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Caecilian Phylogeny and Classification

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2.1 INTRODUCTION

Fifteen years ago, we published a critical review of caecilian phylogeny and classification (Nussbaum and Wilkinson 1989). We hoped to establish some stability in caecilian classification in the face of some highly divergent phylogenetic hypotheses and alternative taxonomic treatments (Wake and Campbell 1983; Duellman and Trueb 1986; Lescure *et al.* 1986; Laurent 1986). We concluded that caecilian phylogeny was too poorly known to provide the basis for a working phylogenetic classification that recognized only well-founded monophyletic groups. Instead, we provided an interim, conservative classification in which 154 nominate species were partitioned into six families with no sub- or suprafamilial ranks other than 34 genera. Up until 1968, all caecilians were placed into a single family, the Caeciliidae, and we recognized that the subsequent removal of distinctive subsets of species in the establishment of additional families had left the Caeciliidae a most likely paraphyletic assemblage of caecilians that did not fit into one of the better circumscribed families. This is reflected in the relative numbers of taxa: well over half of all recognized caecilian species and genera are caeciliids.

Some important milestones have appeared over the last 15 years in caecilian phylogenetics. Since our previous review, the first phylogenetic study of the interrelationships of caecilians based on DNA sequence data was published. Hedges *et al.* (1993) analyzed partial 16S and 12S mt rDNA sequences for 13 caecilian species in 9 genera, including members of four of the family-level taxa recognized in our 1989 classification. Recently, the taxonomic coverage for these molecular markers has begun to expand, so that comparative sequence data are now available for 23 species, 16 genera

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□ This work is dedicated to the memories of John Eric Wilkinson and Annie Wilkinson.

and for representatives of all six families (Wilkinson *et al.* 2002; 2003b). Gower *et al.* (2002), in a study focusing on ichthyophiid caecilians, demonstrated the potential for sequence data from ribosomal and protein coding (cytochrome B) mt DNA to help resolve low level taxonomic problems when the taxonomic sampling is sufficiently dense, and Gower *et al.* (2005) tentatively identified an undescribed cryptic species of Sri Lankan *Ichthyophis* using molecular data. Recently, San Mauro *et al.* (2004) addressed relationships among single representatives of each of the six families with a combination of complete mitochondrial genomes and RAG-1 nuclear gene sequences.

Morphological data sets have also been expanded in terms of taxa and through the discovery of additional characters, and previously assembled data have been critically reviewed and revised to reduce errors (Naylor and Nussbaum 1980; Nussbaum and Naylor 1982; Scheltinga *et al.* 2003, see also Chapter 7 of this volume; Wilkinson and Nussbaum 1996; Wilkinson 1996, 1997). There have also been a few phylogenetic studies of monophyletic subgroups at the genus- or species-level using morphological data (Nussbaum and Hinkel 1994; Wilkinson and Nussbaum 1999; Wilkinson *et al.* 2004).

In our 1989 classification, we provided diagnoses of caeciliid genera based on a core set of characters. Although each genus was understood to have a unique combination of characters, uniquely derived characters supporting the monophyly of most caeciliid genera were simply unknown, and knowledge of the diversity within the more speciose nominate genera was limited to one or a few species. Since 1989, a single genus and 16 species (one of which we consider invalid) have been newly described, and 5 species have been removed from synonymy. In the same period, two genera and 5 species have been lost to synonymy (in addition to those we excluded from our treatment and subsequently synonymized). Little else has changed, and the limited low-level taxonomic activity belies the fact that taxonomy at the species- and genus-level remains in need of careful study and stabilisation. The new genus, *Atretochoana* was established to receive a single species of typhlonectid caecilian with a radically divergent morphology discovered in the course of routine taxonomic work (Nussbaum and Wilkinson 1995). *Atretochoana* is the largest lungless tetrapod and the only known lungless caecilian, and it possesses many unique features associated with a novel cranial architecture (Wilkinson and Nussbaum 1997). Its discovery represents a substantial increase in the perceived diversity of caecilians, and of tetrapods (Donoghue and Alverson 2000), and it serves to emphasise the limited knowledge of caecilian biodiversity.

Overall, taxonomic coverage has remained patchy in both morphological and molecular phylogenetic studies. Consequently, even where inferred relationships for the subset of sampled taxa are well-supported, they are not readily translated into a phylogenetic classification of the entire Order. This is exacerbated by the low-level taxonomic

uncertainties that are currently a major obstacle to progress in caecilian systematics and for caecilian biology more generally. However, some phylogenetic relationships have been confidently established, some more tentatively so, and, importantly, we have a clearer picture of what remains to be done. In this chapter, we present an overview of current understanding of caecilian phylogeny and an update of our 1989 classification.

2.2 CAECILIAN PHYLOGENY

Caecilians constitute one of three extant orders of the amphibian subclass Lissamphibia, which includes all of the extant Amphibia. The caecilians, frogs and toads, salamanders and newts are generally believed to comprise a monophyletic group based on a variety of presumed shared, derived character states such as smooth (externally scaleless) epidermis and the presence of gonadal fat bodies (e.g., Parsons and Williams 1963). That Lissamphibia is monophyletic with respect to extant taxa is strongly supported by molecular data which also tend to support either a sister group relationship between caecilians and salamanders or between caecilians and salamanders plus frogs (e.g., Feller and Hedges 1998; San Mauro *et al.* 2004). However, various hypotheses of polyphyletic origins of the three orders from different fossil taxa have been proposed, and monophyly with respect to several extinct groups of Amphibia is far from uniformly accepted (e.g., Milner 1993; Schoch and Milner 2004).

Regardless of origins and relationships, the three extant orders (Gymnophiona = caecilians; Caudata = salamanders; Anura = frogs) are readily distinguished. Many derived characteristics unambiguously identify all species of Gymnophiona (see Diagnosis below) including the presence of a unique, dual, jaw-closing mechanism (Nussbaum 1977, 1983; Fig. 2.1). The presence of paired tentacular sensory organs on the snout on the edges of, or anterior to, the eyes is unique and can be readily determined with a hand lens even for very small specimens, although in some taxa they become apparent only at or close to metamorphosis and they are not present in larvae. Of course, caecilians also have characteristically elongate, snake-like bodies and completely lack limbs or girdles.

In 1989 we considered caecilian phylogeny to be poorly understood but not completely unknown. Nussbaum (1977, 1979, 1985) had provided good morphological support for the monophyly of two families, the Rhinatrematidae and Scolecomorphidae, and for two hypotheses of interfamilial relationships: that the Rhinatrematidae is the sister taxon of all other caecilians, and that the Scolecomorphidae, Typhlonectidae and Caeciliidae comprise a monophyletic group. We also accepted the monophyly of the Typhlonectidae and had a fairly well-supported phylogeny for the four then recognised typhlonectid genera (Wilkinson 1989). We considered the caeciliids of the Seychelles archipelago to be a

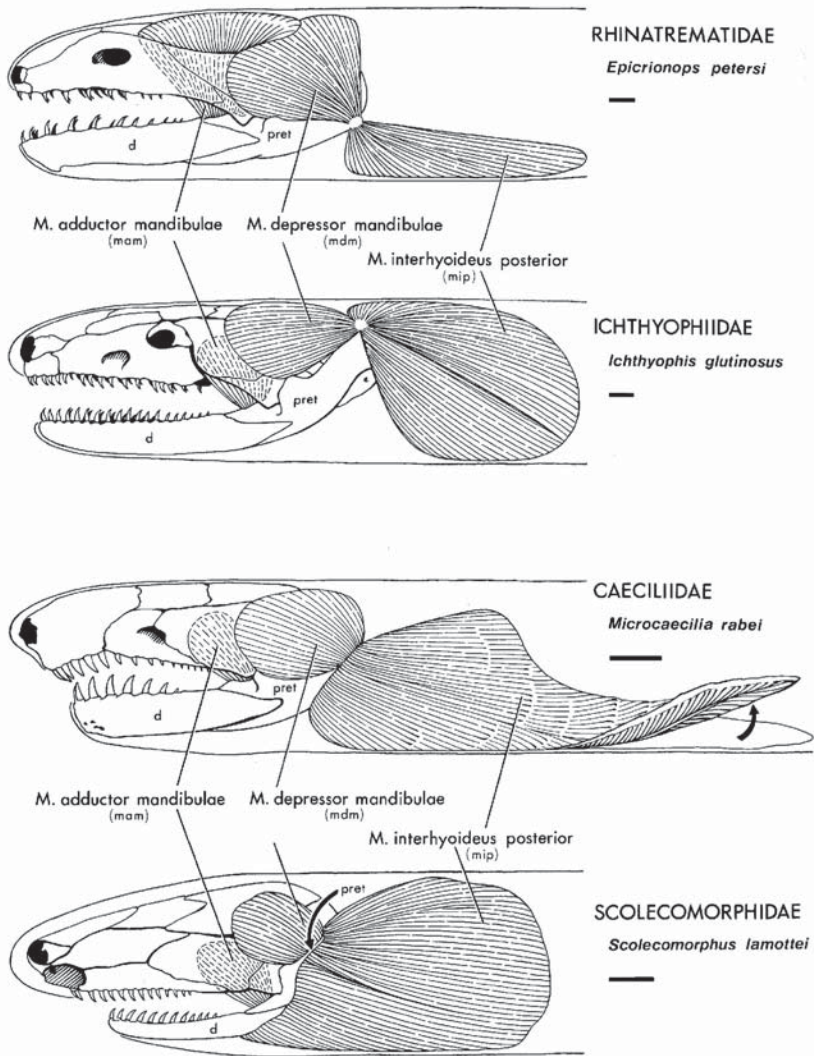


Fig. 2.1. Uniquely derived, dual jaw-closing mechanism, which is diagnostic of caecilians (Nussbaum 1977). The two parts consist of the ancestral jaw-closing mechanism, common to all vertebrates, and a novel component. In the ancestral mechanism, the *m. adductor mandibulae (mam)* pulls up on the lower jaw (*d*, dentary) in front of the articulation of the lower jaw with the skull. In the novel component, the *m. interhyoideus posterior (mip)* pulls down on a process of the dentary (*pret*, or *processus retroarticularis*) that projects posteriorly from the jaw articulation, causing the lower jaw to swing up. The *mip*, normally a throat constrictor, takes on a new function of jaw-closing in caecilians. The *m. depressor mandibulae (mdm)* serves to open the jaws in all caecilians by pulling up on the *pret*. Rhinatrematids have the presumed ancestral condition in which the ancestral jaw-closing mechanism dominates. Ichthyophiids, caeciliids, and scolecomorphids demonstrate progressively increased dominance of the novel component. The lower jaw becomes progressively shorter and the *pret* progressively longer and more curved dorsally in the same evolutionary sequence. The horizontal bar = 1 mm. Adapted from Nussbaum, R. A. 1983. *Journal of Zoology*, London 199: 545-554, Fig. 2.

monophyletic group on the basis of cytogenetic data (Nussbaum and Ducey 1988); and we considered some pairs of caeciliid genera, such as the East African *Afrocaecilia* and *Boulengerula*, Central American *Dermophis* and *Gymnopsis*, and South American *Caecilia* and *Oscaecilia*, to be obviously closely related.

