The Kinematics of Locomotion in Caecilians: Effects of Substrate and Body Shape

ANTHONY HERREL[1,2]* AND G. JOHN MEASEY[2–4]

[1]Département d'Ecologie et de Gestion de la Biodiversité, Museum National d'Histoire Naturelle, Paris, France

[2]Department of Biology, University of Antwerp, Antwerp, Belgium

[3]Applied Biodiversity Research, Kirstenbosch Research Centre, South African National Biodiversity Institute, Claremont, South Africa

[4]Department of Botany and Zoology, Stellenbosch University, Matieland, South Africa
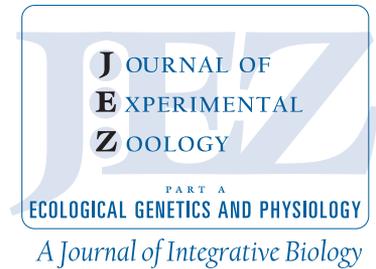
ABSTRACT
Caecilians are limbless amphibians that have radiated extensively in the tropics, and have evolved distinct cranial and postcranial specializations associated with a burrowing lifestyle. Some species are recognized as being surface active, whereas others are dedicated burrowers. Previous authors have demonstrated that some caecilians use a hydrostatic mechanism to generate burrowing forces which is dependent on the existence of skin–vertebral independence. It has been hypothesized that skin–vertebral independence may be lost in extremely elongated species, thus affecting their ability to burrow. Here, we use X-ray video to study the kinematics of locomotion in five species of caecilian differing in their degree of body elongation. Animals were filmed moving in or across different substrates imposing different functional demands on the locomotor system. Our data demonstrate that all species have the ability to perform internal concertina locomotion, but indicate differences between species in the kinematics of locomotion with more elongate species showing a smaller degree of skin–vertebral independence. In all species, locomotion was dependent on the substrate and species switched from using lateral undulation on the surface substrates to the use of whole body or internal concertina in wide and narrow tunnels, respectively. When burrowing in soil, all species used a combination of whole-body and internal concertina locomotion. Additional studies on the ability of different species to generate forces are needed to test whether the reduced skin–vertebral independence in elongate forms has resulted in a decreased ability to generate burrows. *J. Exp. Zool. 313A:301–309, 2010.* © 2010 Wiley-Liss, Inc.

J. Exp. Zool. 313A:301–309, 2010

How to cite this article: Herrel A, Measey GJ. 2010. The kinematics of locomotion in caecilians: effects of substrate and body shape. J. Exp. Zool. 313A:301–309.

Caecilians are limbless amphibians that have radiated extensively in the tropics, and have evolved distinct cranial and postcranial specializations associated with a burrowing lifestyle (Von Schnurbein, '35; Taylor, '68; Gaymer, '71; Gans, '73; Bemis et al., '83; Nussbaum, '83; Renous and Gasc, '86; O'Reilly et al., '97; Summers and O'Reilly, '97; Measey and Herrel, 2006). The majority of species are assumed to be active burrowers that burrow head first into the substrate to establish tunnel systems (Wake, '93). To generate the forces needed to penetrate the soil, caecilians are known to use a hydrostatic mechanism which is dependent on the existence of skin–vertebral independence (O'Reilly et al., '97). Even though typically referred to as skin–vertebral independence, the independence is actually between the vertebral column and the skin, plus associated body-wall musculature (O'Reilly et al., '97).

In general, three major modes of locomotion are known to be used by caecilians: lateral undulation, whole-body and internal concertina locomotion (Fig. 1). During lateral undulation, static push points are used to generate a forward pointing force vector. Kinematically, this is reflected in an undulatory wave passing down the body at the same rate as the animal moves forward. Concertina locomotion, on the other hand, is characterized by the presence of static contact points between the body and substrate, resulting in a static friction force which is used to anchor the body while the remainder of the body is extended or pulled toward the static friction point. Internal concertina is also dependant on the generation of static friction, but in this case the vertebral column is bent inside the body while the body itself remains largely extended (Gans et al., '78; Summers and O'Reilly, '97). This mode of locomotion is thus highly dependent on the existence of some degree of skin–vertebral independence. Fossil
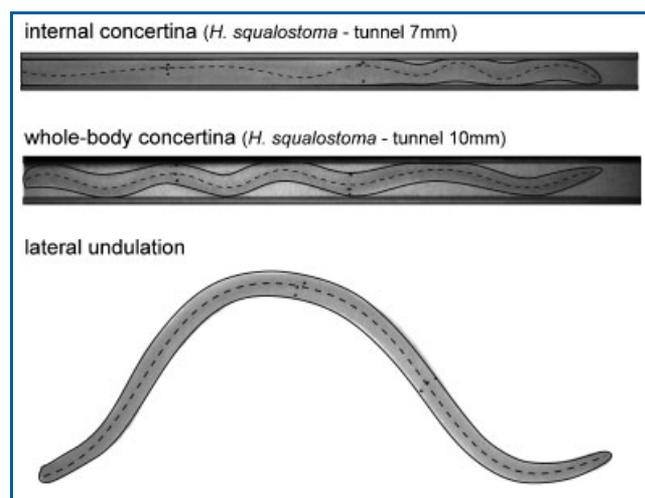

