

## Morphology and function of the head in foetal and juvenile *Scolecormorphus kirkii* (Amphibia: Gymnophiona: Scolecormorphidae)

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The external and musculoskeletal morphology of the head is described for an ontogenetic series of the scolecormorphid caecilian *Scolecormorphus kirkii*. The rostral region of foetuses and juveniles is expanded into large, posterolaterally pointing paraoral processes that are formed by the maxilla. Extraoral teeth are present on the underside of the rostrum and laterally on the paraoral processes. In the foetuses, teeth are covered by epidermal tissue. The endoskeletal part of the foetal skull is largely cartilaginous, but all of the dermal bones, with the exception of the squamosal, are present. The foetal chondrocranium is extensively developed and shows a peculiar, posterolateral process of the nasal capsule that is connected to the trabecula cranii by a transverse bar posterior to the choana, and extends further posterior beyond the level of the posterior end of the pila antotica. Only two *mm. adductor mandibulae* are present, together with two pterygoideus muscles that insert onto the lower jaw. The palatoquadrate and quadrate of foetuses and juveniles, respectively, are highly mobile. It is suggested that the derived head morphology of *Scolecormorphus* foetuses and juveniles is an adaptation to specialized postpartitive feeding. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 96, 491–504.

ADDITIONAL KEYWORDS: Eastern Arc Mountains – feeding – ontogeny – reproductive biology – viviparity.

### INTRODUCTION

Caecilians are elongated, limbless amphibians mostly inhabiting soils in parts of the wet and seasonal tropics and subtropics (Wilkinson & Nussbaum, 2006). Because of a general paucity of external characters, caecilians have often been described as a rather uniform group (Himstedt, 1996). This view is increasingly challenged by recent discoveries of remarkable specializations, including novel modifications of the cardiovascular system (Wilkinson, 1992)

in the caeciliid *Herpele squalostoma* (Stutchbury, 1859) and lunglessness with many associated radical morphological changes (Nussbaum & Wilkinson, 1995) in the typhlonectid *Atretochoana eiselti* (Taylor, 1968).

Caecilians show a remarkably rich diversity of early life-histories. Although comprising only approximately 170 species (Wilkinson & Nussbaum, 2006), caecilians exhibit all main reproductive modes found in other amphibians: oviparity with a free-living aquatic larva, oviparity with direct development, and viviparity. As far as is known, all oviparous caecilians provide brood care in that females guard their egg clutches until hatching (Goeldi, 1899; Sanderson, 1937; Kupfer, Nabhitabhata & Himstedt, 2004).

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Viviparous caecilians have developed different forms of intra-oviductal nutrient transfer, via oviductal secretions and hypertrophied oviductal epithelium, which is scraped by the foetuses equipped with a specialized, deciduous foetal dentition (Wake, 1977; Wake & Dickie, 1998), and/or via modified embryonic gills that function analogous to a placenta (Delsol *et al.*, 1986; Exbrayat & Hraoui-Bloquet, 1992). Kupfer *et al.* (2006) described a novel form of parental care in the direct-developing East African caeciliid *Boulengerula taitanus* Loveridge, 1935, where the young feed on their mother's skin, which is specially modified during a period of post-hatching care. A similar form of nourishment of altricial young has also recently been described in the South American caeciliid, *Siphonops annulatus* (Mikan, 1820; Wilkinson *et al.*, 2008), and has further been postulated for the viviparous caeciliid *Geotrypetes seraphini* (Duméril, 1859; O'Reilly *et al.*, 1998).

The Scolecomorphidae are a little known family of African caecilians comprising the genera *Crotaphatrema* and *Scolecomorphus*, which occur with three species each in West and East Africa, respectively (Taylor, 1969a; Nussbaum, 1985; Lawson, 2000). Scolecomorphids have several morphological characteristics that are unique among caecilians, such as a completely covered fenestra ovalis and no stapes (de Villiers, 1938; Nussbaum, 1985), a supratracheal commissure of the ceratobranchial III + IV (Nussbaum, 1985), and the eye displaced from the orbit and embedded in the base of the tentacle, which, at least in *Scolecomorphus*, protrude with the extrusion of the tentacle (O'Reilly, Nussbaum & Boone, 1996). *Scolecomorphus* is further characterized by spicules on the male phallus (Noble, 1931; Wake, 1998) and a notably kinetic skull (Nussbaum, 1985; Trueb, 1993). Virtually nothing is known about the reproductive biology of *Crotaphatrema*, although Nussbaum (1985) suggested that members of that genus might be oviparous. As far as is known, all species of *Scolecomorphus* are viviparous (Wilkinson & Nussbaum, 2006) but very little is known about development or other aspects of their reproductive biology. Barbour & Loveridge (1928) provided the first evidence for *Scolecomorphus* viviparity by reporting oviductal embryos in *Scolecomorphus uluguruensis* Barbour & Loveridge, 1928. Parker & Dunn (1964) briefly described the dentition of foetal *S. uluguruensis* and Taylor (1968: fig. 360) illustrated an embryo of the same species, but neither of the authors reported any unusual embryonic features. Recently, Loader *et al.* (2003) described a single, morphologically remarkable juvenile of *S. vittatus* (Boulenger, 1895), from the North Pare Mountains of Tanzania. This specimen is characterized by conspicuous, posteroventrally directed paraoral processes that bear teeth on their

aboral sides, an unusually short lower jaw, and other features previously unknown for any life-history stage of scolecomorphids or indeed any caecilian. Loader *et al.* (2003) suggested that this highly divergent juvenile morphology might be indicative of a specialized life-history stage.

In the present study, we describe the external morphology of foetuses and juveniles of *Scolecomorphus kirkii* Boulenger, 1883 from several well-preserved specimens from the Udzungwa Mountains of Tanzania. We also provide the first description of the morphology of the skull and lower jaw and their associated musculature in foetuses and juveniles based on serial sections and computerized three-dimensional reconstructions, gross dissection, and cleared and stained specimens, and discuss functional implications.

## MATERIAL AND METHODS

We studied an ontogenetic series of foetuses, juveniles and adults of *S. kirkii* (see Appendix). We classified as juveniles those free-living animals that are more similar to foetuses than to adults (see below). Animals were collected in the field and either fixed in formalin or ethanol and subsequently stored in ethanol or industrial methylated spirit. No information is available regarding whether any of the juveniles were collected together with an adult or with other juveniles. The nomenclature of cranial musculature follows Kleinteich & Haas (2007).

### SPECIMEN PREPARATION AND INVESTIGATION

Selected specimens (see Appendix) were double stained for bone and cartilage and cleared using a slightly modified protocol based on Taylor & Van Dyke (1985), and the musculature was dissected before applying the final steps of the protocol. Where necessary, contrast was enhanced by staining musculature with an iodine solution (Bock & Shear, 1972). Gross dissections and camera lucida drawings were made using a Nikon SMZ-U stereomicroscope. Specimens for histology were embedded in paraffin, serially sectioned transversely at 8 µm and variously stained with haematoxylin and eosin, Haematoxylin and Masson's trichrome, or Mallory's phosphotungstic acid haematoxylin (Böck, 1989). One foetus was dehydrated, critical point dried, sputter-coated with gold-palladium, and examined using a Hitachi 2500 scanning electron microscopy. The gut contents of one juvenile was prepared as a smear and stained with haematoxylin and eosin (Böck, 1989).

