



A comparative study of locomotion in the caecilians *Dermophis mexicanus* and *Typhlonectes natans* (Amphibia: Gymnophiona)

ADAM P. SUMMERS

Organismic and Evolutionary Biology Program, University of Massachusetts, Amherst, MA 01003-5810, U.S.A.

JAMES C. O'REILLY

Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011-5640, U.S.A.

Received January 1996; accepted for publication September 1996

We compared locomotion of two species of caecilian using x-ray videography of the animals traversing smooth-sided channels and a pegboard. Two channel widths were used, a body width channel and a body width + 20% channel. The terrestrial caecilian, *Dermophis mexicanus*, used internal concertina locomotion in both channels and lateral undulation on the pegboard. The aquatic caecilian, *Typhlonectes natans*, was not able to move at all in the body width channel. In the wider channel *Typhlonectes* proceeded at the same speed as *Dermophis* while using normal, rather than internal, concertina locomotion. On the pegboard, *Typhlonectes* used lateral undulation and achieved 2.5 times the speed managed by *Dermophis*. A phylogenetic analysis of this, and other, evidence shows that (1) internal concertina evolved in the ancestor to extant caecilians and (2) internal concertina locomotion was secondarily lost in the aquatic caecilians.

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ADDITIONAL KEY WORDS—burrowing – phylogenetic analysis – lateral undulation – concertina – internal concertina – Caeciliidae.

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Correspondence to A.P. Summers. email: summers@bio.umass.edu

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INTRODUCTION

Caecilians are limbless amphibians of the order Gymnophiona, circumtropically distributed, with about 160 known species in five families. A monumental work by Taylor (1968) signaled the beginning of an exciting period of inquiry into the systematics (e.g. Nussbaum & Wilkinson, 1989; Wilkinson, 1989; Hedges *et al.*, 1993; Nussbaum & Hinkel, 1994; Wilkinson & Nussbaum, 1996), life history (e.g. Moodie, 1978; Wake, 1980b; Wilkinson, 1992), physiology (e.g. Stiffler *et al.*, 1990; Masood-Parveez *et al.*, 1994; Stiffler & Manokham, 1994), sensory biology (e.g. Himstedt & Fritsch, 1990; Schmidt & Wake, 1990; Wake & Schwenk, 1986; Himstedt & Simon, 1995) and morphology (e.g. Naylor & Nussbaum, 1980; Wake, 1980a, 1994; Nussbaum & Naylor, 1982; Bemis *et al.*, 1983; Nussbaum, 1983) of these creatures. The functional morphology of these animals has received comparatively little attention. Although one group is aquatic or semi-aquatic, the majority of caecilians are fossorial, which in part accounts for the paucity of experimental information on them. The monophyly of the order is well established, and there is an emerging consensus that supports a family level phylogeny (Duellman & Trueb, 1986; Nussbaum & Wilkinson, 1989; Hedges *et al.*, 1993; Wilkinson & Nussbaum, 1996). This paves the way for studies of the evolution of characters within the Gymnophiona.

The study of the kinematics and evolution of limbless locomotion has been a productive endeavour for functional morphologists. Total loss of both pairs of limbs and girdles evolved several times within reptiles and in the caecilians. Extensive examination of locomotion of limbless reptiles has resulted in the definition of a suite of locomotor patterns (Gray, 1946; Lissman, 1950; Gans, 1962, 1986; Gaymer, 1971; Jayne, 1986). These patterns include swimming undulation, lateral undulation, concertina, rectilinear and sidewinding locomotion. Previous workers concluded that all limbless locomotion can be categorized as a variant of one of these modes. Swimming undulation is the familiar means by which fishes and other elongate aquatic organisms move. An undulatory wave passing down the body pushes on the surrounding fluid medium which, combined with the streamlined shape, results in a forward directed force vector. In this mode of locomotion the undulatory wave has a higher velocity than the animal. In contrast, during lateral undulation, the locomotor mode of many terrestrial snakes, static push-points are used to generate the forward pointing force vector. The result is that the undulatory wave passes posteriorly at the same rate as the animal progresses forward. In concertina locomotion, used by snakes in burrows and on smooth surfaces, the animal has some part of its body in static contact with the substrate. This provides a reactive static friction force from which forward motion of the rest of the body is launched (Fig. 1). Gans (1986) proposed an evolutionary sequence of locomotor modes within the terrestrial vertebrates in which concertina locomotion evolved prior to lateral undulation.

