The caecilian amphibian *Scolecomorphus kirkii* Boulenger as prey of the burrowing asp *Atractaspis aterrima* Günther: trophic relationships of fossorial vertebrates

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Abstract

A report is given of an adult caecilian, *Scolecomorphus kirkii*, found in the gut of a specimen of the snake *Atractaspis aterrima* from the Udzungwa Mountains, Tanzania. Both predator and prey are largely fossorial in soil, and their ecology is poorly known, such that this is the first reported predator of any scolecomorphid caecilian. The caecilian was ingested head first and much of the flesh from the anterior of the specimen had been digested. The prey/predator mass ratio is 0.48. This value is substantially higher than reported for *A. aterrima* from West Africa, and refutes the notion that this species feeds only on small prey. Most reported predators of caecilians are snakes, and a brief review is presented.

Key words: Africa, Atractaspididae, diet, Gymnophiona, soil, Tanzania

Résumé

Rapport est donné du cas d'un cécilien adulte, *Scolecomorphus kirkii*, trouvé dans l'intestin d'un serpent *Atractaspis aterrima*, dans les Monts Udzungwa, en Tanzanie. Le prédateur et la proie sont en grande partie fouisseurs et on connaît mal leur écologie, à tel point que ceci est le premier cas rapporté de prédateur d'un cécilien scolécomorphe. Le cécilien a été absorbé la tête la première et une grande partie de la chair de l'avant de l'animal avait été digérée. Le rapport de masse proie/prédateur est de 0,48. Ce chiffre est nettement plus élevé que celui rapporté pour *A. aterrima* en Afrique de l'Ouest et contredit l'idée que cette espèce se nourrit de petites proies. La plupart des prédateurs des céciliens rapportés sont des serpents et on en présente une brève révision.

Introduction

Burrowing asps of the genus *Atractaspis* are venomous, fossorial snakes inhabiting rainforest, woodland, savanna, and semi-desert in mostly tropical Africa and the Arabian peninsula (e.g. Kochva, 2002). Despite their injurious (although rarely fatal, e.g. Spawls & Branch, 1995) potential for humans, very little is known about the natural history of the genus, perhaps because their fossorial lifestyle makes them relatively elusive (e.g. Akani *et al.*, 2001). Data on the diet of *Atractaspis* is scant. For example, Cansdale (1961: 68) wrote that 'It is hard to speak about the feeding habits of snakes which are so poorly known, but their diet is known to include skinks, Worm snakes, small rodents and shrews.' Diet and feeding in *Atractaspis* is of particular interest because of the uncertain phylogenetic position of the Atractaspididae, and an unusual dentition that is highly reduced apart from very long maxillary fangs (e.g. Reinhardt, 1843). This reduced dentition prevents the 'pterygoidwalk' mode of swallowing used by many other higher snakes. Instead, a mechanism convergent with that seen in alethinophidian snakes has evolved in *Atractaspis*. This is perhaps an adaptation to their fossorial habit (Deufel & Cundall, 2003).

Caecilian amphibians (order Gymnophiona) are an inadequately understood and relatively understudied component of tropical vertebrate faunas. As with *Atractaspis*, caecilians are fossorial, elongate and limbless, and their predator–prey relationships are inadequately known. There are few reports of predators of caecilians, and

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apparently none for the endemic African family Scolecomorphidae. Here we add to the meagre knowledge of diet in atractaspidid snakes and the predators of caecilians with a brief report of the discovery of a scolecomorphid caecilian in the gut of an *Atractaspis*.

Material, methods and results

The snake specimen is catalogued in the Zoological Museum of the University of Copenhagen, Denmark (ZMUC) as R68320. ZMUC R68320 was collected during 1997–1998 by residents of the Masisiwe area in the Udzungwa Mountains, Tanzania (08° 17′S, 35°54′E, *c.* 1840 m a.s.l.). Using the key of Broadley & Howell (1991), it is identified as *Atractaspis aterrima*. This identification is based on the single subcaudals and entire anal shield, the short frontal (almost as broad as long), the high number of ventrals (274), and the number of mid-body scale rows (23), a combination of features that is diagnostic for specimens of *A. aterrima* from the Eastern Arc region of East Africa. This species is further distributed westward from Uganda to Senegal. The total length (TL) of ZMUC R68320 is 522 mm, and the mass of the preserved specimen minus gut contents is 27.5 g. Other than the caecilian described below, the only other contents in the gut was a short (36 mm, preserved mass 0.5 g), autotomized section of the tail of an unidentified lizard. The snake is a female. It is in a fairly good condition, although it was beaten during capture so that its skin is ruptured in three places and the vertebral column is broken in one place.

