Developmental morphological diversity in caecilian amphibians: systematic and evolutionary implications

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CHAPTER 7 – SYNOPSIS

The caecilian skull

The skulls of caecilian amphibians are generally heavily ossified, probably as an adaptation to a burrowing life-style practiced by most members of the group (e.g. Peters, 1880; Marcus et al., 1933; Taylor, 1969a; Duellman and Trueb, 1986; Nussbaum and Wilkinson, 1989). In this respect, caecilian skulls differ from those of frogs and salamanders, which are generally less robust and usually have a very open cheek region (Duellman and Trueb, 1986; Trueb, 1993). Caecilians are further characterized by the fusion of individual bones into the larger compound bones typical of the adult caecilian skull (Peter, 1898), which complicates a direct comparison of caecilian adult skulls with those of frogs and salamanders and their putative Paleozoic ancestors. In cases where the adult morphology is highly derived, ontogenetic information is often useful in providing additional support for or against a certain hypothesis. In caecilians, study of the development of the skull is necessary for a better understanding of the adult morphology. Most previous studies of caecilian skull development were limited by the amount of material available (e.g. Marcus et al., 1935; Ramaswamii, 1948) or focused more on specific anatomical regions of the skull (e.g. Peters, 1898; Winslow, 1898; Jurgens, 1971; Wake et al., 1985). Wake and Hanken (1982) provided the first detailed description of the development of the skull in a caecilian, the viviparous caeciliid *Dermophis mexicanus*, and noted that many of the previously reported skull bones, such as quadratojugal or postparietal, do not occur. Wake and Hanken (1982) considered that part of the discrepancy between their and earlier studies, and especially that by Marcus et al. (1935), could be related to different life-histories in the investigated species, which is known to affect skull development in frogs and salamanders (e.g. Hanken et al., 1992; Wake and Hanken, 1996). Müller et al. (2005) studied the development of the skull in *Gegeneophis ramaswamii*, a direct developing species closely related to the species investigated by Marcus et al. (1935), and also found no indications of many of the previously reported multiple skull ossifications, which raised considerable doubts about the validity of these studies. Müller et al. (2005) also demonstrated that the ossification sequence of the direct developing *G. ramaswamii* is considerably different from that of the viviparous *D. mexicanus* (Wake and Hanken, 1982).

In **Chapter 2** of this thesis, I reinvestigated skull development in *Hypogeophis rostratus*, which, together with the closely related *Grandisonia alternans*, had formed the subject of the ontogenetic studies by H. Marcus and his students (e.g. Eifertinger, 1933; Marcus et al. 1933, 1935). Although later studies pointed out inconsistencies (Brand, 1956) and, more recently, incongruence with other taxa (Wake and Hanken, 1982; Müller et al., 2005), the data reported by Marcus and students has been hugely influential in subsequent studies of caecilian skull morphology and amphibian evolution. The results of my investigation are largely incompatible with those of Marcus and students, and I find no evidence for several of the previously reported multiple ossifications, including supra-, infra- and basioccipital, epiotic, pleurosphenoid, preethmoid, posterior vomer, prepalatine, quadratojugal, postparietal, second coronoid, supraangular and complementare. It appears that most of Marcus et al.'s reports of non-existent ossifications are based on false phylogenetic preconception, misinterpretation of the observed morphology and technical error. The ossification sequence of *H. rostratus* is very similar to that of *G. ramaswamii*, although it is at present unclear whether this is related to their direct mode of development or close phylogenetic relationship.

