

A remarkable young *Scolecormorphus vittatus* (Amphibia: Gymnophiona: Scolecormorphidae) from the North Pare Mountains, Tanzania

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Abstract

A description is given of the external morphology of a single young caecilian (gymnophionan) amphibian from the North Pare Mountains, Tanzania, referable to *Scolecormorphus vittatus* (Boulenger, 1895). This is the smallest known free-living *Scolecormorphus*, and it is characterized by many remarkable features previously unrecorded for any life-history stage of any caecilian. The cheeks have conspicuous, posteroventrally divergent paraoral processes that border a concavity on the ventral surface of the snout. The mandibles are very flexible about their articulation with the cranium, and they have a broader curvature than the upper jaw. The dentition is heterogeneous, with adult-like monocuspid teeth in single rows, but also some supernumerary teeth, some of which are bicornute. The posterior parts of the paraoral processes bear a small number of monocuspid teeth that lie outside, and project away from, the mouth. The nuchal region of the body bears a distinctive concavity on the underside of the throat, bordered by longitudinal ridges that terminate in fleshy nipples. All of these features are unknown in adult *Scolecormorphus*, and many are unique for caecilians, and they suggest a highly distinctive life-history stage. The discovery and description of this specimen adds substantially to the currently meagre information on the life history of scolecormorphids and of the diversity of caecilian reproductive biology. Two modes of viviparity in caecilians are identified, with *S. vittatus* resembling the caeciliid *Geotrypetes* in giving birth to small altricial young that seem to require extended post-parturition parental care.

Key words: viviparity, reproduction, Africa, caecilians, morphology, *Scolecormorphus vittatus*

INTRODUCTION

Caecilian amphibians have a variety of reproductive modes, including the classical biphasic amphibian life cycle of oviparity with an aquatic larval stage, as well as oviparity with direct development and viviparity (Wake, 1977a). Our understanding of the evolution of this diversity is hampered by a lack of information on the reproduction and development of most of the c. 160 recognized species of caecilians (Wilkinson & Nussbaum, 1998). The Scolecormorphidae is one of six currently recognized families of caecilians (Duellman & Trueb, 1986; Nussbaum & Wilkinson, 1989; Wilkinson & Nussbaum, 1999) and includes the genera *Scolecormorphus* (three species) and *Crotaphatrema* (three species), from East and West Africa, respectively

(Nussbaum, 1985; Lawson, 2000). Scolecormorphids have several distinctive morphological synapomorphies, including the absence of stapes and the presence of protrusible eyes that migrate from the orbit during development in association with the tentacle (Taylor, 1968; Nussbaum, 1985; O'Reilly, Nussbaum & Boone, 1996). Barbour & Loveridge (1928) reported discovering small embryos in a female *Scolecormorphus uluguruensis*. Subsequently, Parker & Dunn (1964) provided a brief description of the dentition of *S. uluguruensis* embryos as part of their survey of tooth structure and function in the early development of viviparous caecilians, and Taylor (1968: fig. 360) figured one such embryo. As far as we are aware, there have been no other reports of early life-history stages in any species of *Scolecormorphus*. The life history of *Crotaphatrema* is even less well known, though Nussbaum (1985) suggested that this genus may be oviparous, based on his observation of large ova.

In 1973, CAM collected a juvenile caecilian from the herpetologically poorly known North Pare Mountains of

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Northern Tanzania, that is now part of the collections of the Natural History Museum, London (BMNH 1986.609). This specimen is interesting because it is the smallest, and presumably the youngest, known free-living *Scolecormorphus* and because it has distinctive features that are unknown in the adults or young of any other caecilian. Thus this specimen contributes to the meagre knowledge of the reproductive biology of *Scolecormorphus* and to knowledge of the morphological diversity of caecilians. In this paper, a description of the distinctive features of this specimen is provided and its significance discussed.