### THREE-DIMENSIONAL RECONSTRUCTION

For the computerized three-dimensional reconstruction, every third histological section was digitized

using a Leica BD5000 microscope with a digital image capture system. The resulting images were aligned using the software Autoaligner (Bitplane AG) and the alignment corrected manually where necessary. The image stack was imported into the software IMARIS, version 4.0.5 (Bitplane AG) and the contours of the studied elements were marked manually. All relevant structures were reconstructed separately, and then combined and subsequently rendered to produce the final images (see also Supporting Information). Some of the developing dermal bones including the frontal, parietal, and especially the parasphenoid, showed a reticulated growth pattern, with numerous bone trabeculae and small ossification deficiencies at their leading edge. A detailed reconstruction of such bone patterns is not feasible from serial sections and these were reconstructed as solid plates instead. Teeth were not reconstructed.

## RESULTS

### EXTERNAL MORPHOLOGY OF FOETUSES

All foetuses are in a similar state of development. A weakly developed band of dark pigmentation covers the dorsal and dorsolateral sides of the body and stretches from the tip of the snout to the body terminus, excluding the nostrils, tentacles, and the paraoral processes. There is no indication of lateral line organs, spiracular openings, labial folds, or a tail fin. No yolk is visible externally, except for the moderately enlarged intestine that is visible through the venter and seemingly filled with yolk. Three long gills are present laterally behind the head (Fig. 1A), with the second gill being the longest followed by the first and the third. All gills bear numerous gill filaments and appear more similar to the gills of ichthyophiid embryos than those of caeciliids (H. Müller, pers. observ.). The head is broad in dorsal view, with blunt, laterally projecting paraoral processes (Fig. 1B, C, D). The tentacles are in a lateral position, on an imaginary line from the upper corner of the mouth to the nostril, and partly visible dorsally. Somewhat darker pigmented eyes are positioned above and slightly behind the tentacular aperture, but are only faintly visible. In the lateral view, the head is wedge-shaped. The underside of the rostrum is almost completely flat and has a triangular shape. On the underside of the rostrum is a line of approximately eight knob-like protuberances (Figs 1C, 2), each approximately 0.5 mm from, and parallel to, the margin of the mouth. On each side, one or two additional protuberances are present posterolaterally on the paraoral process. At higher magnification, the tip of a tooth can be seen through the epidermis of each protuberance. The upper margin of the mouth and, correspondingly,

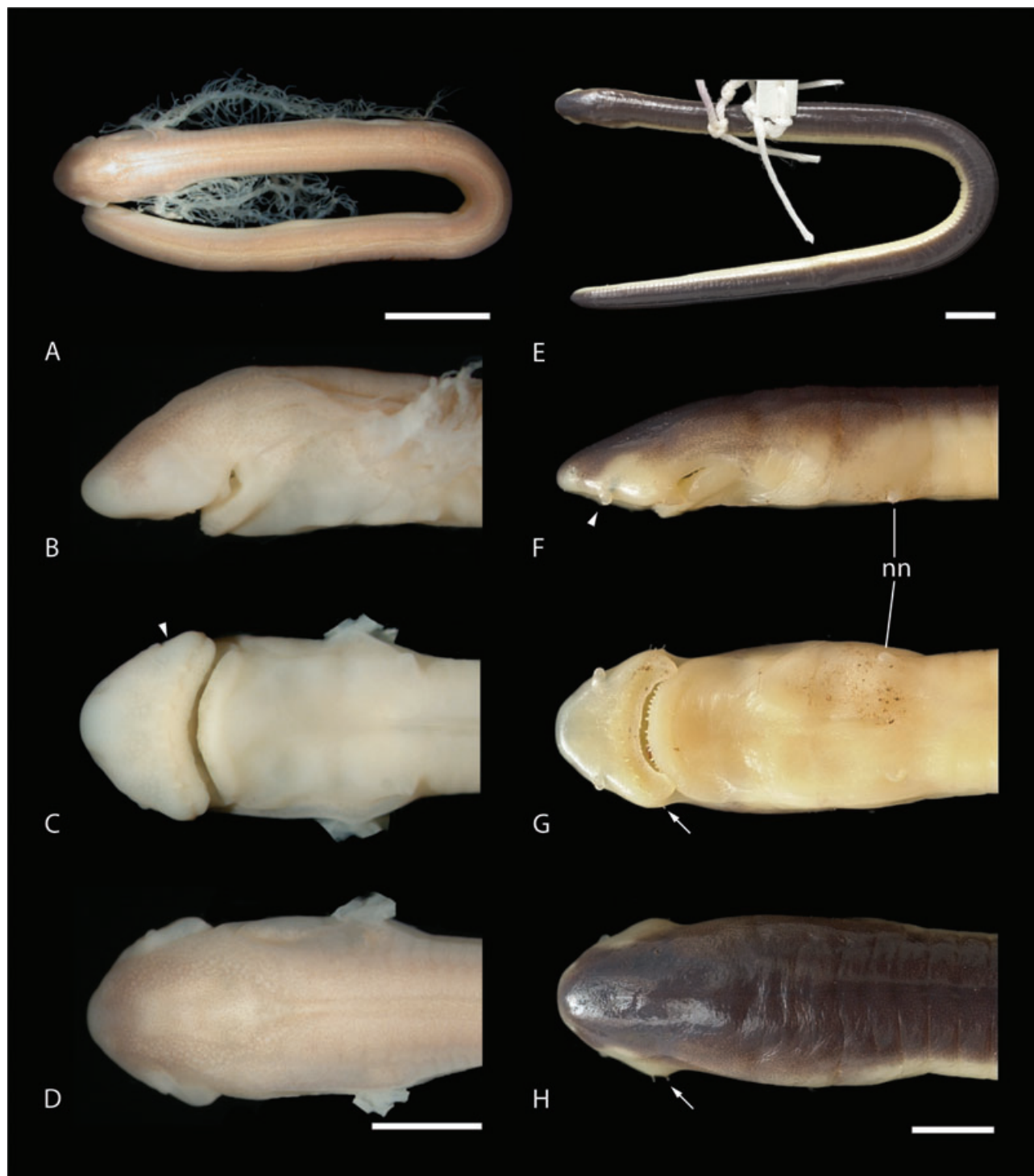
the lower jaw are very broadly rounded (Fig. 1C). The lower jaw bears epidermis-covered dentary teeth on its anterior side, arranged in three rows around the symphysis and two more laterally.