In this section we review current understanding of caecilian phylogeny. Where possible we identify uniquely derived features that unambiguously support hypothesised monophyletic groups of caecilians. Note that inferred relationships of families and of genera that are not monotypic are mostly based on observations of only a subset of the constituent species. Detailed morphological observations and molecular data are lacking for the vast majority of caecilian species. Thus, where we list uniquely derived features supporting the monophyly of a particular group, we do so with the strong caveat that these features may be unknown for some or most of the included species. The relationships we discuss are summarised in Figure 2.2

2.2.1 Rhinatrematidae

Nussbaum (1977) listed six uniquely derived features that support the monophyly of the Rhinatrematidae, a small Neotropical family including the two genera *Rhinatrema* and *Epicrionops* and nine recognised species. Most distinctive of the supporting conditions is the presence of a posterior notch in the squamosal that accommodates a distinct process of the *os basale*. Apart from the lack of a distinct basipterygoid process, Nussbaum's (1977) other derived features of rhinatrematids, the reduction or absence of ceratobranchials 2 and 3; the larynx posterior to the glossal skeleton; and the absence of the *musculus subarcualis rectus* II and III, all relate to the reduction of the posterior hyobranchial apparatus and are unlikely to be completely independent. A *musculus subarcualis rectus* II is now known to be absent in typhlonectids also, although in typhlonectids its absence is associated with the elaboration, rather than reduction, of the buccopharyngeal pump (Wilkinson and Nussbaum 1997), and is surely convergent with the condition in rhinatrematids. Wilkinson (1996) identified two derived cardiovascular features that also support rhinatrematid monophyly, namely the partial division of the normally undivided sinuatrial aperture and the left pulmonary artery supplying the oesophagus rather than the left lung.

None of these features has been documented in all the currently recognised rhinatrematid species, most of which remain unstudied in any detail, but most have been documented for the monotypic *Rhinatrema* and for one or more species of *Epicrionops*. Based on the general similarity of all known rhinatrematids, we do not expect these morphological features to vary much within the family. Rhinatrematid sampling in Wilkinson's (1997) morphological phylogenetic analysis and in the molecular study of Gower *et al.* (2002) was limited to only two species of *Epicrionops* in the former and one *Epicrionops* and the monotypic *Rhinatrema* in the latter. In both analyses, the results were consistent with rhinatrematid monophyly, and the

separation of the rhinatrematids from all other caecilians was well supported. Phylogenetic relationships within the Rhinatrematidae are as yet unstudied. *Epicrionops* differ from *Rhinatrema* primarily in having a longer tail with well-developed haemal arches, a more longitudinal vent, and in retaining a small ceratobranchial 3, all of which are probably ancestral character states. Derived features that support the monophyly of *Epicrionops* are currently unknown.

2.2.2 Non-rhinatrematids — Neocaecilia

The discredited phylogenies of Laurent (1986) and Lescure *et al.* (1986) notwithstanding, since Nussbaum's (1977, 1979) pioneering morphological phylogenetic studies, the basal split in the caecilian tree has been thought to be between the rhinatrematids and all other caecilians. Nussbaum (1977) identified 13 morphological features of rhinatrematids that he considered ancestral and unique within caecilians, with the corresponding derived character states supporting the monophyly of all non-rhinatrematid caecilians. Of these, we currently view five as uniquely derived: sides of parasphenoid converge anteriorly; no contact between quadrate and maxillopalatine; long and recurved retroarticular processes; *musculus interhyoideus posterior* has no insertion on the ceratohyal; and *musculi adductores mandibulae externi* do not meet mid-dorsally. The presence of two rows of trunk neuromasts in larvae is interpreted as an additional unique and ancestral feature of rhinatrematids (Wilkinson 1992a), and Wilkinson (1996) identified five uniquely derived cardiovascular features that also support the monophyly of the non-rhinatrematids: ventricle relatively narrow and elongate; a bipartite *sinus venosus*; *conus arteriosus* not bent to the left; an elongate *truncus arteriosus*; and common systemicocarotid arteries.

Until recently, molecular data have been mostly consistent with, but had not provided compelling support for, the basal split between rhinatrematids and all other caecilians (Hedges *et al.* 1993). Most recent analyses, both morphological (Wilkinson and Nussbaum 1996; Wilkinson 1997) and molecular (Gower *et al.* 2002; Wilkinson *et al.* 2002, 2003b) have assumed that the Rhinatrematidae is the sister group of all other caecilians in order to root the caecilian tree and have not provided any further test of this hypothesis. Although taxon sampling is limited, the extensive mitochondrial and nuclear gene data of San Mauro *et al.* (2004) provide very strong support for non-rhinatrematid monophyly, and we consider it to be a very well supported hypothesis on the basis of diverse morphological and molecular data.

Canatella and Hillis (1993) coined the term Stegokrotaphia for the clade including all non-rhinatrematids. However, this name belies a great diversity of zygotrophaphic scolecomorphids, caeciliids and typhlonectids within the group. For this reason we prefer the anatomically neutral Neocaecilia as a rankless epithet for the suprafamilial clade including all

caecilians with jaw-closing muscles that do not extend onto the top of the skull from the adductor chamber.

2.2.3 Ichthyophiidae

The Ichthyophiidae comprises some 39 species in the two genera *Caudacaecilia* and *Ichthyophis*. *Caudacaecilia* is restricted to South East Asia whereas *Ichthyophis* also has representatives in South Asia. In Nussbaum's (1979) analyses, *Caudacaecilia* and Ichthyophiidae were closely related, but lacked any uniquely derived features that supported their monophyly. In fact, despite the external similarity of all ichthyophiids, and practical difficulty of distinguishing ichthyophiid species (Nussbaum and Gans 1980), only a single feature that supports ichthyophiid monophyly has been reported previously, the presence of angulate annuli on the anteroventral surface (Nussbaum 1977; Wilkinson and Nussbaum 1996). An additional supporting derived feature, a short parasphenoid that does not extend as far anteriorly as the posterior margin of the choanae, is characteristic of all ichthyophiid skulls and of no non-ichthyophiid skulls that we have examined.

Wilkinson (1997) and Wilkinson *et al.* (2002) both recovered the very few ichthyophiids included in their morphological and molecular phylogenetic analyses (three and two species of *Ichthyophis* respectively) as a reasonably well-supported monophyletic group. In contrast, the molecular study of Gower *et al.* (2002) included a broader range of *Ichthyophis* species and yielded optimal trees in which the Ichthyophiidae is paraphyletic with respect to the Uraeotyphlidae. Although this result was not significantly better supported than alternative trees in which the Ichthyophiidae is monophyletic, and thus does not justify any taxonomic changes at this time, it raises the possibility of ichthyophiid parphyly and indicates the need for further phylogenetic study and additional character data. Phylogenetic relationships among ichthyophiids are poorly understood, but Gower *et al.* (2002) suggested that the *Ichthyophis* of Sri Lanka, and those of South East Asia comprise distinct monophyletic groups (see also Bossuyt *et al.* 2004; Gower *et al.* 2005). All recent work supports the idea that the ichthyophiids were present on the Indian plate prior to its collision with Laurasia, and that South East Asian ichthyophiids result from one or more dispersals out of India (Gower *et al.* 2002; Wilkinson *et al.* 2002).

Caudacaecilia and *Ichthyophis* are differentiated by the absence or presence of splenial teeth in adults respectively. Absence of splenial teeth is considered derived within caecilians (Nussbaum 1979) but appears to be quite homoplastic (Nussbaum and Wilkinson 1989). Thus there is only very weak evidence known to support the monophyly of *Caudacaecilia*, no known derived features supporting the monophyly of *Ichthyophis*, and a strong possibility that *Ichthyophis* is paraphyletic with respect to *Caudacaecilia*. No *Caudacaecilia* have been included in any numerical phylogenetic analysis since Nussbaum (1979).

2.2.4 Uraeotyphlidae

The genus *Uraeotyphlus* comprises five nominate species from southern peninsular India. The genus was included in the Caeciliidae by Taylor (1968, 1969) but transferred to its own subfamily within the Ichthyophiidae by Nussbaum (1979). Duellman and Trueb (1986) elevated Nussbaum's Uraeotyphlinae to family level because their phylogenetic analyses suggested that inclusion of the Uraeotyphlinae within Ichthyophiidae rendered the latter paraphyletic. Uraeotyphlids share a combination of ancestral and derived features, but there are no known uniquely derived features that support the monophyly of the genus and family, a consequence of extensive convergence between uraeotyphlids and various caeciliids. Gower *et al.* (2002) included three uraeotyphlid species in their molecular phylogenetic analysis and obtained strong support for monophyly of the group as a whole as well as for relationships among the species. The anterior tentacles, dorsal nares, and recessed subterminal mouths, though not unique, are probably derived within the Ichthyophiidae plus Uraeotyphlidae, providing qualified support for the monophyly of *Uraeotyphlus* (Wilkinson and Nussbaum 1996).