DESCRIPTIVE ACCOUNT

The specimen, BMNH 1986.609, was collected by Charles A. Msuya on 26 December 1973 in Kifula Village, Ugweno, Pare District, Tanzania. It was dug from rich, moist soil in a mixed banana and coffee plantation. Its morphology and provenance supports a referral to *Scolecormorphus vittatus* (Boulenger, 1895) (see Discussion). BMNH 1986.609 has a total length of 72 mm, which is smaller than any previously reported specimens of *Scolecormorphus* other than intrauterine embryos (Barbour & Loveridge, 1928; Parker & Dunn, 1964; Nussbaum, 1985). Some meristic and additional morphometric data for BMNH 1986.609 are given in Table 1, along with comparative data for the otherwise smallest specimen known from the same locality, a 158 mm female in the collections of the California Academy of Sciences (CAS 159952). Comparative photographs of the

two specimens are given in Figs 1 & 2. BMNH 1986.609 differs strikingly from CAS 159952 and from all other adult *S. vittatus* in several features.

In adult scolecormorphids, as in many caecilians, the snout projects anteriorly beyond the margin of the mouth, forming a bluntly rounded subconical rostrum. In contrast, the rostrum of BMNH 1986.609 in lateral view is more wedge-shaped with a more pointed snout tip. On its ventral surface, the rostrum is distinctly concave transversely and its lateral margins form ventrolaterally directed ridges, referred to here as rostral ridges, the apices of which provide a sharper demarcation between the ventral and dorsal surfaces of the rostrum than is seen in other caecilians. More typically, the ventral surface of the caecilian rostrum is convex and without sharp differentiation between the ventral and dorsal surfaces. In adult *Scolecormorphus*, the tentacular apertures are on the ventral surface of the rostrum just anterior to the mouth. In BMNH 1986.609 they are also just anterior to the mouth but are positioned more laterally, in depressions on the lateral surfaces of the rostral ridges, and are barely visible in ventral view (Fig. 3). Compared to CAS 159952, a specimen more than twice its total length, the more laterally placed tentacular apertures of BMNH 1986.609 are also more widely separated (Table 1). The subdermal eyes are more clearly visible in BMNH 1986.609 than in CAS 159952. In BMNH 1986.609 they are close to the tentacular aperture (Table 1) and anterior to the assumed position of the orbit.

The entire mouth and the cheeks (i.e. the sides of the head adjacent to the upper margin of the mouth) of BMNH 1986.609 are highly unusual. In CAS 159952, as is typical of adult caecilians, there is a close fit between the upper and lower jaws when the mouth is closed, and the cheeks do not extend laterally much beyond the lateral margins of the lower jaw and the corresponding lateral margins of the mouth on the upper jaws. In BMNH 1986.609, the cheeks have pronounced posteroventrolateral projections of highly distinctive thickenings, referred to here as paraoral processes (Fig. 3). These do not extend posteriorly to the level of the jaw angle, but instead they diverge from, and partly overlap laterally, a thin web of tissue that forms the upper margin of the corner of the mouth. There is a minor asymmetry in this region in BMNH 1986.609, with the web of tissue on the right side seemingly slightly damaged. The rostral ridges extend onto the paraoral processes, which extends the ventral rostral concavity posterolaterally. The lateral expansion of the paraoral processes, and the cleft between their posteromedial edges and the skin of the corner of the mouth, gives the head anterior to the corner of the mouth a distinctive arrow-shape in ventral or dorsal view (Fig. 3).

In preservation, the lower jaw of BMNH 1986.609 is angled anteroventrally so that the mouth is open. It is very flexible about its articulation with the upper jaw and can be opened more widely than in adult preserved specimens. It is very short and gives the impression of lacking a close fit with the upper jaws when the mouth is closed. However, the mouth can be closed by simultaneously elevating the

Table 1. Morphometric and meristic data for the two specimens of *Scolecormorphus vittatus* shown in Figs 1 & 2. BMNH 1986.609 is the smallest known free-living specimen, while CAS 159952 is the smallest known adult individual from the same locality in the North Pare Mountains, Tanzania. All morphometric data given in mm