Caecilians exhibit all the main reproductive modes known among frogs and salamanders – oviparity with a free-living larva, oviparity with direct development and viviparity (Wilkinson and Nussbaum, 1998). **Chapter 3** investigates the morphology the skull and associated musculature in larvae and adults of representatives of all lineages that are known to have free-living larvae, which presumably represents the ancestral state in caecilians. Despite several obvious differences in detail, larval caecilians share a very similar general morphology that is different from that of adult caecilians. All caecilian larvae are characterized by a gymnokrotaphic skull with a completely open temporal region and a different shaped squamosal to that of the adults. In some taxa (rhinatrematids, ichthyophiids and *Praslinia cooperi*) the squamosal of larvae anchors the quadrate to the skull and has a similar form to that seen in most larval and adult salamanders and frogs (Trueb, 1993; Rose, 2003). Larval caecilians further show a palatal metamorphosis that includes a posterior elongation of the maxilla. As with cranial morphology, larval cranial musculature and hyobranchial morphology is more similar among larvae of different species than between larvae and adults and musculature and the hyobranchial skeleton also undergo metamorphic changes similar in degree to those seen in the skull. This account provides the first descriptions of the skull and hyobranchial skeleton of larval *Uraeotyphlus* spp., larval and adult *Praslinia cooperi*, larval *Sylvacaecilia grandisonae* and larval *Grandisonia spp.*, as well as of the musculature of larval *Epicrionops spp.* and *Rhinatrema bivittatum*, larval *Uraeotyphlus spp.*, larval and adult *P. cooperi*, larval *S. grandisonae* and larval *Grandisonia spp.*

The postembryonic development of the skull in two distantly related direct developing caecilian species with different life-history strategies is investigated in **Chapter 4**. We focussed on the postembryonic development of the skull in *Boulengerula taitanus*, a caeciliid with an extended period of post-hatching parental care, and the caeciliid *Gegeneophis ramaswamii*, which lacks post-hatching parental care. Postembryonic skull development in these two taxa was compared with that of *Ichthyophis* cf. *kohtaoensis*, a species with a free-living aquatic larva, the presumed ancestral condition in caecilians. Compared with *G. ramaswamii*, hatchling *B. taitanus* have a far less developed skull and are unlikely to be able to burrow. Skull development, especially the closure of the cheek region continues during the early postembryonic phase. The general trajectory of skull development in *B. taitanus* is nonetheless similar to that of *G. ramaswamii*, indicating a heterochronic shift in hatching time in the former. Skull development in both species is further characterized by the absence of larval-specific traits seen in larvae of *I.* cf. *kohtaoensis*, which shows that direct development in caecilians is also characterised by ontogenetic repatterning.

Chapter 5 is a closer examination of the unusual form of parental care present in *Boulengerula taitanus*. Although the initial growth and development of most multicellular animals depends on the provision of yolk, there are many varied contrivances by which animals provide additional or alternative investment in their offspring (Clutton-Brock, 1991). Providing offspring with additional nutrition should be favoured by natural selection when the consequent increased fitness of the young offsets any corresponding reduction in fecundity (Smith and Fretwell, 1974). Alternative forms of nutrition may allow parents to delay and potentially redirect their investment. *Boulengerula taitanus* exhibits a remarkable form of parental care and mechanism of parent-offspring nutrient transfer. In this direct developing, oviparous caecilian (Nussbaum and Hinkel, 1994), the skin is transformed in brooding females to provide a rich supply of nutrients for the developing offspring. Young animals are equipped with a specialised dentition, which they use to peel and eat the outer layer of their mother's modified skin. This new form of parental care provides a plausible intermediate stage in the evolution of viviparity in caecilians. At independence, offspring of viviparous and oviparous dermatotrophic caecilians are relatively large despite being provided with relatively little yolk. The specialised dentition of skin-feeding (dermatophagous) caecilians may constitute a preadaptation to the foetal feeding on the oviduct lining of viviparous caecilians.