2.2.5 Ichthyophiidae + Uraeotyphlidae — Diatriata

Nussbaum (1979), and subsequently both Duellman and Trueb (1986) and Hillis (1991), recovered the Uraeotyphlidae as more closely related to caeciliids, scolecomorphids and typhlonectids than to ichthyophiids. The major change in our understanding of higher caecilian phylogeny has been the adoption of the alternative hypotheses that the Uraeotyphlidae plus Ichthyophiidae are a clade. This hypothesis was well supported by morphological data that incorporated newly discovered cardiovascular characters (Wilkinson and Nussbaum 1996; Wilkinson 1997), and it has subsequently received strong support from analyses of gene sequence data (Wilkinson *et al.* 2002, 2003b; San Mauro *et al.* 2004). We currently interpret five uniquely derived features to support the Uraeotyphlidae + Ichthyophiidae clade: circumorbital bone (often termed postfrontal) present, external division of the atrium, an elongate anterior pericardial space, two posterior internal flexures in the *musculus rectus lateralis*, and an internal flexure in the *musculus subvertebralis*. The first of these is somewhat variable in that it may be more or less fused to adjacent elements, and it has been previously considered primitive, but, at least within caecilians, the reverse polarity is more parsimonious. We find the strong and congruent support from morphology and from molecules for this phylogenetic hypothesis to be compelling. We propose Diatriata, as a suitable rankless name for this suprafamilial clade comprising those caecilians with partial external division of their atrium.

2.2.6 The Higher Caecilians — Teresomata

The sister group of the Uraeotyphlidae + Ichthyophiidae, is a clade comprising the Scolecomorphidae, Typhlonectidae and the Caeciliidae, and

informally termed the advanced (Nussbaum 1991) or higher (e.g., San Mauro *et al.* 2004) caecilians. We know of only two putatively unique and derived features of the advanced caecilians, the absence of a true tail, with a true tail being defined compositely as a tapering postcloacal region with internal (vertebrae) and external segmentation (annuli), and the absence of internal flexures in the *musculus rectus lateralis* (Nussbaum and Naylor 1982; Wilkinson 1997). However, this grouping has been recovered in all numerical phylogenetic analyses of morphology or molecules, and with strong support. Compared to its sister clade, the advanced caecilians appear to be more speciose, and the group is much more diverse in morphology, ecology and life history. Its distribution is more cosmopolitan, with representatives in all areas where caecilians are found except South East Asia. The informally named 'advanced caecilians' has stood the test of time, and we suggest Teresomata as a rankless name for this suprafamilial clade, which encompasses the Scolecomorphidae, Typhlonectidae, and paraphyletic Caeciliidae. These caecilians lack true tails and have, for the most part, more rounded (teres) ends to their bodies (soma) than rhinatrematids, ichthyophiids and uraeotyphlids.

2.2.7 Scolecomorphidae

The Scolecomorphidae was established by Taylor (1969) for a few distinctive African caecilians. It currently comprises the West African *Crotaphatrema* and East African *Scolecomorphus*, each with three nominate species. These genera share many distinctive, derived morphological features that provide strong support for scolecomorphid monophyly. These include the absence of stapes and *foramina ovales*, absence of internal processes on lower jaws, a transverse bar extending between the posteromedial edges of the posteriormost ceratobranchial elements of the glossal skeleton (Nussbaum 1977), and a mobile eye attached to the base of the tentacle (Taylor 1968; Nussbaum 1981, 1985; O'Reilly *et al.* 1996). No *Crotaphatrema* have been included in any numerical phylogenetic analyses, but Wilkinson (1997) included all three *Scolecomorphus* species in his morphological phylogenetic analysis, and two species were included in the Wilkinson *et al.* (2003b) molecular phylogenetic study. In both cases there was strong support for the monophyly of *Scolecomorphus*, which is supported by the presence of a uniquely large diastema between the vomerine and palatine dental series. Monophyly of *Crotaphatrema* is supported by the particular form of stegokrotaphy in which the upper temporal fossa is obliterated by an outgrowth of the parietal (Nussbaum 1985). Wake (1998) suggested a close relationship between *S. kirkii* and *S. vittatus* on the basis of similar phallus morphology.

2.2.8 Typhlonectidae

The Typhlonectidae was established by Taylor (1968) for a group of Neotropical caecilians that he believed were aquatic and which are now considered to be either aquatic or semi-aquatic (Nussbaum and Wilkinson

1987; 1989). As currently conceived, the family includes five genera, three of which are monotypic. A highly distinctive derived feature that supports typhlonectid monophyly is the fused, sac-like form of the foetal gills (Wilkinson 1989; Wilkinson and Nussbaum 1999). This feature is known in all typhlonectids for which fetuses have been examined but remains unknown in *Potomotyphlus* and *Atretochoana*. Wilkinson and Nussbaum (1999) identified six additional features that appeared to be unique and derived in typhlonectids. These are: small tentacular apertures and (non-protrusible) tentacles, relatively dorsally oriented occipital condyles, a ventral process of the squamosal bracing against the maxillopalatine, M-shaped ceratohyals, a sliding articulation between the third and fourth ceratobranchials, and the *musculus subvertebralis pars ventralis* with a scalloped origin.

Wilkinson's (1997) morphological phylogenetic analysis found strong support for the pairing of the only two typhlonectids, *Chthonerpeton indistinctum* and *Typhlonectes natans*, that it included, and is the only study to have provided a numerical phylogenetic test of typhlonectid monophyly (which has never been seriously questioned). Well-supported relationships within the Typhlonectidae have been inferred on the basis of extensive morphological data (Wilkinson and Nussbaum 1999; see Fig. 2.2). Although monophyly of *Chthonerpeton* has not been established, the generotype, *C. indistinctum*, lies outside a group including all other typhlonectid genera. *Nectocaecilia*, which is believed to be semi-aquatic, is the sister group of a clade of fully aquatic, finned caecilians that comprises *Atretochoana*, *Potomotyphlus*, and *Typhlonectes*. *Potomotyphlus* appears to be the sister genus of the lungless *Atretochoana* on the basis of a number of features associated with a reduction in pulmonary respiration.

2.2.9 Caeciliidae

As currently conceived, the Caeciliidae appears to be a relatively heterogeneous and paraphyletic assemblage comprising all those caecilians that have never been removed to another family. Molecular data strongly support the paraphyly of the Caeciliidae with respect to the Typhlonectidae, recovering *Caecilia* as more closely related to *Typhlonectes* than to a broad range of other caeciliids (Hedges *et al.* 1993; Wilkinson *et al.* 2002, 2003b). Hedges *et al.* (1993) proposed removing caeciliid paraphyly by recognising the typhlonectids at the sub-familial rather than familial level, but in the absence of a better understanding of the relationships among higher caecilians this action would only shift the problem of paraphyly to a different taxonomic level. Paraphyly of the Caeciliidae with respect to the Scolecomorphidae is also suggested by the most recent molecular phylogenetic study (Wilkinson *et al.* 2003b). Phylogenetic analyses based on morphology are less clear cut, with caeciliid monophyly or paraphyly with respect to both the Typhlonectidae and Scolecomorphidae achieved under alternative weighting schemes (Wilkinson 1997) and thus not well-supported. A single derived feature, an elongate *musculus interhyoideus*

posterior (Fig. 2.1), supports the monophyly of the Caeciliidae. However, given the strong molecular support for caeciliid paraphyly, the shorter form of the muscle in typhlonectids must be presumed to be due to reversal, presumably associated with their zygotrophy.

We have only limited understanding of the relationships among caeciliids. Some relationships are suggested by taxonomic history. *Oascaecilia* was established by Taylor (1968) through the partitioning of *Caecilia* on the basis of a single difference (the eye covered with bone or not) of dubious value. Although both genera are thus of uncertain monophyly, we are content to assume that they are jointly monophyletic based on their overall similarity in external morphology and cranial architecture. Similarly, *Luetkenotyphlus* was established through partitioning of *Siphonops*, and these genera are presumed to be closely related to each other and to *Mimosiphonops* (Wilkinson and Nussbaum 1992), although we know of no uniquely derived characters of this group or of any of its constituent genera. The Central American species of the genera *Dermophis* and *Gymnophis* are presumed to be jointly monophyletic on the basis of their overall similarity in morphology and reproduction. They differ in the presence or absence of splenial teeth and whether the eye is covered with bone, features which appear highly homoplastic in caecilians and which do not convince us of the monophyly of either genus. Of the caeciliid taxa studied thus far, molecular data strongly support a close relationship of *Dermophis* (and by implication *Gymnophis*) with the African genus *Schistometopum*, reflecting a previous taxonomic association.

Among Old World caeciliids, molecular evidence supports the monophyly of the caeciliids of the Seychelles, which Nussbaum and Ducey (1988) had argued previously on the basis of cytological data. All species of the Seychellean caeciliid clade have been included in molecular phylogenetic analyses, an atypical level of taxonomic coverage for caecilians. These data convincingly identify *Praslinia* as the sister taxon to a *Grandisonia* + *Hypogeophis* clade, without resolving the relationships within this latter clade. They suggest that *Grandisonia*, which (like the Seychellean clade as a whole) lacks any known uniquely phenotypic derived traits, is paraphyletic with respect to *Hypogeophis*. Among the sampled taxa, the molecular data also provide strong support for the Indian caeciliid *Gegeneophis* being the sister-group of the Seychelles caeciliids (Wilkinson *et al.*, 2002; 2003b), suggesting the possibility of an Indo-Seychellean caeciliid clade that we might expect to also include the thus far unstudied Indian caeciliid *Indotyphlus*. An Indo-Seychellean connection for caecilians was predicted on the basis of biogeographic and plate tectonics considerations (Nussbaum 1984). Molecular data also support, albeit not strongly, the pairing of the East African *Boulengerula* and West African *Herpele*.

Wilkinson (1997) considered the available morphological data to be insufficient to unravel relationships within the higher caecilians. We interpret the failure of analyses based on morphology to support those

relationships that are well supported by molecular data, including the monophyly of the Seychellean caeciliids, the Indo-Seychellean clade, and the *Dermophis-Schistometopum* grouping, to further indicate the current limitations of the morphological data rather than undermining the molecular results. Morphological data have provided very useful phylogenetic characters, but broader and deeper sampling of characters and taxa are needed, particularly within the higher caecilians. Although relationships within the higher caecilians are poorly resolved in our relatively conservative consensus phylogeny (Fig. 2.2), sampling of taxa for both morphological and molecular phylogenetic study is improving.