### EXTERNAL MORPHOLOGY OF JUVENILES

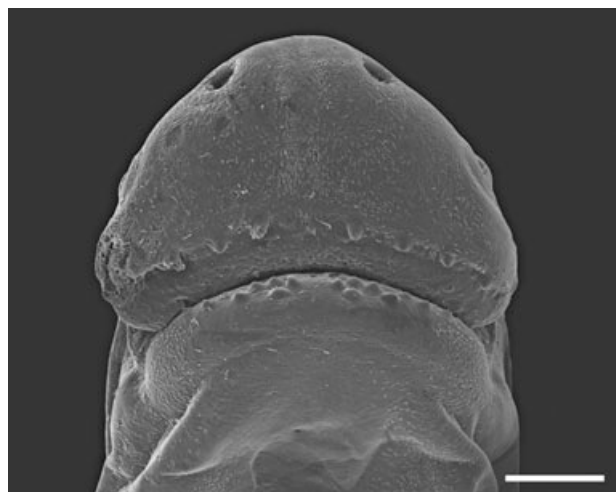
The three juveniles are similar in appearance to the foetuses. They have a well-developed band of dark pigmentation that covers the dorsal and dorsolateral sides of the body and stretches from the tip of the snout to the body terminus, similar to the adult coloration (Fig. 1E, F). Areas around the nostrils, the bases of the tentacles and the paraoral processes are free of pigmentation. The tentacles are slightly protruded and visible dorsally in all specimens (Fig. 1H). The ventral side of the rostrum is markedly convex transversely. Erupted premaxillary–maxillary teeth are present in the positions corresponding to the protuberances seen in the foetuses (Fig. 1G). All are relatively large, straight and bicuspid, with the labial cusp very small and close to the apex. An additional one or two teeth are found on the lateral side of the paraoral processes, pointing laterally, posterolaterally or dorsolaterally (Fig. 1G, H). Teeth found laterally on the paraoral processes and those in a more lateral position on the underside of the rostrum show clear signs of wear. This is more pronounced in the two larger specimens, where some of these teeth are worn down to almost the level of the skin. The teeth of the lower jaw are erupted and two kinds are present. Lancet-shaped, so-called ‘foetal’ teeth are found in an anterior position and are arranged in three to four rows, with four rows confined to the symphyseal region. The largest of these are the innermost, with the outer rows being successively smaller. The outer rows of teeth show heavy wear, again more so in the larger juveniles. Towards the jaw articulation, teeth are large and monocusped and arranged in a single row. The posterior part of the gut is filled by a whitish, amorphous mass that superficially resembles yolk. A haematoxylin and eosin stained smear revealed it to be composed of numerous small spheres, some cellular debris including isolated nuclei, and a few soil particles.

### MUSCULOSKELETAL MORPHOLOGY OF FOETUSES

The endocranium of the foetuses is almost completely cartilaginous (Fig. 3). The only endocranial ossifications present are the exoccipital, the processus retroarticularis, and perichondral ossifications surrounding the mandibular symphysis. The nasal capsule is prominently developed. Most of the floor of the anterior part of the nasal capsule is cartilaginous, except for a relatively small fenestra prechoanalis



**Figure 1.** (A) Total dorsal view of a foetal *Scolecomorphus kirkii* (Scol 2) and a close-up of the head in lateral (B), ventral (C), and dorsal (D) views. Note the long external gills in (A); arrow head marks the tentacle anlage in (C). (E) Total dorsal view of a juvenile *Scolecomorphus kirkii* (AMNH A156899) and a close-up of the head in lateral (F), ventral (G), and dorsal (H) view. Arrow head points to tentacle in (F); also note the eye seen as a dark spot at the base of the tentacle. Arrows point to extraoral teeth on the lateral sides of the paraoral process. nn, nuchal nipples. Scale bars = 5 mm in (A, E) and 2 mm elsewhere.

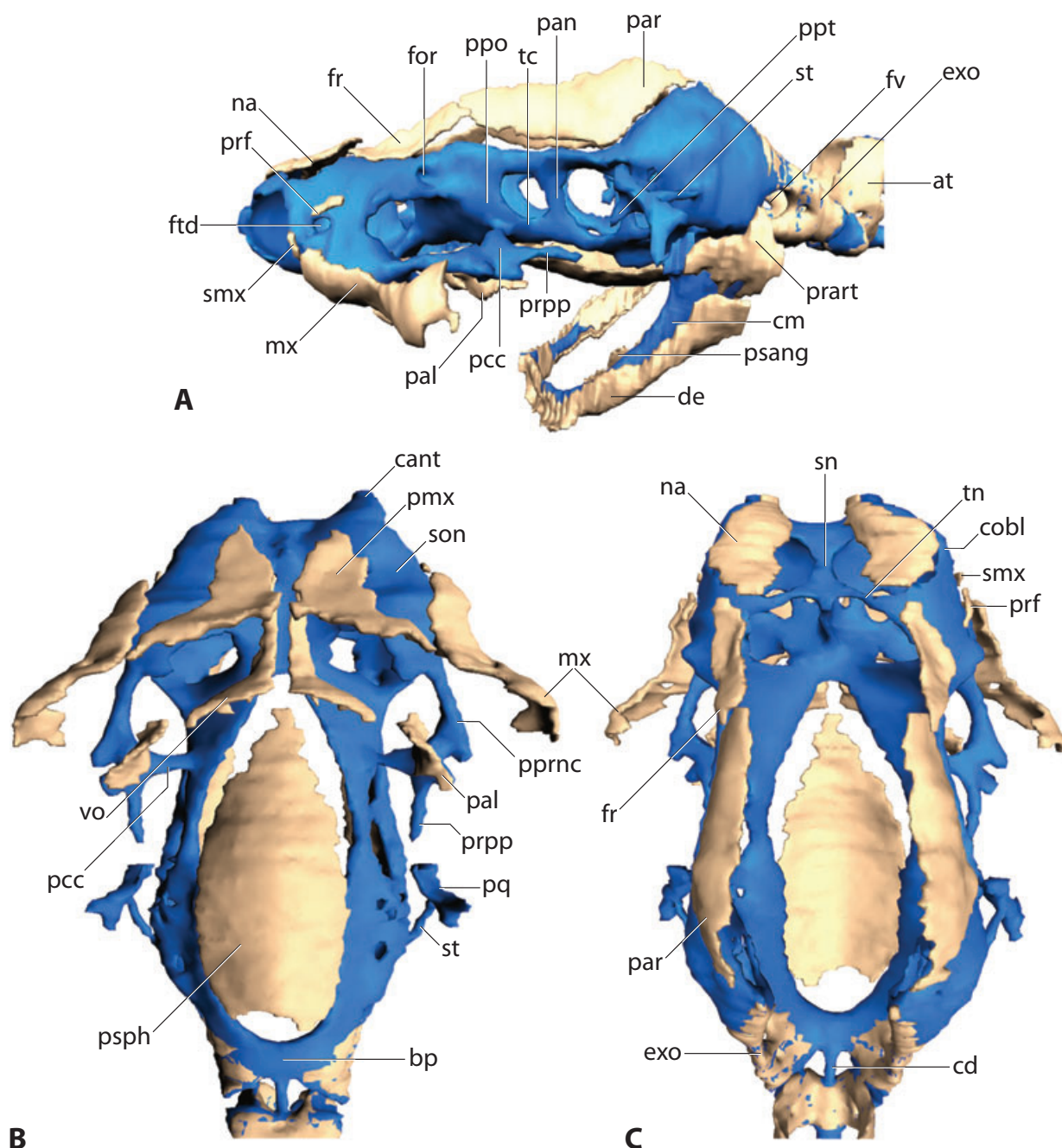


**Figure 2.** Scanning electron microscopy photograph of the ventral side of the head of a foetal *Scolecomorphus kirkii* (Scol 3). Note the epidermis covered teeth on the upper and lower jaw. Scale bar = 0.5 mm.

