Developmental morphological diversity in caecilian amphibians: systematic and evolutionary implications

Müller, H.

Citation

Müller, H. (2007, November 8). *Developmental morphological diversity in caecilian amphibians: systematic and evolutionary implications*. Leiden University Press. Retrieved from https://hdl.handle.net/1887/12462

CHAPTER 1 – INTRODUCTION

Caecilian amphibians (Gymnophiona) – an introduction

Caecilian or Gymnophiona, together with frogs (Anura) and salamanders (Caudata), constitute the three living orders of the Amphibia. Caecilians are often thought of as the least known major group of tetrapods, and certainly of the three living orders of amphibians. They are elongated snake-like amphibians completely lacking limbs and girdles and they have a primarily terrestrial, surface-cryptic or burrowing lifestyle as adults, except for the Typhlonectidae, a South America group that are secondarily aquatic or semiaquatic (Taylor, 1968; Wilkinson and Nussbaum, 1999). The majority of the approximately 170 recognized species inhabit the wet tropics of Central and South America, Africa and Asia, with some species also reaching the subtropics of South America and Asia (Wilkinson and Nussbaum, 2006). The current distribution is commonly accepted to reflect an Gondwanan origin of the group (Duellman and Trueb, 1986; Hedges et al., 1993; Wilkinson et al., 2002; San Mauro et al., 200).

Compared to frogs and salamanders, very little information is available on many aspects of caecilian biology (see Himstedt, 1996 for most comprehensive recent review). Their secretive, mostly burrowing lifestyle and tropical distribution are very likely the main reason that caecilians are rarely encountered in the field, unless special sampling effort is made (e.g. Malonza and Müller, 2004; Measey, 2004; Gower and Wilkinson, 2005), and thus likely responsible for their poor representation in museum collections. Many morphological specialisations of caecilians are also attributable to their burrowing lifestyle, including their compact and heavily ossified skull that is unlike that of salamanders and especially frogs (Taylor, 1969a; Trueb, 1993). Caecilians possess a unique sensory organ, the tentacle, which is derived from structures of the eye and associated musculature and glands (Sarasin and Sarasin, 1887-1890; Billo and Wake, 1987) and which serves as chemo-mechanosensory organ that is probably used by the animal to detect surface-borne scent molecules and also to orient itself within its burrow (Himstedt and Simon, 1995). Six families of caecilians are currently recognized (Wilkinson and Nussbaum, 2006; but see Frost et al. 2006). Although caecilians are relatively uniform in their external appearance (Himstedt, 1996), recent research has uncovered a remarkable degree of morphological (e.g. Nussbaum and Wilkinson, 1995; Wilkinson, 1992a; Gower and Wilkinson, 2002), ecological (e.g. Gower et al., 2004, Jones et al., 2006), and life history diversity (Wake, 1977; Loader et al., 2003; Kupfer et al., 2004, 2006;).

The fossil record of caecilians is poor and consists exclusively of isolated vertebrae of uncertain affinities from the Palaeocene of Brazil and Bolivia (Estes and Wake, 1972; Rage, 1986; Rage, 1991), the Upper Cretaceous of Sudan (Evans et al., 1996; Werner, 1994) and the Miocene of Colombia (Hecht and LaDuke, 1997). Further fossil vertebrae referred to *Dermophis* are known from the Quaternary of Mexico (Wake et al., 1999). Two putative stem-group caecilians exist. The older, *Eocaecilia micropodia* from the Lower Jurassic of Arizona, USA, is known from about 30 specimens of variable completeness. It possesses limbs, albeit reduced in size, and shows a modestly elongated trunk (Jenkins and Walsh, 1993). The second taxon, *Rubricacaecilia monbaroni* from the Lower Cretaceous of Morocco, is known from several isolated bone fragments, and it might also have limbs (Evans and Sigogneau-Russel, 2001). Recent time tree analyses suggest that the crown group had already started to diversify at the time the aforementioned stem group representatives existed (San Mauro et al., 2005; Roelants et al., 2007).

Phylogenetic relationships of caecilians

The phylogenetic relationships of caecilians with regard to other amphibians have been a matter of debate for well over a century. They were initially considered to be degenerate snakes, until Johannes Müller (1831a) discovered gill slits in a larva of an ichthyophiid and thus established that caecilians are amphibians. The exact relationships of caecilians to other amphibians, however, remained controversial. Some authorities considered caecilians to be closely related to certain Palaeozoic forms (e.g. Wiedersheim, 1879, Kingsley, 1902), whereas others considered them to be closely related to, or even within, salamanders (Sarasin and Sarasin, 1887-1890). In 1901, Gadow proposed the Lissamphibia concept in its current usage: all three Recent orders of living amphibians form a monophyletic group that arose from a single lineage of Palaeozoic amphibians. This was in contrast to Haeckel (1866) who originally proposed Lissamphibia as the name for the group comprising frogs and salamanders, to the explicit exclusion of caecilians. The Lissamphibia concept (sensu Gadow, 1901), however, was largely ignored during the first half of the 20th century and many researchers propagated a closer relationship of caecilians with various Palaeozoic groups, than with frogs and salamanders. The most prominent of these were Harry Marcus and his students, who studied various aspects of caecilian anatomy and development, and considered caecilians to be living representatives of so-called stegocephalian amphibians, in particular aistopods (e.g. Eifertinger, 1933; Marcus, 1933; Marcus et al., 1935).

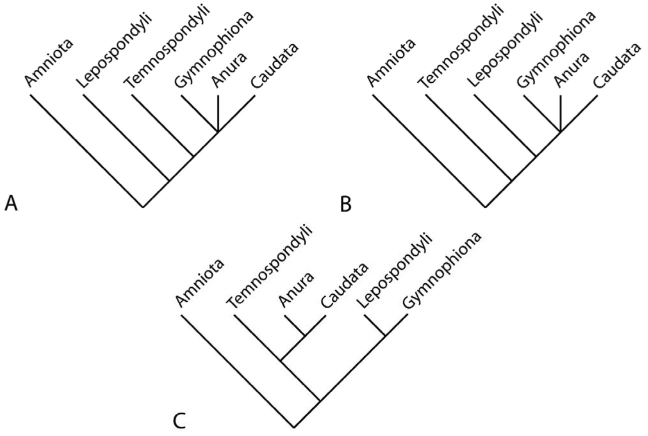

Fig. 1. Phylogenetic relationships of living amphibians: **A** Temnospondyls are ancestors of a monophyletic Lissamphibia, **B** Lepospondyli are ancestors of a monophyletic Lissamphibia, **C** Lissamphibians are diphyletic, frogs and salamanders related to temnospondyls, caecilians related to lepospondyls. See text for further