	BMNH 1986.609	CAS 159952
No. of primary annuli	121	125
Total length	72	157
Width at mid-body	2.8	5.6
Snout tip to first nuchal groove	4.8	5.6
Snout tip to second nuchal groove	6.0	7.3
Snout tip to third nuchal groove	7.2	10.1
Lower jaw tip to jaw angle	2.2	3.1
Snout tip to jaw angle	3.9	4.4
Head width at jaw angle	2.7	3.1
Head width at occiput	3.0	3.8
Internarial distance	1.1	1.3
Intertentacular distance	2.1	1.6
Eye spot to tentacle	0.4	Eye not visible
Eye spot to naris	1.3	Eye not visible
Tentacle to naris	0.8	0.7
Length of terminal shield	2.2	3.6

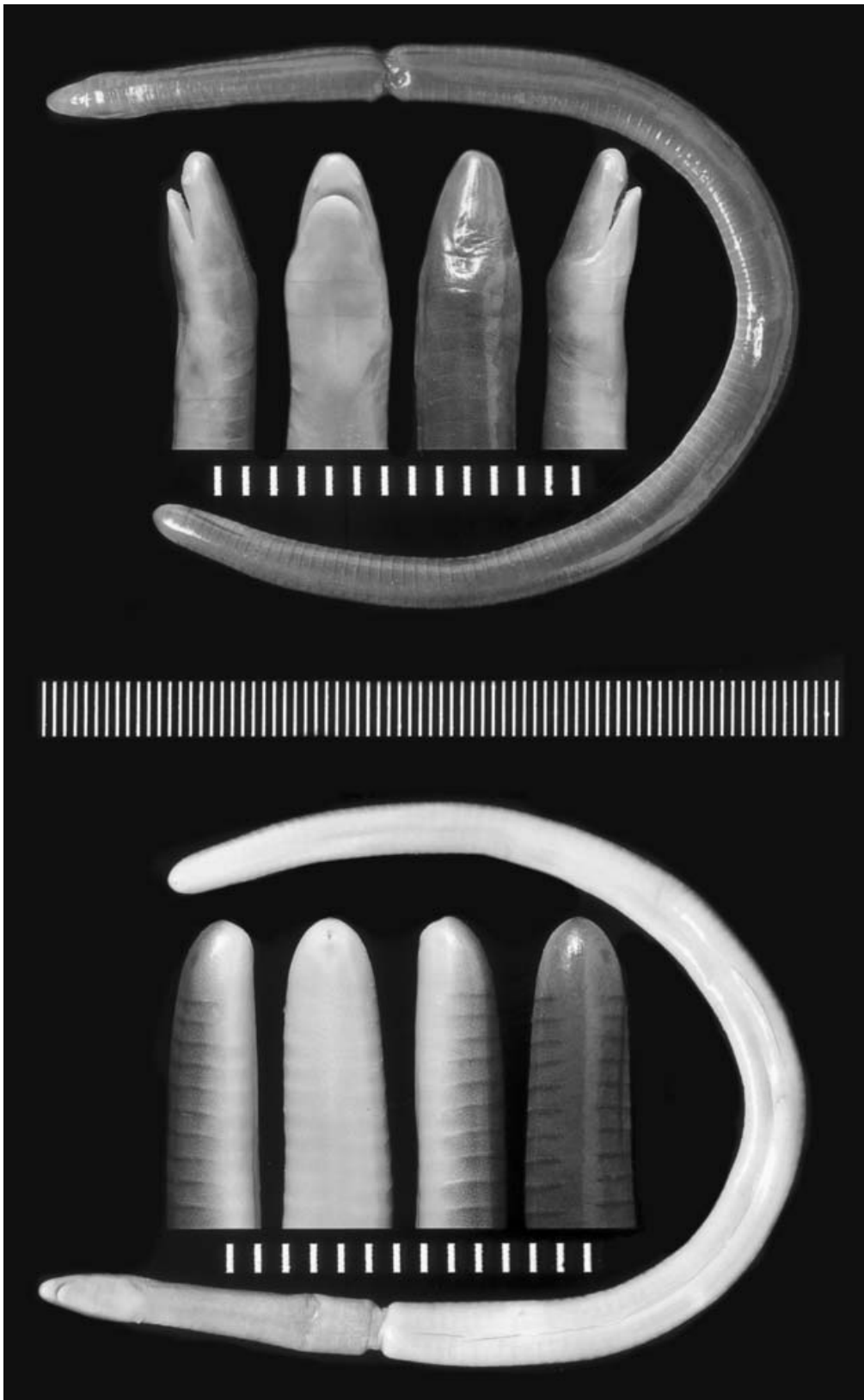


Fig. 1. *Scolecormorphus vittatus* CAS 159952. Whole specimen in dorsal and ventral views, with detail of head and vent region. Scale bars in mm.