The caecilian (ZMUC R0277, Fig. 1) removed from the gut of ZMUC R68320 is a mature female, based on examination of its gonads. It has a TL of 356 mm and preserved mass of 13.2 g. Identification of species of *Scolecomorphus* is largely determined by colour pattern (Nussbaum, 1985), and ZMUC R0277 is identified as *Scolecomorphus kirkii*. In addition to its colour pattern, the numbers of annuli (147) and vertebrae (158) are within the known range for females of this species (140–152 and 150–165, respectively; n = 23, Nussbaum, 1985).

Given its orientation in the snake's gut, the caecilian is interpreted as having been ingested head first. Its anterior end is heavily digested with most of the skin and other, outer soft tissue of the cranium and mandibles having been

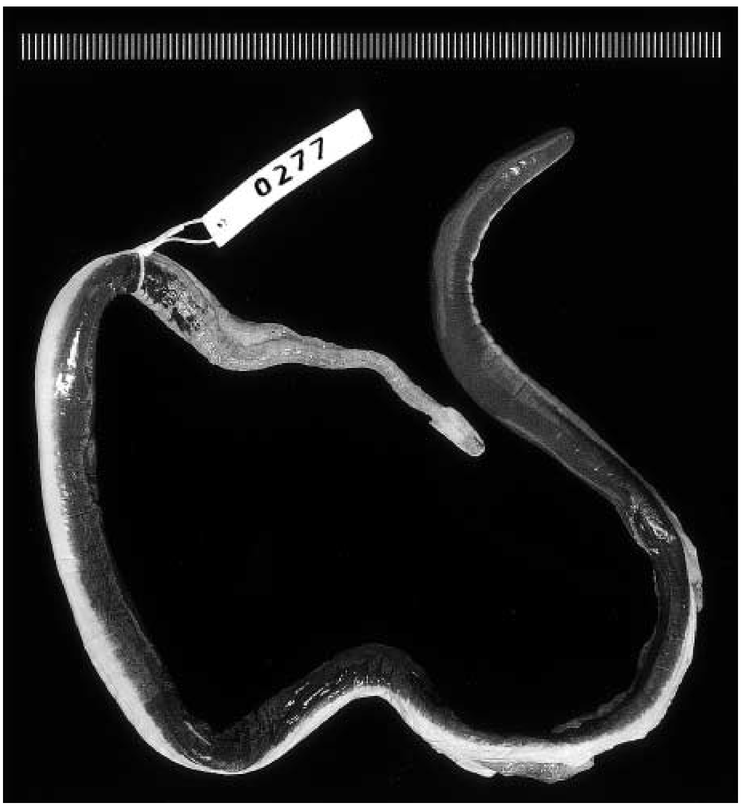

Fig 1 Dorsal view of a partially digested caecilian amphibian, *Scolecomorphus kirkii*, removed from the gut of a specimen of the atractaspidid snake *Atractaspis aterrima* from Tanzania. Scale bar in millimetres.

removed so that many of the bony elements are exposed. The eyes remain in place in the tentacular grooves. The skin is missing from the anterior of the body, up to the level of about the 24th annulus. Much of the flesh is also missing from this region, including the more superficial 'external muscular sheath' (Nussbaum & Naylor, 1982). Deeper muscle remains attached to the vertebrae so that only a very small amount of bone is directly visible. A similar pattern of loss of flesh from the head was reported by Barbour & Loveridge (1928) for an individual of the Tanzanian caeciliid *Boulengerula boulengeri* extracted from the gut of the elapid snake *Elapsoidea nigra*. The amount of flesh remaining intact on the anterior of ZMUC R0277 increases steadily up to the 24th annulus. From the 24th to about the 60th annulus, the body and skin are in good condition. From about the 60–117th annulus, the body wall is notably flaccid and there are substantial patches where the outer layer of skin is missing. This might be attributable to imperfect preservation, to the fact that the snake was damaged, or perhaps it instead indicates that the caecilian was bitten and possibly envenomated here by the *A. aterrima*. The remaining length of the specimen, from about the 118th annulus to the posterior terminus, is in good condition with no indication of any external damage. X-ray examination revealed no damage to any of the bones of the cranial, mandibular, or axial skeleton.