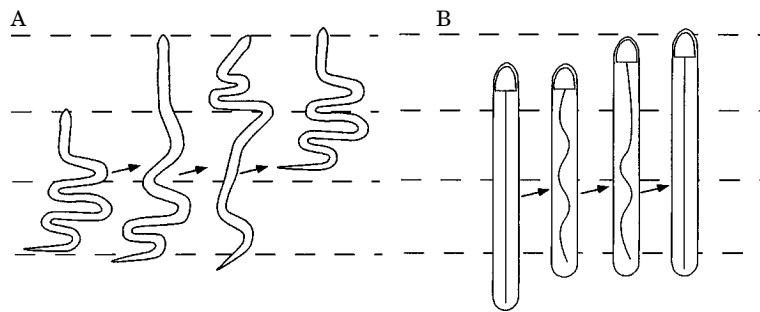


Figure 1. A comparison of normal concertina (A) and internal concertina (B). Concertina is shown in a snake traversing a smooth surface. Internal concertina is shown in a caecilian moving in a burrow. The vertebral column and skull are superimposed on the outline of the caecilian.

In contrast to reptiles, locomotion in caecilians has received little attention. Presumably the aquatic caecilians proceed by swimming or lateral undulation, while the fossorial ones use concertina or lateral undulation, as in fossorial reptiles (Renous & Gasc, 1986). In an early investigation, based on dissections of *Hypogeophis*, von Schnurbein (1935) concluded that the vertebral column should be able to move independently from the skin. Her remarks indicate that this animal maintains the cross-sectional shape of the body using hydrostatic pressure. She envisioned the free moving skin acting much like the tread on a tractor, alternately being moved forward and, after being anchored to the substrate, used to drag the vertebral column and viscera forward. In examining the locomotion of a live *Hypogeophis*, Gaymer (1971) made a preliminary report of 'vermiform locomotion'. In this locomotor mode the vertebral column is thrown into waves within the body, which are in static contact with the body wall and in turn with the substrate. This contact provides a static friction reaction force so that as these waves are progressively straightened from anterior to posterior the animal makes forward progress. Gans (1973) argued that this method, also used by some amphisbaenians and snakes, is really a special case of concertina locomotion that he named 'internal concertina'. Internal concertina, like regular concertina, relies on throwing the vertebral column into waves and on sites of static friction which provide reaction forces to forward motion. They differ only in whether the whole body or just the vertebral column is bent into waves. A well studied case of internal concertina locomotion is burrow extension by 'freight train locomotion' in the uropeltid snake *Rhinophis* (Gans *et al.*, 1978).

This study is a comparison of the locomotor kinematics of two species of caecilian in the family Caeciliidae, *Dermophis mexicanus* and *Typhlonectes natans*. *Dermophis mexicanus* is a terrestrial, fossorial member of the subfamily Dermophiinae, with a distribution from southern Mexico to Columbia (Duellman & Trueb, 1986). It inhabits a wide variety of soil types (Wake, 1980b), and is an accomplished burrower (Ducey *et al.*, 1993; Wake, 1993). *Typhlonectes natans* is a member of the subfamily Typhlonectinae from South America. It is totally aquatic and is presumed to use swimming undulation in the water column and lateral undulation when proceeding along the bottom or through submerged bottom structure. The goals of our study are two-fold. First we present a comparative study of locomotor ability and kinematics in caecilians. Second, we have used the data from this study, and the literature, to determine an evolutionary sequence of locomotor modes within the Gymnophiona.

METHODS

Husbandry and surgery

Caecilians were obtained from commercial dealers. *Dermophis mexicanus* were maintained in separate plastic boxes, in moist potting soil, on a diet of earthworms. *Typhlonectes natans* were maintained in a 40 l aquarium, in 10 cm deep, 25°C spring water, also on a diet of earthworms.