Figure 1. Figure illustrating different locomotor types observed in caecilians: internal concertina (top), whole-body concertina (middle), and lateral undulation (bottom). Figures are based on images extracted from X-ray videos (see supplementary videos S1–3). For reasons of clarity, the outline of the body has been traced by a solid line; the vertebral column is indicated by the dashed line; the black dots indicate the markers inserted under the skin and on the vertebral column. Note that although the skin and vertebral column move together during lateral undulation and whole-body concertina movements, the vertebral column moves independently from the skin during internal concertina locomotion (stronger bending of the vertebral column relative to the skin). During whole-body concertina locomotion, the animal uses bends of the body to secure itself against the sides of the tunnel while extending or pulling other parts of the body. During internal concertina, the animal has no space to bend its entire body, but rather secures the skin to the tunnel and bends the vertebral column inside the body wall.

evidence of limbed caecilians, showing a set of primitive traits associated with the postcranial skeleton (Jenkins et al., 2007), suggests that the presence of skin–vertebral independence (i.e. movements of the vertebral column independent of skin movement), and thus also hydrostatic locomotion, may be a derived condition for caecilians.

Despite a relatively conserved overall morphology, caecilians have radiated into a variety of ecological niches (Taylor, '68). For example, a study on two sympatric East African caecilians suggested that one of the species (*Scolecomorphus*) was surface active, whereas the other (*Boulengerula*) was found exclusively in compact soils (Gower et al., 2004; see also Measey, 2004). Similarly, in West Africa, Burger and co-workers (2004) found seven *Geotrypetes* but no *Herpele* in pitfall traps, despite both being present at the site. Morphologically, these pairs of species demonstrate traits which might be expected to correlate with an increased tendency to burrow: blunt stegokrotaphic skulls, globulose tentacles (*Herpele* and *Boulengerula*), or be more surface active: a zygokrotaphic skull and long tentacles orientated to the ground in *Scolecomorphus* and *Geotrypetes* (Gower et al., 2004; AH and GJM, personal observation). The tendency and burrowing speeds of different species have also been compared experimentally, showing that some (*Dermophis*) are more proficient in harder substrates, whereas others (*Schistometopum*) preferred to burrow into existing tunnels (Ducey et al., '93).

The genera *Typhlonectes*, *Potomotyphlus*, and *Chthonerpeton* (together known as the Typhlonectinae) have long been considered to have radiated secondarily into the aquatic niche (Taylor '68), which is supported by recent molecular phylogenies (e.g. San Mauro et al., 2004; Roelants et al., 2007; Wollenberg and Measey, 2009). Associated with the transition to an aquatic lifestyle, these animals have lost their skin–vertebral independence and are unable to move through narrow tunnels (Summers and O'Reilly, '97). In wider tunnels, these animals use whole-body concertina and on land and in water they move using lateral undulation (Summers and O'Reilly, '97; AH personal observation). It has been suggested that skin–vertebral independence may also have been lost in extremely elongate caecilians, owing to the lack of coelomic space available for the vertebral column to generate bends (Summers and O'Reilly, '97). If so, the evolution of elongate body shapes in caecilians could affect their ability to create burrows and may confine them to the use of existing burrow systems.

Here, we provide kinematic data on locomotion in five species of caecilians, differing in their degree of overall body elongation. Whereas *S. thomense*, *G. seraphini*, and *H. squalostoma* are rather stocky forms, *B. taitanus* and *B. fischeri* are among the most elongated caecilians in overall body shape (Fig. 2; note, however, that they do not have the highest number of vertebrae). Using X-ray videography, we quantify the degree of skin–vertebral independence and the ability of these species to use
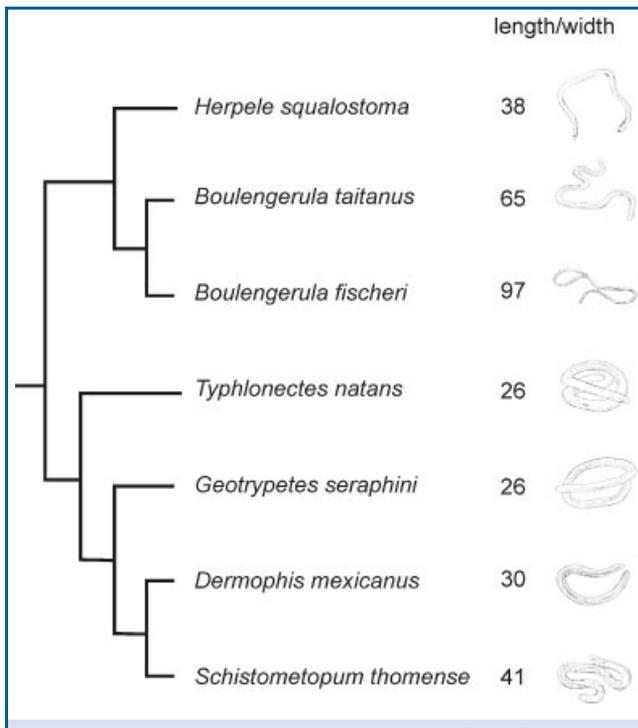
Figure 2. Cladogram, based on Roelants et al., (2007), illustrating the relationships between the species included in this study and in Summers and O'Reilly ('97). To the right of the species names, the body elongation index (length/width) is indicated. Cartoons illustrate the difference in body shape. Note how the two *Boulengerula* species are very elongate relative to the other species included in our study.