In 1963, Parsons and Williams revived the Lissamphibia as a monophyletic group comprising all Recent amphibians and provided a large number of characters in support of their monophyly. Most subsequent workers have accepted the Lissamphibia although different Palaeozoic groups have been proposed as being ancestral to the Lissamphibia (see Schoch and Milner, 2004, for most recent comprehensive review). The majority of studies considered Lissamphibians to be derived from Temnospondyli (e.g. Parsons and Williams, 1963; Milner, 1988; Bolt, 1991; Trueb and Cloutier, 1991; Ruta et al., 2003; Schoch and Milner, 2004), whereas Laurin (1998) and Laurin and Reisz (1997) recently proposed an origin of the Lissamphibia from among the Lepospondyli. Other authors, however, considered Lissamphibia to be paraphyletic with regard to Palaeozoic amphibians and considered frogs, salamanders and caecilians to be derived from different Palaeozoic lineages. According to this so-called diphyly hypothesis, frogs and salamanders arose from temnospondyl dissorophoids and caecilians from lepospondyl microsaurs (Carroll, 2000; Carroll et al., 2004; see Fig. 1C), with which they share at least a superficially similar skull morphology (see Fig. 4). Nussbaum (1983) considered lepospondyl lysorophids to be the closest relatives of caecilians. Løvtrup (1985), however, considered caecilians to be more closely related to amniotes than to other caecilians, while Jarvik (1980) considered frogs on the one hand and salamanders and caecilians on the other to be independently derived from osteolepiform and, respectively, porolepiform sarcopterygians. Both hypotheses received no subsequent support and are not currently in fashion.

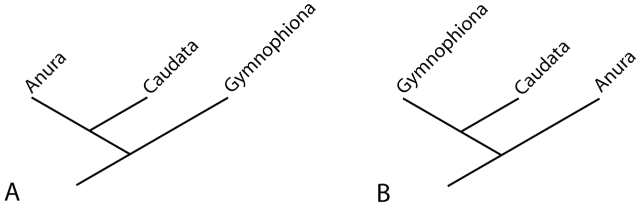

Fig. 2. A The Batrachia hypothesis: frogs and salamanders are sistergroups to the exclusion of caecilians. **B** The Procera hypothesis: caecilians and salamanders form a monophyletic group to the exclusion of frogs.

Two competing hypotheses currently exist regarding the relationships of the three lissamphibian groups – frogs, salamanders and caecilians – to each other. Most studies based on both morphological (e.g. Rage and Janvier, 1982; Milner, 1988; McGowan and Evans, 1995; Trueb and Cloutier, 1991) and molecular data (e.g. Venkatesh et al. 2001; Zardoya and Meyer 2001; San Mauro et al 2005; Roelants et al 2007) support frogs as the sister group of salamanders, to the exclusion of caecilians (Fig. 1A). The clade comprising frogs and salamanders has been termed Batrachia (Milner, 1988). Earlier molecular studies (e.g. Hedges et al., 1990; Hedges and Maxson, 1993; Feller and Hedges, 1998), which used comparatively small datasets relative to more recent studies (e.g. San Mauro et al 2005; Roelants et al 2007), recovered caecilians as the sister group of salamanders, to the exclusion of frogs (Fig. 1B). This Procera hypothesis, named for the clade comprising caecilians and salamanders, also received some limited morphological support based on the skeletal anatomy of *Eocaecilia micropodia*, a putative stem group caecilian (Jenkins and Walsh, 1993). The question of the relationships among the three living orders and to Palaeozoic groups is further compounded by the poor fossil record of frogs, salamanders and especially caecilians. It is obvious that all three groups are very different in their general morphology and many aspects of their biology, and that each group seems to have acquired their specialized morphology at a very early point in their evolutionary history (Zardoya and Meyer, 2001; Schoch and Milner, 2004; Roelants et al., 2007), with hardly any plausible intermediates being currently known.

Caecilian intrarelationships

Although caecilians made an early appearance in the scientific literature (Seba, 1735), their alpha- and higher level diversity was long presumed to be relatively low. An important early student of caecilian systematics was Wilhelm C. H. Peters, who described several new species and genera and also provided the first hypothesis of caecilian intrarelationships (e.g. Peters, 1880). During the first half of the 20th century Emmett R. Dunn (e.g. 1942) made important contributions to the systematics and taxonomy of American caecilians while Arthur Loveridge (e.g. Loveridge, 1936) and especially H. W. Parker (e.g. 1936; 1958) advanced the understanding of African caecilians. The most important contribution to caecilian taxonomy was made by Edward H. Taylor, who not only revised and described many of the currently recognized species (e.g. Taylor 1960, 1968, 1969b), but also erected the families Ichthyophiidae and Typhlonectidae (Taylor, 1968), and Scolecomorphidae (Taylor, 1969c). Subsequently, Nussbaum (1977) recognized the Rhinatrematidae as a family distinct from ichthyophiid caecilians. In 1979, Nussbaum erected the family Uraeotyphlidae to accommodate the genus *Uraeotyphlus*, which had previously been placed in the Caeciliidae. Four of these families are relatively small and have more restricted distributions: the Rhinatrematidae (two genera, nine species) and Typhlonectidae (five genera, 13 species) occur in South America, the Uraeotyphlidae (one genus, five species) in India, while the Scolecomorphidae (two genera, six species) are confined to mountainous areas of East and West Africa (Wilkinson and Nussbaum, 2006). The second largest family, the Ichthyophiidae (two genera, 37 species) occur in South and South East Asia. By far the largest and most heterogeneous family is the Caeciliidae (21 genera, 100+ species), which occur in Central and South America, Africa, the Seychelles and India (Wilkinson and Nussbaum, 2006).

In contrast to frogs and salamanders, where various hypothesis of familial relationships have been proposed (e.g. Ford and Cannatella, 1993; Weisrock et al., 2005; Wiens et al., 2005; Frost et al., 2006), estimates of familial relationships in caecilians have been relatively stable. There is numerous morphological and molecular evidence that Rhinatrematidae are the sister group to all other living caecilians (e.g. Nussbaum, 1977; Wilkinson, 1992b; Wilkinson, 1996; Hedges et al., 1993; San Mauro et al. 2005; Roelants et al. 2007). Nussbaum (1979), and Duellman and Trueb (1986) and Hillis (1991), using family level taxa and a subset of characters from Nussbaum (1979), recovered a clade comprising the Caeciliidae, Typhlonectidae and Scolecomorphidae, a group informally known as the advanced (Nussbaum, 1991) or higher (San Mauro et al., 2004) caecilians. In their analyses, Uraeotyphlidae, Ichthyophiidae and Rhinatrematidae were recovered as successively more distant outgroups to the higher caecilians. Wilkinson and Nussbaum (1996) and Wilkinson (1997) found strong support for a sister group relationship of Ichthyophiidae and Uraeotyphlidae (=Diatria, Wilkinson and Nussbaum, 2006), which together form the sister group to higher caecilians (=Teresomata, Wilkinson and Nussbaum, 2006). A monophyletic Diatria have been recovered as the sister group to