Three individuals of each species, ranging from 280–350 mm SVL, were used in this study. In order to visualize the skin during x-ray videography, we subcutaneously marked animals in the mid-body region with injected lead markers. Fine wire markers, 1 mm long, were delivered through a 20 gauge hypodermic needle while the animal was under anaesthesia (0.1% MS222 [tricainemethane-sulfonate], buffered to pH 7.0 with sodium bicarbonate). Markers in *Dermophis* were implanted posterior to the termination of the right lung, approximately halfway down the body. Four markers were implanted, two on each side, six to ten annuli apart. In *Typhlonectes* markers were implanted unilaterally when it was established by observation that there was synchronous movement of the skin of the left and right sides. Animals were allowed to recover from implantation of the markers for at least 6 hours.

Locomotion

Each animal was placed in a wetted acrylic channel, rectangular in cross section, with a height of 55 mm and adjustable width. Initially the width matched the maximum body width of the specimen. While *Dermophis* could traverse this channel, *Typhlonectes* could not, so the channel was widened to the maximum body width + 20%. Subsequently both *Dermophis* and *Typhlonectes* were filmed in channels that were body width + 20% wide. Each individual was recorded moving a full body length through the wider channel five separate times with a 1–5 minute rest between each trial. After a rest period of at least 6 hours, each animal was filmed moving on a Plexiglas pegboard with 5 mm acrylic pegs placed on center in a 50 mm square grid. The board was misted with water before each experiment. Each of the six animals was run five times on the pegboard. No attempt was made to elicit maximal speed during any of these trials. Finally, two of the three *Dermophis* were filmed moving through a polyethylene container with 15 cm of moist potting soil. The soil was loosely packed, but x-ray videography showed some areas of higher compaction. Several minutes of locomotion were recorded for each animal. Locomotion in the channel, on the pegboard, and through the soil was filmed with a Siemens cineradiographic apparatus, positioned for dorso-ventral projection. Images were recorded from the fluoroscope using a Hitachi CCD video camera at 60 fields per second, shuttered at 1/250 sec. These animals were not euthanized after the experiments and remain in the live collection at the University of Massachusetts.

Data analysis and statistics

After initial viewing of the video tapes one sequence was selected for analysis from each trial. For channel passage our criterion was that the selected portion

clearly show all the markers in the frame for a full locomotor cycle. Similarly, for the pegboard, a sequence with high contrast and a visible marker was selected. This process yielded a data set with five entries for each of six individual caecilians for two locomotor modes. We analysed the tapes using a Panasonic AG 1970 VCR, a Sony PVM 1351Q monitor, and a Mitutoyo digital caliper. Displacement variables were measured by tracing the position of the markers and a reference vertebra on acetate film attached to the face of the monitor, then measuring the distances traversed during a locomotor cycle with the digital caliper. The timing of kinematic events was determined by using the jog/shuttle control to play the tapes field by field. Maximum strain in the skin of *Dermophis* was computed by measuring the maximum and minimum distance between ipsilaterally implanted markers.

For locomotion in the channel, three variables were compared between species: the distance covered in a locomotor cycle (*stride length*), the average velocity (*speed*) and the maximum displacement of a reference vertebra with respect to the skin (*skin-vertebral distance*). The comparison was made with a nested analysis of variance (Sokal & Rohlf, 1995). In this analysis, the species is a fixed, independent variable, and each of the aforementioned kinematics variables is, in turn, the dependent variable. Individuals are nested within species to provide a measure of the individual variation. For the pegboard data the only dependent variable was *speed*, otherwise the analysis was the same.

Phylogenetic analysis

The phylogeny of the Gymnophiona in this paper (Fig. 4) is based on that of Duellman and Trueb (1986), with the placement of the family Uraeotyphlidae suggested by Wilkinson and Nussbaum (1996). We use this phylogeny as a working hypothesis, having made no attempt to reinterpret or synthesize character sets in order to generate a new tree.

