, 2(12), 291–300.
- Cuvier, G. (1829) *Le Règne Animal* (2nd ed), Déterville and Crochard, Paris.
- Doherty-Bone, T.M., Kebuh Ndifon, R., San Mauro, D., Wilkinson, M., LeGrand, G.N. & Gower, D.J. (2011) Systematics and ecology of the caecilian *Crotaphatrema lamottei* (Nussbaum) (Amphibia: Gymnophiona: Scolecomorphidae). *Journal of Natural History*, 45, 827–841.
- Duellman, W.E. & Trueb, L. (1986) *Biology of Amphibians*. McGraw-Hill Book Co., New York.
- Duméril, A.M.C. (1859) Reptiles et poissons de l'Afrique occidentale. Étude précédée de considérations générales sur leur distribution géographique. *Archives du Muséum d'Histoire Naturelle, Paris*, 10, 137–268.
- Duméril, A.M.C. & Bibron, G. (1841) *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles, Vol. 8*. Librairie Encyclopédique de Roret, Paris.
- Dunn, E.R. (1942) The American caecilians. *Bulletin of the Museum of Comparative Zoology, Harvard*, 91, 339–540.
- Dunn, E.R. (1945) A new caecilian of the genus *Gymnopsis* from Brazil. *American Museum Novitates*, 1278, 1.
- Evans S.E. & Sigogneau-Russell, D. (2001) A stem-group caecilian (Lissamphibia: Gymnophiona) from the Lower Cretaceous of North Africa. *Paleontology*, 44, 259–273.
- Fitzinger, L.J. (1826) *Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften nebst einer Verwandtschaftstafel und einem Verzeichnisse der Reptiliensammlungen des K. K. zoologischen Museums zu Wien*. J. G. Heubner, Wien.
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de S. R.O., Channing, A., Wilkinson, M., Donnellan, S.C. Raxworthy, C.J., Campbell, J.A., Blotto, B., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J., Green, D.M. & Wheeler, W.C. (2006) The amphibian tree of life. *Bulletin of the American Museum of Natural History*, 297, 1–370.
- Gower, D.J. & Wilkinson, M. (2009) Gymnophiona. Pp. 369–372 in (S.B. Hedges and S. Kumar, eds) *The Timetree of Life*. Oxford University Press, New York.
- Gower D.J., Kupfer, A., Oommen, O.V., Himstedt, W., Nussbaum, R.A., Loader, S.P., Presswell, B., Müller, H., Krishna, S.B., Boistel, R. & Wilkinson, M. (2002) A molecular phylogeny of ichthyophiid caecilians (Amphibia: Gymnophiona: Ichthyophiidae): out of India or out of South East Asia? *Proceedings of the Royal Society London B*, 269, 1563–1569.
- Gower, D.J., Wilkinson, M., Sherratt, E. & Kok, P.J.R. (2010) A new species of *Rhinatrema* Duméril & Bibron (Amphibia: Gymnophiona: Rhinatrematidae) from Guyana. *Zootaxa*, 2391, 47–60.
- Gower, D.J., San Mauro, D., Giri, V., Bhatta, G., Govindappa, V., Kotharambath, R., Oommen, O.V., Fatih, F.A., Mackenzie-Dodds, J.A., Nussbaum, R.A., Biju, S.D., Shouche, Y.S. & *Wilkinson, M. (2011) Molecular systematics of caeciliid caecilians (Amphibia: Gymnophiona) of the Western Ghats, India. *Molecular Phylogenetics and Evolution* 59, 698–707.

- Guérin-Méneville, M.F.E. (1838) [1829–1844] *Iconographie du Règne Animal de G. Cuvier o représentation d'après nature de l'une des espèces le plus remarquables et souvent non encore figurées, de chaque genre d'animaux. Avec un texte descriptif mis au courant de la science. Ouvrage pouvant servir d'atlas a tous les traités de zoologie. Tome I, Reptiles*. J. B. Baillière, Paris.
- Hedges, S.B., Nussbaum, R.A. & Maxson, L.R. (1993) Caecilian phylogeny and biogeography inferred from mitochondrial DNA sequences of the 12S rRNA 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. Pp. 7–31 in (S.K. Sessions and D.M. Green, eds) *Amphibian Cytogenetics and Evolution*. Academic Press, San Diego.