2.2.10 Prospects

The relatively small number of species of Gymnophiona means that a fairly comprehensive phylogeny for the major lineages of caecilians is a realistic

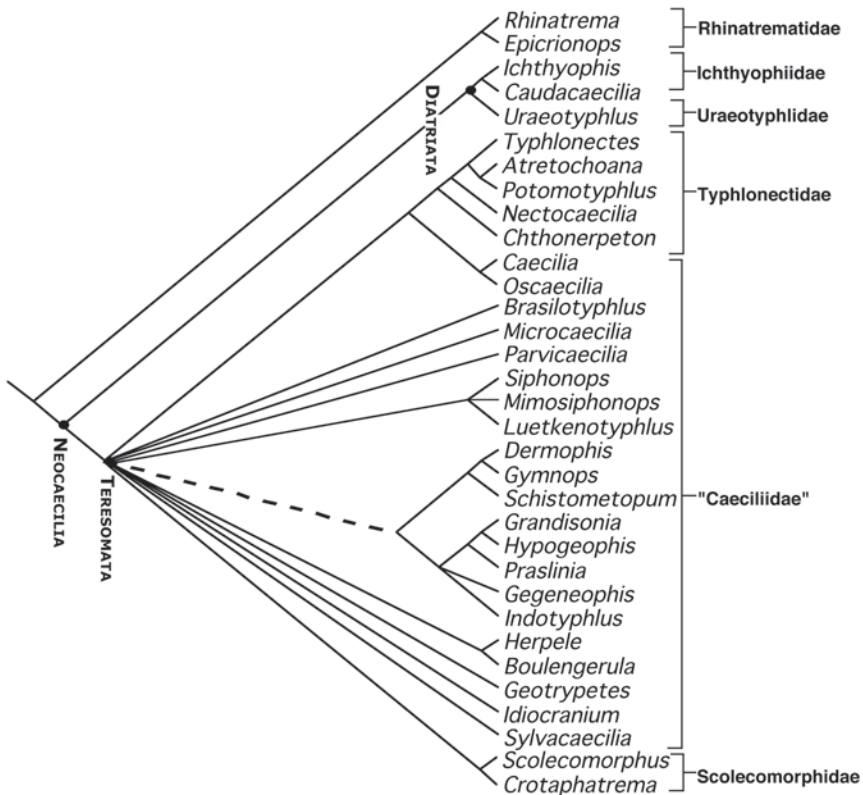


Fig. 2.2. Summary (consensus) phylogeny of caecilian constructed manually and based on the results of previous numerical phylogenetic analyses and inferences from taxonomy as described in the text. The dashed line indicates particularly uncertain monophyly highlighting the potential for the branches from the main polytomy, including many unstudied taxa, to perhaps lie within this group. Note that monophyly of many genera is at best uncertain and that there is a need for much more detailed, low-level, taxonomic work. Original.

short-term goal that we believe is within reach, and will be reached in the near future. At lower taxonomic levels the systematic foundations are not so good. Until about 1972, caecilian taxonomy was dominated by E. H. Taylor who described many species that have not withstood subsequent scrutiny and have been lost to synonymy. The reduction in numbers of recognised species has more or less balanced the description of new species since Taylor's time, and the work of checking and testing Taylor's species-level taxonomic work remains largely incomplete. Most caecilian species are poorly known and poorly circumscribed, impinging on all aspects of their biology (e.g., Gower and Wilkinson, 2005), and taxonomic uncertainty and instability can be expected to continue for some time. However, molecular phylogenetic studies at low taxonomic levels are proving useful in helping to delimit and distinguish morphologically similar species in genera such as *Ichthyophis*, where identification to species is notoriously difficult and the existing taxonomy exceedingly problematic. Molecular studies should facilitate taxonomic work while providing the low-level phylogenies needed to study caecilian evolution in detail. Ultimately any understanding of caecilian species, be it derived from molecules or morphology or (preferably) both, will depend on collecting sufficient (i.e., much more) new material across many taxa. Traditionally, caecilians have been poorly sampled in the field, but this is improving. We think it likely that many new caecilian species will be discovered, both in research collections and through additional collecting. It is noteworthy that the majority of new species described in the 15 years since our last review have been described in the last five years, perhaps indicating a rise in interest and the beginnings of a new era of taxonomic discovery (e.g., Gower *et al.*, 2004). As caecilian taxonomy stabilises, and the rate of losses to synonymy decreases, we expect the overall number of recognised caecilian species to increase, and we suspect that the number of currently recognised species is a considerable underestimate of their actual diversity.

2.3 CLASSIFICATION

The classification presented here includes no major changes from our previous summary (Nussbaum and Wilkinson 1989), because we think none is warranted by the current state of knowledge. We draw attention to three important studies of the taxonomy of regional caecilian faunas by Pillai and Ravichandran (1999), Savage and Wake (2001) and Lynch (1999) that provide recent keys. We prefer to accept the paraphyly of the Caeciliidae for the time being, in the belief that the best way of removing it will only become apparent with a more comprehensive understanding of the relationships of caeciliid genera, particularly those that remain unstudied phylogenetically. Formal taxonomic revision aimed at removing the paraphyly now, although well-intended, would be incomplete and unlikely to promote stability in the meanings of names. Thus we use the same six-family system and same format as in 1989, but with updated

species lists and synonymies. Where possible, we have indicated derived features for genera that are not monotypic and where this has not been discussed above, but our diagnoses rely upon unique combinations of features, not all of which are themselves unique. Reference to a pseudoectopterygoid (Wilkinson and Nussbaum 1992) is to the separate palatal bone that lies between the pterygoid (process of the quadrate) and the maxillopalatine in some caeciliids. We also prefer to use inner mandibular for those teeth usually referred to as splenials. In both cases our usage is intended to avoid asserting homologies for which there is no good evidence.

ORDER GYMNOPHIONA RAFINESQUE 1814

Diagnosis. Lissamphibia without limbs and girdles; with paired sensory tentacles on the snout; with a dual jaw-closing mechanism consisting of the ancestral component (*musculus adductor mandibulae* pulling up on ramus of lower jaw) and a unique, novel component (*musculus interhyoideus posterior* pulling back and down on retroarticular process of lower jaw); with an eversible phallus in males formed by the posterior part of the cloaca; with an *os basale*; trunk vertebrae with enlarged basipophyseal processes; atlas without a *tuberculum interglenoideum*.

Content. 6 families, 33 genera, 170 species.

Distribution. Pantropical, except for Madagascar and southeast of Wallace's Line. Distribution includes some subtropical areas.

Remarks. Jenkins and Walsh (1993) described a 'caecilian' fossil, *Eocaecilia*, from the Jurassic of North America and more recently Evans and Sigogneau-Russell (2001) described a 'stem-group caecilian' *Rubricacaecilia* from the Lower Cretaceous of North Africa. This fossil taxon, based on a brief description that has yet to be significantly expanded, has seemingly been universally accepted as a caecilian with little, if any, critical discussion. Unlike living caecilians, *Eocaecilia* has small limbs, and thus, by the diagnosis given above, it is not a gymnophionan (= caecilian). The presence or absence of limbs in the fragmentary *Rubricacaecilia* is unclear, but it has other features, notably the atlas has a *tuberculum interglenoideum*, which places it outside our Gymnophiona. Evans and Sigogneau-Russell (2001) supported Trueb and Cloutier's (1991) use of "Apoda Oppel 1811 for the crown group alone and Gymnophiona Rafinesque for the clade comprising stem-group taxa + Apoda", a use also adopted by Schoch and Milner (2004). Our previous and present diagnoses of Gymnophiona are based on the living species, and they exclude what Evans and Sigogneau-Russell view as stem-group caecilians. Neontologists use the term Gymnophiona to convey generalities about the living caecilians that may not hold or may not be known in the stem group. Changing the meaning of Gymnophiona means that general statements in the literature, such as 'Gymnophiona are legless', become technically incorrect, and neontologists, who comprise the bulk of caecilian researchers would have to learn to adopt Apoda in order

to make generalisations about the living caecilians. The latter name is also problematic because zoological classification is festooned with other uses of it, most importantly the homonymy with *Apoda* Haworth 1809, a genus of moth. We believe clarity would be best served if the use of *Apoda* in caecilian classification were completely abandoned. We see no good reason to rediagnose *Gymnophiona* in order to accommodate relatively poorly known fossil taxa that, while possibly closely related to caecilians, are not caecilians in the sense in which the term is generally used. A. Family *Rhinatreumatidae* Nussbaum 1977 (Fig. 2.3 A, B)

Diagnosis. *Gymnophiona* with true tails consisting of a postcloacal segment with vertebrae, myomeres, and complete skin annuli; primary annuli divided by secondary and tertiary grooves; all annular grooves orthoplicate; numerous scales in all annular grooves and in some of the dorsal grooves of the collars; strongly zygotrophic skulls with the *musculi adductores mandibulae externi* passing through the temporal fossae to meet at the midline of the skull along the interparietal suture; maxillopalatine in contact with the quadrate; squamosal widely separated from the frontal, notched posteriorly, the notch opposing a dorsolateral process of the *os basale*; premaxillae and nasals present as separate bones; mouth terminal; retroarticular process of lower jaw short and not curved dorsally; *musculus interhyoideus* posterior short; stapes pierced by stapedia artery; tentacle immediately anterior to or on the anterior edge of eye; eyes visible externally, in a socket in the maxillopalatine; hyobranchium of adults with only three ceratobranchial elements decreasing in size posteriorly, with the larynx situated posterior to the hyobranchium (not enclosed between the two arms of the posteriormost ceratobranchials); hyobranchial elements of larvae mineralized, hyobranchium of metamorphosed individuals cartilaginous; *truncus arteriosus* short; atrium undivided externally.

Content. 2 genera, 9 species.

Distribution. Northern South America.

Remarks. There has been no change in the taxonomy of the *Rhinatreumatidae* since our review of 1989, and no species description or other taxonomic actions since Taylor (1968).

1. *Epicrionops* Boulenger 1883

Type species: *Epicrionops bicolor* by original monotypy.