Discussion

Spawls *et al.* (2002): 439) stated that 'virtually nothing is known' of the natural history of *A. aterrima*, and this is, to the best of our knowledge, the first report of this genus feeding on caecilians. That *Atractaspis* feed on other highly fossorial, elongate lower vertebrates, at least occasionally, is demonstrated by reports of scolecophidian snakes (Barbour & Loveridge, 1928: 137; Loveridge, 1933: 279) and an amphisbaenian squamate (Loveridge, 1951: 202) in the gut of specimens from Uganda and Tanzania. Akani *et al.* (2001) reported that the gut and faeces contents of three individuals of *A. aterrima* from Nigeria were snakes (including the colubrid *Natriciteres* sp.) and forest skinks (*Panaspis* sp.). For at least four sympatric species of *Atractaspis*, Akani *et al.* reported an overall statistically significant positive relationship between predator size and prey size, and that 'although the sample size was small', the slopes of this relationship were significantly different among the species studied, with *A. aterrima* taking the proportionately smallest prey.

The predator mass : prey mass values given by Akani *et al.* (2001) were largely for fresh specimens, and the predator mass values included gut contents (L. Luiselli, pers. comm.). Assessing an accurate comparable ratio in the present case is problematic because mass was only measured for the preserved predator and prey, and both values will undoubtedly be lower than they were in life – the snake has a midventral incision along much of its length, and the caecilian is partly digested. Additionally, this study is based on a minimal sample, and the following, limited interpretation must be treated with care.

Prey/predator mass ratio (MR; equivalent to the weight ratio WR of Greene, 1983) have been calculated from the preserved masses. The greatest WR value for *A. aterrima* recorded by Akani *et al.* from their Nigerian sample was about 0.06 (Akani *et al.*'s Fig. 1). In the present Tanzanian case, MR = 0.32 (0.48 if predator mass is recorded minus gut contents), which is almost an order of magnitude greater, and about one and a half times the value of the greatest MR value for any of the species of *Atractaspis* reported by Akani *et al.* (2001) (Fig. 1). The MR value reported here for the Tanzanian specimens is, of course, associated with measurement error caveats, but it might be taken to indicate that *A. aterrima* does not necessarily tend 'to prey upon very small prey' (Akani *et al.*, 2001: 92).

Even including gut contents and allowing for a 10% decrease in mass upon preservation in alcohol (as reported for lizards by Colbert, 1967), the mass (*c.* 70 to >118 g) of three Nigerian specimens of *A. aterrima* given by Akani *et al.* (2001) (Fig. 1) is substantially greater than the mass of the Tanzanian specimen under consideration here, despite the latter being longer. This is also true for seven West African *A. aterrima* in the collections of The Natural History Museum, London (TL 279–645 mm; preserved mass 5.2–48.2 g). For ZMUC Tanzanian specimens of *A. aterrima*, the largest male has a TL of 660 mm and a preserved mass of 71 g (n = 3), and the largest female a TL of 670 mm and of mass 53 g (n = 3). The two heaviest *A. aterrima* reported by Akani *et al.* were females that were gravid, but their *c.* 70 g specimen was not (L. Luiselli, pers. comm.), and the apparent discrepancy between the two studies is not fully explained by reduction in mass caused by preservation. The relationship between mass and length in fresh and preserved *Atractaspis* requires further investigation.

If there is truly a great variation in relative prey size within *A. aterrima*, then this might be attributable to a large number of factors, potentially including geography and the presence of sympatric species of *Atractaspis*. Simpler hypotheses are also worth considering, and it might be noted that 'feeding both on small and large prey is common for most snakes' (Marques, 1996). Furthermore, it is known that some snakes can change their diet under various circumstances (e.g. de Queiroz *et al.*, 2001), so that the proportionately very small size of the prey taken by the two largest *A. aterrima* reported by Akani *et al.* (2001), might conceivably be related to their gravidity. Clearly, more data are needed for a satisfactory assessment of diet in *Atractaspis*.