Chapter 6 describes the external and musculoskeletal morphology of the head in an ontogenetic series of the scolecomorphid caecilian *Scolecomorphus kirkii*. The rostral region of foetuses and juveniles in this viviparous species is expanded into large, posterolaterally pointing paraoral processes that are formed by the maxilla. Extraoral teeth that show signs of wear are present on the underside of the rostrum in front of the mouth and laterally on the paraoral processes. In foetuses the extraoral teeth are covered by epidermal tissue, which suggests that the peculiar morphology is indicative of a specialized post parturition feeding stage in *Scolecomorphus* (see also Loader et al., 2003). The endoskeletal part of the foetal skull is largely cartilaginous, while all of the dermal bones, with the exception of the squamosal, are well developed. The foetal chondrocranium is extensively developed and shows a peculiar posteriorly directed process of the lamina orbitonasalis posterolaterally, which is joined by a transverse bar joining the pila preoptica posterior to the choana, and a posteriorly directed lateral process (postpalatine process) that extends parallel to the trabecular cartilage beyond the level of the posterior end of the pila antotica. A similar chondrocranial morphology is unknown from any other caecilian taxon. Only two primary jaw adductor muscles are present, together with two pterygoideus-like muscles that insert onto the lower jaw. The palatoquadrate, respectively quadrate of foetuses and juveniles shows a high degree of mobility. Compared with the limited data available on skull development in other viviparous species Wake and Hanken, 1982; Reiss and O'Reilly, 1999), results suggest profound diversity in early skull development and highlight the need for more comparative data on viviparous caecilians.

Phylogenetic position of caecilians

Much has been written about the phylogentic relationships between caecilians and other amphibians, Recent or fossil, and much will undoubtedly be written in the future. Of the various hypotheses put forward regarding caecilian relationships (e.g. Kingsley, 1902; Marcus et al., 1935; Nussbaum, 1983; Løvtrup, 1985; Carroll and Currie, 1975; Laurin and Reisz, 1997; Anderson, 2001; McGowan, 2002; Carroll et al., 2004; Schoch and Milner, 2004) only three are currently being considered seriously. Two of these recover Lissamphibia as a monophyletic group that has its origin from either among the Temnospondyli (e.g. Parsons and Williams, 1963; Milner, 1988; Bolt, 1991; Trueb and Cloutier, 1991; Ruta et al., 2003; Schoch and Milner, 2004; Ruta and Coates, in press) or the Lepospondyli (Laurin and Reisz, 1997; Laurin, 1998). Most authors favour a temnospondyl origin of Lissamphibia, although support for the lepospondyl hypothesis is not significantly worse (Ruta and Coates, in press). The third hypothesis, which postulates a separate origin of frogs from temnospondyls and caecilians from lepospondyls, with salamanders variously derived from either group, has repeatedly been proposed (Carroll and Currie, 1975; Carroll, 2000; Schoch and

Carroll, 2003; Carroll et al., 1999, 2004), but received no support in any of the recent quantitative phylogenetic analyses (see above).

In this regard, it is worthwhile stressing again the phylogenetic importance of metamorphosis in all Recent amphibians (Schoch and Milner, 2004). Caecilians share with frogs and salamanders a similar suite of metamorphic patterns, ranging from changes in the soft anatomy, such as the epidermal structure (Duellman and Trueb, 1986) or cranial musculature (Bauer, 1997; Haas, 2001), to metamorphic changes in the skeleton (Duellman and Trueb, 1986). Cranial changes include the conspicuous posterior elongation of the maxilla upon metamorphosis and changes in the palatal region, including a widening of the interpterygoid vacuities (Reiss, 1996, 2002; Schoch and Milner, 2004). Frogs and salamanders are further characterized by a more pronounced condensation of ossification events into the metamorphic period (Roček and van Dijk, 2006; Schoch, 2002a, 2002b). Caecilians differ in that the larval skull has more or less the adult set of bones already upon hatching, but they undergo extensive fusion and remodelling of certain bones, such as maxilla and squamosal, upon metamorphosis (see **Chapter 3**). However, the circumorbital of ichthyophiids and uraeotyphlids only forms during metamorphosis, and the formation of the maxillopalatine in rhinatrematids, which might also incorporate a postfrontal element, is unknown.