Fig. 2. *Scolecomorphus vittatus* BMNH 1986.609. Whole specimen in dorsal and ventral views, with detail of vent region. Scale bars in mm.

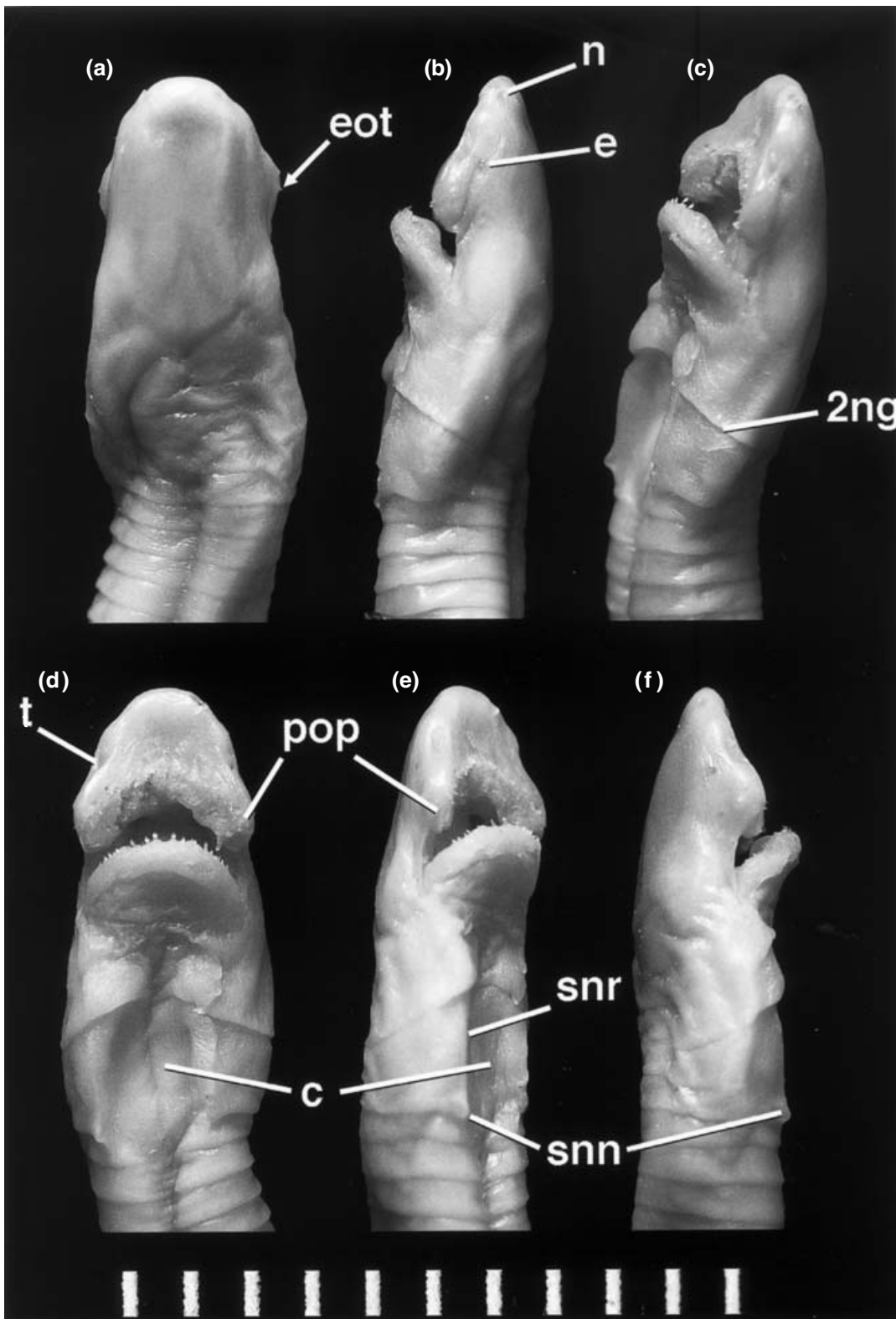


Fig. 3. *Scolecormorphus vittatus* BMNH 1986.609. Head and anterior of body in: (a) dorsal; (b) left lateral; (c) left ventrolateral; (d) ventral; (e) right ventrolateral; (f) right lateral views. c, subnuchal concavity; e, eye; eot, position of extraoral teeth on outer aspect of paraoral process; n, external naris; pop, paraoral process; snn, subnuchal nipple; snr, subnuchal ridge; t, tentacular fossa; 2ng, second nuchal groove. Scale bar in mm.

lower jaw and pushing downwards and backwards on the snout. This seems to flex the cranium. It also widens the angle between the paraoral processes.

Adult scolecomorphids have pointed and recurved monocusped teeth in three series, the dentary series in the lower jaw and the premaxillary–maxillary and prevomeropalatine series in the upper jaw. Nussbaum (1985) reported that the numbers of these teeth in *S. vittatus* vary between 17–31, 14–25 and 9–21, respectively, and tooth counts for CAS 159952 fall within these ranges (Table 1). The teeth of BMNH 1986.609 and their arrangement differ in several respects from those of adult scolecomorphids. They are mostly very small, which makes precise observations of number, morphology and disposition difficult without further preparation. They are also irregular in these respects, making the interpretation of pattern details subjective. Our description is one possible interpretation of these details.

The anterior margins of the upper jaws of BMNH 1986.609 bear a series of premaxillary–maxillary (PMM) teeth. This series is irregular as is the anterior margin of the upper jaws, and there is some damage to the adjacent gingivae, especially on the left side. The series comprises 19 teeth, 10 on the right and nine on the left, that extend from the midline onto the paraoral processes. The teeth are monocusped and recurved, as in adults. There are two similar but