- Jenkins, F.A. & Walsh, D.M. (1993) An Early Jurassic caecilian with limbs. *Nature*, 365, 246–250.
- Jenkins, F.A., Walsh, D.M. & Carroll, R.L. (2007) Anatomy of *Eocaecilia micropodia*, a limbed caecilian from the early Jurassic. *Bulletin of the Museum of Comparative Zoology, Harvard*, 158, 285–366.
- Laurent, R.F. (1984) Heterogenidad de la familia Caeciliidae (Amphibia-Apoda). *Acta Zoologica Lilloana*, 37, 199–200.
- Laurent, R.F. (1986) Ordre des Gymnophiones. Pp. 595–608. In P.-P. Grass and M. Delsol (eds), *Trait de Zoologie, Vol 14, Amphibiens*, Masson, Paris, France.
- Lescure, J., Renous, S. & Gasc, J.-P. (1986) Proposition d'une nouvelle classification des amphibiens gymnophiones. *Mémoires de la Société Zoologique de France*, 43, 145–177.
- Linnaeus, C. (1758) *Systema Naturae* (10th Ed), Laurentii Salva, Holmiae.
- Loader, S.P., Pisani, D., Cotton, J.A., Gower, D.J., Day, J.J. & Wilkinson, M. (2007) Relative timescales reveal multiple origins of parallel disjunct distributions of African caecilian amphibians. *Biology Letters*, 3, 505–508.
- Mikan, J.C. (1820) *Delectus florum et faunae Brasiliensis*. Title page, dedication, preface, and 24 plates all unnumbered. J. C. Mikan, Vindobonae.
- Müller, J. (1832) Beiträge zur Anatomie und Naturgeschichte der Amphibien. *Zeitschrift für Physiologie*, 4, 190–275.
- Noble, G.K. (1924) Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition 1909-1915. Part III. Amphibia: with abstracts from the field notes of Herbert Lang and James P. Chapin. *Bulletin of the American Museum of Natural History*, 49, 147–347.
- 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 caecilians (Amphibia: Gymnophiona) of the family Scolecomorphidae. *Occasional Papers of the Museum of Zoology, University of Michigan*, 713, 1–49.
- Nussbaum, R.A. (1988) On the status of *Copeotyphlinus syntremus*, *Gymnopsis oligozona*, and *Minascaecilia sartoria* (Gymnophiona: Caeciliidae): A comedy of errors. *Copeia*, 1988, 921–928.
- Nussbaum, R.A. & Wilkinson, M. (1989) On the classification and phylogeny of caecilians (Amphibia: Gymnophiona), a critical review. *Herpetological Monographs*, 3, 1–42.
- Nussbaum, R.A. & Wilkinson, M. (1995) A new genus of lungless tetrapod: a radically divergent caecilian (Amphibia: Gymnophiona). *Proceedings of the Royal Society of London B*, 261, 331–335.
- Parker, H.W. (1936) The amphibians of the Mamfe Division, Cameroons (1) Zoogeography and systematics. *Proceedings of the Zoological Society of London*, 1, 64–163.
- Parker, H.W. (1941) The caecilians of the Seychelles. *Annals and Magazine of Natural History*, 11(7), 1–17.
- Parker, H.W. (1958) Caecilians of the Seychelles Islands with description of a new species. *Copeia*, 1958, 71–17.
- Peters, W. (1874) Über neue Amphibien (*Gymnopsis*, *Siphonops*, *Polypedates*, *Rhacophorus*, *Hyla*, *Cyclodus*, *Euprepes*, *Clemmys*). *Monatsbericht der Deutschen Akademie der Wissenschaften zu Berlin*, 1874, 616–624.
- Peters, W. (1879) Über die Eintheilung der Caecilien und insbesondere über die Gattungen *Rhinatrema* und *Gymnopsis* *Monatsbericht der Deutschen Akademie der Wissenschaften zu Berlin*, 1879, 924–943.