internal concertina locomotion, test how different substrates affect the type of locomotion used, and test for differences between species in the kinematics of locomotion associated with different substrates. More generally, using our own data and earlier published data on two additional species (*D. mexicanus* and *T. natans*; see Summers and O'Reilly, '97), we explored how the evolution of elongate body shapes may have affected locomotor style and kinematics in these caecilians.

MATERIALS AND METHODS

Animals

Caecilians were obtained directly from the field (*S. thomense*, *B. taitanus*, and *B. fischeri*) or through commercial dealers (*G. seraphini* and *H. squalostoma*). Animals were transferred to the lab at the University of Antwerp and kept individually in 2L containers containing moist potting soil, and were maintained on a diet of earthworms and crickets. All experiments were approved by the University of Antwerp animal ethics committee.

Cineradiography

X-ray video recordings were made using Redlake MotionPro (Tallahassee, Florida) digital high-resolution camera attached to the image intensifier of a Philips Optimas M200 X-ray system (The Netherlands). X-rays were generated at 40 kV and animals were filmed moving across or in different substrates. To help visualize the movements of the skin relative to the vertebrae, two sets of three small (1 mm) radio-opaque markers were inserted subcutaneously at different locations along the body (an anterior set of markers at one-third of the animal's body length and a posterior set of markers at two-thirds of the animal's body length) under general anesthesia (MS222). One marker was inserted dorsally on the vertebrae and the other two of a set were inserted in the same or adjacent body segment, but laterally just under the skin. The latter markers moved in conjunction with the skin as was demonstrated earlier and confirmed by our cineradiographic images (see also Summers and O'Reilly, '97). Markers were inserted into three individuals of the species *S. thomense*, *G. seraphini*, *H. squalostoma*, and *B. taitanus*. For *B. fischeri*, we were able to insert only two markers (one dorsal and one lateral) in a single individual owing to the extremely thin and elongate shape of this species (body diameter < 4 mm). Animals were induced to move through a narrow plexiglass tunnel that was only slightly larger than the width of their body and through a 10 mm wide tunnel, which was wider than the maximal body width of all individuals. Additionally, we obtained movies of animals moving across a wetted towel (a moist, high friction surface) and while burrowing in a natural substrate (plexiglass aquarium filled with potting soil–60 × 40 × 3 cm) for all species except *H. squalostoma*. For *B. fischeri*, *H. squalostoma*, and *G. seraphini*, additional recordings were made while the animals were moving across a smooth plexiglass substrate. At least two trials, obtained on different days, were recorded for each individual from which we selected cycles in which the animal moved continuously through the field of view of the camera at constant speed. Because of these selection criteria and unwillingness of some species, such as *B. fischeri*, to move continuously, the numbers of cycles analyzed varied considerably for the different species (see Table 2).

For each individual across all substrates, we selected locomotor sequences where movements were continuous for at least three locomotor cycles that involved the regions associated with the implanted markers where possible. All markers were digitized at a frequency of 20–50 Hz using Didge (Image Digitizing Software v. 2.2.0; Alistair Cullum). Coordinates were scaled and smoothed using a zero phase shift, fourth-order low pass Butterworth filter at 1–3 Hz (implemented by Sam Van Wassenbergh). Distances between skin and vertebral markers were calculated based on the raw displacement data, smoothed, and the changes in velocity calculated using numerical differentiation. We calculated skin–vertebral displacement as the distance between the vertebral marker and one of the lateral

markers. Based on the displacement and velocity profiles over time of the anterior vertebral marker, we calculated the stride length (horizontal displacement of the vertebral marker during one full locomotor cycle) and stride frequency (i.e. number of cycles per second; see Fig. 3). We also extracted peak velocity of the vertebral marker and the mean velocity for all cycles analyzed (Fig. 3). Individual means of all variables were calculated and used in subsequent analysis. Thus, each individual is represented by a single entry for each substrate to avoid pseudoreplication of the data.