smaller teeth just anterior to the two most anteromedial members of the PMM series. These can be considered supernumerary and distinct from the PMM series *per se*. In addition, there are two small teeth that seem to have bicornute crowns. These also lie outside the arc of the main PMM series and can also be interpreted as supernumerary, although they are in line with gaps in the PMM series (between the third and fourth, and between the fourth and fifth posteriormost teeth of the left and right sides, respectively) and might be displaced members of that series. On each side there is an additional patch of four pointed monocusped teeth lying on the outer (lateral and dorsolateral) surface of the paraoral processes posteriorly. These teeth lie some distance outside of the mouth, beyond the rostral ridges. These extraoral teeth point upwards and outwards, although the two most dorsal members of each patch are barely erupted through the skin. We are unable to determine whether any teeth corresponding to the prevomeropalatine series of adults are present.

On the lower jaw of BMNH 1986.609 there are at least two rows of teeth in at least some places. All are monocusped and somewhat recurved. Of these, a major row comprises 23 teeth, 11 on the left and 12 on the right, that extend from the mandibular symphysis to near to the corner of the mouth. The most anteromedial teeth of this row are distinctly larger than the others and they differ from those of adult *Scolecomorphus* in having a relatively broad subterminal tooth crown (broader than the base) with an apical point. More posterolateral teeth are smaller and have a more narrow crown similar to the adult condition. An additional short tooth row comprising about six teeth on the left and three on the right lies labial to the anteromedial teeth of the main row. These teeth are very small, occupy the anterior margin of the mouth and

are directed more anterodorsally. A single additional large tooth lies lingual to the large anteromedial teeth of the main series on the right side.