Teresomata in all subsequent molecular studies of caecilian relationships (e.g. Wilkinson et al., 2002, 2003; San Mauro et al., 2004; Frost et al., 2006; Roelants et al., 2007). Recently, Frost et al (2006) synonymized Uraeotyphlidae with Ichthyophiidae based on the apparent paraphyly of *Ichthyophis* with regard to *Uraeotyphlus* (Gower et al., 2002; Frost et al., 2006). They further synonymized both the Scolecomorphidae and Typhlonectidae with the Caeciliidae because of the paraphyly of the latter regarding the former two groups. However, while the paraphyly of Caeciliidae with regards to Typhlonectidae has long been recognized (e.g. Nussbaum, 1979; Hedges et al., 1993; Wilkinson, 1997; Wilkinson et al., 2002; Wilkinson et al., 2003), the paraphyly of Ichthyophiidae with regard to Uraeotyphlidae (Gower et al., 2002; Frost et al., 2006) has not been universally demonstrated (see Roelants et al., 2007) and merits further investigation. Further uncertain is the position of the Scolecomorphidae, which might be either basal to Caeciliidae plus Typhlonectidae (Roelants et al., 2007) or within Caeciliidae (Wilkinson et al., 2003; Frost et al., 2006). Here I follow the taxonomy of Wilkinson and Nussbaum (2006).

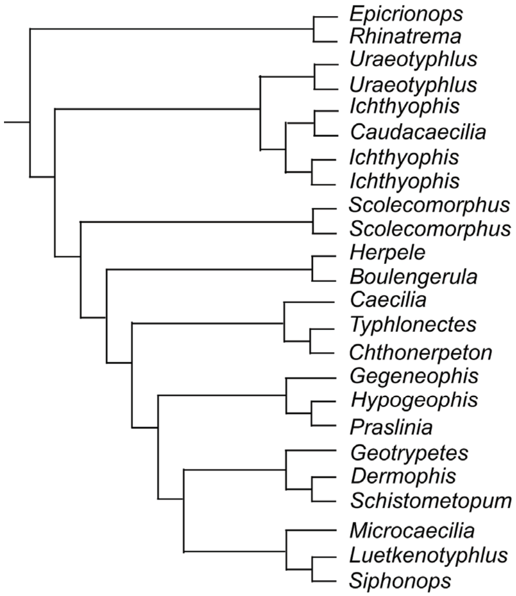

Fig. 3. Phylogenetic relationships of caecilians according to Roelants et al. (2007).

Since Nussbaum (1979) presented the first numerical analysis of caecilian intrarelationships, several studies have addressed this issue focussing on either larger scale relationships (e.g. Hay et al., 1995; Hedges and Maxson, 1993; Hedges et al., 1993; Frost et al., 2006; Roelants et al. 2007), intrafamilial or intrageneric relationships (e.g. Straub, 1985; Wilkinson and Nussbaum, 1999; Gower et al., 2002) or certain geographic areas (e.g. Hass et al., 1993; Gower et al., 2002; Wilkinson et al., 2002, 2003; Wake et al., 2004). Most of these studies are particularly interesting with regard to the relationships within the Caeciliidae, which is by far the largest and most diverse group in terms of ecology, morphological differentiation or life-history (Himstedt, 1996; Wilkinson and Nussbaum, 2006). While the position of some taxa like *Siphonops* is variable in several analyses (e.g. Wilkinson et al., 2003; Frost et al., 2006; Roelants et al., 2007), other relationships are consistently recovered in various analyses using different datasets, which lends some confidence to these results. Among these are the monophyly of the Seychellean caeciliids (e.g. Hass et al., 1993; Wilkinson et al., 2003), the sister group relationship of the Seychellean clade and *Gegeneophis* (e.g. Wilkinson et al., 2003; Roelants et al., 2007), the grouping of *Herpele* and *Boulengerula*, though deeply divergent, (Wilkinson et al., 2003; Frost et al., 2006; Roelants et al., 2007), and the sister group relationship of *Caecilia* and Typhlonectidae that renders the Caeciliidae paraphylectic (Hedges et al., 1993; Wilkinson et al., 2003; Frost et al., 2006; Roelants et al., 2007). Figure 3 shows the most recent phylogeny recovered by Roelants et al. (2007) using a large molecular data set and the most diverse sampling to date.

Skull morphology of caecilians

All caecilian species possess a heavily ossified skull (see Fig. 4 A, B) that is in stark contrast to the loftier and almost fragile skull morphologies seen especially in most frogs (Trueb, 1993). The fenestration of the cheek region is strongly reduced (a condition known as zygokrotaphy) and most species have a temporal region that is completely covered by bone (stegokrotaphy). Even the orbit is be completely covered by bone in some species with greatly reduced eyes. The peculiar morphology of the caecilian skull is considered by virtually all authors to be an adaptation to a burrowing lifestyle (e.g. Müller, 1831b; Peters, 1880; Marcus et al., 1933; Taylor, 1969a; Duellman and Trueb, 1986; Nussbaum, 1998; Nussbaum and Wilkinson, 1989). There appears to be a correlation between the degree of the reduction of the temporal gap or the recession of the mouth and the degree of burrowing ability and subterranean lifestyle (Ramaswami, 1941; Taylor, 1969a; Teodecki et al., 1998; Gower et al., 2004).

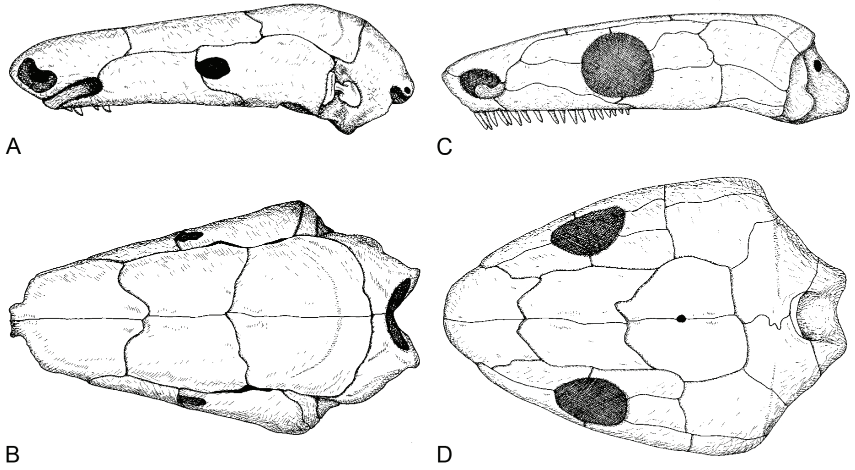

Fig. 4. Lateral (A) and dorsal (B) view of the skull of the adult caecilian *Hypogeophis rostratus* (modified from Taylor, 1969a). Lateral (C) and dorsal (D) view of the skull of the lepospondyl microsaur *Rhynchonkos* (from Carroll and Currie, 19675).