We mapped the evolution of concertina locomotion onto the phylogeny of the Gymnophiona using MacClade software (Maddison & Maddison, 1992). The ability to move by internal concertina was determined for Typhlonectidae and Caeciliidae by the experiments discussed above. Dissections and data from the literature provided inferences about internal concertina in Ichthyophiidae and Rhinatrematidae. A single character was coded as the presence or absence of the ability to perform internal concertina. The program displayed the most parsimonious explanation for the evolution of this character given the phylogeny we provided.

RESULTS

Dermophis mexicanus

In the initial experiment on locomotion in a body width channel, all three individuals always performed internal concertina locomotion. The same kinematics were observed in the trials conducted in a channel 20% wider than the body, with the exception that the whole body was thrown into waves at the end of a locomotor

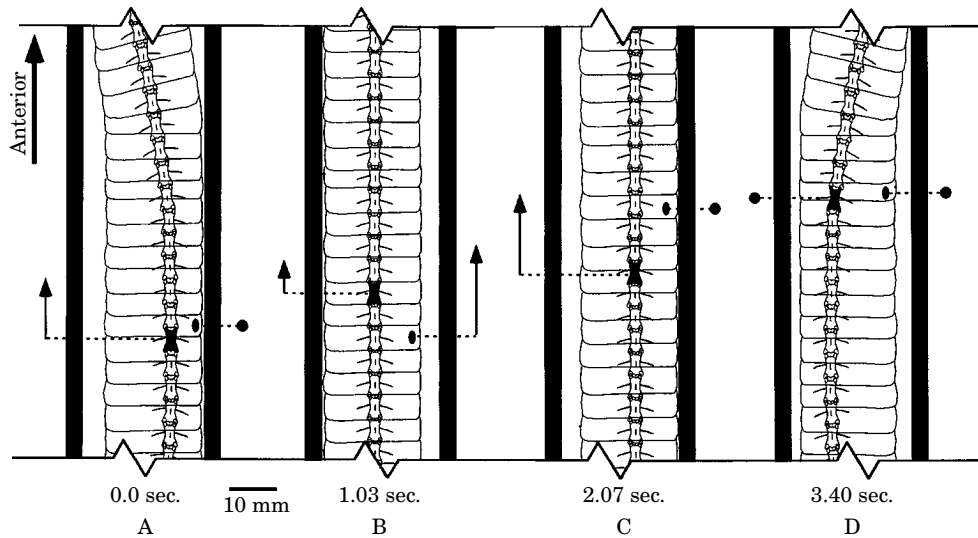


Figure 2. *Dermophis mexicanus*. Drawings of four frames from an x-ray video of *Dermophis* performing internal concertina in a body width + 20% channel. The mid-body region is illustrated, with anterior towards the top of each drawing. The lead marker implanted in the skin is indicated by a black oval. A shaded reference vertebra is also indicated. The relative speed of these two points is indicated by the length of the attached arrow.

TABLE 1. Average \pm standard error ($n=15$) of three kinematic variables measured from x-ray videos of *Dermophis mexicanus* and *Typhlonectes natans* during locomotion in a channel and on a pegboard. Stride length is the distance moved in one locomotor cycle. S-V is the average distance that a mid-body vertebra moves relative to the skin during a locomotor cycle

	Channel		Pegboard	
	<i>D. mexicanus</i>	<i>T. natans</i>	<i>D. mexicanus</i>	<i>T. natans</i>
Speed (mm/s)	4.8 \pm 0.33	5.0 \pm 0.68	20.2 \pm 3.0	55.5 \pm 10.8
Stride Length (mm)	48 \pm 3.6	72 \pm 6.5	—	—
S-V (mm)	15.2 \pm 1.1	1.2 \pm 0.31	0.0	0.0

cycle (Fig. 2). During a typical locomotor cycle the spinal column is thrown into waves within the body as the animal shortens itself (Fig. 2A). The spinal column then starts to move forward without the skin moving. A reference vertebra can be seen to move forward two vertebral lengths before the skin starts to move (Fig. 2B). As both skin and vertebrae move forward, the skin moves faster and overtakes the reference vertebra, passing as many as three vertebral lengths ahead of it (Fig. 2C). The skin comes to a stop first, and, as the spine is once again thrown into waves, the reference vertebra gains ground on the skin, eventually returning to its original position (Fig. 2D). The distance covered by one of these locomotor cycles (*stride length*) averaged 48 mm, and the animal proceeded at an average rate of 4.8 mm/sec. The average distance that the reference vertebra was displaced relative to the skin was 15.2 mm, or approximately 4 vertebral segments (Table 1). The average longitudinal strain in the skin was 8.4%, within the normal range for vertebrate skin (Wainwright *et al.*, 1976)

