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Rotational feeding in caecilians: putting a spin on the evolution of cranial design

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Caecilians are a poorly known group of amphibians with a highly derived skull and cranial musculature that has evolved in response to their specialized head-first burrowing lifestyle. They possess a unique jaw-closing system, which is shown to be capable of generating considerable bite forces for its head width (1.09±0.34 and 0.62±0.31 N for *Schistometopum thomense* and *Boulengerula taitanus*, respectively). However, comprehensive dietary studies indicate that there is no need for large bite forces, since most caecilians appear to be generalist predators of subterranean macrofauna. Here, we demonstrate, based on *in vivo* external and X-ray video recordings of animals feeding, that long-axis body rotations are used independent of prey size by these two species of caeciliid caecilians when feeding underground. Further, we show that individuals are capable of generating a substantial spinning force, which is greater than their bite force (1.35±0.26 and 1.02±0.18 N, respectively). These observations shed light on the functional and the evolutionary significance of several unique features of the cranial design in derived caecilians; spinning may allow the individuals to judge prey size and subsequently reduce oversized prey within gape limits.

Keywords: Gymnophiona; feeding behaviour; bite force; burrowing

1. INTRODUCTION

Caecilians are an elongate and completely limbless order of amphibians, most of which are soil-dwelling predators of the wet tropics. In association with their burrowing habit, most terrestrial species have sturdy, compact skulls, recessed mouths and reduced eyes sometimes covered by the bones of the skull roof. As the head-first burrowing lifestyle of caecilians puts severe constraints on maximal head diameter (Wake 1993; O'Reilly 2000), the external jaw closer muscles, positioned at the side of the head, are strongly reduced in size in derived caecilians (Bemis *et al.* 1983; Nussbaum 1983; O'Reilly 2000). However, the presence of a mobile quadrate (streptostyly) and a unique jaw-closing system involving the large and well-developed interhyoideus posterior muscle, positioned in line with the head (and thus not increasing the head diameter), suggests that these animals can generate considerable bite forces with the mouth closed (Summers & Wake 2005).

Large bite forces are typically associated with the consumption of unusually large or hard prey in a variety of small vertebrates (e.g. Herrel *et al.* 2002, 2004, in press). Surprisingly, recent comprehensive dietary accounts indicate no apparent need for large bite forces. Most caecilians appear to be generalist predators with the majority of prey items being earthworms and subterranean arthropods (Delêtre & Measey 2004; Gaborieau & Measey 2004; Kupfer *et al.* 2005). Yet, observations of feeding behaviour in caecilians that could shed light on this apparent paradox are rare due to the subterranean existence of these animals (Tanner 1971; O'Reilly 2000; Summers & Wake 2005).

In this study, we use *in vivo* external and X-ray video recordings of animals feeding to report the first quantitative data on caecilian feeding behaviour in semi-natural conditions. Complementary recordings of bite and spin force in the same individuals provide crucial insights into the function of the unique cranial design of derived caecilians.

2. MATERIAL AND METHODS

(a) *Husbandry*

Six *Boulengerula taitanus* and six *Schistometopum thomense* were used in the experiments. Animals were housed in Plexiglass aquaria (60×40×3 cm) filled with a mixture of sand and potting soil. The caecilians were kept individually or in pairs and were fed weekly with earthworms (*Eisenia fetida*, ∅ 2.8 mm) and crickets (*Achetae domestica*, ∅ 3.4 mm) *ad libitum*. All the animals established well-defined tunnel systems in which they moved when foraging.

(b) *Video recordings*

Animals were filmed using a Redlake MotionPro high-resolution digital camera set at 50 frames s^{-1}. Two custom-made arrays of eight ultrabright red light-emitting diodes were used to provide the necessary illumination. The red light did not disturb the animals and the feeding behaviour could be recorded in tunnels adjacent to the Plexiglass (see video 1 in electronic supplementary material). The animals were filmed between 18.00 and midnight as they showed most interest in food during these times.

(c) *X-ray video recordings*

X-ray video recordings were made using Redlake MotionPro digital high-resolution camera attached to the image intensifier of a Philips Optimas M200 X-ray system. X-rays were generated at 40 kV and animals were filmed inside their tunnels. To help visualize the movements of the animals, sets of small radio-opaque markers were inserted subcutaneously at two locations along the body under general anaesthesia (MS222).

(d) *Force measurements*

Rotational forces were recorded in three dimensions using a custom-designed piezoelectric Kistler force platform. Animals were hand held and induced to bite a short metal plate (covered with a thin layer of cloth) that was bolted to the force platform. After biting down on the plate, animals volitionally started spinning and forces were recorded.

Static bite forces were measured using piezoelectric Kistler force transducers (range±50 N) positioned in a custom-made holder. Animals were induced to bite the bite plates through which unidirectional pull was exerted on the transducer (see Herrel *et al.* 1999 for a detailed description of the set-up). During the bite force measurements animals were prevented from engaging in long-axis body rotations.

3. RESULTS

Our observations show that two species of caeciliid caecilians (*S. thomense* and *B. taitanus*) always use long-axis rotations when feeding underground (see

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Table 1. Body dimensions, force measurements and feeding behaviour in two caecilian species studied here (mean ± s.e.).