Caecilian skull morphology has been of considerable interest to many morphologists since the early days of comparative morphology, and a surprising amount of literature on adult skull morphology is available (see Straub, 1985 for a detailed list of the older literature on caecilian skull morphology and Wake, 2003 for a more recent summary). Dugés (1835) was among the first to provide a detailed examination of the caecilian skull. He and others (e.g. Wiedersheim, 1879) proposed that some of the large ossifications of the adult caecilian skull, such as the os basale (comprising the posterior part of the endocranium including the otic capsules as well as the floor of the braincase) are likely the product of a fusion of several individual ossifications during ontogeny. The composite nature of several of the bones that form the caecilian cranium was later corroborated by ontogenetic information (e.g. Peter, 1898; Eifertinger, 1933; Marcus et al., 1935). In addition to the aforementioned os basale, all adult caecilians have the lower jaw elements fused into two large bones, the pseudodentary and pseudoangular, and the maxilla and palatine are fused to form the maxillopalatine in the adult cranium. The sphenethmoid has further been thought to be comprised of several individual endocranial ossifications (Marcus et al. 1935, Wake and Hanken, 1982; Müller et al., 2005) although there is controversy regarding how many elements are actually involved. These so-called compound bones are characteristic of the caecilian cranium and there is a phylogenetic trend towards an increased fusion of bones within the group. Rhinatrematids, ichthyophiids, uraeotyphlids and scolecomorphids are all characterized by separate nasal, premaxilla and septomaxilla bones, whereas the anterior snout region of caeciliids and typhlonectids is formed by the paired nasopremaxillae (Marcus et al., 1933; Taylor 1969a). Rhinatrematids, ichthyophiids, uraeotyphlids and scolecomorphids retain separate prefrontal bones that are absent in caeciliids and typhlonectids. However, a small element in a similar position but thought to be a lacrimal is incorporated into the maxillopalatine in caeciliids (Marcus et al., 1935; Müller et al., 2005). Ichthyophiids and uraeotyphlids further possess a circumorbital thought to be homologous with a postfrontal (Trueb, 1993).

A further phylogenetically variable feature is the degree of the closure of the cheek region (Taylor, 1969a; Trueb, 1993). Several taxa (rhinatrematids, uraeotyphlids, typhlonectids, *Scolecomorphus*, *Geotrypetes*) have zygokrotaphic skulls, in which a temporal gap separates the squamosal and parietal, whereas the remaining taxa have a stegokrotaphic or at least weakly stegokrotaphic (some ontogenetic variation is bound to occur) skull that has a completely closed cheek region. Zygokrotaphy in rhinatrematids is different from that of the remaining zygokrotaphic taxa in that the primary jaw adductor musculature extends onto the dorsal side of the skull (Nussbaum, 1983). Most authorities consider zygokrotaphy as exhibited by rhinatrematids to be the ancestral condition for Recent caecilians with stegokrotaphy being secondarily evolved (e.g. Sarasin and Sarasin, 1887-1890; Peter, 1898; de Beer, 1937; Ramaswami, 1941; Nussbaum, 1977, 1983; Wake and Hanken, 1982), although some have argued for stegokrotaphy as the plesiomorphic condition (e.g. Marcus et al., 1933, 1935; Carroll and Currie, 1975). The reconstruction of the ancestral condition is complicated by the recent discovery of the putative stem line caecilian *Eocaecilia micropodia* that has a clearly stegokrotaphic skull, which has been considered as a decisive support for stegokrotaphy being the ancestral condition in caecilians (Jenkins and Walsh, 1993; Carroll, 2000).

Development of the caecilian skull

Due to the paucity of suitable material, very few studies exist that have described the development of the skull in caecilians in any detail. Most studies of caecilian skull development, especially in the older literature, focus on either specific anatomical regions and do not present a coherent overview of cranial development (e.g. Peter, 1898; Jurgens, 1971; Reiss, 1996) or are based on single or few specimens (e.g. Winslow, 1898; Marcus et al., 1935; Ramaswami, 1948). Only relatively recently have larger developmental series been examined and described in detail (Wake and Hanken, 1982; Müller et al., 2005). Wake et al. (1985) further described skull development in *Typhlonectes compressicauda* but focused only on the regression of the cartilage associated with increasing ossification during development. Interestingly, skull development and life-history seem to be linked as indicated by different ossification sequences in direct-developing and viviparous species (Wake and Hanken, 1982; Müller et al., 2005), but this is based on very sparse taxon sampling.

The most influential early work on caecilian skull development was the account of Marcus et al. (1935) on the development of the skull in *Hypogeophis rostratus* and *Grandisonia alternans*, which was at this time considered to be a species of *Hypogeophis*. In this and previous papers (e.g. Eifertinger, 1933; Marcus, 1933) Marcus and co-authors described the skull and lower jaw as being composed of several individual bones that fuse during ontogeny to form the compound bones of the adult skull. Although the composite nature of several of the adult skull bones had already been demonstrated by Peter (1898), the high number of separate ossification centres reported by Marcus et al. (1935), and thus the high extent of fusion occurring in the caecilian cranium, aroused much interest and was highly influential in the debate concerning their systematic position (e.g. de Beer, 1937). More importantly, the results of Marcus et al. (1935) were often seen as representing the standard in cranial development of Gymnophiona. Accordingly, in many subsequent studies on caecilian skull morphology (e.g. Ramaswami 1948; Brand 1956; Visser 1963) authors commented on several fused bones, the presence of which was more assumed than observed. Subsequent workers, however, pointed out inconsistencies (Brand, 1956) and, more recently, incongruence (Wake and Hanken, 1982; Müller et al., 2005) with results reported by Marcus and students.

Caecilian life-history

Despite being a comparatively small group, caecilians exhibit all the major life history modes seen in frogs and salamanders: oviparity with a free-living larva (e.g. Sarasin and Sarasin, 1887-1890), oviparity with direct development (e.g. Brauer, 1897) and viviparity (e.g. Peters, 1874). Fertilization is internal in caecilians via the phallus, a copulatory organ derived from parts of the hindgut and unique within lissamphibians (Gower and Wilkinson, 2002). Eggs of oviparous species are usually large (Exbrayat, 2006) and females guard their eggs where known (e.g. Sarasin and Sarasin, 1887-1890; Brauer, 1897; Sanderson, 1937, Kupfer et al., 2004, 2006). Species with free-living larvae undergo a metamorphosis to attain the adult-like morphology, although very little information is available on caecilian metamorphosis in general (e.g. Fox, 1987; Fritzsch, 1990; see also Wake, 2006). Viviparous species are characterized by smaller eggs and various forms of maternally provided, intraoviductal nutrition (Wake, 1977). Several recent studies have further drawn attention to a previously unsuspected degree of reproductive diversity among caecilians. O'Reilly et al. (1998) described altricial young in the viviparous *Geotrypetes seraphini* and Loader et al. (2003) described a young *Scolecomorphus vittatus* and suggested that two different modes of viviparity occur in caecilians. One mode is characterized by large young that are independent at birth whereas species of the second mode give birth to altricial young that receive some form of extended post-parturition parental care. Kupfer et al. (2006) described altricial young in a direct developing caecilian, *Boulengerula taitanus* from Kenya that feed on the specially modified skin of their mother and is further characterized by so-called foetal teeth, and suggested that this life-history might have been a plausible intermediate step in the evolution of viviparity in caecilians.