Diagnosis. *Rhinatreumatids* with three ceratobranchial arches in adults; a longitudinal cloacal opening; relatively long tail consisting of more than 11 postcloacal annuli; more than one row of scales per annular groove.

Content. 8 species: *bicolor*, *columbianus*, *lativittatus*, *marmoratus*, *niger*, *parkeri*, *peruvianus*, *petersi*.

Distribution. Colombia, Ecuador, Peru, and Venezuela.

2. *Rhinatrema* Duméril & Bibron, 1841

Type species: *Caecilia bivittata* Guérin-Méneville 1829, by monotypy.



Colour
Figure

Fig. 2.3 contd

Diagnosis. Rhinatrematids with two ceratobranchial arches in adults; more transverse or subcircular cloacal opening; relatively short tail consisting of 11 or fewer postcloacal annuli; a single row of scales per annular groove.

Content. 1 species: *bivittatum*.

Distribution. Brazil, French Guiana, Guyana, and Surinam.

Remarks. Nussbaum and Hoogmoed (1979) noted the rarity of *Rhinatrema bivittatum* in scientific collections. Recent fieldwork in French Guiana yielded considerable additional material suggesting the species is not particularly rare in the wild (Wilkinson, Gower and Kupfer, unpublished).

B. Family Ichthyophiidae Taylor 1968 (Figs. 2.3C, D; 2.6A, B)

Diagnosis. Gymnophiona with true tails; skull stegokrotaphic; *musculi adductores mandibulae externi* confined beneath the skull roof, not meeting middorsally; distinct septomaxillae, premaxillae, nasals, and prefrontals; circumorbitals (postfrontals) distinct or partially or entirely fused to maxillopalatine or squamosal; frontal and squamosal in contact; no dorsolateral process on *os basale*; no posterior notch in squamosal; quadrate and maxillopalatine broadly separated; stapes pierced by stapedia artery; mouth nearly terminal; retroarticular process of lower jaw curved dorsally; *musculus interhyoideus posterior* short; tentacular opening between the eye and nostril, usually closer to the eye and below the eye-nostril line; ceratohyal arch U-shaped; four ceratobranchial arches in larvae, arches 3 and 4 fused in adults; larynx positioned between the distal ends of fused arches 3 and 4; all primary annuli subdivided by secondary and tertiary grooves in metamorphosed individuals; annular grooves angulate ventrally over most of the body, orthoplicate posteriorly only; numerous scales present in all but perhaps a few anterior annular grooves of adults; aortic arches proximal to the heart fused into an elongate *truncus arteriosus*; atrium partially divided externally.

Content. 2 genera, 37 species.

Distribution. India, Sri Lanka, and southeast Asia including southern Philippines and Indo-Malaysian Archipelago northwest of Wallace's Line.

1. *Caudacaecilia* Taylor 1968

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

Diagnosis. Ichthyophiids without inner mandibular teeth.

Content. 5 species: *asplenia*, *larutensis*, *nigroflava*, *paucidentula*, *weberi*.

Distribution. Borneo, Malay Peninsular, Philippines, Sumatra.

Remarks. Taylor (1968) and Nussbaum and Gans (1980) examined specimens of *Caudacaecilia* (cf. *asplenia*) from Sri Lanka in museums, but

Fig. 2.3 contd

Fig. 2.3 A-B. Adult *Rhinatrema bivittatum* (Rhinatreematidae) from French Guiana; the tentacle (small white spot) is on the anterior edge of the eye; photo by Peter Stafford. **C-D.** Adult *Ichthyophis bannanicus* (Ichthyophiidae) from Mengla, Yunnan, China; the tentacle is just above the mouth and closer to the eye than to the naris; photo by Edmund D. Brodie, Jr.

concluded that there was some doubt about the collection data. Recent caecilian surveys in Sri Lanka have not revealed additional specimens attributable to this genus.

2. *Ichthyophis* Fitzinger 1826

Type species. *Caecilia glutinosa* Linnaeus 1758, by original monotypy.

Diagnosis. Ichthyophiids with splenial teeth.

Content. 34 species: *acuminatus*, *atricollaris*, *bannanicus*, *beddomei*, *bernisi*, *biangularis*, *billitonensis*, *bombayensis*, *dulitensis*, *elongatus*, *garoensis*, *glandulosus*, *glutinosus*, *humphreyi*, *husaini*, *hypocyaneus*, *javanicus*, *kohtaoensis*, *laosensis*, *longicephalus*, *malabaricus*, *mindanaoensis*, *monochrous*, *orthoplicatus*, *paucisulcus*, *peninsularis*, *pseudangularis*, *sikkimensis*, *singaporensis*, *subterrestris*, *sumatranus*, *supachaii*, *tricolor*, *youngorum*.

Distribution. South East Asia, India, Sri Lanka, southern Philippines, western Indo-Australian Archipelago.

Remarks. Two new species of *Ichthyophis* (*husaini* and *garoensis*) were described by Pillai and Ravichandran (1999), and Gower *et al.* (2005) suggested the presence of an undescribed cryptic species in Sri Lanka. Kupfer and Müller (2004) provided a rediagnosis of *I. supachii*. *I. longicephalus* (Pillai 1986) was overlooked and not included in our previous treatment (Nussbaum and Wilkinson 1989).

C. Family Uraeotyphlidae Nussbaum 1979 (Fig. 2.4 A, B)

Diagnosis. Gymnophiona with true tails; weakly stegokrotaphic skulls; *m. adductor mandibulae externi* confined beneath the skull roof but may be visible through a small opening between the squamosal and parietal; number and arrangement of skull and lower jaw bones and configuration of the hyobranchium as in the Ichthyophiidae; Stapes imperforate; *m. interhyoideus posterior* short; mouth recessed or subterminal; tentacular opening far forward, below nostril; external nares relatively dorsal, most primary annuli divided by secondary grooves, a few anterior primary annuli may not be subdivided, or primary and higher-order annuli indistinguishable externally; annular grooves do not completely encircle the body; scales present; aortic arches proximal to the heart fused into an elongate *truncus arteriosus*; atrium partially divided externally.

Content. 1 genus, 5 species.

Distribution. Southern peninsular India.

Remarks. The diagnosis (of Nussbaum and Wilkinson 1989) has been modified to account for new information on the diversity of uraeotyphlid annulation patterns (Gower and Wilkinson in prep.; Nussbaum, pers. obs.).

1. *Uraeotyphlus* Peters 1879

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

Diagnosis. As for the family.

Content. 5 species: *interruptus*, *malabaricus*, *menoni*, *narayani*, *oxyurus*.

Distribution. Southern peninsular India, Kerala, Karnataka and Tamil Nadu.

Remarks. Pillai and Ravichandran (1999) described *U. interruptus* from Kerala since our (Nussbaum and Wilkinson 1989) review.

D. Family Scolecomorphidae Taylor 1969 (Fig. 2.5 C, D, E)

Diagnosis. Gymnophiona that lack stapes and *foramina ovales*; septomaxillae and prefrontals present; no internal process on the pseudoangular bone; no *m. levator quadrati*; *m. interhyoideus posterior* short; a distinctive hyobranchium in which the flattened distal ends of the fourth branchial arch are connected by a transverse bar above the larynx; all primary annuli undivided; aortic arches proximal to the heart fused into an elongate *truncus arteriosus*; atrium undivided externally.

Content. 2 genera, 6 species.

Distribution. East and equatorial West Africa.

1. *Crotaphatrema* Nussbaum 1985

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

Diagnosis. Scolecomorphids without temporal fossae; without diastemata between the vomerine and palatine series of teeth; and with the maxillary series extending further posteriorly than the palatine series.

Content. 3 species: *bornmuelleri*, *lamottei*, *tchabalmbaboensis*.

Distribution. Cameroon.

Remarks. Lawson (2000) added *C. tchabalmbaboensis* to the known species of *Crotaphatrema*.

2. *Scolecomorphus* Boulenger 1883

Type species. *Scolecomorphus kirkii* Boulenger 1883, by original monotypy.

Diagnosis. Scolecomorphids with temporal fossae; with diastemata between the vomerine and palatine series of teeth; and with all or most of the palatine teeth posterior to the maxillary teeth.

Content. 3 species: *kirkii*, *uluguruensis*, *vittatus*.

Distribution. East Africa: Malawi, and Tanzania.

Remarks. The phallus of all *Scolecomorphus* species is equipped with cartilaginous spines or spicules (Taylor 1968; Wake 1998). This may be a uniquely derived character of the genus but the condition in *Crotaphatrema* is undocumented.

E. Family Caeciliidae Rafinesque 1814 (Figs. 2.4 C, D; 2.5 A; 2.6 C-F)

Diagnosis. Gymnophiona with nasal and premaxilla fused; septomaxilla, prefrontal, postfrontal and pterygoid lost or fused to adjacent bones; pseudoectopterygoid present or not; maxillopalatine widely separated from quadrate; temporal fossae usually absent, if present, *m. adductor mandibulae externi* do not pass dorsally through the fossae; *M. interhyoideus posterior* long, with posterior portion extending as far as the sixth trunk myomere;