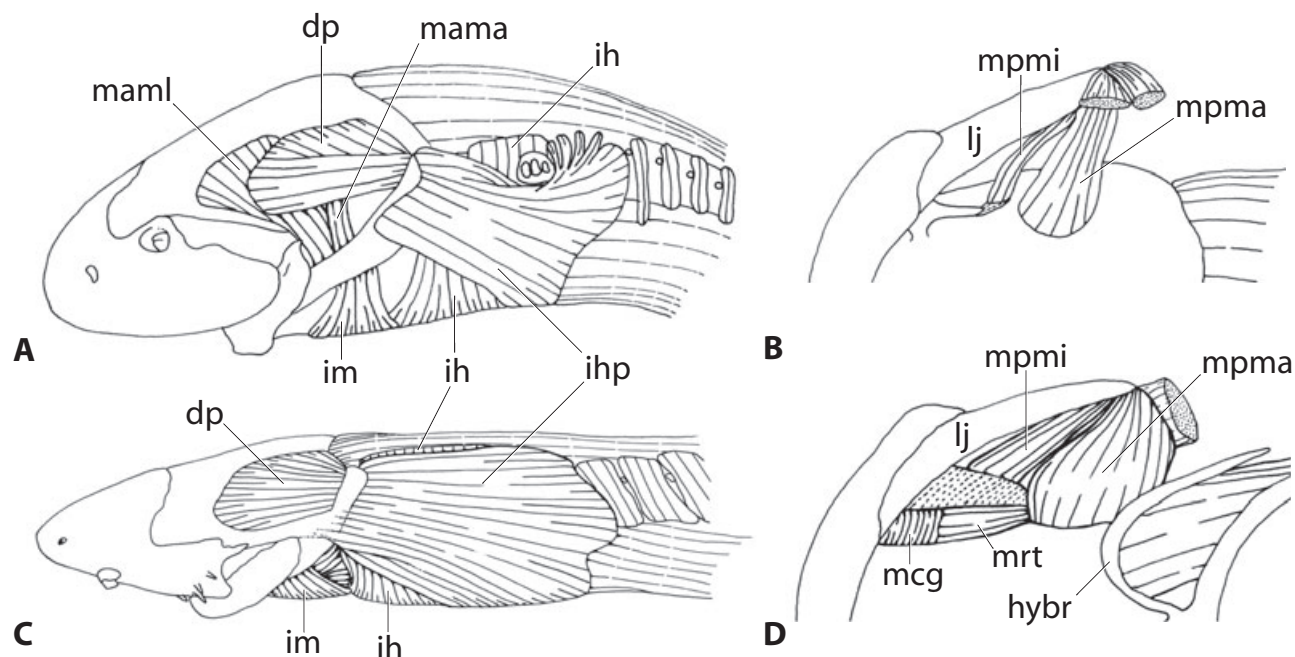
and a smaller, medial foramen for a ventral branch of the nervus ophthalmicus profundus. Further caudally, a very large fenestra endochoanalis is bordered by the trabecular plate and pila preoptica medially, the solum nasi anteriorly and anterolaterally, and a posterolateral process of the nasal capsule posterolaterally. The posterior border of the fenestra endochoanalis is formed by a transverse bar joining the trabecula cranii, ventral to the pila preoptica (lamina orbitonasalis of Jurgens, 1971) and the posterolateral process of the nasal capsule (Fig. 3B). Posterior to this transverse bar, a process extends parallel to the trabecula cranii beyond the level of the posterior end of the pila antotica (Fig. 3). This posteriorly directed process is provisionally termed the postpalatal process in reference to its position posterior to the initial position of the palatine, whereas the transverse bar is provisionally termed the postchoanal commissure (Fig. 3). The lateral wall of the nasal capsule is pierced by a foramen for the passage of the tentacular ducts (homologous to the nasolacrimal ducts of other amphibians; Sarasin & Sarasin, 1887–1890). The dorsal aspect of the capsule is characterized by a large fenestra that is bordered anteriorly by the slender cupula anterior, the cartilago obliqua laterally, the septum nasi medially, and the slender tectum nasi posteriorly. The medial part of the nasal capsule is formed by the septum nasi. A processus prenasalis is absent. Posteroventral to the septum nasi, between the anterior parts of the fenestrae endochoanalis, is a broad trabecular plate that is formed by the fusion of the trabeculae cranii. A simple, cartilaginous stapes is present and extends

from the posterior side of the palatoquadrate to the lateral side of the otic capsule. The stapes is in intimate contact with the palatoquadrate and is apparently fused to the lateral wall of the otic capsule. A fenestra ovalis is absent and the lateral side of the otic capsule is completely chondrified. The notochord extends anteriorly onto the basal plate but does not project into the fenestra basicranialis.

With the exception of the squamosal, the full complement of adult dermal bones is present (Fig. 3). The premaxilla consists of a well-defined dental lamina that spans almost the entire width of the nasal capsule, and a broad, triangular processus alaris that covers the ventromedial part of the anterior half of the nasal capsule. The maxilla lies lateral to the premaxilla and extends posteriorly from just rostral of the fenestra prechoanalis, covering the ventrolateral side of the posterior half of the nasal capsule. At the level of the posterolateral tip of the premaxilla, the maxilla extends into the posterolaterally directed paraoral process. A foramen for the nervus maxillaris is present where the maxilla is flexed outward. The maxilla becomes increasingly medially concave towards its posterior end and attains a C-shape in transverse sections. Immediately anterodorsal to the maxilla is a small, plate-like septomaxilla. The prefrontal, approximately twice the size of the septomaxilla, is a narrow plate extending posterodorsally from above the tentacular duct foramen. The nasal is comparatively broad and covers the dorsolateral side of the nasal capsule. The nasals are widely separated by a midline gap approximately the width of a single nasal. Posterior to the nasal, the frontal covers the dorsolateral side of the anterior part of the brain. Posterior to the frontal is the parietal, which covers most of the dorsolateral side of the braincase. Frontal and parietal both have a reticulated leading edge, with numerous small ossification deficiencies, best seen in the cleared and stained specimen. Nasal and frontal are separated, whereas the frontal and parietal overlap slightly (Fig. 3C). The vomer consists of a dental lamina and a conspicuous, slender, anteriorly directed process that extends dorsally to the premaxilla. The dental lamina of the vomer has two dorsally directed processes that enclose the ramus palatinus VII (Fig. 3B). Lateral to the posterior end of the vomer is the small palatine, which rests on the posterolateral process of the nasal capsule, at the level of the postchoanal commissure. The palatine has an intimate contact with the chondrocranium and is moulded around parts of the posterolateral process and postchoanal commissure. The fenestra basicranialis is almost completely filled by the parasphenoid, except for an anterior medial and lateral gap, and a smaller posterior medial gap just anterior to the basal plate.