Statistical Analyses

All data were Log_{10}-transformed before analysis to meet the assumptions for parametric analyses. First, we tested whether body length had an effect on the kinematics of movement, using a MANCOVA with body length as covariate and species and substrate as our fixed factors. As the effect of body length (Wilk's
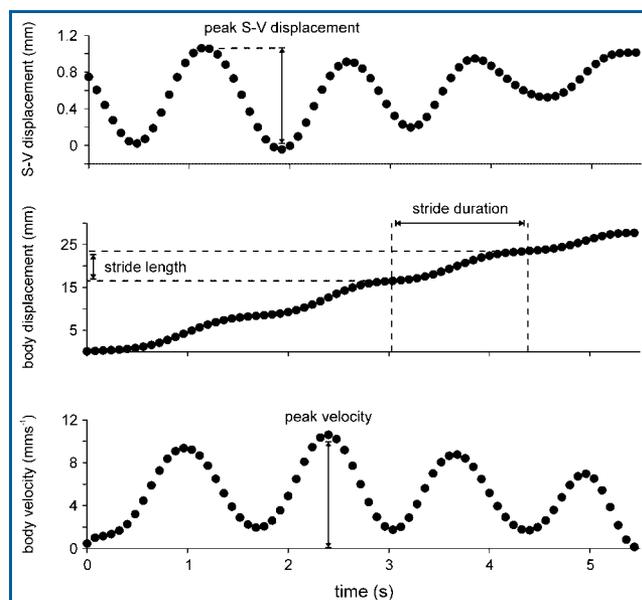

Figure 3. Graphs illustrating the kinematic variables extracted from the X-ray data. The top graph illustrates the changes in skin–vertebral displacement for a *Boulengerula taitanus* moving through a tunnel equal to its body width. From the displacement profile, we extracted the peak skin–vertebral displacement for each cycle. The middle graph illustrates the cumulative displacement through time of the anterior vertebral marker. Based on the velocity profile of the same marker, calculated by numerical differentiation of the displacement over time (bottom graph), locomotor cycles were identified and the stride length (i.e. the distance moved across one locomotor cycle) was calculated. Based on the velocity profile we also calculated the peak forward velocity of the anterior vertebral marker.

Lambda $= 0.82$; $F = 0.67$; $P = 0.67$) was nonsignificant, we removed it from subsequent analyses. Next, kinematic data were analyzed using a MANOVA with species and substrate as fixed factors. Univariate ANOVAs coupled to Bonferroni post hoc tests were used to explore which kinematic variables differed between species and substrates, respectively, for those variables not showing significant substrate by species interaction effects. All analyses were performed using SPSS v. 15 for windows.

RESULTS

The substrates used in our study induced different types of locomotion in the species studied, ranging from lateral undulation on smooth substrates (100% of the cycles in all recordings in all species tested; see Table 1) to internal concertina locomotion in narrow tunnels (100% of all trials in all species, except *B. fischeri* and *H. squalostoma*). On a high friction substrate (wet towel), species used lateral undulation, sometimes accompanied by internal concertina (Table 1). In soil, all species relied on a combination of whole-body concertina and internal concertina locomotion (Table 1). Although in a wide tunnel the two *Boulengerula* species relied entirely on whole-body concertina, *G. seraphini*, *H. squalostoma*, and *S. thomense* used a combination of internal and whole-body concertina locomotion.

Multivariate analyses of variance showed that both substrate (Wilks' Lambda $= 0.23$; $F = 2.06$; $P = 0.007$) and species (Wilks' Lambda $= 0.03$; $F = 6.91$; $P < 0.001$) effects were highly significant, indicating that the kinematics of movement differed between species and are dependent on substrate type. Interaction effects were also significant (Wilks' Lambda $= 0.05$; $F = 1.54$; $P < 0.014$) suggesting that the effect of substrate was not identical for all species. However, subsequent ANOVAs indicated that interaction effects were significant only for the displacement of the posterior markers ($F_{12,53} = 2.71$; $P = 0.012$) and maximal velocity ($F_{12,53} = 2.17$; $P = 0.04$). Consequently, no univariate tests for species or substrate effects were performed on these two variables.

Substrate effects were significant for the displacement of the anterior ($F_{4,53} = 7.72$; $P < 0.001$) marker set only. Post hoc tests showed that the displacement of the anterior marker set, during locomotion on a smooth substrate and the wet towel, was significantly different from locomotion in tunnels or in the soil (all $P < 0.05$), with marker displacement being smallest during locomotion on a smooth surface (Table 2; Fig. 4). Tests for effects of substrate for each species separately mimicked the overall results but, in addition, showed that peak velocity was greater in the narrow and wide tunnel than on a towel for *B. taitanus* ($P = 0.029$).

Species effects were significant for all variables (anterior markers: $F_{4,53} = 15.64$; $P < 0.001$; stride length: $F_{4,53} = 9.80$; $P < 0.001$; stride velocity: $F_{4,53} = 11.40$; $P < 0.001$), except stride frequency ($F_{4,53} = 2.61$; $P = 0.054$). Post hoc tests indicated that locomotion in *S. thomense* was significantly different from all

Table 1. Summary of the type of locomotion used on different substrates by different species.