Colour
Figure

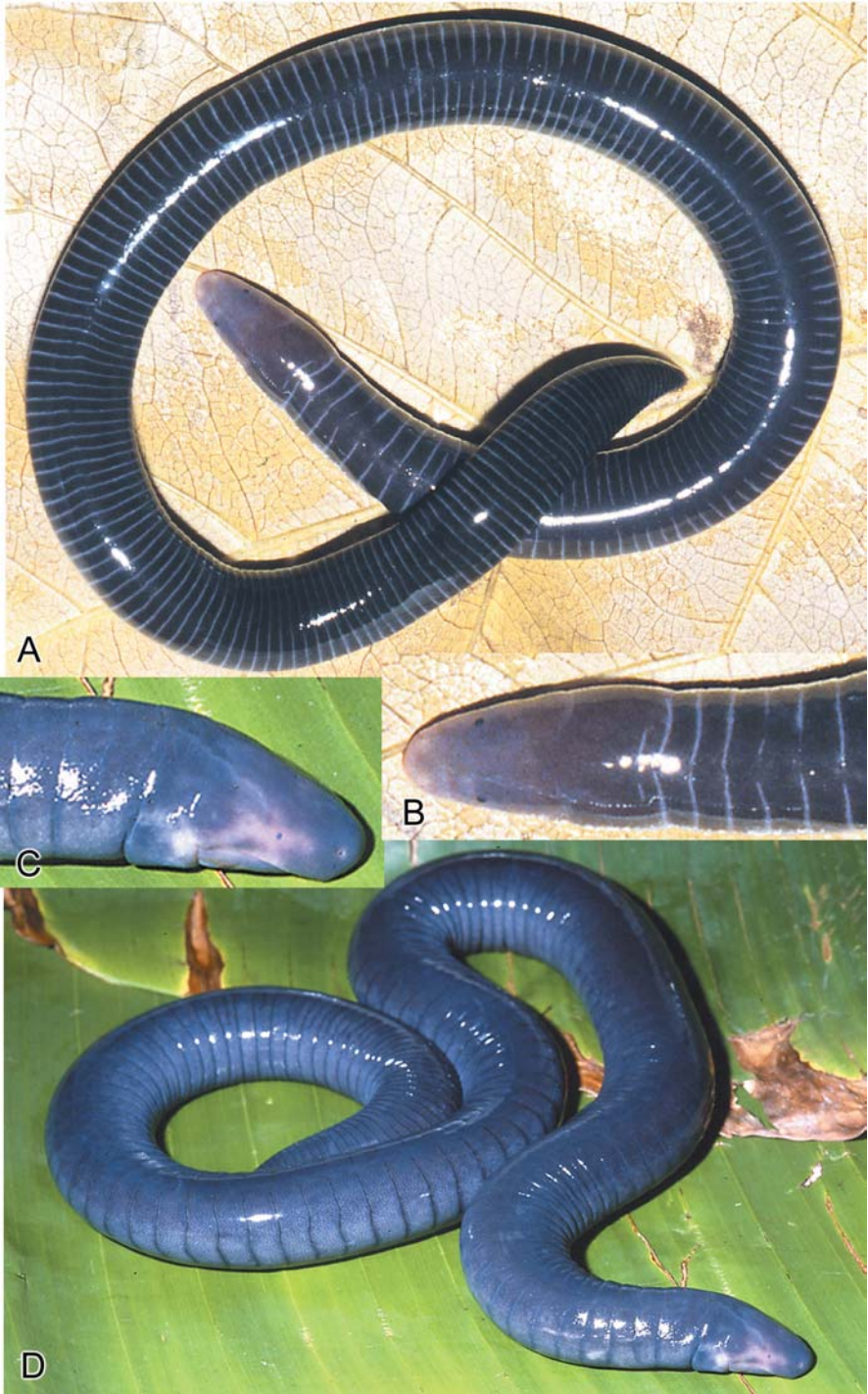


Fig. 2.4 contd

M-shaped ceratohyal arch; larynx between distal ends of fused third and fourth ceratobranchials; no tail; some, none, or all primary annuli subdivided by secondary grooves; no tertiary grooves; scales present or absent; external gills of embryos in three rami (one ramus may be reduced or vestigial), not fused and sac-like; aortic arches proximal to the heart fused into an elongate *truncus arteriosus*; atrium undivided externally.

Content. 21 genera, 98 species.

Distribution. Tropical Central and South America, equatorial East and West Africa, islands of the Gulf of Guinea, Seychelles Archipelago, and India.

Remarks. During the late 1980's and early 1990's, the name "Caeciliidae" was used for this family in an attempt to remove the homonymy of Caeciliidae Rafinesque, 1814 (Amphibia) with Caeciliidae Kolbe, 1880 (Insecta). The problem is outlined in Moore *et al.* (1984). In 1996, the Commission on Zoological Nomenclature, under its plenary powers, ruled (Opinion 1830, BZN 53(1):68-69) that Caeciliidae Rafinesque, 1814 is the valid amphibian name, and the insect name was changed to Caeciliusidae Kolbe, 1880.

1. *Boulengerula* Tornier 1897

Type species. *Boulengerula boulengeri* Tornier 1897, by monotypy.

Diagnosis. Caeciliids with eye (if present) under bone; no temporal fossae; mesethmoid exposed between frontals or not; inner mandibular teeth present or not; no secondary grooves; no scales; tentacular opening nearer to eye than to external naris; an unsegmented terminal shield; no narial plugs; a strong diastema between the vomerine and palatine teeth present or not; a vertical keel on the end of the terminal shield.

Content. 6 species: *boulengeri*, *changamwensis*, *denhardti*, *fischeri*, *taitana*, *uluguruensis*.

Distribution. Kenya, Malawi, Tanzania and Rwanda.

Remarks. Nussbaum and Hinkel (1994) placed *Afrocaecilia* in the synonymy of *Boulengerula* and described *B. fischeri*. Wilkinson *et al.* (2004) removed *B. denhardti* from the synonymy of *Schistometopum gregorii*. Their phylogenetic analyses using Nussbaum and Hinkel's morphological data were unable to resolve well-supported relationships within the genus. Monophyly of the genus is not seriously in question. Many of the diagnostic features are derived within the Neocaecilia although none of them uniquely so, and in molecular analyses, grouping of the two species of *Boulengerula* included thus far is well supported (Wilkinson *et al.* 2003b).

Fig. 2.4 cont'd

Fig. 2.4 A-B. Adult or subadult *Uraeotyphlus* sp. (Uraeotyphlidae) from the Western Ghats, peninsular India; note the dorsal orientation of the eyes and external nares, and the undivided primary annuli on the anterior portion of the body; photo by John Measey. **C-D.** Adult *Caecilia* cf. *tentaculata* (Caeciliidae) from South America; note the lack of undivided primary annuli over most of the body, but with some subdivided primaries posteriorly; the tentacle cannot be seen, because it is directed ventrally from the "shelf" below the external naris; photo by Peter Stafford.



Colour
Figure

Fig. 2.5 contd

2. *Brasilotyphylus* Taylor 1968

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

Diagnosis. Caeciliids with eye under bone; no temporal fossae; mesethmoid covered by frontals; no splenial teeth; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no terminal shield; a very short series of premaxillary-maxillary teeth, not extending posterior of the choanae; a strong diastema between the vomerine and palatine teeth; a vertical keel on the body terminus.

Content. 1 species: *braziliensis*.

Distribution. Brazil.

Remarks. The affinities of this genus, which has similarities to *Boulengerula* in the Old-World and *Microcaecilia* in the New, are quite unclear at present (Nussbaum and Hinkel 1994).

3. *Caecilia* Linnaeus 1758

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

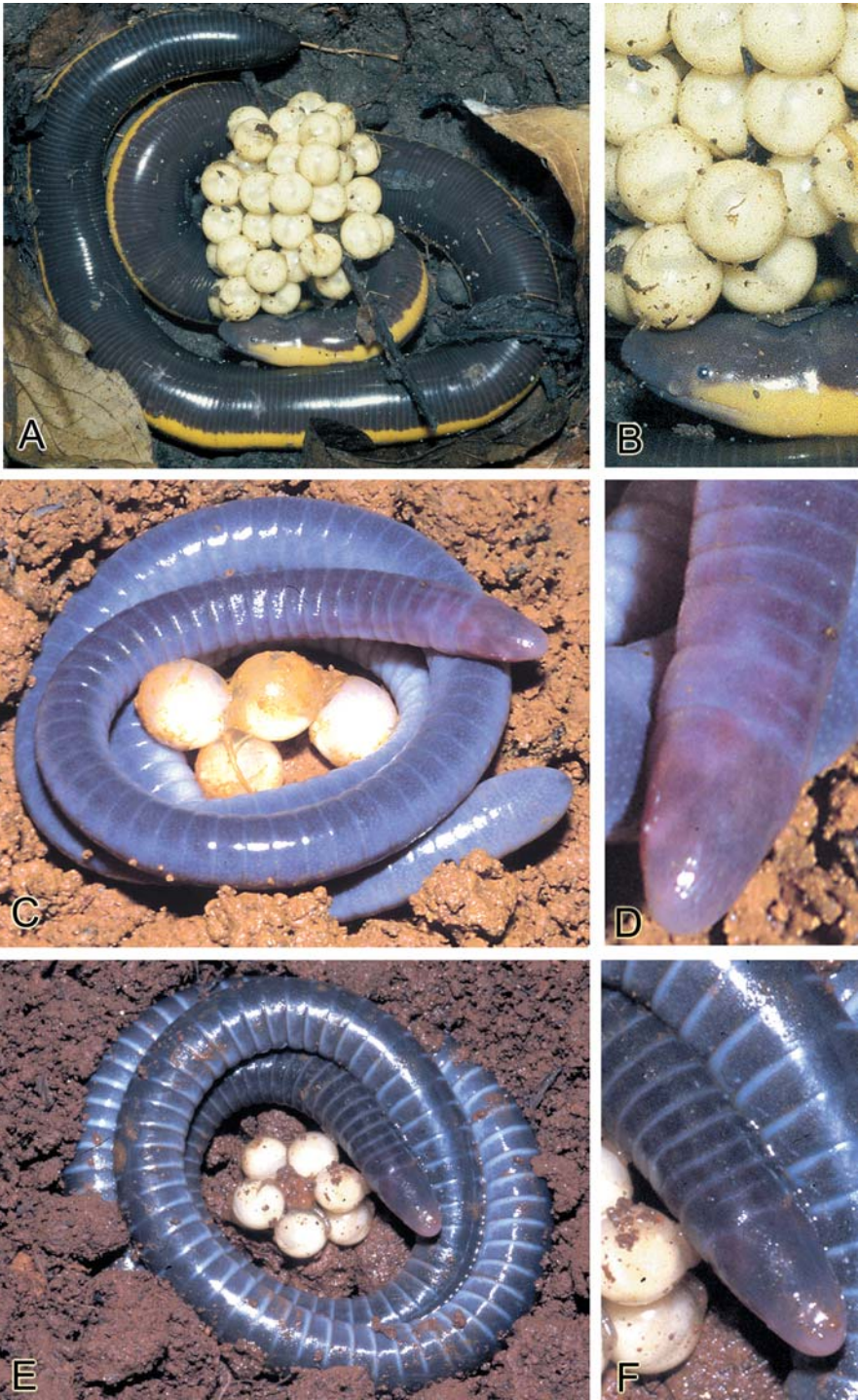
Diagnosis. Caeciliids with eye not covered with bone; no temporal fossae; mesethmoid exposed between frontals; splenial teeth present; secondary grooves present or absent; scales present or absent; subdermal scales present or absent; tentacular opening directly below external naris, closer to naris than to eye; unsegmented terminal shield present or not; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel; teeth relatively few and large, usually replaced alternately in groups; vomeropalatine tooth row displaced posteriorly, not parallel to premaxillary-maxillary tooth row, diverging from the latter anteriorly forming an angle where the two rows meet rather than a semicircle.