Although the reproductive mode is known for fewer than half of the nominal species (Wake, 2006), interpolation from species with known reproductive mode to congeners provides a reasonable estimate of the distribution of reproductive modes in caecilians. The majority of species appear to be oviparous with direct development, followed by oviparity with a free-living larva (Wilkinson and Nussbaum, 1998). Viviparity is found in approximately one fifth of all species, which is a considerably higher proportion than in frogs or salamanders, where true viviparity is exceedingly rare (Wake, 1977). The phylogenetic distribution of the main reproductive modes in caecilians suggests several instances of independent evolution of viviparity and possibly direct development (Wilkinson et al. 2003; see Chapters 4 and 8). Life-history is further likely to have an impact on skull development and the limited available information seems to indicate differences between viviparous and non-viviparous species at least. Wake and Hanken (1982) discovered an altered sequence of skull ossification in the viviparous *Dermophis mexicanus*, in which bones involved in jaw articulation develop early as compared to non-viviparous species, and attributed this to active intraoviductal feeding early during ontogeny.

Aims of this thesis

The aims of this thesis are threefold: firstly to investigate the development of the caecilian skull in order to address the inconsistencies between earlier investigations (e.g. Marcus et al., 1935) on caecilian skull development and more recent studies (Wake and Hanken, 1982; Müller et al., 2005), secondly to investigate the metamorphosis of the caecilian skull and its associated musculature in species with free-living aquatic larvae in order to analyse and document the changes occurring during metamorphosis and their bearing on interpretations of caecilian skull evolution, and thirdly to investigate the influence of different reproductive modes on the development of the skull. Chapter 1 provides a general introduction to caecilian amphibians and their inter- and intrarelationships. It further highlights the particularities of the caecilian skull compared to other recent and fossil amphibians, and summarizes current knowledge about its development, and also provides a short introduction to caecilian life-history. Chapter 2 investigates the development of the skull, lower jaw and hyobranchial skeleton of *Hypogeophis rostratus*, which was the subject of extensive study by the Marcus school during the 1920s and 1930s. Marcus and his students reported a surprisingly high number of separate ossifications that occur during the development of the skull in this and a closely related species. Their results proved very influential in the debate about the phylogenetic position of caecilians and the evolution of their unique skull morphology, although more recent studies (Wake and Hanken, 1982; Müller et al., 2005) have failed to confirm several of the observations of Marcus and his students. Chapter 3 investigates the morphology of larvae and adults of all taxa known to have a biphasic life-history. The more basal branching caecilian taxa Rhinatrematidae, Ichthyophiidae and Uraeotyphlidae (as well as several caeciliids) are characterised by oviparity with a free-living, usually aquatic larva that subsequently undergoes a metamorphosis to attain the adult-like morphology. Metamorphosis in caecilians is very poorly known, with no information being available for many of the taxa concerned. The metamorphic changes are analysed and their bearing on the ground pattern of the cranium of caecilians addressed. The following three chapters focus on aspects of the developmental diversity of caecilians. Chapter 4 compares the posthatching development of the skull in two different direct-developing species with that of a species with free-living larvae. Chapter 5 describes the remarkable form of post-hatching parental care in *Boulengerula taitanus* that involves juveniles feeding on their mother's own skin, while Chapter 6 describes and analyses the unusual morphology of the head in foetal and juvenile *Scolecomorphus kirkii*. Chapter 7 provides a synopsis of the key findings of this thesis and provides a look forward to the future of studies on caecilian development.

References

Billo R, Wake MH. 1987. Tentacle development in *Dermophis mexicanus* (Amphibia, Gymnophiona) with a hypothesis of tentacle origin. J Morphol 192:101–110.

Bolt JR. 1991. Lissamphibian origins. In: Schultze H-P Trueb L (eds.) Origins of the Higher Groups of Tetrapods, pp. 194–222.

Brand DJ. 1956. The cranial morphology of *Scolecomorphus ulugurensis* (Barbour and Loveridge). Ann Univ Stellenbosch 32(A):1–25.

Brauer A. 1897. Beiträge zur Kenntniss der Entwicklungsgeschichte und der Anatomie der Gymnophionen. Zool Jahrb Anat 10:277–472.

Carroll, R.L. 2000. *Eocaecilia* and the origin of caecilians. In: Heatwole H, Carroll RL (eds.) Amphibian biology, Vol. 4: Palaeontology. pp. 1402–1411. Surrey Beatty & Sons, Chipping Norton.

Carroll RL, Currie PJ. 1975. Microsaurs as possible apodan ancestors. Zool J Linn Soc 57:229–247.

Carroll RL, Boisvert C, Bolt J, Green DM, Philip N, Rolian C, Schoch RR. 2004. Changing patterns of ontogeny from osteolepiform fish through Permian tetrapods as a guide to the early evolution of land vertebrates. In Arratia G, Wilson MVH, Cloutier R. (eds.) Recent advances in the origin and early radiation of vertebrates. Pp 321–343. Pfeil, Munich.

de Beer GR. 1937. The development of the vertebrate skull. Oxford: Oxford University Press. 554 p.

Duellmann WE, Trueb L .1986. Biology of amphibians. New York: McGraw–Hill Book Co. 670 p.

Dugès A. 1835. Recherches sur l'ostéologie et la myologie des Batrchiens à leurs différens âges. Mém prés a l'acad sc Paris sc math et phys 6:21–209.

Dunn ER. 1942. The American caecilians. Bull Mus Comp Zool 91:437-540.

Eifertinger L. 1933. Die Entwicklung des knöchernen Unterkiefers von *Hypogeophis*. Beitrag zur Kenntnis der Gymnophionen XX. Z Anat Entwicklungsgesch 101:534–552.

Estes R, Wake MH. 1972. The first fossil record of caecilian amphibians. Nature 239:228–231.

Evans SE, Milner AR, Werner C. 1996. Sirenid salamanders and a gymnophionan amphibian from the Cretaceous of the Sudan. Paleontol 39:77–95.