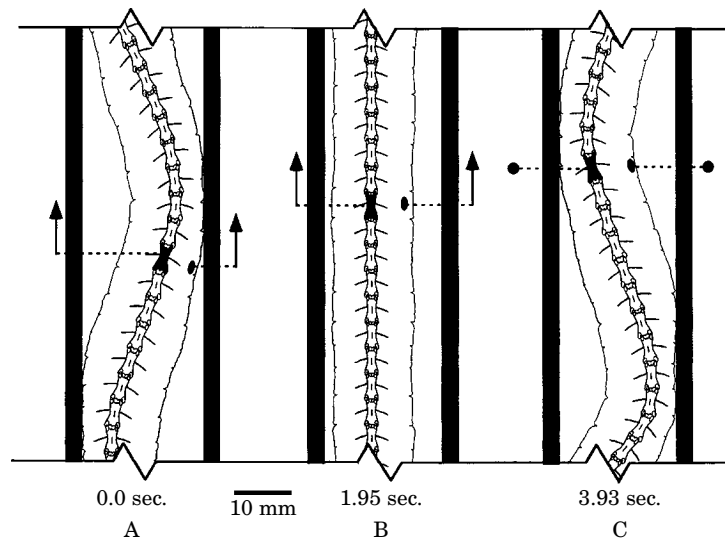


Figure 3. *Typhlonectes natans*. Drawings of three frames from an x-ray video of *Typhlonectes* performing normal concertina locomotion in a body width +20% channel. The mid-body region is illustrated, with anterior towards the top of each drawing. The lead marker implanted in the skin is indicated by a black oval. A shaded reference vertebra is also indicated. The relative speed of these two points is indicated by the length of the attached arrow.

The pegboard apparatus elicited lateral undulation from all three experimental animals. The pegs were used as push points during forward movement. There was no measurable displacement of the reference vertebra relative to the skin during lateral undulation. Lateral undulation proved to be on average four times faster than internal concertina.

While burrowing in soil, the animals exhibited both lateral undulation and internal concertina. It seemed that internal concertina was used when the animal encountered harder packed soil, shown as a darker area in the video x-ray. There were several instances when it was using both modes of locomotion simultaneously, with the anterior region doing lateral undulation while a more posterior region was doing internal concertina. During both modes of burrowing *Dermophis* uses dorso-ventral flexion of its head to push the soil out of the way. We only collected data from two of our three animals, and both were buccal pumping at all times during burrowing.

Typhlonectes natans

Individuals of this species did not move forward in a channel that was only one body width across. Every animal placed in the channel showed distress by exuding copious amounts of mucus. None exhibited concertina locomotion, although they did manage to rotate about their long axis by thrashing the head. When the channel was widened to body width +20% across, all three animals performed normal, rather than internal, concertina locomotion. This was clearly different from the internal concertina of *Dermophis* in that the vertebrae did not move significantly with respect to the skin (Fig. 3). There was some slight movement of the skin relative to

TABLE 2. Results of nested ANOVA analysis contrasting locomotion variables for *Dermophis mexicanus* and *Typhlonectes natans* during channel passage and on a pegboard. The species effect and the individual effect are shown for each variable. * $P < 0.05$

	Speed		Channel Stride Length		S-V		Pegboard Speed	
	Species	Individual	Species	Individual	Species	Individual	Species	Individual
d.f.	1	4	1	4	1	4	1	4
MS	6.525	8.281	4225.4	427.3	12769	49.9	16330	1598
F	0.788	3.482	9.89	1.57	256.1	0.510	10.2	5.34
P	0.42	0.019*	0.035*	0.21	<0.01*	0.73	0.033*	<0.01*

the vertebrae, but it appeared that this was the result of deformation of the skin as it pressed against the channel walls. In spite of the different locomotor mode, the speed of forward progress was not significantly different from the values for *Dermophis*.