**Figure 3.** Three-dimensional reconstruction of the skull of a foetal *Scolecomorphus kirkii* (Scol 1) in lateral (A), ventral (B), and dorsal (C) views. Lower jaw omitted in (B) and (C); cartilage blue, bone light coloured. at, atlas; bp, basal plate; cant, cupula anterior; cd, chorda dorsalis; cm, cartilago meckeli; cobl, cartilage obliqua; de, dentary; exo, exoccipital; for, foramen orbitonasale; fr, frontal; ftd, tentacular duct foramen; fv, foramen vagi; mx, maxilla; na, nasal; pal, palatine; pan, pila antotica; par, parietal; pcc, postchoanal commissure; pmx, premaxilla; ppo, pila preoptica; pprnc, posterolateral process of the nasal capsule; ppt, processus pterygoideus palatoquadrati; pq, palatoquadrate; prart, processus retro-articularis; prf, prefrontal; prpp, postpalatal process; psang, pseudoangular; psph, parasphenoid; smx, septomaxilla; sn, septum nasi; son, solum nasi; st, stapes; tc, trabecula cranii; tn, tectum nasi; vo, vomer. Scale bar = 1 mm.



**Figure 4.** Lateral view (A) of the superficial musculature of the head region and close-up (B) of the pterygoeus musculature in ventral view in a foetus of *Scolecomorphus kirkii* (Scol 2). Note that the lower jaw has been slightly moved laterally in (B). Musculature (C, D) of a juvenile *Scolecomorphus kirkii* (AMNH A156899) corresponding to the views in (A) and (B). dp, *m. depressor mandibulae*; hybr, hyobranchial skeleton; ih, *m. interhyoideus*; ihp, *m. interhyoideus posterior*; im, *m. intermandibularis*; lj, lower jaw; mama, *m. add. mand. articularis*; mamml, *m. add. mand. longus*; mcg, *m. constrictor glandulae*; mpma, *m. pterygoideus major*; mpmi, *m. pterygoideus minor*; mrt, *m. retractor tentaculi*. Not to scale.

Two *mm. adductor mandibulae* are present (Fig. 4A). The *m. add. mand. articularis* originates from the anteromedial side of the palatoquadrate and inserts dorsally on the lower jaw immediately in front of the jaw articulation. The much larger *m. add. mand. longus* originates from the lateral side of the parietal and the taenia marginalis, and inserts dorsally on the lower jaw, in front of the insertion of the *m. add. mand. articularis*. The two muscles are separated by the ramus mandibularis V. Lateral to these muscles is the *m. depressor mandibulae*, which originates from the fascia covering the *m. add. mand. longus*, the parietal and dorsal part of the otic capsule, and inserts onto the dorso-medial side of the processus retroarticularis of the lower jaw. It covers the dorsal half of the *m. add. mand. longus* and the otic capsule. Medial to the lower jaw, two trigeminus innervated muscles are present. A large *m. pterygoideus major* (Fig. 4B; see Discussion) originates from the ventral side of the anterior otic capsule and attaches to the medial side of the processus retroarticularis. Anterior to the *m. pterygoideus major* is a small muscle, the *m. pterygoideus minor*, which originates from the postpalati-

nal process via a tendon and also attaches to the medial side of the lower jaw, close to the jaw articulation (Fig. 4B). Although both muscles run parallel along the lower jaw, they are completely discrete and have a different fibre orientation, with the fibres of the *m. pterygoideus major* being more oblique and those of the *m. pterygoideus minor* running almost parallel to the lower jaw. The fan-like *m. intermandibularis* has a moderately broad origin on the medial side of the pseudoangular, anterior of the jaw articulation, and inserts in a mid-ventral fascia. Its insertion slightly overlaps the *m. interhyoideus* at its posterior end. The facialis innervated *m. interhyoideus posterior* has an anterior slip that is slightly narrower than the *m. intermandibularis* and originates from the ventral edge of the processus retroarticularis and inserts in the mid-ventral fascia. A larger, posterior slip of the *m. interhyoideus posterior* originates from the mid-ventral fascia ventrally and the fascia overlying the epaxial and hypaxial musculature and inserts on the lateral and ventral edge of the processus retroarticularis. The ventral-most fibres of the *m. interhyoideus posterior* have a more anterolateral

attachment on the lower jaw, very close to the jaw articulation and in line with the anterior limit of the articular facet. Posteriorly, this muscle fans out dorsally behind the gill attachment site (Fig. 4A).

#### MUSCULOSKELETAL MORPHOLOGY OF JUVENILES

The ossification of the smallest juvenile is much advanced compared to the foetus, although the shape of its skull is similar (Fig. 5). Most of the endocranium is well ossified, apart from parts of the nasal capsule (cupula anterior, parts of the solum nasi, and cartilago obliqua). Except for the cupula anterior, the cartilaginous parts of the nasal capsule are reduced to some extent compared to the foetus. Most of the anterior endocranium is incorporated into the sphenethmoid ossification, but the postchoanal commissure remains cartilaginous, and seems to buttress the maxillopalatine against the sphenethmoid. The postpalatine process has disappeared, although some of it appears to have been incorporated into the maxillopalatine (Fig. 5B; see below). Two blocks of cartilage remain dorsal and ventral to the optic foramen representing the orbital and trabecular cartilages respectively (Fig. 5A). The posterior neurocranial ossifications have fused with the parasphenoid to form the composite os basale, similar to that of the adult except for some incomplete ossification around the carotid foramen. A large, cartilaginous, bar-shaped processus basalis articulates with the base of the processus pterygoideus quadrati. Another articulation between the os basale and the quadrate exists at the anterodorsal limit of the otic capsule, where a short, cartilaginous process articulates with the dorso-medial tip of the quadrate. Both articulations are rather loose, with the elements somewhat separated but bound by connective tissue. A small, rod-shaped cartilaginous stapes lies posterior to the quadrate (Fig. 5A, B). A cartilaginous area on the posterior edge of the quadrate is possibly a facet for articulation with the stapes, although the two elements are not in contact. All dermal bones are well developed. The squamosal covers the anterolateral aspect of the quadrate and slightly overlaps the prefrontal anteriorly. The squamosal has a loose articulation with the maxillary part of the maxillopalatine anteroventrally, and there is a broad temporal opening between it and the parietal and os basale medially, through which the *m. add. mand. longus* is visible. Nasal, frontal, and parietal are similar in shape to the adult condition (Nussbaum, 1985), but not as well sutured medially, leaving the sphenethmoid partly exposed between the antimeres of frontal and nasal (Fig. 5C). The septomaxilla and especially the prefrontal are greatly expanded and similar to those of the adult, except for the relatively wide sutures between the