Looking at the fossil record, several temnospondyl groups exhibit ontogenetic changes that are reminiscent of the metamorphic changes seen in Recent amphibians (Schoch 2002a) albeit far less pronounced. The enlargement of the interpterygoid vacuities, for instance, also seems to characterise certain temnospondyls (Reiss, 2002). However, the foreshortened maxilla of larval Recent amphibians and its posterior elongation during metamorphosis is not found in any Palaeozoic amphibian group (Schoch 2002a) and seems to be a possible lissamphibian synapomorphy (Reiss, 2002). The temnospondyl branchiosaurid *Apateon* furthermore exhibits a cranial ossification sequence that is very similar to that of salamanders (Schoch 2002b; Schoch and Carroll, 2003), although a frustrating lack of data on other relevant groups prohibits further conclusions to be drawn. Ontogenetic studies of lepospondyls are scant because of a general absence of suitable material, although the few available data seem indicate a complete absence of metamorphosis-like changes in cranial ontogeny (Anderson, 2003). It is also of importance to note that metamorphic changes reminiscent of lissamphibians are only found within the Dissorophoidea and not in all temnospondyls (Schoch, 2002a). Dissorophoidea comprises several taxa, such as branchiosaurids and doleserpetontids, regarded as closely related to lissamphibians, or at least some subtaxa of lissamphibians (e.g. Parsons and Williams, 1963; Milner, 1988, Trueb and Clouthier, 1991; Schoch and Carroll, 2003; Schoch and Milner, 2004). Ontogenetic studies indicate a progressive condensation of metamorphic events in dissorophoids as compared to other temnospondyls (Schoch 2004; Witzmann and Pfretzschner, 2003; Witzmann, 2005) and it seems likely that metamorphosis evolved within a taxon comprising dissorophoids and lissamphibians. The greater condensation of metamorphic events in lissamphibians as compared to dissorophoids seems to have occurred partly within the lissamphibian stem-line and partly within crown group lissamphibians (Roček and van Dijk, 2006).

Carroll (2000) and Anderson (2001) considered *Eocaecilia* and, by implication, caecilians to be nested within Microsauria. The presence of metamorphosis in caecilians, however, is a strong indication of a close relationship with both frogs and salamanders, as well as with certain temnospondyls, rather than lepospondyls. Schoch and Milner (2004) have further pointed out various dissorophoid features of *Eocaecilia* and regarded the similarities of *Eocaecilia* and the microsaur *Rhynchonkos* to be associated with a similar, burrowing life-style and not necessarily indicative of common descent. All this would speak for a temnospondyl origin of caecilians, rather than for lepospondyl affinities, and discount both hypotheses of a diphyly or lepospondyl origin of lissamphibians (e.g. Carroll and Currie, 1975; Laurin and Reisz, 1997; Laurin, 1998; Carroll, 2000; Carroll et al., 1999, 2004).

Ontogentic data further clearly indicate that caecilians have a reduced set of skull bones (Wake and Hanken, 1982; Müller et al., 2005; Müller, 2006; see