Lateral undulation was elicited on the pegboard, as it was for *Dermophis*, and, similarly, the vertebrae did not move relative to the skin during locomotion. The rate of travel was five times that for concertina locomotion, and two and half times as fast as *Dermophis* (Table 1).

Statistical analysis (Table 2) shows that there is no significant difference between the speed of the two species while traversing the channel. There is a significant difference in stride length, and in the distance that the skin moves relative to the vertebrae. For locomotion on the pegboard the speed difference between the species was significant ($P < 0.05$).

DISCUSSION

We have shown, with x-ray video, that *Dermophis mexicanus* is capable of the same type of internal concertina locomotion described in another terrestrial caecilian *Hypogeophis rostratus* (Gaymer, 1971). Quantification of vertebral excursions relative to the skin demonstrated that the vertebral muscle mass moves up to five vertebral segments relative to the sub-dermal muscle mass in *Dermophis*. These results suggest that a loose connection between the vertebral column/axial musculature and the skin/body wall musculature is a necessary condition for internal concertina locomotion. Furthermore, in species for which observations of live specimens are not available, we propose the presence of such a loose connection is a morphological indicator of the ability to perform internal concertina.

In contrast to *Dermophis*, *Typhlonectes* is incapable of internal concertina locomotion. The implication is either that they have lost the loose connection between body wall musculature and the axial muscle mass, or that they do not have the motor pattern for internal concertina. *Typhlonectes* traverses the channel at the same rate of speed as *Dermophis*, but we speculate that the internal concertina mode of locomotion is better suited to hard packed soils. The comparison between the channel speed and pegboard speed of the two species indicates that (1) lateral undulation is a faster mode of locomotion and (2) *Typhlonectes* is a better lateral undulator than *Dermophis*. We have some reservations about the second conclusion as there was no attempt to elicit maximal locomotor responses from either species.

The biomechanics and anatomy of internal concertina locomotion has been well studied in the uropeltid snake *Rhinophis* (Gans *et al.*, 1978). The kinematics of internal concertina in *Rhinophis* are quite different from those found in *Dermophis*. In the anterior third of its body the uropeltid has red rather than white muscle, and the connection between the body wall musculature and the axial muscle mass is loose. During burrowing *Rhinophis* throws the anterior third of the vertebral column into very tight bends that serve to double the width of the body. This widens the tunnel, decreasing kinetic friction on the remainder of the body, and provides a strong site of static friction from which to launch the next head ramming event. In contrast, our results show that *Dermophis* throws the whole spine, from atlas to terminal vertebra, into waves that are much less extreme than those of the uropeltid. The tunnel is not appreciably widened, and the main purpose is the establishment of a large site of static friction that is used to counter the reaction force of the head ramming into the soil.

Dissection and manipulation of freshly killed and preserved *Epicrionops petersi* (Rhinatrematidae) and *Ichthyophis kohtaoensis* (Ichthyophiidae) shows a loose connection between the vertebral muscle mass and the dermal muscle mass (Naylor & Nussbaum, 1980). In addition, both families are fossorial, and *Ichthyophis* is known to burrow as effectively as some caeciliids (Ducey *et al.*, 1993). On this basis we assert that both of these families are capable of internal concertina locomotion.

As an aside, many members of the family Caeciliidae are extremely narrow bodied. This would make them less efficient at internal concertina locomotion because a narrow cross section limits the space available to arrange the vertebrae in waves within the body. Indeed, we speculate that the ability to use internal concertina has been lost in all very narrow caeciliids.