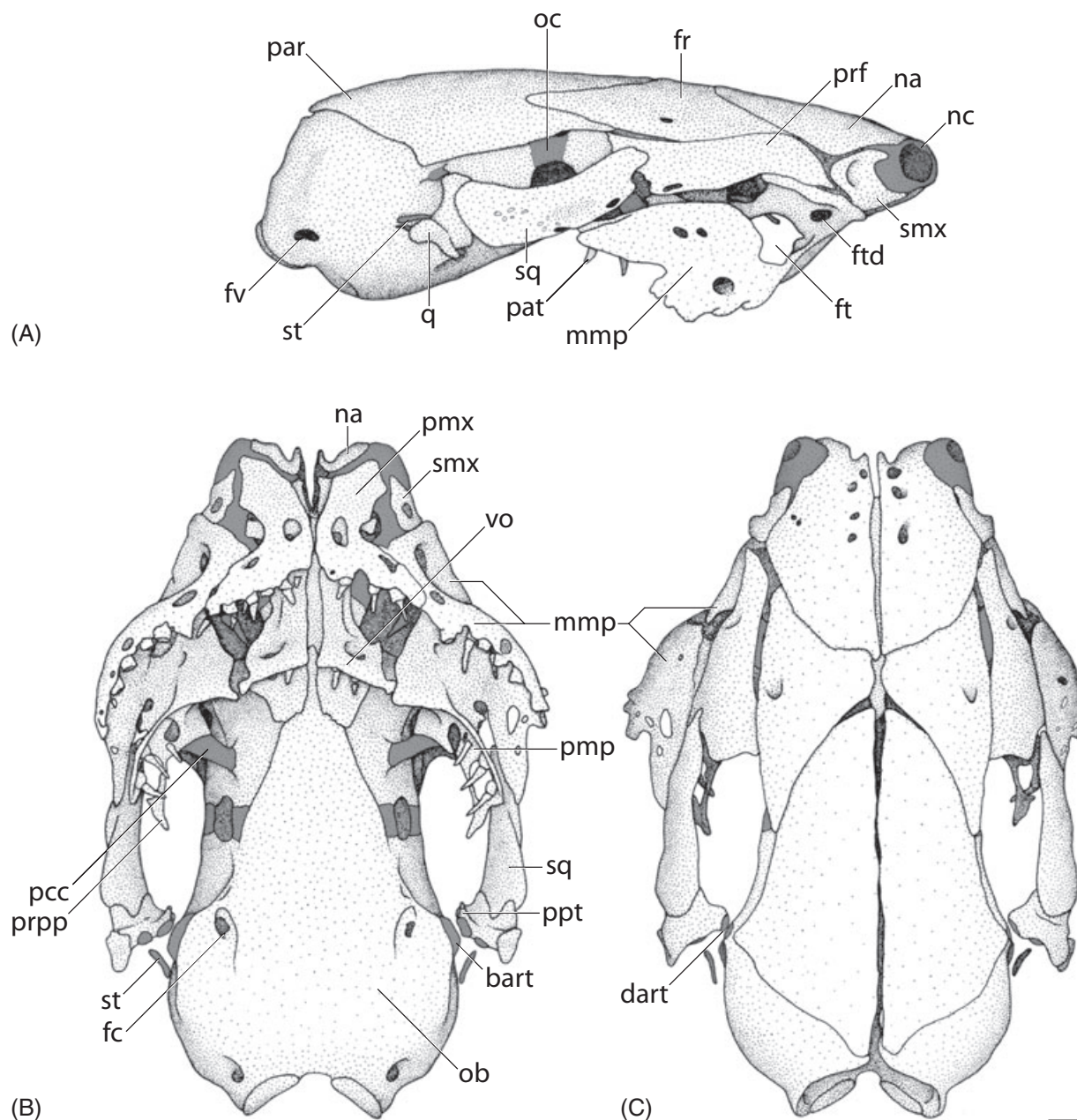
elements. The premaxilla is similar to that of the foetus, but distinctly more crescent-shaped in ventral view. Its dental lamina in particular is broader than in the adult, and the element as a whole is proportionately larger. The maxilla and palatine are fused to form the maxillopalatine, with the palatine broadly fused with the maxilla at its anterior end but the elements being separated by a narrow gap further posteriorly. The maxillopalatine has a complex structure, consisting of a broad, laterally expanded maxillary shelf that supports the maxillary and extraoral teeth seen at the lateral extremity of the paraoral process (note that most of the tooth-crowns have detached from their sockets during preparation and are omitted in Fig. 5). In the lateral view (Fig. 5A), the maxillary part of the maxillopalatine has an almost wing-like shape that greatly increases the depth of the anterior half of the skull. At least part of the postpalatine process appears to have been incorporated into the palatine part of the maxillopalatine, as indicated by ossifying cartilage in its medial-most, posterior part. The anterior process of the vomer has expanded and a short, broad palatine shelf is present posterior to the vomerine tooth row, giving it a shape similar to that of the adult. The premaxillary-maxillary arcade lies ventral to the level of the vomero-palatine arcade because the dental shelves of the premaxilla and maxilla are expanded and postero-ventrally directed. This is in contrast to the adult, where both arcades are approximately at the same level (Nussbaum, 1985).

Changes in musculature from the foetuses are slight (Fig. 4C). The *mm. add. mand. longus et articularis* are covered by the squamosal and *m. depressor mandibulae* and are barely visible in lateral view. The only more pronounced ontogenetic change is in the *m. interhyoideus posterior*, which has considerably expanded dorsally following the loss of the external gills (Fig. 4C). In all respects, the musculature of the juvenile is similar to the adult condition, except for a proportionately larger *m. intermandibularis* in adults in association with a more elongated lower jaw. Additionally, the fibres of the adult *m. pterygoideus major* are more steeply inclined because of the extended and more dorsally recurved processus retroarticularis.

#### DISCUSSION

Foetal and juvenile *S. kirkii* have a head morphology that differs remarkably from that of adults. The chondrocranium, and especially the nasal capsule, of the foetus is remarkably well developed and more robust than in embryos or foetuses of most other species described so far (Peter, 1898; Wake, Exbrayat & Delsol, 1985; Müller, Oommen &





**Figure 5.** Juvenile skull of *Scolecomorphus kirkii* (AMNH A156899) in lateral (A), ventral (B), and dorsal (C) views. Bone stippled, cartilage stippled with grey shading. bart, basal articulation of quadrate; dart, dorsal articulation of quadrate; fr, frontal; ftd, tentacular duct foramen; ft, tentacular foramen; fv, foramen vagi; mmp, maxillary part of the maxillopalatine; na, nasal; nc, nasal capsule; ob, os basale; oc, orbital cartilage, pal, palatine; par, parietal; pat, palatine tooth; pcc, postchoanal commissure; pmp, palatine part of the maxillopalatine; pmx, premaxilla; ppt, process pterygoideus quadrati; prf, prefrontal; prpp, postpalatine process; q, quadrate; smx, septomaxilla; sq, squamosal; st, stapes; vo, vomer. Scale bar = 1 mm.

Bartsch, 2005; Müller, 2006), where most of the elements are slender bars or thin plates that give the impression of a less robust structure. This is in stark contrast to the endocranium of adult *Scolecomorphus*, which have the most reduced nasal

capsule known among adult caecilians (Brand, 1956; Wake, 2003). The posterolateral process of the nasal capsule, postchoanal commissure, and postpalatine process found in foetal and juvenile *S. kirkii* are unique among caecilians investigated so far. Notable

also is the presence of a rudimentary stapes (absent in adults) in both the foetal and juvenile *S. kirkii*, which requires a slight modification of the diagnosis (Wilkinson & Nussbaum, 2006) of *Scolecophoridae*. The most distinctive foetal/juvenile feature, however, is the radically divergent morphology of the premaxillary–maxillary arcade and associated structures. As far as can be determined from external observations, the distinctive morphology of foetal and juvenile *S. kirkii* also pertain to juvenile *S. vittatus* (Loader *et al.*, 2003) and foetal *S. uluguruensis* (R. A. Nussbaum, pers. comm.) and can reasonably be assumed to be characteristic of (and homologous across) early life stages of *Scolecophorus*.