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

Distribution. Eastern Panama and northern and central South America.

Fig. 2.5 contd

Fig. 2.5 A. Adult female *Schistometopum thomense* (Caeciliidae) and new-born from Ilha São Tomé, Gulf of Guinea; the species is viviparous; photo by Ronald A. Nussbaum. **B.** Adult *Chthonerpeton indistinctum* (Typhlonectidae) from southern South America; this species is terrestrial/semi-aquatic, whereas other species of the family are fully aquatic; photo by John Measey. **C-E.** Adult *Scolecophorus kirkii* (Scolecophoridae) from Tanzania; the eye, which rides on the base of the tentacle, is shown under the skin and skull bones in the nearly resting position (C), in the nearly maximally protruded position (D), and in the fully protruded position (E) in which the eye is carried completely outside of the skull on the base of the tentacle; there is a pigmentless area of the skin over the track of the eye as it moves back and forth with the tentacle, which presumably allows light to pass through the skin and stimulate the retina; see O'Reilly *et al.* (1996) for details; photos by Daniel Boone.



Colour
Figure

Fig. 2.6 contd

Remarks. *Caecilia* is the largest genus of caecilians in the New World and has a broad distribution. Over half the species were described by E. H. Taylor, and most are poorly characterised and delimited. Surprisingly, there have been no new species described and little taxonomic work on the group since 1989 despite the clear need for the latter. A helpful treatment of the *Caecilia* of Colombia is given by Lynch (1999). Summers and Wake (2001) redescribed the holotype of *C. volceni*. *C. isthmica* was accidentally omitted from our previous treatment (although counted in the total number of species).

4. *Dermophis* Peters 1879

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

Diagnosis. Caeciliids with eye not covered with bone; no temporal fossae; mesethmoid covered or exposed; no splenial teeth; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 7 species: *costaricensis*, *glandulosus*, *gracilior*, *mexicanus*, *oaxacae*, *occidentalis*, *parviceps*.

Distribution. Southern Mexico south to northwestern Colombia.

Remarks. Following our 1989 comment that some of the species of *Dermophis* considered invalid by Savage and Wake (1972) were valid, Savage and Wake (2001) resurrected four species from the synonymies they had previously proposed.

5. *Gegeneophis* Peters 1879

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

Diagnosis. Caeciliids with eye under bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening midway between eye and external naris; no unsegmented terminal shield; narial plugs on tongue; no diastema between vomerine and palatine teeth; terminal keel present or absent.

Content. 8 species: *carnosus*, *danieli*, *fulleri*, *krishni*, *madhavai*, *nadkarnii*, *ramaswamii*, *seslachari*.

Fig. 2.6 contd

Fig. 2.6 A. Adult female *Ichthyophis kohtaoensis* (Ichthyophiidae) from Thailand guarding her clutch of early-stage embryos; the species is oviparous with indirect development; the nest is terrestrial; the hatchling larvae make their way to nearby streams where they grow and eventually metamorphose into terrestrial subadults; photo by Alex Kupfer. **B.** Adult female *Boulengerula boulengeri* (Caeciliidae) from Tanzania guarding her early-stage embryos in a terrestrial nest; the species is oviparous with direct development (no larval stage); photo by Alex Kupfer. **C.** Adult *Boulengerula taitanus* (Caeciliidae) from the Taita Hills, Kenya, guarding her early-stage embryos in a terrestrial nest; the species is oviparous with direct development; photo by Alex Kupfer.

Distribution. India.

Remarks. Five new species of *Gegeneophis* have recently been described from Maharashtra (Ravichandran *et al.* 2003; Giri *et al.* 2003) Karnataka (Pillai and Ravichandran 1999; Bhatta and Srinivasa 2004) and Goa (Bhatta and Prasanth 2004). Giri *et al.* (2003) also revised the generic diagnosis. No uniquely derived traits are known for this genus.

6. *Geotrypetes* Peters 1880

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

Diagnosis. Caeciliids with eye not covered with bone; temporal fossae present; mesethmoid exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to external naris than to eye; no unsegmented terminal shield; narial plugs present on tongue; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 3 species: *angeli*, *pseudoangeli*, *seraphini*.

Distribution. Equatorial West Africa and Bioko Island.

Remarks. Nussbaum and Pfreder (1998) noted that *Schistometopum garzonheydti* from Bioko is a junior synonym of *Geotrypetes seraphini*. *Geotrypetes seraphini* have a distinctively shaped *os basale* (pers. obs.) and unique arrangements of cranial muscles and anterior trunk muscles (Sheps *et al.* 1997; Wilkinson, unpublished) which, if present in the other species, would provide strong support for the monophyly of the genus.

7. *Grandisonia* Taylor 1968

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

Diagnosis. Caeciliids with eye not covered with bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present on more than half of the primary annuli, may be missing on some anterior primaries; scales present; tentacular opening variable in position, may be closer to external naris than to eye, nearly midway between eye and external naris, or slightly closer to eye; no unsegmented terminal shield; narial plugs present on tongue; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 4 species: *alternans*, *brevis*, *larvata*, *sechellensis*.

Distribution. Seychelles Archipelago.

Remarks. *Grandisonia diminutiva* is based on juvenile specimens of *G. sechellensis* (Nussbaum, unpublished). The small “tail” that Taylor (1968) considered to be diagnostic of *G. diminutiva* does not exist, and the rest of the characteristics of the type series fall well within the range of *G. sechellensis*.

8. *Gymnopsis* Peters 1874

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

Diagnosis. Caeciliids with eye covered by bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to eye than to

external naris; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 2 species: *multiplicata*, *syntrema*.

Distribution. Guatemala south to Panama.

Remarks. The complicated history of the taxonomy of *Gymnopsis syntrema* was reviewed by Nussbaum (1988). Wake (in Savage and Wake 2001: 52) indicated that she 'disagrees with Nussbaum's concept of *Gymnopsis* as it relates to *G. syntremus* [sic]' and would treat the issue elsewhere.

9. *Herpele* Peters 1879

Type species: *Caecilia squalostoma* Stutchbury 1834, by original monotypy.

Diagnosis. Caeciliids with eye under bone; no temporal fossae; mesethmoid slightly visible or not dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to external naris than to eye; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 2 species: *multiplicata*, *squalostoma*.

Distribution. Equatorial West Africa, including the Gulf of Guinea island, Bioko (Fernando Po).

Remarks. The status of *Herpele multiplicata*, a species known only from a holotype specimen that is now lost, was recently reviewed by Wilkinson *et al.* (2003a) who wrongly gave the date of description of *H. squalostoma* as 1859 instead of 1834. *H. squalostoma* has an unusual arrangement of its systemic arches that is unique among vertebrates (Wilkinson 1992b), which, if present also in *H. multiplicata*, would provide good evidence of monophyly of the genus.

10. *Hypogeophis* Peters 1879

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

Diagnosis. Caeciliids with eye in socket, not under bone; no temporal fossae; mesethmoid not exposed dorsally; secondary grooves present, confined to posterior third or less of body; scales present; tentacular opening far forward, closer to external naris than to eye; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 1 species: *rostratus*.

Distribution. Seychelles Archipelago.

11. *Idiocranium* Parker 1936

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

Diagnosis. Caeciliids with eye not under bone; no temporal fossae; mesethmoid widely exposed dorsally; frontals reduced, not in contact with maxillaries; nasal in contact with squamosal; splenial teeth present;

secondary grooves present; scales present; tentacular opening closer to external naris than to eye; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 1 species: *russelli*.

Distribution. Cameroon.

12. *Indotyphlus* Taylor 1960

Type species: *Indotyphlus battersbyi* Taylor 1960, by original designation and monotypy.

Diagnosis. Caeciliids with eye not under bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; narial plugs on tongue; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 2 species: *battersbyi*, *maharashtraensis*.

Remarks. Giri *et al.* (2004) recently described the second known species of *Indotyphlus*, noting that the narial plugs are not particularly small in either species, a feature we previously included in the generic diagnosis. We know of no uniquely derived traits.

Distribution. India, northern Western Ghats.

13. *Luetkenotyphlus* Taylor 1968.

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

Diagnosis. Caeciliids with eye not under bone; no temporal fossae; dorsal exposure of mesethmoid unknown; no splenial teeth; no secondary grooves; no scales; tentacular opening closer to eye than to external naris; an unsegmented terminal shield; no narial plugs; premaxillary-maxillary series of teeth short, not extending posterior to the choanae; no diastema between vomerine and palatine teeth; a diastema between anterior ends of the two series of vomerine teeth in adults; no terminal keel.

Content. 1 species: *brasiliensis*.

Distribution. Argentina, Brazil, Paraguay.

Remarks. Nussbaum (1986) and Nussbaum and Wilkinson (1989) used the spelling “Lutkenotyphlus” for this genus, because we assumed that Lütken is not a German word. This assumption was based on the fact that Christian Frederik Lütken, for whom the genus is named, is Danish, and his ancestry is also Danish. However, under a strict interpretation of the rules of zoological nomenclature—when it doubt consider a word with an umlaut to be a German word—our earlier spelling appears to have been an unjustified emendation.

14. *Microcaecilia* Taylor 1968

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

Diagnosis. Caeciliids with eye under bone; no temporal fossae; mesethmoid not exposed dorsally; no splenial teeth; secondary grooves

usually present, absent in one species; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; terminal keel present or absent.

Content. 5 species: *albiceps*, *rabei*, *supernumeraria*, *taylori*, *unicolor*.