Genus	Species	Substrate	Mode	%
Boulengerula	*fischeri*	Smooth	Lateral undulation	100
		Soil	Whole body+internal concertina	100
		Towel	Lateral undulation	100
		Narrow tunnel	Whole body+internal concertina	100
		Wide tunnel	Whole-body concertina	100
Boulengerula	*taitanus*	Soil	Whole body+internal concertina	57
			Internal concertina	43
		Towel	Lateral undulation	83
			Lateral undulation+internal concertina	17
		Narrow tunnel	Internal concertina	100
		Wide tunnel	Whole-body concertina	33
			Whole body+internal concertina	67
Geotrypetes	*seraphini*	Smooth	Lateral undulation	100
		Soil	Whole body+internal concertina	20
			Internal concertina	80
		Soil compact	Whole body+internal concertina	67
			Internal concertina	33
		Towel	Lateral undulation	100
		Narrow tunnel	Internal concertina	100
		Wide tunnel	Whole body+internal concertina	100
Schistometopum	*thomense*	Soil	Internal concertina	43
			Whole body+internal concertina	57
		Towel	Lateral undulation	20
			Lateral undulation+internal concertina	80
		Narrow tunnel	Whole body+internal concertina	11
			Internal concertina	89
		Wide tunnel	Whole body+internal concertina	100
Herpele	*squalostoma*	Smooth	Lateral undulation	100
		Narrow tunnel	Internal concertina	66
			Whole body+internal concertina	34
		Wide tunnel	Whole body concertina	34
			Whole body+internal concertina	66

other species, except *H. squalostoma*, in the displacement of the anterior marker set ($P<0.001$; Fig. 5), with skin–vertebral displacements being significantly greater in *S. thomense* and *H. squalostoma*. In addition, differences between *H. squalostoma* and *G. seraphini* were also significant ($P = 0.011$), with *H. squalostoma* showing significantly greater skin–vertebral independence. Differences in stride length were significant between *H. squalostoma* and all other species, with *H. squalostoma* utilizing significantly greater strides. Stride velocity was also significantly different between *H. squalostoma* and the other species (all $P<0.05$), except *G. seraphini* ($P = 0.07$). Additionally, differences in velocity between *B. taitanus* and *G. seraphini* were also significant ($P = 0.002$), with *G. seraphini* being significantly faster (see Table 2; Fig. 5).

DISCUSSION

Our data unequivocally show that all species in our study, including the extremely elongated *B. fischeri* (length/width = 97), show skin–vertebral independence and use internal concertina locomotion to move through narrow tunnels and while burrowing in soil. Consequently, our data do not support the hypothesis that internal concertina is lost in very narrow caeciliids (Summers and O'Reilly, '97). However, data on other elongated forms (e.g. *Oscaecilia*; length/width = 69; see Renous and Gasc, '89) would be needed to test the generality of these results. Additionally, it would be important to test the performance implications of the observed variation in skin–vertebral independence (i.e. variation in burrow force), as this might provide insights into the ecology and distribution of

Table 2. Summary of the locomotor characteristics of the different species moving across different substrates.

Species	Ni	SVL	Substrate	Nc	Displ. ant. markers (mm)	Displ. post. markers (mm)	Mean vel. (mm/s)	Stride freq. (mm)	Stride length (Hz)	Peak inst. vel. (mm/s)
B. fischeri	1	173	Smooth	1	0.3	0.2	3.5	0.5	1.9	2.8
			Soil	2	0.4±0.4	1.0±1.1	6.8±0.2	0.7±0.1	4.7±0.7	7.0
			Towel	1	0.2	0.2	13.6	0.5	6.6	13.6
			Wt	2	0.4±0.1	0.2±0.2	12.5±1.8	1.2±0.4	14.4±2.5	21.0
			Nt	2	0.5±0.4	0.6±0.02	5.7±0.7	0.7±0.1	4.2±0.05	7.5
B. taitanus	3	265±33	Soil	8	1.0±0.3	1.1±0.5	9.5±8.9	0.6±0.3	3.7±1.0	7.4±2.5
			Towel	8	0.3±0.2	0.4±0.1	3.5±1.5	0.8±0.2	2.6±1.2	3.9±1.7
			Wt	7	0.7±0.3	0.7±0.3	6.4±2.6	0.6±0.2	3.4±1.8	10.2±3.2
			Nt	8	1.6±1.1	0.7±0.2	9.6±3.4	0.7±0.1	6.2±1.8	10.8±1.8
G. seraphini	3	198±20	Smooth	8	0.2±0.04	1.3±1.1	32.2±36.6	1.9±1.1	69.8±97.3	102.6±130.0
			Soil	12	0.8±0.4	0.6±0.1	13.3±3.7	0.8±0.5	8.9±2.8	19.6±2.4
			Soil (c)	3	0.7±0.02	0.8±0.2	9.9±0.8	1.2±0.4	12.2±4.4	20.7±3.1
			Towel	7	0.2±0.1	0.3±0.1	6.8±1.8	1.6±0.2	10.9±3.8	15.2±7.4
			Wt	5	1.3±0.7	0.7±0.2	14.5±2.5	0.8±0.5	11.0±6.9	24.0±18.6
			Nt	12	0.5±0.3	1.3±0.4	6.5±4.3	0.9±0.5	4.4±1.2	11.4±3.8
S. thomense	3	215±25	Soil	9	4.6±0.5	3.8±0.2	11.1±1.1	0.5±0.1	5.0±1.2	12.0±1.5
			Towel	7	1.3±0.7	1.9±0.7	10.3±3.4	0.7±0.1	6.8±3.4	12.7±6.4
			Wt	10	2.3±1.0	2.5±0.7	8.8±0.6	0.6±0.1	5.3±0.8	13.3±1.3
			Nt	8	3.1±1.7	3.1±1.6	9.6±1.0	0.4±0.2	3.9±1.3	9.3±2.5
H. squalostoma	3	245±52	Smooth	18	0.6±0.4	0.3±0.1	43.5±27.0	1.4±0.2	32.2±17.1	106.3±62.8
			Wt	17	3.6±2.6	1.9±0.6	23.9±17.7	0.9±0.4	27.6±14.5	51.8±31.8
			Nt	12	1.9±0.6	2.0±0.2	16.6±4.3	0.6±0.3	30.3±4.3	39.0±10.4