Adult skull morphology is quite similar in all species of *Scolecophorus* (Peter, 1895; Brand, 1956; Taylor, 1969b; Nussbaum, 1985; Wake, 2003), with some substantial differences from other caecilians that appear to be related to a highly mobile cheek region (Nussbaum, 1985; Trueb, 1993). Caecilian skull kinesis has been discussed previously, as summarized by Wake & Hanken (1982). De Villiers (1938) and Brand (1956) considered the squamosal to be tightly bound to the prefrontal in *Scolecophorus* and, in the absence of a quadrato-stapedial articulation, interpreted the skull of *Scolecophorus* to be monimostylic and therefore akinetic. However, based on various species, models of caecilian skull kinesis have recently been proposed, which are all based on a mobile cheek region, with this unit consisting of the quadrate, squamosal and, to a varying extent, the maxillopalatine (Straub, 1985; Wilkinson & Nussbaum, 1997). The absence of stapes (and fenestra ovals) is diagnostic for the *Scolecophoridae* (Taylor, 1969a; Nussbaum, 1985) and eliminates one of the points of articulation between the cheek and the os basale characteristic of other caecilians (Wilkinson & Nussbaum, 1997). Additionally, the basipterygoid process, which is mostly cartilaginous, is greatly enlarged and projects relatively far lateral from the base of the skull. This expansion is consistent with it supporting enhanced lateral displacement of the cheek in this region. The combination of the absence of a pterygoid and the processus pterygoideus quadrati being only an inconspicuous ledge (contra Brand, 1956), renders the cheek less robust in *Scolecophorus* and probably more flexible than in other adult caecilians. The first two of these features are partly convergent with *Atretochoana eiselti*, a large lungless typhlonectid caecilian with a highly kinetic skull (Wilkinson & Nussbaum, 1997). Also absent in *Scolecophorus* is the processus internus of the lower jaw, which may be related to its increased mobility.

The mandibular arch musculature in *Scolecophorus* is relatively simple compared to other caecilians (Wilkinson & Nussbaum, 1997; Kleinteich & Haas,

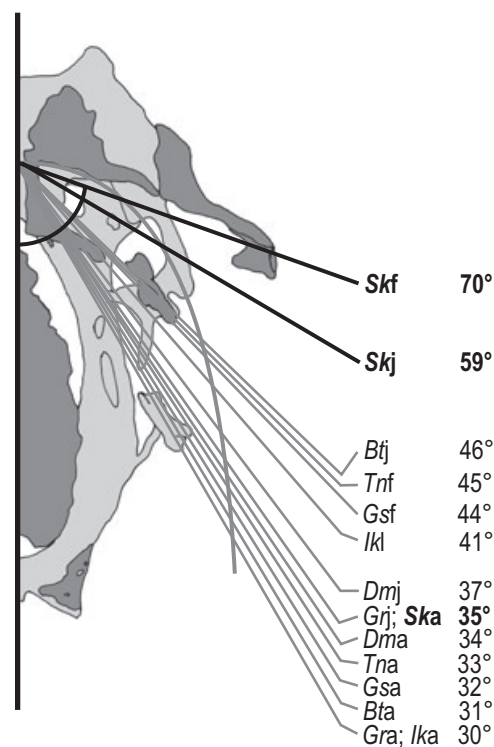
2007) with no *m. add. mand. internus* (de Villiers, 1938; Brand, 1956). The *m. levator quadrati* is also absent (de Villiers, 1938; Brand, 1956). Previously unreported in any *Scolecophorus* is the presence of two *m. pterygoideus*-like muscles. In most other caecilians, the single *m. pterygoideus* originates from either the pterygoid or the pterygoid process of the quadrate and inserts on the medial side of the processus retroarticularis (Wilkinson & Nussbaum, 1997; Kleinteich & Haas, 2007). In *S. kirkii*, the smaller, anterior muscle, which we termed *m. pterygoideus minor* in the present study, originates from the post-palatinal process in the foetus, and later from the maxillopalatine, via a strong fascia. The larger, posterior muscle, termed *m. pterygoideus major* in the present study, originates from the lateroventral neurocranium, just underneath and behind the processus basipterygoideus. Both pterygoideus muscles attach on the medial side of the processus retroarticularis. A pterygoid is apparently absent in *Scolecophorus* and the processus pterygoideus quadrati is rather small and dorsally displaced. Based on topological relationships, it seems most likely that the two muscles are derived from the single ancestral *m. pterygoideus* retained in other caecilians, which split and shifted its origin. In contrast to our observations, de Villiers (1938) mentioned the *m. pterygoideus* as being well developed in *S. uluguruensis* without noting any subdivisions, whereas Brand (1956) described it as arising from the ventral edge of the processus pterygoideus quadrati as in other caecilians. The reported differences between *S. kirkii* and *S. uluguruensis* might be the result of interspecific variation, although it might be possible that the peculiar architecture of the *m. pterygoideus* complex in *Scolecophorus* has previously been overlooked because of the close association of the two pterygoideus muscles in histological sections. However, the presence of two discrete units of the *m. pterygoideus*, at least in *S. kirkii*, suggests a more complex function of this muscle in cranial kinesis. Although wary of inferring action from static morphology, we suspect that this contributes, in conjunction with the absence of an internal process on the lower jaw, to increased mobility of the lower jaw and probably the cheek itself. Increased kinesis of the quadrate-squamosal complex is known to substantially increase bite force in adult caecilians (Summers & Wake, 2005). Again, it is noteworthy that kinesis in *A. eiselti* is also associated with the differentiation of the *m. pterygoideus* into two parts (Wilkinson & Nussbaum, 1997), which shifted their origin from the processus pterygoideus quadrati to a fascia arising from the posterior edge of the maxillopalatine.

Available ecological information (Gower *et al.*, 2004; Jones, Loader & Gower, 2006) indicates that *S. vittatus* is more active above ground than sympatric

caecilian species and feeds predominantly on large, surface active earthworms. Jones *et al.* (2006) suggested that the mobile cheek region in *Scolecormorphus* is advantageous for handling large, soft-bodied prey.

IS THERE A MORPHOLOGICALLY SPECIALIZED POSTPARITIVE FEEDING STAGE IN *SCOLECOMORPHUS*? Developmental changes in the premaxillary-maxillary arcade in caecilians are mainly the result of a posterior extension of the maxillary arcade during ontogeny. One of the main differences between foetal and juvenile *Scolecormorphus* and comparable ontogenetic stages of other caecilians is that the premaxillary-maxillary arcade forms a very broad arc that is oriented at a large angle to the sagittal axis (Fig. 6). This is associated with an almost transverse orientation of the dental lamina of the premaxilla and the large, out turned maxillary arcade. It is noteworthy, however, that besides *S. kirkii*, the largest angles are seen in foetuses and hatchlings of species known or suspected to scrape-feed in their early ontogeny (Fig. 6). There appears to be a gradual decrease in angle between the foetal and the juvenile stage in *S. kirkii*. However, a large gap separates the juvenile and adult morphologies and, at present, it is unclear whether the transition between them is a gradual one or more climactic, metamorphosis-like, although the latter is perhaps more likely. The gap in total length between sampled foetuses and juveniles is similar to that between the largest juvenile showing the particular morphology and the smallest adult-like specimen. However, the difference in orientation of the premaxillary-maxillary arcade between foetuses and juveniles is relatively small, whereas that between juvenile and adult morphology is much larger. It appears therefore as if some accelerated transformation from the juvenile to the adult-like morphology occurs between 110 mm and 150 mm total length in *S. kirkii*.