Chapter 2) similar to frogs and salamanders, and that the heavily ossified caecilian skull likely evolved secondarily as an adaptation to a burrowing life-style from a gymnokrotaphic or zygokrotaphic ancestor (see **Chapter 3**). This raises questions regarding the caecilian affinities of the putative stem-line caecilian *Eocaecilia micropodia*. An open temporal region is present in the earliest known stem-group representatives of frogs and salamanders (and their descendants), and we have argued that a similar condition is also characteristic of the last common ancestor of living caecilians (**Chapter 3**). The Albanerpetontidae, a group of small, salamander-like forms that has been variously placed as stem-group salamanders, stem-Batrachia, stem-Lissamphibia, or sistergroup to Gymnophiona (Milner, 1988; Gardner, 2001; McGowan, 2002; Ruta et al., 2003; Ruta and Coates, in press), also possessed an open temporal region. Accepting *Eocaecilia* as a stem-line caecilian implies convergent evolution of a zygokrotaphic skull in caecilians and other lissamphibians, as well as convergent loss of various skull bones (Schoch and Milner, 2004; but see also Ruta et al., 2003). Considering the characters that link *Eocaecilia* and modern caecilians, it is noteworthy that several of these are linked to a burrowing life-style and therefore possibly more prone to convergence as has been argued for similarities between *Rhynchonkos* and *Eocaecilia* (Schoch and Milner, 2004). This raises the possibility of an alternative placement of *Eocaecilia* within dissorophoids, but removed from the immediate ancestry of caecilians. Further investigation of the relationships of caecilians and *Eocaecilia* seems warranted and should receive particular attention in future studies of temnospondyl and lissamphibian phylogeny.

Future work

Recent work including this thesis (e.g. Wilkinson, 1996; Wilkinson and Nussbaum, 1996; O’Reilly et al., 1997; Loader et al., 2003; Kupfer et al., 2006; Chapters 2, 3, 4, 5, 6) has demonstrated in an impressive way a previously unsuspected diversity of caecilian amphibian biology, ranging from morphology to life-history evolution. In the general amphibian literature, however, caecilians have traditionally been considered to be a fairly homogenous group with little differentiation among its members. Somewhat paradoxically, this view has apparently been held not because, but despite of previous research or the lack thereof. The prevailing notion in the scientific literature seems to be that caecilians are rare, difficult to collect and somehow remarkably similar to each other, although a similar statement could be similarly applied to such intensively studied groups as whales and dolphins. The research presented in this thesis has – yet again – shown a remarkable diversity of caecilians in developmental morphology and other aspects of their biology. However, in as much as recent work has improved our understanding of caecilian biology, there are still large gaps in our current knowledge, especially regarding the basic biology of numerous species and their phylogeny, which frustratingly hamper further progress at the moment. Active fieldwork seems to be the key to continued and fast progress in caecilian research. For instance, further fieldwork, combined with behavioural observations, seems almost guaranteed to provide decisive evidence on the function of the peculiar morphology of juvenile *Scolecomorphus* described in **Chapter 6** and by Loader et al. (2003). A similar assumption seems justified in view of the function of the peculiar foetal dentition in non-viviparous caecilians (**Chapter 5**) and its possible association with skin feeding in species other than *Boulengerula taitanus* (as predicted in Chapter 5). Further research should focus on skull development in additional taxa, and especially rhinatrematids because a better understanding of their development is likely to advance our understanding on the phylogenetic position of caecilians more than previously studied groups (see **Chapter 3**). More and detailed ontogenetic studies would also provide more data to test evolutionary trends within caecilians in a more detailed way than currently possible. A particular emphasis should be placed on direct developing and viviparous species to test for hypotheses of independent life-history evolution (**Chapter 3, 4, 5**). Caecilians would further make a promising target for the study of body elongation and limb reduction in tetrapods and seem well suited to complement genetic and morphological studies in other limbless and elongated groups such as snakes (Cohn and Tickle, 1999). Again, this is most likely achieved by increased future field work efforts. Although recent years have seen an advance in or understanding of caecilian intrarelationships (Gower et al., 2002; Wilkinson et al., 2003; San Mauro et al., 2004; Frost et al., 2006; Roelants et al., 2007) and especially an emerging consensus on the relationships within the Caeciliidae, the largest and most diverse group, more effort is needed to establish the robust phylogenetic framework needed for the study of caecilian evolution. Increased fieldwork will generate more samples for these taxonomic and systematic studies. Taxa exhibiting interesting but understudied life histories, such as *Sylvacaecilia grandisonae* with free-living larvae or the direct-developing, miniaturized *Idiocranium russeli* (Wake, 1985) should be targeted in future fieldwork.

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