- Peters, W. (1880) Über Schädel von zwei Coecilien *Hypogeophis rostratus* und *Hypogeophis seraphini*. *Sitzung Bericht Geschichte Naturforschung Frankfurt*, 1880, 53–55.
- Pillai, R.S. & Ravichandran, M.S. (1999) Gymnophiona (Amphibia) of India a taxonomic study. *Records of the Zoological Survey of India Occasional Papers*, 172, 1–117.
- Rafinesque, C.S. (1814) Fine del Prodromo d'Erpetologia Siciliana. *Specchio delle Scienze o Giornale Enciclopedico di Sicilia, Palermo*, 2, 102–104.
- Ramaswami LS. (1941). Some aspects of the cranial morphology of *Uraeotyphlus narayani* Seshachar (Apoda). *Records of the Indian Museum*, 43, 143–207.
- Reinhardt, J.T. & Lütken, C.F. (1861) Bidrag til kundskab om Brasiliens Padder og Krybdyr. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening Kjobenhaun*, 1861(10–15), 143–242.
- Roelants, K., Gower, D.J., Wilkinson, M., Loader, S.P., Biju, S.D., Guillaume, K. & Bossuyt, F. (2007) Patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences*, 104, 887–892.
- San Mauro, D. (2010) A multilocus timescale for the origin of extant amphibians. *Molecular Phylogenetics and Evolution*, 56, 554–561.
- San Mauro, D., Gower, D.J., Oommen, O.V., Wilkinson, M. & Zardoya, R. (2004) Phylogeny of caecilian amphibians (Gymnophiona) based on complete mitochondrial genomes and nuclear 1. *Molecular Phylogenetics and Evolution*, 33, 413–427.
- San Mauro, D., Vences, M., Alcobendas, M., Zardoya, R. & Meyer, A. (2005) Initial diversification of living amphibians pre-

- dated the breakup of Pangaea. *American Naturalist*, 165, 590–599.
- San Mauro, D., Gower, D.J., Zardoya, R. & Wilkinson, M. (2006) A hotspot of gene order rearrangement by tandem duplication and random loss in the vertebrate mitochondrial genome. *Molecular Biology and Evolution*, 23, 227–234.
- San Mauro, D., Gower D.J., Massingham, T., Wilkinson, M., Zardoya, R. & Cotton, J.A. (2009) Experimental design in caecilian systematics: phylogenetic information of mitochondrial genomes and nuclear *rag1*. *Systematic Biology*, 58, 425–438.
- Stejneger, L. (1893) On some collections of reptiles and batrachians from East Africa and the adjacent islands, recently received from Dr. W. L. Abbott and Mr. William Astor Chanler, with descriptions of new species. *Proceedings of the United States National Museum*, 16, 711–741.
- Stutchbury, I. (1834) Description of a new species of the genus of the genus *Chamaeleon*. *Transactions of the Linnaean Society of London*, 1(17), 362.
- Taylor, E.H. (1960a) A new caecilian genus in India. *University of Kansas Science Bulletin*, 40, 31–36.
- Taylor, E.H. (1960b) On the caecilian species *Ichthyophis monochrous* and *Ichthyophis glutinosus* and related species. *University of Kansas Science Bulletin*, 40, 37–120.
- Taylor, E.H. (1968) *The caecilians of the World*. University of Kansas Press, Lawrence, Kansas.
- Taylor, E.H. (1969) A new family of African Gymnophiona. *University of Kansas Science Bulletin*, 48, 297–305.
- Taylor, E.H. (1970) A new caecilian from Ethiopia. *University of Kansas Science Bulletin*, 48, 849–854.
- Tornier, G. (1896) (1897) Die Kriechtiere Deutsch-Ost-Afrikas. Beiträge zur Systematik und Descendenzlehre, Reimer, Berlin.
- Wagler, J. (1828) Auszüge aus seinem Systema Amphibiorum. *Isis, von Oken*, 21, 740–744.
- Wake, M.H. (1987) A new genus of African caecilian (Amphibia: Gymnophiona). *Journal of Herpetology*, 21, 6–15.
- Wake, M.H. & Campbell, J.A. (1983) A new genus and species of caecilian from the Sierra de las Minas of Guatemala. *Copeia*, 1983, 857–863.