Evans SE, Sigogneau-Russel D. 2001. A stem-group caecilian (Lissamphibia: Gymnophiona) from the Lower Cretaceous of North Africa. Paleontol 44:259–273.

Exbrayat J-M. 2006 Modes of parity and oviposition. In: Exbrayat J-M, editor. Reproductive Biology and Phylogeny of Gymnophiona (Caecilians). Enfield: Science Publishers. p. 303–323.

Ford LS, Canatellla DC. 1993. The major clades of frogs. Herpetol Monogr 7:94–117.

Feller AE, Hedges SB. 1998. Molecular evidence for the early history of living amphibians. Mol Phylogenet Evol 9**:**509–516.

Fox H. 1987. On the fine structure of the skin in larval, juvenile and adult Ichthyophis (Amphibia: Caecilia). Zoomorphology 107:67–76.

Fritzsch B. 1990. The evolution of metamorphosis in amphibians. J Neurobiol 21:1011–1021.

Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, de Sa RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto B, Moler P, Drewes RC, Nussbaum RA, Lynch J, Green DM, Wheeler WC. 2006. The amphiban tree of life. Bull Am Mus Nat Hist 297:1–370.

Gadow H. 1901. Amphibia and reptiles. London, Macmillan & Co. 668 pp.

Gower DJ, Wilkinson M. 2002. Phallus morphology in caecilians and its systematic utility. Bull Nat Hist Mus (Zool). 68:143–154.

Gower DJ, Wilkinson M. 2005. Conservation biology of caecilian amphibians. Conserv Biol 19:45–55.

Gower DJ, Kupfer A, Oommen OV, Himstedt W, Nussbaum RA, Loader SP, Presswell B, Müller H, Krishna SB, Boistel R, Wilkinson M. 2002. A molecular phylogeny of ichthyophiid caecilians (Amphibia: Gymnophiona: Ichthyophiidae): Out of India or out of Eurasia? Proceedings of the Royal Society London, Series B 269:1563–1569.

Gower DJ, Loader SP, Moncrieff CB, Wilkinson M. 2004. Niche separation and comparative abundance of *Boulengerula boulengeri* and *Scolecomorphus vittatus* (Amphibia: Gymnophiona) in an East Usambara forest, Tanzania. Afr J Herpet 53:183–190.

Haeckel E. 1866. Generelle Morphologie der Organismen. Zweiter Band. Allgemeine Entwickelungsgeschichte der Organismen. Berlin: Georg Kramer. 462 pp.

Hass CA, Nussbaum RA, Maxson LR. 1993 Immunological insights into the evolutionary history of caecilians (Amphibia: Gymnophiona): relationships of the Seychellean caecilians and a preliminary report on family-level relationships. Herpetol Monogr 7:56–63.

Hay JM, Ruvinsky I, Hedges SB, Maxson LR. 1995. Phylogenetic relationships of amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA. Mol Biol Evol 12:928–937.

Hecht M, LaDuke TC. 1997. Limbless tetrapods. In: Kay RF, Madden RH, Cifelli RL, Flynn JJ (eds.) Vertebrate paleontology in the neotropics. The Miocene fauna of La Venta, Colombia. Smithsonian Institution Press, Washington.

Hedges SB, Maxson LR. 1993. A molecular perspective on lissamphibian phylogeny. Herpetol Monogr 7:27–42.

Hedges SB, Moberg KD, Maxson LR. 1990. Tetrapod phylogeny inferred from 18s and 28s ribosomal RNA sequences and a review of the evidence for amniote relationships. Mol Biol Evol 7:607–633.

Hedges SB, Nussbaum RA, Maxson LR. 1993 Caecilian phylogeny and biogeography inferred from mitochondrial DNA sequences of the 12s and 16s rRNA genes (Amphibia: Gymnophiona). Herpetol Monogr 7:64–76.

Hillis DM. 1991. The phylogeny of amphibians: current knowledge and the role of cytogenetics. In: Sessions SK, Green DM (eds.) Amphibian cytogenetics. Academic Press, San Diego. Pp. 7–31.

Himstedt W. 1996. Die Blindwühlen. Westarp, Magdeburg.

Himstedt W, Simon D. 1995. Sensory basis of foraging behaviour in caecilians (Amphibia: Gymnophiona). Herpetol J 5:266–270

Jarvik E. 1980. Basic Structure and Evolution of Vertebrates. Vol I. Academic Press, London, New York, Toronto, Sydney and San Francisco, 575 pp.

Jenkins FA, Walsh DM. 1993. An Early Jurassic caecilian with limbs. Nature 365:246–249.

Jones DT, Loader, SP, Gower DJ. 2006. Trophic ecology of East African caecilians (Amphibia: Gymnophiona), and their impact on forest soil invertebrates. J Zool 269:117–126.

Jurgens JD. 1971. The morphology of the nasal region of Amphibia and its bearing on the phylogeny of the group. Ann Univ Stellenbosch 46:1–146.

Kingsley JS. 1902. The systematic position of the caecilians. Tufts Coll Studies, Sci Ser 7:323–344.

Kupfer A, Nabhitabhata J, Himstedt W. 2004. Reproductive ecology of female caecilian amphibians (genus *Ichthyophis*): a baseline study. Biol J Linn Soc 83:207–217.

Kupfer A, Müller H, Antoniazzi MM, Jared JC, Greven H, Nussbaum RA, Wilkinson M. 2006. A novel form of parental investment by skin feeding in a caecilian amphibian. Nature 440:926–929.

Laurin M. 1998. The importance of global parsimony and historical bias in understanding tetrapod evolution. Part I. Systematics, middle ear evolution and jaw suspension. Ann Sci Nat 1998:1–42.

Laurin M, Reisz R. 1997. A new perspective on tetrapod phylogeny. In: Sumida S, Martin KL (eds). Amniote origins – completing the transition to land. Acad Press, New York. Pp 9–59.

Loader SP, Wilkinson M, Gower DJ, Msuya CA. 2003. A remarkable young *Scolecomorphus vittatus* (Amphibia: Gymnophiona: Scolecomorphidae) from the North Pare Mountains, Tanzania. J Zool Lond 259:93–101.

Løvtrup S. 1985. On the classification of the taxon Tetrapoda. Syst Zool 34:463–470.

Loveridge A. 1936. Scientific results of an expedition to rainforest regions in eastern Africa. VII Amphibians. Bull Mus Comp Zool Harvard 79:369–430.

Marcus H. 1933. Zur Entstehung des Unterkiefers von *Hypogeophis*. Beitrag zur Kenntnis der Gymnophionen XX. Anat Anz 77:178–184.

Marcus H, Stimmelmayr E, Porsch G. 1935. Die Ossifikation des Hypogeophisschädels. Beitrag zur Kenntnis der Gymnophionen XXV. Gegenbaurs Morphol Jb 76:375–420.