As far as we are aware, this is the first report of any predator of the African endemic Scolecomorphidae. In life, *S. kirkii* have a striking colour pattern comprising a very dark dorsum and a strongly contrasting (Fig. 1), pinkish venter. Nussbaum (1998: 54) has suggested that the bright colouration of some caecilians might be aposematic, associated with possible skin toxins. It might be speculated that the striking colour pattern of *S. kirkii* is, at least in part, an adaptation to avoid predation, but *A. aterrima* do not seem to be deterred by this and/or any toxins that this caecilian might produce.

Species of *Scolecomorphus* are known only from Malawi and Tanzania in East Africa, where they inhabit rainforest of the highlands, including the Udzungwa, Uluguru, Usambara and Pare Mountains of the Eastern Arc (Nussbaum, 1985). Caecilians other than *Scolecomorphus* are known from some of the western part of the range of *A. aterrima*, but apparently the only report of their predators is of the fossorial, venomous atractaspidid *Polemon acanthias* preying on the caeciliid *Geotrypetes seraphini* in Ghana (Cole, 1967).

As with many aspects of the biology of caecilians, knowledge of their predators is inadequate. Taylor (1968: 393) suggested that for terrestrial caecilians 'doubtless snakes and carnivorous birds are the most active predators'. For snakes, this is supported in that they are the taxa in the vast majority of literature reports of caecilian predators. These reports include preying on the caeciliid *Caecilia intermedia* and an unspecified caecilian by the fossorial/cryptic, nonvenomous colubrid *Ninia atrata* and the venomous elapid *Micrurus ancoralis ancoralis*, respectively, in Colombia (Boulenger, 1913); the semi-aquatic typhlonectid *Chthonerpeton indistinctum* by the aquatic, diurnal aglyphous colubrid *Sordellina punctata* in Brazil (Procter, 1923); several individuals of the caeciliid *B. boulengeri* by the mostly nocturnal, fossorial/cryptic and venomous elapid *E. nigra* in Tanzania (Barbour & Loveridge, 1928: 182; Jakobsen, 1997: 65); the caeciliid *Siphonops annulatus* by the largely nocturnal, venomous colubrid *Clelia clelia* (Sawaya, 1937) and *Siphonops* sp. by the nocturnal, venomous elapid *Micrurus coralinus* (Marques & Sazima, 1997) and the venomous *M. decoratus* (Marques, 2002) in Brazil; the caeciliid *Caecilia gracilis* by the fossorial, nonvenomous aniliid *Anilius scytale* in Surinam (Taylor, 1968: 34; Nussbaum & Hoogmoed, 1979); the caeciliid *Gymnopis multiplicata* by the venomous elapid *Micrurus multifasciatus hertwigi* (Burger, 1997) in Costa Rica; the caeciliids *Microcaecilia* sp. and *Oscaecilia* sp. by the venomous elapid *Micrurus lemniscatus* in Brazilian Amazonia (Martins & Oliveira, 1998); the ichthyophiid *Ichthyophis* sp. by the nocturnal, venomous elapid *Bungarus candidus* (Grossmann & Schäfer, 2000) and the fossorial, nonvenomous cylindrophiid *Cylindrophis ruffus* in Thailand (Greene, 1983; Kupfer *et al.*, 2003). Neotropical coral snakes of the venomous elapid genus *Micrurus* are clearly the most commonly reported snakes preying on caecilians. Roze (1996: 60) reports that among nine species of *Micrurus* known to prey on caecilians, *M. m. mipartitus* from Panama and Colombia, and *M. bocourti* from Ecuador and Peru, are 'known to feed only on caecilians'. Marques & Sazima (1997) found that although caecilians are a significant prey item of species of *Micrurus*, their most common prey are amphisbaenian fossorial reptiles.

Some, but not all, of the records of snakes preying on caecilians report the headfirst ingestion of prey. Marques & Sazima (1997) suggest that instances of tail-first ingestion of fossorial vertebrates by elapid coral snakes are associated with underground feeding. Where reported snake predators are not fossorial or semi-fossorial, they are often nocturnal and/or the caecilian has been found being ingested while moving on the surface (e.g. Burger, 1997; Grossmann & Schäfer, 2000; Kupfer *et al.*, 2003). However, the sample size is currently very small and more data are required before any firm general conclusions can be drawn.

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