- Wake, M.H. & Donnelly, M.A. (2010) A new lungless caecilian (Amphibia: Gymnophiona) from Guyana. *Proceedings of the Royal Society of London B*, 227 (1683), 915–922.
- Werner, F. (1899) Ueber Reptilien und Batrachier aus Togoland, Kamerun, und Deutsch-Neu-Guinea, Grössenteils aus dem K. Museum für Naturkunde in Berlin. *Verhandlungen Zoologische-Botanische Gesellschaft in Wien*, 49, 132–157.
- Wilkinson, M. (1989) On the status of *Nectocaecilia fasciata* Taylor, with a discussion of the phylogeny of the Typhlonectidae (Amphibia: Gymnophiona). *Herpetologica*, 45, 23–36.
- Wilkinson, M. (1997) Characters, congruence and quality: a study of neuroanatomical and traditional data in caecilian phylogeny. *Biological Reviews*, 72, 423–470.
- Wilkinson, M., Loader, S.P., Gower, D.J., Sheps, J.A. & Cohen, B.L. (2003) Phylogenetic relationships of African caecilians (Amphibia: Gymnophiona): insights from mitochondrial rRNA gene sequences. *African Journal of Herpetology*, 52, 83–92.
- Wilkinson, M. & Nussbaum, R.A. (1992) Taxonomic status of *Pseudosiphonops ptychodermis* Taylor and *Mimosiphonops vermiculatus* Taylor (Amphibia: Gymnophiona: Caeciliidae), with description of a new species. *Journal of Natural History*, 26, 675–688.
- Wilkinson, M. & Nussbaum, R.A. (1996) On the phylogenetic position of the Uraeotyphlidae (Amphibia: Gymnophiona). *Copeia*, 1996, 550–562.
- Wilkinson, M. & Nussbaum, R.A. (1997) Comparative morphology and evolution of the lungless caecilian *Atretochoana eiselti* (Taylor) (Amphibia: Gymnophiona: Typhlonectidae). *Biological Journal of the Linnean Society*, 62, 39–109.
- Wilkinson, M. & Nussbaum, R.A. (1999) Evolutionary relationships of the lungless caecilian *Atretochoana eiselti* (Amphibia: Gymnophiona: Typhlonectidae). *Zoological Journal of the Linnean Society*, 126, 191–123.
- Wilkinson, M. & Nussbaum, R.A. (2006) Caecilian phylogeny and classification. Pp. 39–78 in (J.-M. Exbrayat, ed.) *Reproductive Biology and Phylogeny of Gymnophiona (caecilians)*. Science Publishers, Inc., Enfield, New Hampshire, U.S.A.
- Wilkinson, M., Oommen, O.V., Sheps, J.A. & Cohen, B.L. (2002) Phylogenetic relationships of Indian caecilians (Amphibia: Gymnophiona) inferred from mitochondrial rRNA gene sequences. *Molecular Phylogenetics and Evolution*, 23, 401–407.
- Zhang, P. & Wake, M.H. (2009) A mitogenomic perspective on the phylogeny and biogeography of living caecilians (Amphibia: Gymnophiona). *Molecular Phylogenetics and Evolution*, 53, 479–491.

APPENDIX. Abbreviations of osteological features used in Figures 2-11.

af—antorbital fenestra	p—parietal
c—circumorbital bone (= postfrontal of some authors)	pa—pseudoarticular
cf—carotid foramen	pc—processus condyloides of the pseudoarticular
ch—choana	pd—pseudodentary
cp—canalis primordialis	pf—prefrontal
en—external naris	pi—processus internus of the pseudoarticular
f—frontal	pm—premaxilla
fm—foramen magnum	pq—pterygoid process of the quadrate
fo—foramen ovalis	pt—pterygoid
i—inner mandibular tooth series	q—quadrate
j—jugular foramen	r—retroarticular process of the pseudoangular
m—maxillopalatine	s—stapes
me—mesethmoid	sf—stapedial foramen
n—nasal	sm—septomaxilla
np—nasopremaxilla	sq—squamosal
ob—os basale	ta—tentacular aperture
oc—occipital condyle	v—vo mer
o—orbit	