Marcus H, Winsauer O, Hueber A. 1933. Der kinetische Schädel von *Hypogeophis* und die Gehörknöchelchen. Beitrag zur Kenntnis der Gymnophionen XVIII. Z Anat Entwicklungsgesch 100:149–193.

Malonza PK, Müller H. 2004. A rediscovery after two decades: the Changamwe lowland caecilian *Boulengerula changamwensis* Loveridge, 1932 (Amphibia: Gymnophiona: Caeciliidae). J East Afr Nat Hist 93:57–61.

McGowan G, Evans SE. 1995. Albanerpetontid amphibians from the Cretaceous of Spain. Nature 373:143–145.

Measey GJ. 2004. Are caecilians rare? An East African perspective. J East Afr Nat Hist 93:1–21.

Milner AR. 1988. The relationships and origin of living amphibians. In: Benton MJ (ed) The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds. Systematics Association Special Volume No 35A, Clarendon Press, Oxford, pp 59–102.

Müller J. 1831a. Kiemenlöcher einer jungen Caecilia hypocyanea. Isis 24:709–711.

Müller J. 1831b. Beiträge zur Anatomie und Naturgeschichte der Amphibien. Z Physiol 4:190–275.

Müller H, Oommen OV, Bartsch P. 2005. Skeletal development of the direct developing caecilian *Gegeneophis ramaswamii* Taylor, 1964 (Amphibia: Gymnophiona: Caeciliidae). Zoomorphol 124:171–188.

Nussbaum RA. 1977. Rhinatrematidae: a new family of caecilians (Amphibia: Gymnophiona). Occas Pap Mus Zool Univ Mich 682:1–30.

Nussbaum RA .1979. The taxonomic status of the caecilian genus *Uraeotyphlus* Peters. Occas Pap Mus Zool Univ Mich 687:1–20.

Nussbaum RA. 1983. The evolution of a unique dual jaw-closing mechanism in caeilians (Amphibia: Gymnophiona) and its bearing on caecilian ancestry. J Zool Lond 199:545–554.

Nussbaum RA. 1991. Cytotaxonomy of caecilians. In: Sessions SK, Green DM (eds.). Amphibian cytogenetics and evolution. Pp 22–76. Acad Press, San Diego.

Nussbaum RA. 1998. Caecilians. In: Cogger HG, Zweifel RG (eds.). Encyclopedia of reptiles and amphibians. Pp 52–59. Acad Press, San Diego.

Nussbaum RA, Wilkinson M. 1989. On the classification of caecilians (Amphibia: Gymnophiona), a critical review. Herpetol Monogr 3:1–42.

Nussbaum RA, Wilkinson M. 1995. A new genus of lungless tetrapod: a radically divergent caecilian (Amphibia: Gymnophiona). Proc Roy Soc Lond B 261:331-335.

O'Reilly JC, Fenolio D, Rania LC, Wilkinson M. 1998. Altriciality and extended parental care in the West African caecilian *Geotrypetes seraphini* (Gymnophiona: Caeciliidae). Am Zool 38:187A.

Parker HW. 1936. Amphibians from Liberia and the Gold Coast. Zool Meded 19:87–102.

Parker HW. 1958. Caecilians of the Seychelles Islands with description of a new subspecies. Copeia 1958:71–76.

Parsons TS, Williams EE. 1963. The relationships of the modern Amphibia: a re-examination. Q Rev Biol 38:26–53.

Peter K. 1898. Die Entwicklung und funktionelle Gestaltung des Schädels von *Ichthyophis glutinosus*. Morphol Jahrb 25:555–628.

Peters WCH. 1874. Über die Entwicklung der Caecilien und insbesondere der Caecilia compressicauda. Monatsber Akad Wiss Berlin 1874:45–49.

Peters WCH. 1880. Über die Eintheilung der Caecilien und insbesondere über die Gattungen *Rhinatrema* und *Gymnopis*. Monatsb Akad Wiss Berlin 1880:924–943.

Rage JC. 1986. Le pluis ancien Amphibien apode (Gymnophiona) fossile. Remarques sur la répartition et l'histoire paleobiogeographique des Gymnophiones. Com Rend Acad Sci Paris 302:1033–1036.

Rage JC. 1991. Gymnophionan amphibian from Early Paleocene (Santa Lucia Formation) of Tiupampa: the earliest known Gymnophiona. In: Suarez-Socuro R (ed.) Fosiles y facies de Bolivia, 1. Vertebrados. Rev tec yac petro fisc Boliv 12:499–501.

Rage JC, Janvier P. 1982. Le problème de la monophylie des amphibien actuels, a la lumière des nouvelles données sur les affinités des tétrapodes. Geobios 6:65–83.

Ramaswami LS. 1941. Some aspects of the cranial morphology of Uraeotyphlus narayani Seshachar (Apoda). Rec Indian Mus 43:143–207.

Ramaswami LS. 1948. The chondrocranium of *Gegenophis* [sic] (Apoda, Amphibia). Proc Zool Soc London 118:752–760.

Reiss J. 1996. Palatal metamorphosis in basal caecilians (Amphibia: Gymnophiona) as evidence for lissamphibian monophyly. J Herpetol 30:27–39.

Roelants K, Gower DJ, Wilkinson M, Loader SP, Biju SD, Guillaume K, Moriau L, Bossuyt F. 2007. Global patterns of diversification in the history of modern amphibians. PNAS 104:887–892.

Ruta M, Coates MI, Quicke DLJ. 2003. Early tetrapod relationships revisited. Biol Rev 78:251–345.

San Mauro D, Gower DJ, Oommen OV, Wilkinson M, Zardoya R. 2004. Phylogeny of caecilian amphibians (Gymnophiona) based on complete mitochondrial genomes and nuclear RAG1. Mol Phylogenet Evol 33:413–427.

San Mauro D, Vences M, Alcobendas M, Zardoya R, Meyer A. 2005. Initial Diversification of Living Amphibians Predated the Breakup of Pangaea. Am Nat 165:590–599.

Sanderson IT. 1937 *Animal Treasure*. New York: The Viking Press.

Sarasin P, Sarasin F. 1887–1890. Ergebnisse Naturwissenschaftlicher Forschungen auf Ceylon in den Jahren 1884–1886. Band 2: Zur Entwicklungsgeschichte und Anatomie der ceylonesischen Blindwühle *Ichthyophis glutinosus*. Wiesbaden: C.W. Kreidel's Verlag. 263 p.

Schoch RR, Milner AR. 2004. Structure and implications of theories on the origin of lissamphibians. In: Arratia G, Wilson MHV, Cloutier R, editors. Recent advances in the origin and early radiation of vertebrates. München: Verlag Dr Friedrich Pfeil. p. 345–377.