BMNH 1986.609 also has an unusual nuchal region. In adult caecilians, the ventral surface of the nuchal region, referred to here as the throat, shows little differentiation from the adjacent anterior body region. In adult *Scolecomorphus*, the main distinguishing features are the absence of annular grooves and the presence of a weak and narrow mid-ventral longitudinal nuchal groove (Fig. 1). In BMNH 1986.609, in contrast, there is a distinctive concavity on the throat that occupies most of the ventral surface of the second nuchal collar and has straight-sided lateral margins that are demarcated by longitudinal subnuchal ridges. The concavity extends onto the first nuchal collar anteriorly, but is less well indicated and seemingly less regular there. Posteriorly, it is continuous with a narrow but pronounced mid-ventral groove that extends across approximately the first 20 annuli (and reappears intermittently along the length of the body). The right subnuchal ridge terminates at the posterior margin of the second nuchal collar in a distinctive fleshy posteroventrally projecting nipple (Fig. 3). It seems that an antimeric nipple was present on the left sub-nuchal ridge also, but this region is damaged and most of the nipple is missing. The second nuchal groove of BMNH 1986.609 is much more pronounced than in adult *Scolecomorphus*. Unlike the adult condition, in which the groove is more or less transverse (Fig. 2), in BMNH 1986.609 it extends obliquely across the lateral nuchal region (Fig. 3).

X-ray examination reveals BMNH 1986.609 to be mostly poorly ossified. Only the otic capsules, the margins of the foramen magnum and the atlas, the floor of the braincase (os basale and parasphenoid) and to a lesser degree the next three anteriormost vertebrae and the posteriormost (pseudangular) parts of the lower jaw including the retroarticular processes, appear relatively well-ossified. An additional 20–25 anterior vertebrae that become progressively less distinct can be seen. Vertebrae cannot be distinguished further posterior and are presumed to be cartilaginous. No ossification is apparent within the paraoral processes. X-rays revealed the presence of some radio-opaque material in the hindgut. Dissection revealed that this included soil and mineral particles. The hindgut also contained a loosely aggregated flaky white substance but no recognizable remains of prey items.

DISCUSSION

The morphology of BMNH 1986.609 supports a referral to the genus *Scolecomorphus* rather than to any other East African caecilian genus. It differs from *Schistometopum* and *Sylvacaecilia* in lacking secondary annuli and in possessing a terminal shield, and from *Schistometopum*, *Sylvacaecilia* and *Boulengerula* in possessing a longitudinal rather than a transverse vent. The specimen can be fairly confidently referred to

Scolecormorphus vittatus. Nussbaum's (1985) key to the species of *Scolecormorphus* is based entirely on coloration. Although the colour is weakly indicated in BMNH 1986.609, either because it was poorly developed and/or because it has faded, a dark dorsal band is faintly indicated which is consistent with that reported for *S. vittatus*. In addition, the number of annuli of BMNH 1986.609 is 121, which lies outside the reported ranges (Nussbaum, 1985) for *S. kirkee* (130–152) and *S. uluguruensis* (124–149) but within the known range for *S. vittatus* (120–148). Provenance also supports the referral to *S. vittatus*. Although the caecilian fauna of the North Pare mountains is poorly known, the only caecilian species reported from this region is *S. vittatus*, and adult material from the same locality was assigned to this species by Howell & Msuya (1980) and Nussbaum (1985).

Judged against current knowledge of the morphology of caecilians, BMNH 1986.609 is highly unusual. In particular, the shape of the head is dominated by unique dentigerous paraoral processes which form lateral expansions of the upper jaws. Comparable features are unknown in any life-history stage of any caecilian species. It is unlikely that these bilaterally symmetrical features are artefacts or otherwise anomalous, and they are interpreted as evidence of a novel cranial morphology and functional morphology of the mouth in early life-history stages of at least *S. vittatus*. The deep mid-ventral groove along the anterior trunk and sporadically elsewhere is probably an artefact of preservation. Dehydration in preservative can affect the shape of external surfaces in caecilians. The concavity on the nuchal region does not seem to be artefactual, but this needs to be tested by examination of additional material. The hypothesis that nuchal features are artefacts does not explain the symmetry of the subnuchal ridges or their termination at the posterior margin of the second nuchal collar in fleshy nipples. Whether or not the nuchal concavity is functionally associated with the rostral concavity and/or with the mouth, the co-occurrence of these features suggests the existence of a highly distinctive life-history stage in *Scolecormorphus*.

