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Developmental morphological diversity in caecilian amphibians: systematic and evolutionary implications

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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).

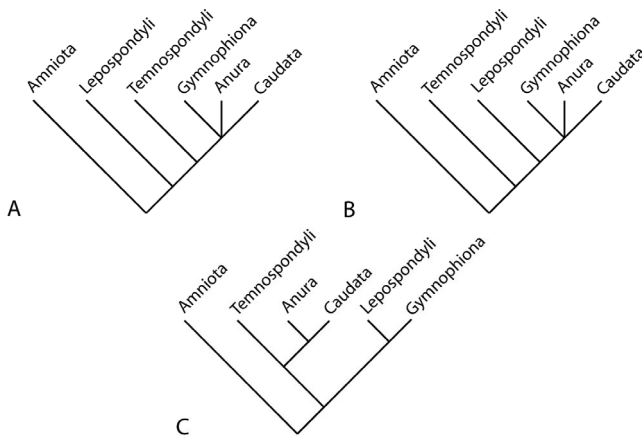


Fig. 1. Phylogenetic relationships of living amphibians: **A** Temnospondyls are ancestors of a monophyletic Lissamphibia, **B** Lepospondyli are ancestors of a monophyletic Lissamphibia, **C** Lissamphibians are diphylectic, frogs and salamanders related to temnospondyls, caecilians related to lepospondyls.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

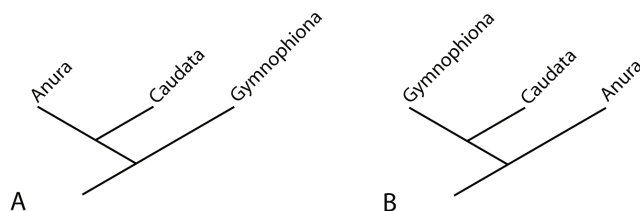


Fig. 2. **A** The Batrachia hypothesis: frogs and salamanders are sistergroups to the exclusion of caecilians. **B** The Procera hypothesis: caecilians and salamanders form a monophyletic group to the exclusion of frogs.

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).

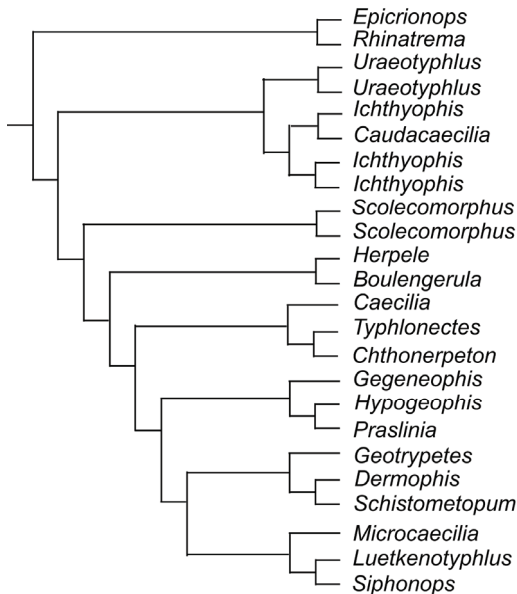


Fig. 3. Phylogenetic relationships of caecilians according to Roelants et al. (2007).

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 paraphyletic (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 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).

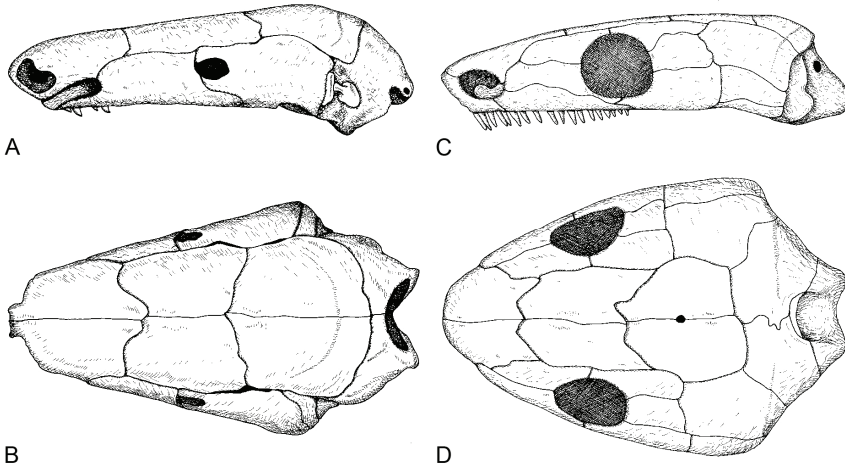


Fig. 4. Lateral (A) and dorsal (B) view of the skull of the adult caecilian *Hypogeophis rostratus* (modified from Taylor, 1969a). Lateral (C) and dorsal (D) view of the skull of the lepospondyl microsauro *Rhynchonkos* (from Carroll and Currie, 19675).

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, *Scolecormorphus*, *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; Fritsch, 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 *Scolecophorus 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 *Scolecormorphus 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.

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