	S. thomense	*B. taitanus*	
body length (mm)	212.45 ± 28.20	240.3 ± 28.01	
mass (g)	7.09 ± 2.57	4.55 ± 1.67	
head length (mm)	8.49 ± 0.89	6.19 ± 0.50	
head width (mm)	5.19 ± 0.54	3.69 ± 0.39	
bite force (N)	1.09 ± 0.34	0.62 ± 0.31	
spinning force (N)	1.35 ± 0.26	1.02 ± 0.18	
feeding behaviour			
	earthworm	earthworm	cricket
no. of spins per minute	4.7 ± 0.94	9.0 ± 1.55	10.5 ± 4.13
percentage of time spent spinning	7.6 ± 2.24	17.3 ± 2.97	12.6 ± 6.08
rotation (deg.)	189.4 ± 22.21	293.3 ± 30.96	103.5 ± 6.68

videos 1–3 in electronic supplementary material). The spinning behaviour occurred independent of the type (crickets and earthworms) of prey taken. Remarkably, this behaviour continued to be used even with the smallest of prey items used (first instar crickets, ∅ 2.1 mm) indicating that prey reduction may not be the only function of this behaviour.

Spinning behaviour took up a significant proportion of the time spent eating (table 1). However, the smaller species, *B. taitanus*, rotated less per spin when feeding on crickets compared to earthworms (table 1). Moreover, *B. taitanus* used more rotations (9.0 versus 4.7 per minute on an average) and spent more time using rotational feeding (17.3 versus 7.6% of the feeding event) than the larger *S. thomense* (table 1). Crickets were also offered as prey items to *S. thomense*, but they were not observed feeding on these during the recording sessions.

Our data confirm that bite forces are relatively high for both the species of caecilians studied (table 1) and larger than bite forces in most small vertebrates of similar head dimensions (e.g. Herrel *et al.* in press). However, our observations on prey handling suggest that bite force is not used to reduce prey size (see Gaborieau & Measey 2004), but rather suggest that long-axis body rotations effectively allow individuals to overcome their gape limitations where needed (figure 1*b*).

4. DISCUSSION

Our data on freely moving animals feeding underground based on X-ray and conventional video recordings suggest that rotational feeding is an important component of their feeding behaviour (figure 1, videos 1–3 in electronic supplementary material). Although this behaviour has been previously recorded for caecilians (Tanner 1971; Bemis *et al.* 1983; O'Reilly 2000; Summers & Wake 2005), it has never been studied quantitatively and the functional significance has remained unclear (O'Reilly 2000). Long-axis body rotations are known from various groups of vertebrates, including reptiles (crocodiles) and fishes (eels), and are assumed to assist gape-limited predators that do not possess highly kinetic skulls in the reduction of large prey (Cott 1961; Helfman & Clark 1986).

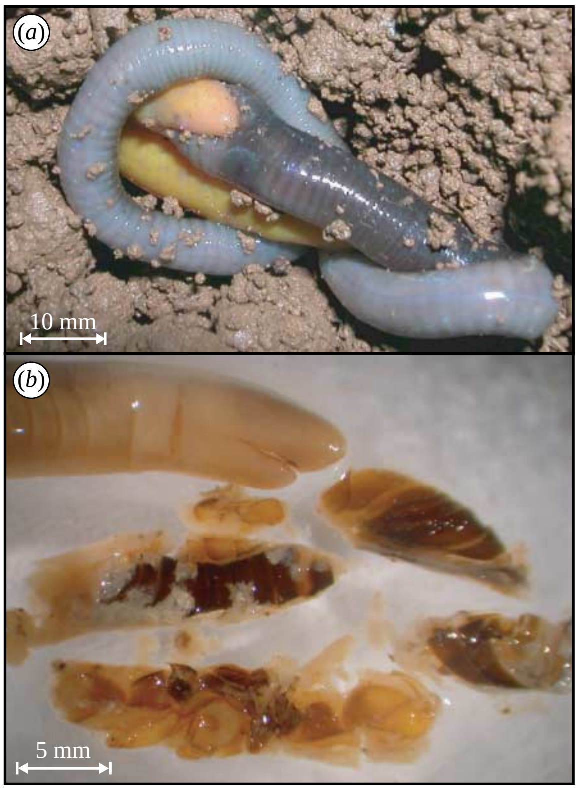

Figure 1. (*a*) Adult *Schistometopum thomense* eating an earthworm. The caecilian (yellow) is almost completely inside its burrow and has hold of a megascolecid earthworm, which has just been spun. As a result, the earthworm has been twisted around its long axis. (*b*) Photograph of the head of a preserved adult *Boulengerula boulengeri* with a single large prey item that was retrieved from its stomach. Note how the prey is completely torn, so that it can fit through the mouth of the caecilian. Our observations show that twisting can indeed be used to reduce larger prey.

Our observations show that large prey are indeed reduced by spinning (figure 1*b*), allowing the caecilians to overcome gape limitations (see also Helfman & Clark 1986). However, our results show that spinning is used when feeding on smaller prey as well. As these rotations occur underground, failure to keep the jaws closed forcefully could result in the prey or the substrate levering the jaws ultimately resulting in their dislocation. Measurements of the forces exerted during long-axis rotations indicate that they can surpass 10 times body mass and are even slightly higher than the actual bite forces keeping the jaws shut (table 1). Thus, our observations that caecilians frequently use long-axis body rotations when feeding, combined with the fact that these rotations impart significant torques on the head and jaws of the animal, may explain the origin of the unique jaw configuration in derived caecilians (Bemis *et al.* 1983; Nussbaum 1983; O'Reilly 2000; Summers & Wake 2005), which allows them to generate large bite forces with their jaws closed (Summers & Wake 2005).

While the reduction of oversized food items remains the most common explanation for long-axis body rotations during feeding, existing data on prey diameter and gape size (Delêtre & Measey 2004) suggest that caecilian prey are rarely oversized. We speculate that spinning serves a further purpose in narrow, dark tunnels for animals with limited sensory capabilities (see Himstedt & Simon 1995). On first contact with a prey item, caecilians are unable to determine their relative size or mass. Spinning, and the feedback on the amount of spin force required, may provide valuable and continuous information about the size of the prey item and hence the amount of handling time and energy required by the predator.

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