Displ. ant. markers, displacement of the anterior markers; displ. post. markers, displacement of the posterior markers; freq, frequency; inst, instantaneous; Nc, number of cycles analyzed; Ni, number of individuals; nt, narrow tunnel; SD, standard deviation; subst, substrate; SVL, snout–vent length; vel, velocity; wt, wide tunnel.
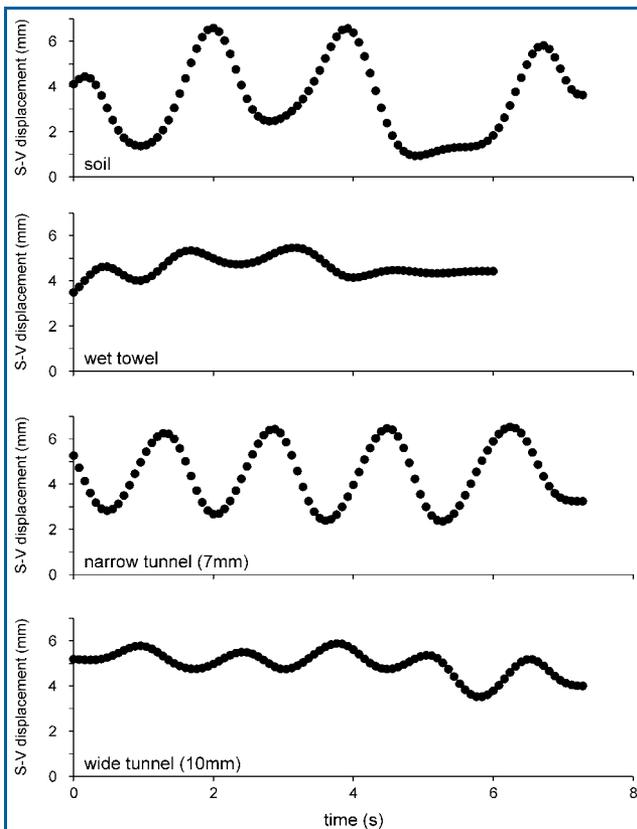
Figure 4. Skin–vertebral displacement graphs for *Schistometopum thomense* while moving across/in different substrates. Note how the skin–vertebral displacements are greatest when moving through a narrow tunnel or while burrowing in soil. In wide tunnels and on a high-friction surface, the displacement is reduced as animals switch to whole-body concertina and lateral undulation on these two substrates respectively.

Figure 5. Skin–vertebral displacement graphs for the five species included in our study while moving through tunnels equal to their body diameter. Note the difference in the magnitude and frequency of the skin–vertebral displacements between species (see also Table 1), with *B. fischeri* showing the smallest displacement of all species. Note also the different scale on the Y-axis for the displacement graph of *S. thomense* and *H. squalostoma* compared with the other species.

caecilians of different body shapes. Based on our results, we predict that burrowing forces should be greatest in *S. thomense* and *H. squalostoma*, as these species showed the greatest degree of skin–vertebral independence of the species included in our study. Additionally, it would be important to explore how the kinematics of locomotion is affected in species characterized by high vertebral numbers, such as members of the genera *Oscaecilia* or *Caecilia*. Even though our data illustrate that overall body shape affects locomotion, animals of similar shapes (i.e. length/width ratio) but with different vertebral numbers could show very different patterns of locomotion, as a higher vertebral number would likely allow for more acute bending and shorter wavelengths.