Distribution. Ecuador, French Guiana, Guyana, Surinam, Venezuela.

Remarks. *Microcaecilia* lacks any known uniquely derived features supporting its monophyly. Our previous diagnosis included the absence of a terminal keel, but this is present in at least *M. unicolor* (Wilkinson, unpublished). Nussbaum (unpublished) has examined specimens from northern Brazil that appear to be assignable to *Microcaecilia*.

15. *Mimosiphonops* Taylor 1968

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

Diagnosis. Caeciliids with eye in socket, not under bone; presence or absence of temporal fossae and dorsal exposure of mesethmoid unknown, probably as in *Siphonops*; splenial teeth present; no secondary grooves; no scales; tentacular opening nearly equidistant between eye and external naris; an unsegmented terminal shield; no narial plugs; a diastema between vomerine and palatine teeth; no terminal keel.

Content. 2 species: *reinhardti*, *vermiculatus*.

Distribution. southern Brazil.

Remarks. Wilkinson and Nussbaum (1992) placed *Pseudosiphonops* in the synonymy of *Mimosiphonops* and *P. ptychodermis* in the synonymy of *M. vermiculatus*. Wake (2003) gave separate accounts for *Pseudosiphonops* and *Mimosiphonops* in her review of caecilian osteology but did not comment on the earlier proposed synonymy and presented no evidence that would count against it. *Mimosiphonops* lacks known uniquely derived traits. Within the siphonofoms (*Mimosiphonops*, *Luetkenotyphlus*, *Siphonops*) the relatively anterior tentacle position, more strongly recessed mouths, and strong diastema between the vomerine and palatine teeth are probably derived.

16. *Osaecilia* Taylor 1968

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

Diagnosis. Caeciliids with eye under bone; no temporal fossae; mesethmoid exposed dorsally; splenial teeth present; secondary grooves present; scales present; subdermal scales present or absent; tentacular opening directly below external naris, closer to naris than to eye; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel; teeth relatively few and large, replaced alternately in groups; vomeropalatine tooth row displaced posteriorly, not parallel to premaxillary-maxillary tooth row, diverging from the latter anteriorly forming an angle where the two rows meet rather than a semicircle.

Content. 9 species: *bassleri*, *elongata*, *equatorialis*, *hypereumeces*, *koepckeorum*, *ochrocephala*, *osae*, *polyzona*, *zweifeli*.

Distribution. Southern central and northern South America, Central America (Costa Rica).

Remarks. Lahanas and Savage (1992) described *O. osae* from Costa Rica since our last summary (Nussbaum and Wilkinson 1989).

17. *Parvicaecilia* Taylor 1968

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

Diagnosis. Caeciliids with eye not under bone; presence or absence of a temporal fossae and dorsal exposure of mesethmoid unknown; no splenial teeth; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; premaxillary-maxillary series of teeth short, not extending posterior to the choanae; no diastema between the vomerine and palatine teeth; no terminal keel.

Content. 2 species: *nicefori*, *pricei*.

Distribution. Colombia.

Remarks. We know of no uniquely derived traits of this poorly known genus.

18. *Praslinia* Boulenger 1909

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

Diagnosis. Caeciliids with eye not under bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; teeth small, uniform in size, more than 50 per row, except for splenials; mouth terminal; secondary grooves present; scales present; tentacular opening adjacent to anterior edge of eye; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 1 species: *cooperi*.

Distribution. Seychelles Archipelago.

19. *Schistometopum* Parker 1941

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

Diagnosis. Caeciliids with eye in socket, not under bone; no temporal fossae; mesethmoid exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 2 species: *gregorii*, *thomense*.

Distribution. Kenya, Tanzania, Gulf of Guinea islands.

Remarks. Nussbaum and Pfrender (1998) noted that *S. ephale* is a geographic variant of *S. thomense*; *S. brevirostre* is a junior synonym of *S. thomense*; and *S. garzonheydti* is a junior synonym of *Geotrypetes seraphini*. Gower and Wilkinson (2002) suggested that the species of *Schistometopum*

share a uniquely derived phallus ornamentation, and there is strong support for monophyly from molecular data (Wilkinson *et al.*, 2003b).

20. *Siphonops* Wagler 1828

Type species: *Caecilia annulata* Mikan 1820, by original monotypy.

Diagnosis. Caeciliids with eye in socket, not under bone; no temporal fossae; mesethmoid exposed dorsally; no splenial teeth; no secondary grooves; no scales; tentacular opening closer to eye than to external naris; an unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 5 species: *annulatus*, *hardyi*, *insulanus*, *leucoderus*, *paulensis*.

Distribution. Argentina, Bolivia, Brazil, Colombia, Ecuador, Guyana, Paraguay, Peru, Venezuela, and probably Uruguay, Surinam, and French Guiana.

Remarks. We know of no uniquely derived traits. The three species *annulatus*, *leucoderus*, *paulensis* have a distinctive and presumably derived colour pattern with a blue background and whitish annular ring, but this is shared with the species of *Mimosiphonops* suggesting that *Siphonops* may be paraphyletic.

21. *Sylvacaecilia* Wake 1987

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

Diagnosis. Caeciliids with eye not under bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel.

Content. 1 species: *grandisonae*.

Distribution. Ethiopia.

F. Family Typhlonectidae Taylor 1968 (Fig. 2.5 B)

Diagnosis. Gymnophiona with the same number and arrangement of skull bones as caeciliids, but pseudoectopterygoid never present and mesethmoid always covered by frontals; temporal fossae present; eye never under bone; splenial teeth present; teeth monocuspid; *m. interhyoideus* posterior short; tentacle small; choanae large with well developed valves; narial plugs present; relatively large cloacal disk; viviparous; embryonic gills fused into a large, sac-like structure on each side; undivided primary annuli only, or some primary annuli with pseudosecondary grooves; aortic arches proximal to the heart fused into an elongate *truncus arteriosus*; atrium partially divided externally.

Content. 5 genera and 12 species.

Distribution. South America.

1. *Atretochoana* Nussbaum and Wilkinson 1995.

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

Diagnosis. Typhlonectids with sealed choanae; no lungs; no pulmonary blood vessels; postcranial jaw articulation; posteriorly directed and elongate stapes; novel stapedial muscle; the tentacular aperture intermediate in position between eye and external naris; tentacular groove not covered with bone; body laterally compressed with a middorsal fin; unknown habit, but suspected to be lotic-torrential.

Content. 1 species: *eiselti*.

Distribution. 'South America'.

Remarks. The holotype of *A. eiselti* lacks detailed locality data, but is labelled "South America". Wilkinson *et al.* (1998) reported the second known specimen of *A. eiselti*, which is also without data but suspected to be from Brazil.

2. *Chthonerpeton* Peters 1879

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

Diagnosis. Typhlonectids with the tentacular aperture intermediate in position between eye and external naris; tentacular groove not covered with bone; foetal gills attaching laterally to the nuchal region, the two gill bases well separated dorsally; no lateral compression of the body; no middorsal ridge or free fold (fin); left lung rudimentary; external naris ovate; choanal valve aperture along entire length of valve; cloacal disk subcircular; semiaquatic habit.

Content. 8 species: *arii*, *braestrupi*, *exile*, *indistinctum*, *noctinectes*, *onorei*, *perissodus*, *viviparum*.

Distribution. Northern Argentina, Brazil, Ecuador, Uruguay.

Remarks. The two species *C. arii* (Cascon and Lima-Verde 1994) and *C. noctinectes* (Silva *et al.* 2003) were described since 1989. Based on specimens in Museum collections, there appears to be a number of undescribed *Chthonerpeton* (Wilkinson, unpublished). Uniquely derived traits of *Chthonerpeton* are unknown, but the type species, *C. indistinctum* lacks a distinct *m. rectus lateralis*, a highly unusual condition unknown in other caecilians. If true of the other species this would provide strong support for the monophyly of the genus.

3. *Nectocaecilia* Taylor 1968

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

Diagnosis. Typhlonectids with the tentacular aperture close behind external naris; tentacular groove partially roofed by bone in adults; fetal gills attaching dorsolaterally, the two gill bases slightly separated middorsally; no lateral compression of the body; no dorsal free fold or ridge; left lung well developed; subcircular cloacal disk; external naris subtriangular; choanal valve aperture along entire length of the valve; semiaquatic habit.

Content. 1 species: *petersii*.

Distribution. Venezuela.

Remarks. Wilkinson (1996b) placed *N. haydee* (Roze 1963) in the synonymy of *Typhlonectes natans*.

4. *Potomotyphlus* Taylor 1968

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

Diagnosis. Typhlonectids with the tentacular aperture close behind external naris; tentacular groove partially roofed with bone in adults; foetal gills unknown; body laterally compressed; middorsal free fold or ridge present; left lung well developed, dilated, much wider than right lung; head small relative to body; cloacal disk subcircular posteriorly with a narrower anterior portion; external naris subtriangular; choana extremely large; choanal valve with aperture restricted to a small funnel-like flap; aquatic habit.

Content. 1 species: *kaupii*.

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

5. *Typhlonectes* Peters 1879

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

Diagnosis. Typhlonectids with tentacular aperture close behind external naris; tentacular groove partially roofed by bone in adults; foetal gills attaching dorsally, the two gill bases fused with no separation; body laterally compressed, at least posteriorly, in adults; a middorsal ridge or free fold present; left lung well developed; cloacal disk, subcircular; external naris subtriangular; choanal valve aperture along full length of valve; habit aquatic.

Content. 2 species: *compressicauda*, *natans*.

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

Remarks. *T. cunhai* was described by Cascon *et al.* (1991) but its validity has been questioned (Wilkinson and Nussbaum 1997). Based on recent examination (Wilkinson, unpublished) we consider the holotype to be indistinguishable from *T. compressicauda* and thus place *T. cunhai* in the synonymy of *T. compressicauda* (Dumeril and Bibron, 1841). Wilkinson (1991; 1996c) provided formal synonymies for several species recognised by Taylor (1968) but not included in our previous treatment (Nussbaum and Wilkinson 1989). Wilkinson and Nussbaum (1999) identified nine uniquely derived characters supporting monophyly of the genus.

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