Little is known of the life history of *Scolecormorphus*. Based on Barbour & Loveridge's (1928) finding of embryos of *Scolecormorphus uluguruensis*, it has been assumed that all *Scolecormorphus* are viviparous (Nussbaum, 1979; Duellman & Trueb, 1986; Wilkinson & Nussbaum, 1998). Foetuses of viviparous caecilians have distinctive dentitions with multiple rows of small teeth, often with distinct cusp forms that are believed to be used in intra-oviductal feeding (Parker, 1956; Wake, 1977b). With respect to *S. uluguruensis*, Parker & Dunn (1964) briefly reported that: 'Thirty-seven of the fetuses, measuring from 24 to 36 mm, have been examined. All are in approximately the same stage of development, which would indicate a brief mating season, and all were still coiled and possessed triradiate, plumose external gills. There are no signs of erupted teeth in specimens of less than 30 mm, which retain some yolk, but older individuals of 30–36 mm have two staggered rows along the premaxillary-maxillary arch and a similar row along

the outer aspect of the lower jaw. The individual teeth are not of the adult bicuspid [sic] type, but in a free-living specimen of 85 mm these are present in single series along the dentaries, premaxillae, maxillae, vomers, and palatines'. Unfortunately, Parker & Dunn also reported that this material is now lost and they did not describe the form of the embryonic teeth in any detail.

At 72 mm total length, BMNH 1986.609 is the smallest free-living *Scolecormorphus* known and presumably the youngest. It is poorly ossified and is probably a newborn. While it is thought unlikely that some demineralization has occurred in preservative, this cannot be ruled out, and should be checked when more material is available. The specimen has no scar tissue indicating the site of the previous attachment of gills. The second nuchal groove of adult *Scolecormorphus* occupies the position in which gills might be expected in *Scolecormorphus* embryos, and the more oblique form of this groove in BMNH 1986.609 may betray the previous presence of gills. Other than Parker & Dunn (1964), reported total length ranges (Barbour & Loveridge, 1928; Nussbaum, 1985) for the three currently recognized species are 163–463 mm for *S. kirkee*, 140–360 mm for *S. uluguruensis* and 140–376 mm for *S. vittatus*. Assuming that the life history of *S. vittatus* is similar to that of *S. uluguruensis*, and that Parker & Dunn (1964) did not overlook similar features in the 85 mm juvenile that they examined, then the peculiar head morphology seen in BMNH 1986.609 does not seem to persist in young *Scolecormorphus* for very long after parturition. Logically, these features are either characteristic of a post-parturition life-history stage or they are present also in (late) foetuses. The presence in BMNH 1986.609 of marginal tooth rows in which large adult-type teeth are accompanied by smaller teeth with supernumerary elements and occasional bicornute crowns, as well as the rather broad and short lower jaws, is significant. These are associated with foetuses of newborns of other viviparous caecilians (Wake, 1977b) and it is considered probable that the paraoral processes of BMNH 1986.609 are also characteristic of *Scolecormorphus* foetuses rather than being elaborated for a short post-natal period. Whether the nuchal concavity and extra oral dentition are also present in foetuses and whether all the unusual features of BMNH 1986.609 are functional in foetuses and/or in newborns is unclear (see later).