As demonstrated by earlier authors, the type of substrate caecilians move in has a strong impact on the type of locomotion used (Renous et al., '93; Summers and O'Reilly, '97). For example, *D. mexicanus* switches from using lateral undulation on a peg
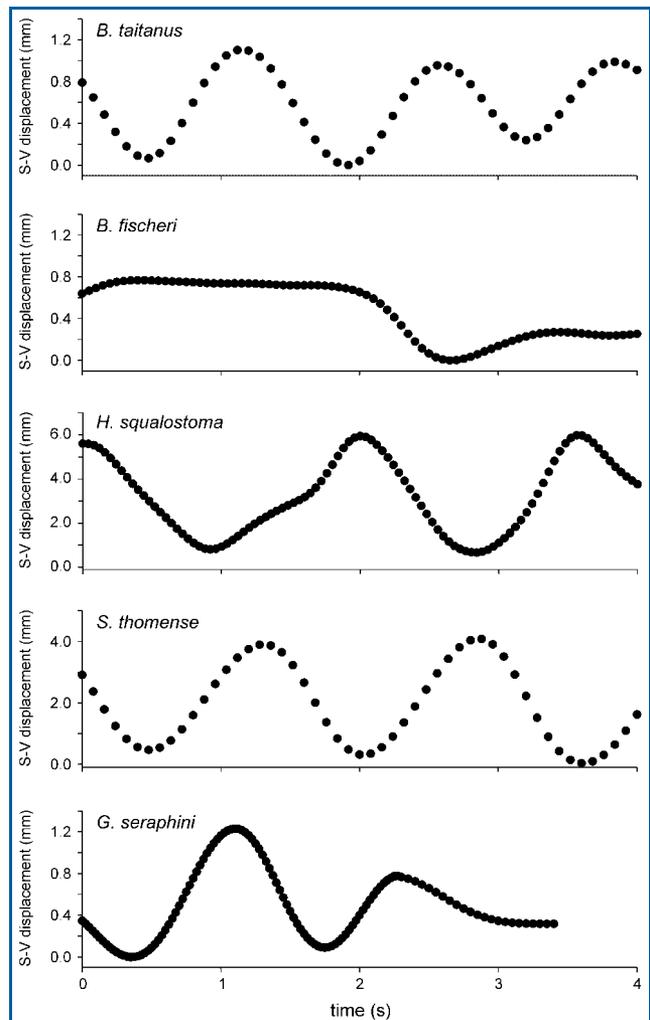
board to using a combination of lateral undulation and internal concertina when burrowing in soil, and using exclusively internal concertina when moving in narrow tunnels (Summers and O'Reilly, '97). *T. natans*, an aquatic species, was, however, unable to perform internal concertina but used whole-body concertina when placed in wider tunnels and lateral undulation on a peg board (Summers and O'Reilly, '97). *Grandisonia alternans* and *Hypogeophis rostratus*, two typically surface-dwelling species from Seychelles, used lateral undulation on a high-friction substrate (Renous et al., '93). However, whereas *G. alternans* used

concertina, *H. rostratus* used rectilinear locomotion in narrow tunnels (Renous et al., '93). Our data also indicate strong substrate effects, and all species switch from lateral undulation on a smooth or high friction surface to the use of concertina in wide tunnels and internal concertina in narrow tunnels (Table 1).

However, none of the species in our study was observed to use lateral undulation while burrowing. Moreover, rectilinear locomotion was never observed in our animals. When burrowing in soil, the animals in our study used a combination of whole-body and internal concertina. One potential explanation for the discrepancy between our observations and those reported earlier (Summers and O'Reilly, '97) may be that the soil we used in our trials was more compact. Indeed, Summers and O'Reilly ('97) mention that *Dermophis* switched to the exclusive use of internal concertina when encountering more tightly packed soils. *S. thomense*, on the other hand, always includes internal concertina in all substrates, either in isolation or in combination with whole-body concertina or lateral undulation, suggesting that this species may be unable to decouple the use of internal concertina from locomotion. The degree of skin–vertebral independence in *S. thomense* was, however, markedly different for different substrates (Fig. 4). In contrast to the data for *Dermophis* (Summers and O'Reilly, '97), all species in our study used whole-body concertina, in some cases (Table 1).