We consider that the ability to burrow using internal concertina arose in the common ancestor of all recent Gymnophiona and was lost at least once, in the typhlonectids (Fig. 4). It is not difficult to propose an explanation for the disappearance of this locomotor ability in the typhlonectids. All members of this family, whose habits are known, are aquatic or semi-aquatic and use lateral and swimming undulation rather than concertina as the primary locomotor modes. The loss could be attributed to (1) the effects of disuse, or, and we think more likely, (2) an advantage to having the two muscle masses tightly connected. A tight joining of these muscle masses would result in greater force transmission between the dermal musculature and the spinal musculature making lateral undulation more efficient. This supposition is supported by the higher undulatory speed of *Typhlonectes* as compared to *Dermophis* in these experiments.

Ducey *et al.* (1993) concluded that *Dermophis mexicanus* was willing to burrow in more compacted soils than several other caecilians. It has been observed that, while many fossorial caecilians are confined to friable soils, *Dermophis* exploits a wide range of soil types (Wake, 1980b). Our observation that the animal will switch from lateral undulation to internal concertina when it encounters more tightly packed soil shows that the latter is a more powerful burrowing mode. Perhaps the ability to switch from lateral undulation in friable soils to internal concertina when more compact soils are encountered explains *Dermophis*' burrowing aptitude.

In demonstrating the kinematics of internal concertina and the presence/absence of this trait among gymnophionans we highlight two areas that beg further inquiry. First, studying the distribution of internal concertina locomotion in other groups of caecilians, in particular the uraeotyphlids, scolecomorphids and a diversity of

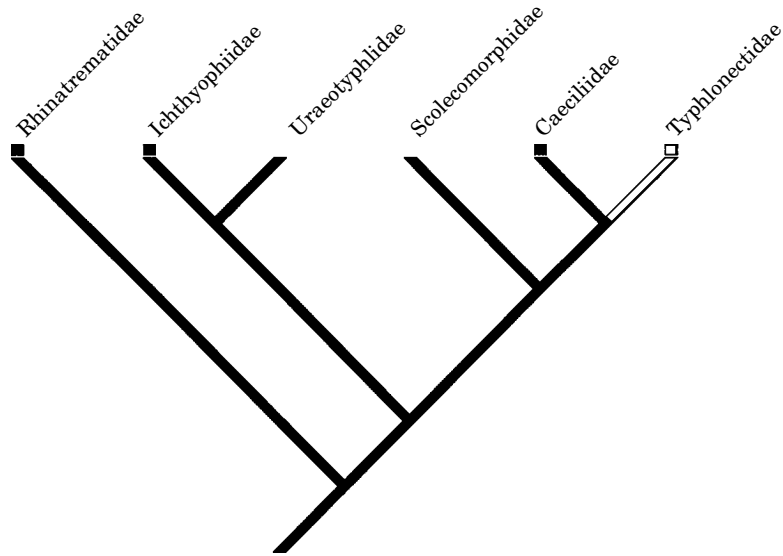


Figure 4. The ability to perform internal concertina locomotion mapped on a phylogeny of the Gymnophiona. The box at the branch terminal represents the fixed character state assigned to that taxon (Maddison & Maddison, 1992).

caeciliids would give further insight into the evolution of this complex locomotor mode. Second, a thorough biomechanical study of one species could explain the mechanical system responsible for force production during burrowing, an important contribution to the body of knowledge on limbless locomotion.

ACKNOWLEDGEMENTS

This research was supported by NSF grants IBN9306466 to Dave Carrier and IBN9419892 to Beth Brainerd, and by a grant from the Margaret E. and Howard E. Bigelow Gift to the University of Massachusetts Amherst. Karel Liem kindly provided lab space to APS during these experiments. Farish Jenkins generously allowed us to use the cineradiography equipment at the Museum of Comparative Zoology, Harvard University and provided much needed technical assistance. The cineradiography equipment is supported in part by NSF grants BSR87-06820 and BSR85-11867 to Farish Jenkins. Animals were obtained through the diligent efforts of Rob MacInnes, Glades Herp Inc., Ft. Meyers, FL. We thank Beth Brainerd, Kiisa Nishikawa, Willy Bemis, Nate Kley and Pam Kwiatkowski for constructive comments on the manuscript and Hans Hoppler for translating and discussing von Schnurbein's (1935) paper.

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