In most caecilians, the cheek region proximal to the corner of the mouth is supported chiefly by a bony quadrato-squamosal arch. In zygotrophic caecilians, this arch forms the lateral margin of the upper temporal fenestra (Nussbaum, 1977). Typically, the stapes articulates with the quadrate and connects the arch to the braincase posteriorly. Given only superficial morphological information on a single specimen, we are wary of drawing functional conclusions *per se*. However, based on the apparent absence of any ossification within the paraoral processes of BMNH 1986.609, we speculate that the paraoral processes of young *Scolecormorphus* are soft-tissue structures that are not supported by any lateral expansions of the quadrato-squamosal arch. In

the typhlonectid *Atretochoana eiselti*, an unusual lateral expansion of the cheeks, associated with an enlarged gape, is correlated with a loss of the articulation between the quadrate and the stapes and the consequent freeing of the cheek from the posterior of the braincase (Wilkinson & Nussbaum, 1997). Scolecomorphids are unusual among caecilians in lacking a stapes, and thus in having a potentially less constrained cheek region, and the possibility of a relationship between foetal adaptation and adult morphology here is intriguing. The extreme flexibility of the lower jaw suggests a highly kinetic skull but the mobility of the expanded cheeks is not clear from BMNH 1986.609, and a better understanding of its novel cranial morphology requires more detailed anatomical study of additional material.

Some caecilians have a distinctive, deciduous 'foetal' dentition that sometimes extends outside the mouth, onto the external surface of the lower jaw (Parker, 1956; Wake, 1980; Wilkinson, 1991). In contrast, the extraoral teeth of BMNH 1986.609 are not of the 'foetal' type, and are on the upper jaw, on the dorsolateral surfaces of the paraoral processes. These are unreported in any life-history stage of any caecilian species and are highly unusual. Extraoral teeth have been reported in some fish, where they have been ascribed a hydrodynamic function (Sire, 2001). There may be several possible functions for these teeth in foetal or neonatal caecilians (involving for example communication and feeding), but we are confident only that they lack any hydrodynamic function in these soil-dwelling animals.

A further set of peculiar features of BMNH 1986.609 are the concavities and associated ridges and fleshy nipples on the snout and throat. These features contribute to an overall impression of an animal that is adapted to feeding on or clinging to a surface. Foetal caecilians are believed to feed *in utero* upon secretions and cells of the hypertrophied maternal oviduct lining, and the young of some species may feed upon maternal skin secretions (O'Reilly, Fenolio *et al.*, 1998; M. Wilkinson, R. A. Nussbaum & C. Jared, pers. obs., as reported in Pennisi, 1999). The concavities of BMNH 1986.609 could conceivably facilitate association with and/or feeding from either a flexible oviduct lining or the firmer and more concave external surface of the mother. The presence of environmental debris (mineral and soil particles) in the hindgut is evidence that BMNH 1986.609 had ingested material subsequent to its birth, suggesting that this life-history stage is a feeding stage and is not simply quiescent.

There seem to be at least two modes of viviparity in caecilians. Mode I caecilians (typhlonectids, the Central American caeciliids *Gymnopsis* and *Dermophis*, and the West African caeciliid *Schistometopum thomense*) give birth to well-developed and well-ossified, precocial young that appear immediately capable of an independent existence. Some traces of characteristic foetal features (e.g. of the dentition) may be present in newborns (Taylor, 1955; Parker & Dunn, 1964; Wake, 1977b) but they mostly resemble adults. Mode II caecilians (the West African caeciliid *Geotrypetes*) give birth to smaller and more altricial young that seem to require extended

post-parturition parental care (Wake, 1977b; O'Reilly, Fenolio *et al.*, 1998). Mode II newborns resemble younger mode I foetuses, and differ substantially from adult caecilians, for example in their dentition, in lacking pigment, and in being weakly ossified. BMNH 1986.609 is also generally weakly ossified and on that limited basis, *Scolecomorphus* seems to be most similar to mode II viviparous caecilians.

Throughout our discussion we have assumed that the unusual features of BMNH 1986.609 are typical of a life-history stage that is common to all *Scolecomorphus* species, and that we can meaningfully discuss the life history of *Scolecomorphus*. This assumption needs to be tested through the collection of additional material of all species of *Scolecomorphus*, encompassing a better range of life-history stages than are currently known for any species. If our assumption is correct, then paraoral processes, extraoral teeth, rostral and throat concavities, ridges and nipples, all of which are obviously derived within the Gymnophiona, will provide further compelling evidence for the monophyly of *Scolecomorphus*. If our assumption is incorrect, they should provide useful evidence of phylogenetic relationships within this fascinating genus.

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