The different species included in our study also differed significantly in the kinematics of locomotion. The greatest difference observed was in the degree of skin–vertebral independence, which was significantly greater in *S. thomense* and *H. squalostoma* compared with the other species (Table 2). Although the most elongated species in our data set (*B. fischeri*) had the smallest degree of skin–vertebral independence, the second most elongated species (*B. taitanus*) had a skin–vertebral independence that was similar to *G. seraphini* which is much stockier. Skin–vertebral independence in all species in our study was, however, much smaller than observed for *D. mexicanus* which attained nearly 15 mm (Summers and O'Reilly, '97), more than 5 times the greatest value observed in our study (Table 2). Even though the individuals used by Summers and O'Reilly ('97) were about 1.5 times bigger than our animals, this cannot explain the enormous difference between these species and suggests that *D. mexicanus* may be highly specialized. Indeed, in the article measuring burrowing speed and the tendency to burrow in different caecilians, Ducey and co-workers ('93) observed that *Dermophis* was the fastest burrower, and also more inclined to burrow in general and to burrow into more compacted soils. *S. thomense* was much slower and showed a lower tendency to burrow, but preferred using existing burrows where possible (Ducey et al., '93). Clearly, additional data on the degree of skin–vertebral independence and the speed and force that animals can generate while burrowing are needed to test whether increased skin–vertebral independence is indeed correlated with a greater burrowing performance. Moreover, data on other taxa including the basal most groups, such as Rhinatrematids and Ichthyophids, are needed to better understand the evolution of locomotion in this group.

LITERATURE CITED

Bemis WE, Schwenk K, Wake MH. 1983. Morphology and function of the feeding apparatus in *Dermophis mexicanus* (Amphibia, Gymnophiona). Zool J Linn Soc 77:75–96.

Burger M, Branch WR, Channing A. 2004. Amphibians and reptiles of Monts Doudou, Gabon: species turnover along an elevational gradient. Calif Acad Sci Mem 28:145–186.

Ducey PK, Formanowicz DR, Boyet L, Mailloux J, Nussbaum RA. 1993. Experimental examination of burrowing behavior in caecilians (Amphibia, Gymnophiona)—effects of soil compaction on burrowing ability of four species. Herpetologica 49:450–457.

Gaymer R. 1971. New method of locomotion in limbless terrestrial vertebrates. Nature 234:150–151.

Gans C. 1973. Locomotion and burrowing in limbless vertebrates. Nature 242:414–415.

Gans C, Dessaur HC, Baic D. 1978. Axial differences in musculature of uropeltid snakes: the freight-train approach to burrowing. Science 199:189–192.

Gower DJ, Loader SP, Wilkinson M, Montcrieff CB. 2004. Niche separation and comparative abundance of *Boulengerula boulengeri* and *Scolecomorphus vittatus* (Amphibia: Gymnophiona) in an East Usamabara forest, Tanzania. Afr J Herp 53:183–190.

Jenkins Jr FA, Walsh DM, Carroll RL. 2007. Anatomy of *Eocecilia micropodia*, a limbed caecilian of the Early Jurassic. Bull Mus Comp Zool 158:285–365.

Measey GJ. 2004. Are caecilians rare? An East African perspective. J East Afr Nat Hist 93:1–21.

Measey GJ, Herrel A. 2006. Rotational feeding in caecilians: putting a spin on the evolution of cranial design. Biol Lett 2:485–487.

Nussbaum RA. 1983. The evolution of a unique dual jaw closing mechanism in caecilians (Amphibia: Gymnophiona) and its bearing on caecilian ancestry. J Zool Lond 199:545–554.

O'Reilly JC, Ritter DA, Carrier DR. 1997. Hydrostatic locomotion in a limbless tetrapod. Nature 386:269–272.

Renous S, Gasc JP. 1986. Le fouissage des gymnophiones (Amphibia): hypothèse morphofonctionelle fondée sur la comparison avec d'autres vertèbres apodes. Zool Jahrbuch Anat 114:95–130.

Renous S, Gasc JP. 1989. Body and vertebral proportions in Gymnophiona (Amphibia): diversity of morphological types. Copeia 1989:837–847.

Renous S, Gasc JP, Ineich P. 1993. Données préliminaires sur les capacités locomotrices des Amphibiens Gymnophiones. Ann Sci Nat Zool Paris 14:59–79.

Roelants K, Gower DJ, Wilkinson M, Loader SP, Biju SD, Guillaume K, Bossuyt F. 2007. Patterns of diversification in the history of modern amphibians. Proc Natl Acad Sci 104:887–892.

San Mauro D, Gower DJ, Oommen OV, Wilkinson M, Zardoya R. 2004. Phylogeny of caecilian amphibians (Gymnophiona) based on complete mitochondrial genomes and nuclear RAG1. Mol Phyl Evol 33:413–427.

Summers AP, O'Reilly JC. 1997. Kinematics of locomotion in two species of caecilian, *Typhlonectes natans* and *Dermophis mexicanus*. Zool J Linn Soc 121:65–76.

Taylor EH. 1968. The caecilians of the world. Lawrence: University of Kansas Press.

von Schnurbein AF. 1935. Der bewegungsapparat von Hypogeophis. Beitrag zur Kenntnis der Gymnophionen XXIII. Morph Jahrbuch 75:315–330.

Wake MH. 1993. The skull as a locomotor organ. In: Hanken J, Hall BK, editors. The skull, volume 3. Chicago: University of Chicago Press. p 197–240.

Wollenberg KC, Measey GJ. 2009. Why colour in subterranean vertebrates? Exploring the evolution of colour patterns in caecilian amphibians. J Evol Biol 22:1046–1056.