Foetuses of all viviparous taxa studied to date have a specialized, deciduous dentition (Parker & Dunn, 1964), which is assumed to be used in scrape feeding from the hypertrophied oviduct lining (Wake, 2003) and it is tempting to interpret the distinctive morphology of foetal *S. kirkii* as an adaptation to intra-oviductal feeding. Several lines of evidence, however, suggest instead a role in postparitve feeding. First, the lining of the oviduct does not seem to be hypertrophied (H. Müller, S. P. Loader, pers. observ.). Second, juveniles of *S. vittatus* (Loader *et al.*, 2003) and *S. kirkii* (present study) both had an amorphous, flaky, white substance in their hindguts, showing that juveniles of both species have apparently similar feeding habits that are distinct from the usual spectrum of



**Figure 6.** Orientation of the premaxillary-maxillary arcade in various caecilian species plotted onto an outline drawing of the investigated foetus of *Scolecormorphus kirkii*, in ventral view. Lines indicate the angle of the premaxillary-maxillary arcade in various species and life-history stages, with the grey parabola representing the typical orientation of the arcade found in other caecilian species. Angles were measured from the medial end of the dental lamina of the premaxilla to the posterior, functional end of the dentary lamina of the maxilla or maxillary part of the maxillopalatine, usually indicated by the last tooth. Angles for *Dermophis mexicanus* measured from Lessa & Wake (1992), others are from specimens from the Natural History Museum, London. Btj, *Boulengerula taitanus* juvenile; Bta, *B. taitanus* adult; Dmj, *Dermophis mexicanus* juvenile; Dma, *D. mexicanus* adult; Grj, *Gegeneophis ramaswamii* juvenile; Gra, *G. ramaswamii* adult; Gsf, *Geotrypetes seraphini* foetus; Gsa, *G. seraphini* adult; Skf, *Scolecormorphus kirkii* foetus; Skj, *S. kirkii* juvenile; Ska, *S. kirkii* adult; Tnf, *Typhlonectes natans* foetus, Tna, *T. natans* adult.

primarily invertebrate prey of adults (Jones *et al.*, 2006). Third, in the foetus of *S. kirkii*, the tooth crowns of the premaxillary-maxillary and dentary arcade are still covered by the epidermis and likely to be nonfunctional. By contrast, all teeth are erupted in the investigated juveniles and show clear signs of wear.

Specialized, so-called 'foetal' teeth are now known to occur also in hatchlings of direct developing caecilians (Wilkinson & Nussbaum, 1998) and Kupfer

*et al.* (2006) recently suggested that 'foetal' teeth may have first evolved in direct developing, skin feeding caecilians and were later co-opted for intra-oviductal feeding in viviparous forms. The presence of specialized teeth in fetuses and juveniles is therefore not necessarily indicative of intra-oviductal feeding in viviparous caecilians. In some aspects, *S. kirkii* may be intermediate morphologically and behaviourally between direct-developing forms with 'foetal' teeth in altricial hatchlings and post-hatching skin-feeding (Kupfer *et al.*, 2006; Wilkinson *et al.*, 2008), and viviparous forms with intra-oviductal feeding and fully developed, precocial neonates (Wake, 1977). Taken at face value, the limited evidence leads us to hypothesize that neonate *Scolecormorphus* feed on maternal skin rather than the fetuses feeding on the oviduct lining, and we interpret the presence of a strong ventral concavity of the cephalic and nuchal region in juveniles as an adaptation to such postparturitive feeding (Loader *et al.*, 2003). Unfortunately, our ontogenetic sequence is incomplete and probably lacking in late fetuses/early newborns that would clarify whether there is any intra-oviductal feeding. *Scolecormorphus* is potentially very important for understanding caecilian life-history evolution and should be particularly targeted in future studies on the evolution of viviparity in caecilians to test the evolutionary scenario proposed by Kupfer *et al.* (2006). Clearly, more observations especially of live animals are needed for further functional interpretations of the unusual juvenile morphology.

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## APPENDIX

List of specimens of *Scolecormorphus kirkii* from the Udzungwa Mountains, Tanzania, examined. Museum collection acronyms: AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London.

Number	Locality	Life-history stage	Size (in mm)	Preparation
Scol 1, ex. BMNH2005.890	West Kilombero Scarp Forest	Foetus	41	Serial sections, three-dimensional reconstruction, angles
Scol 2, ex. BMNH2005.890	West Kilombero Scarp Forest	Foetus	43	Dissection, cleared and stained
Scol 3, ex. BMNH2005.890	West Kilombero Scarp Forest	Foetus	43	Scanning electron microscopy
AMNH A156899	Njokamoni River drainage, Udzungwa Mountains NP	Juvenile	93	Dissection, cleared and stained
AMNH A156897	Njokamoni River drainage, Udzungwa Mountains NP	Juvenile	104	–
AMNH A156898	Njokamoni River drainage, Udzungwa Mountains NP	Juvenile	106	–
BMNH2005.895	West Kilombero Scarp Forest	Subadult	159	–
BMNH2005.894	West Kilombero Scarp Forest	Subadult	209	–
BMNH2005.891	West Kilombero Scarp Forest	Adult	295	Serial sections
BMNH2005.893	West Kilombero Scarp Forest	Adult	350	–
BMNH2005.890	West Kilombero Scarp Forest	Adult	402	–

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Video clips S1–4.** AVI films of three-dimensional reconstructions (surface rendering) of a horizontally sectioned foetal *Scolecormorphus kirkii*, showing the chondrocranium (S1), the head skeleton (S2), the head skeleton with *mm. add. mandibulae* and *ptergoideus* (S3), and the head skeleton including most of the musculature. For an explanation of the structures, see Figs 3, 4, 5. Colour codes: blue, cartilage; beige, bone; brown, musculature. **VRML file S1.** VRML file of three-dimensional reconstruction (surface rendering) of a horizontally sectioned foetal *Scolecormorphus kirkii*, showing the chondrocranium including the cartilago meckeli. Colour codes: blue, cartilage; beige, bone. The VRML file was produced from histological sections with the software IMARIS. The VRML file can be viewed using any VRML client. These clients are small programs (cookies) that enable the observer to interactively rotate and move the models in the internet browser (Internet Explorer, Netscape, Firefox, etc.). The models have been tested with the Cortona VRML client for Windows XP. The Cortona VRML client is available at: <http://www.parallelgraphics.com/products/cortona/> and follow the instructions. After installation open the VRML file in an internet browser. The animation can be freely rotated and investigated using the tool palette. If the animation is not in the centre of the screen click on the button ‘fit’ in the right bottom corner of the Cortona handling bar.

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