Seba, A. 1735. Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimis expressio, per universam physices historiam. Opus, cui, in hoc rerum genere, nullum par exstitit. Ex toto terrarum orbe collegit, digessit, et depingendum curavit. Tomus II. - pp. [1-32], 1-154, pl. 1-114. Amsterdam.

Straub JO. 1985. Contributions to the cranial anatomy of the genus Grandisonia Taylor 1968 (Amphibia: Gymnophiona). PhD thesis, Univ. Basel, 129 p.

Taylor EH. 1960. On the caecilian species *Ichthyophis monochrous* and *Ichthyophis glutinosus* and related species. Univ Kans Sci Bull 40:37–120.

Taylor EH. 1968. The caecilians of the world: a taxonomic review. Lawrence: University of Kansas Press. 848 p.

Taylor EH. 1969a. Skulls of Gymnophiona and their significance in the taxonomy of the group. Univ Kans Sci Bull 48:585–687.

Taylor EH. 1969b. Miscellaneous notes and descriptions of new forms of caecilian. Univ Kans Sci Bull 48:281–296.

Taylor EH. 1969c. A new family of African Gymnophiona. Univ Kans Sci Bull 48:297–305.

Teodecki EE, Brodie ED, Formanowicz DR, Nussbaum RA. 1998. Head dimorphism and burrowing speed in the African caecilian *Schistometopum thomense* (Amphibia: Gymnophiona). Herpetol **54**: 154–160.

Trueb L. 1993. Patterns of cranial diversity among the Lissamphibia. In: Hanken J, Hall BK (eds) The skull, volume 2: Patterns of structural and systematic diversity. University of Chicago Press, Chicago and London, pp 255–343.

Trueb L, Cloutier R. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). In: Schultze H-P, Trueb L (eds) Origin of the Higher Groups of Tetrapods: Controversy and Consensus. Cornell University Press, Ithaca, pp 175–188.

Venkatesh B, Erdmann MV, Brenner S. 2001. Molecular synapomorphies resolve evolutionary relationships of extant jawed vertebrates. Proc Nat Acad Sci 98:11382–11387.

Visser MHC. 1963. The cranial morphology of *Ichthyophis glutinosus* (Linné) and *Ichthyophis monochrous* (Bleeker). Ann Univ Stellenbosch A 38:67–102.

Wake MH. 1977. Fetal maintenance and its evolutionary significance in the Amphibia: Gymnophiona. J Herpetol 11:379–386.

Wake MH. 2003. The osteology of caecilians. In: Heatwole H, Davis M, editors. Amphibian biology, Vol 5 Osteology. Chipping Norton: Surrey Beatty. p. 1809–1876.

Wake MH. 2006. A brief history of research on gymnophionan reproductive biology and development. In: Exbrayat J-M, editor. Reproductive Biology and Phylogeny of Gymnophiona (Caecilians). Enfield: Science Publishers. p. 1–37.

Wake MH, Hanken J. 1982. Development of the skull of *Dermophis mexicanus* (Amphibia: Gymnophiona), with comments on skull kinesis and amphibian relationships. J Morphol 173:203–223.

Wake MH, Exbrayat J-M, Delsol M. 1985. The development of the chondrocranium of *Typhlonectes commpressicaudus* [sic] (Gymnophiona), with comparison to other species. J Herpetol 19:68–77.

Wake MH, Parra Olea G, Sheen JP. 2004. Biogeography and phylogeny of certain New World caecilians. In: Donnelly MA, Crother BI, Guyer C, Wake MH, White M (eds.) Ecology and evolution in the tropics: a herpetological perspective. Univ Chicago Press, Chicago.

Wake TA, Wake MH, Lesure RG. 1999. First Quaternary fossil record of caecilians from a Mexican archaeological site. Quat Res 52:138–140.

Weisrock DW, Harmon LJ, Larson A. 2005. Resolving Deep Phylogenetic Relationships in Salamanders: Analyses of Mitochondrial and Nuclear Genomic Data. Syst Biol 54:758–777.

Werner C. 1994. Der erste Nachweis von Gymnophionen (Amphibia) in der Kreide (Wadi-Milk-Formation, Sudan). N Jahrb Geol Pal 1994:633–640.

Wiedersheim R. 1879. Die Anatomie der Gymnophionen. Gustav Fischer, Jena, 101 pp.

Wiens JJ, Bonett RM, Chippindale PT. 2005. Ontogeny discombobulates phylogeny: paedomorphosis and higher-level salamander relationships. Syst Biol 54:91–110.

Wilkinson M. 1992a. Novel modification of the cardiovascular system in the West African caecilian *Herpele squalostoma* (Amphibian: Gymnophiona: Caeciliidae). J Zool 228:277–286.

Wilkinson M. 1992b. The phylogenetic position of the Rhinatrematidae (Amphibia: Gymnophiona): evidence from the larval lateral line system. Amph-Rept 13:74–79.

Wilkinson M. 1996 The heart and aortic arches of rhinatrematid caecilians (Amphibia: Gymnophiona). Zool J Linn Soc118:135–150.

Wilkinson M. 1997. Characters, congruence and quality: a study of neuroanatomical and traditional data in caecilian phylogeny. Biol Rev 72:423–470.

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

Wilkinson M, Nussbaum RA. 1997. Comparative morphology and evolution of the lungless caecilian *Atretochoana eiselti* (Taylor) (Amphibia: Gymnophiona: Typhlonectidae). Biol J Linn Soc 62:39–109.

Wilkinson M, Nussbaum RA. 1998. Caecilian viviparity and amniote origins. J Nat Hist 32:1403–1409.

Wilkinson M, Nussbaum RA. 1999. Evolutionary relationships of the lungless caecilian *Atretochoana eiselti* (Amphibia: Gymnophiona: Typhlonectidae). Zool J Linn Soc 126:191–223.

Wilkinson M, Nussbaum RA. 2006. Caecilian phylogeny and classification. In: Exbrayat J-M, editor. Reproductive Biology and Phylogeny of Gymnophiona (Caecilians). Enfield: Science Publishers. p. 39–78.

Wilkinson M, Sheps JA, Oommen OV, Cohen BL. 2002. Phylogenetic relationships of Indian caecilians (Amphibia: Gymnophiona) inferred from mitochondrial rRNA gene sequences. Mol Phyl Evo 23:401–407.

Wilkinson M, Loader SP, Gower DG, Sheps JA, Cohen BL. 2003. Phylogenetic relationships of African caecilians (Amphibia: Gymnophiona): insights from mitochondrial rRNA gene sequences. Afr J Herp 52: 83–92.

Winslow GM. 1898. The chondrocranium of the Ichthyopsida. Bull Essex Inst 28:87–141.

Zardoya R, Meyer A. 2000. Mitochondrial evidence on the phylogenetic position of caecilians (Amphibia: Gymnophiona). Genetics 155:765–77.