

Hydrostatic locomotion in a limbless tetrapod

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Caecilians are an ancient and enigmatic group of limbless, burrowing amphibians found throughout most of the humid tropics^{1,2}. Over the past 100 million years, the majority of caecilian lineages seem to have retained a series of highly derived musculoskeletal traits from a common ancestor. Among these features are unusually oriented body wall muscles³ and a vertebral column that moves independently of the skin⁴⁻⁹. Until now, these strange characteristics have defied a satisfying functional explanation. Our data suggest that the unique morphology of caecilians enables them to power locomotion hydrostatically by applying force to a crossed-helical array of tendons that surrounds their body cavity. Using this system, the Central American *Dermophis mexicanus* can generate approximately twice the maximum forward force as similar-sized burrowing snakes that rely solely on longitudinally oriented musculature of the body wall and vertebral column for forward force production. Although many groups of invertebrates use hydrostatic systems to move¹⁰⁻¹³ and many vertebrates use hydrostatic systems in localized body parts^{13,14}, caecilians are the first vertebrates known to use the entire body as a hydrostatic system for locomotion.

Because caecilian ribs are not ventrally directed and cannot support their bodies, previous workers have suggested that caecilians maintain body shape during locomotion by means of hydrostatic pressure generated by the unusually vertical muscles of their body wall^{3,4,15,16}. To test this hypothesis, we monitored pleuroperitoneal pressures during vigorous locomotion by implanting air-filled catheters in the vestigial left lung of four specimens of *Dermophis mexicanus* and recording pressure changes with a differential pressure transducer. We expected pleuroperitoneal pressure to vary across different modes of locomotion, but to remain fairly constant within each mode. However, to our surprise, in all four subjects pleuroperitoneal pressure varied cyclically during concertina locomotion. In this mode of locomotion, caecilians use movements

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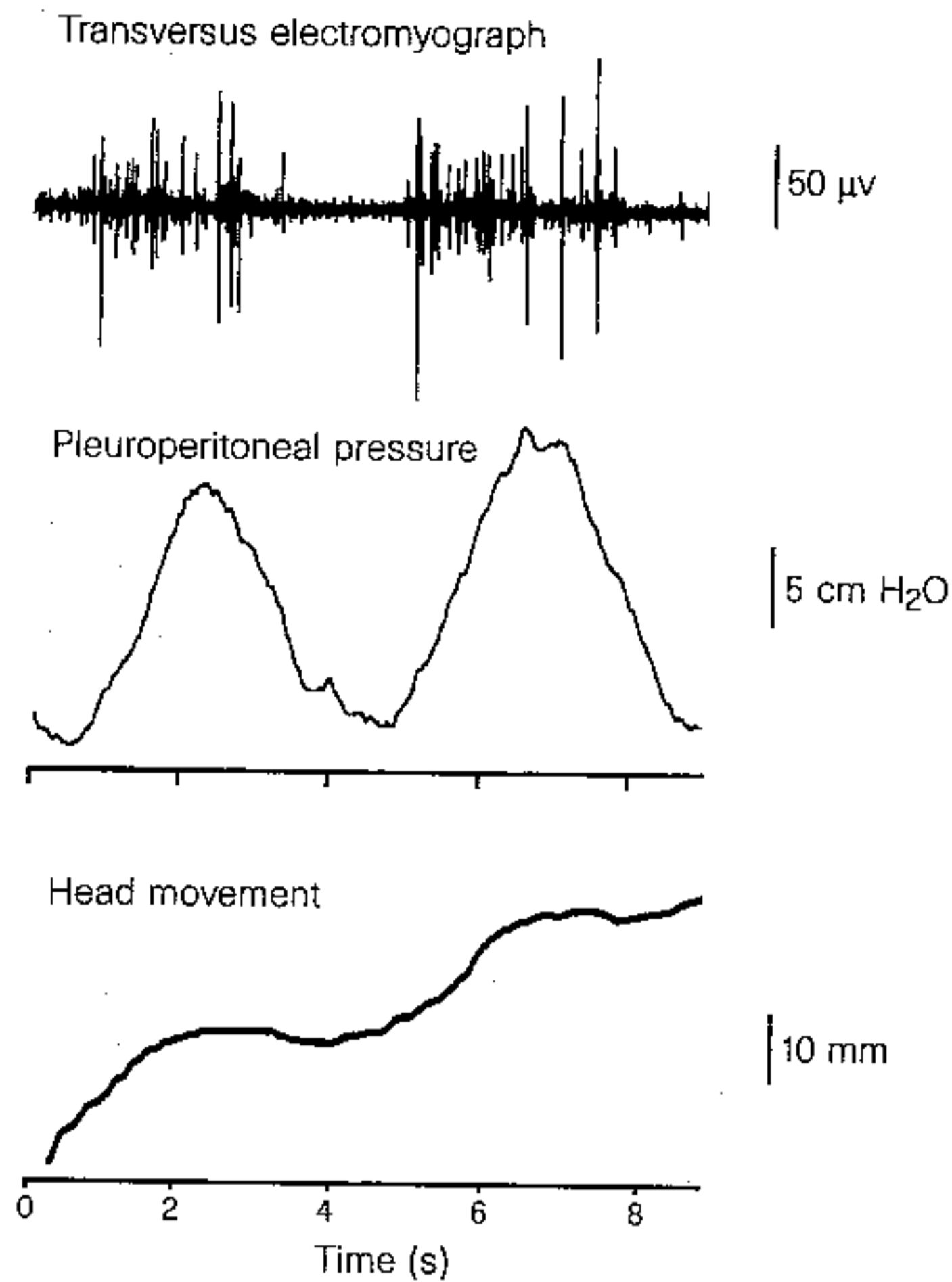


Figure 1 An example of the temporal relationship among activity of the m. transversus, pleuroperitoneal pressure and forward velocity of the head in a *Dermophis* (40 cm total length) performing concertina locomotion. As the m. transversus becomes active, pressure rises and the head is thrust forward. This pattern led us to the hypothesis that the vertically oriented muscles of the body wall might be contributing to forward force production.

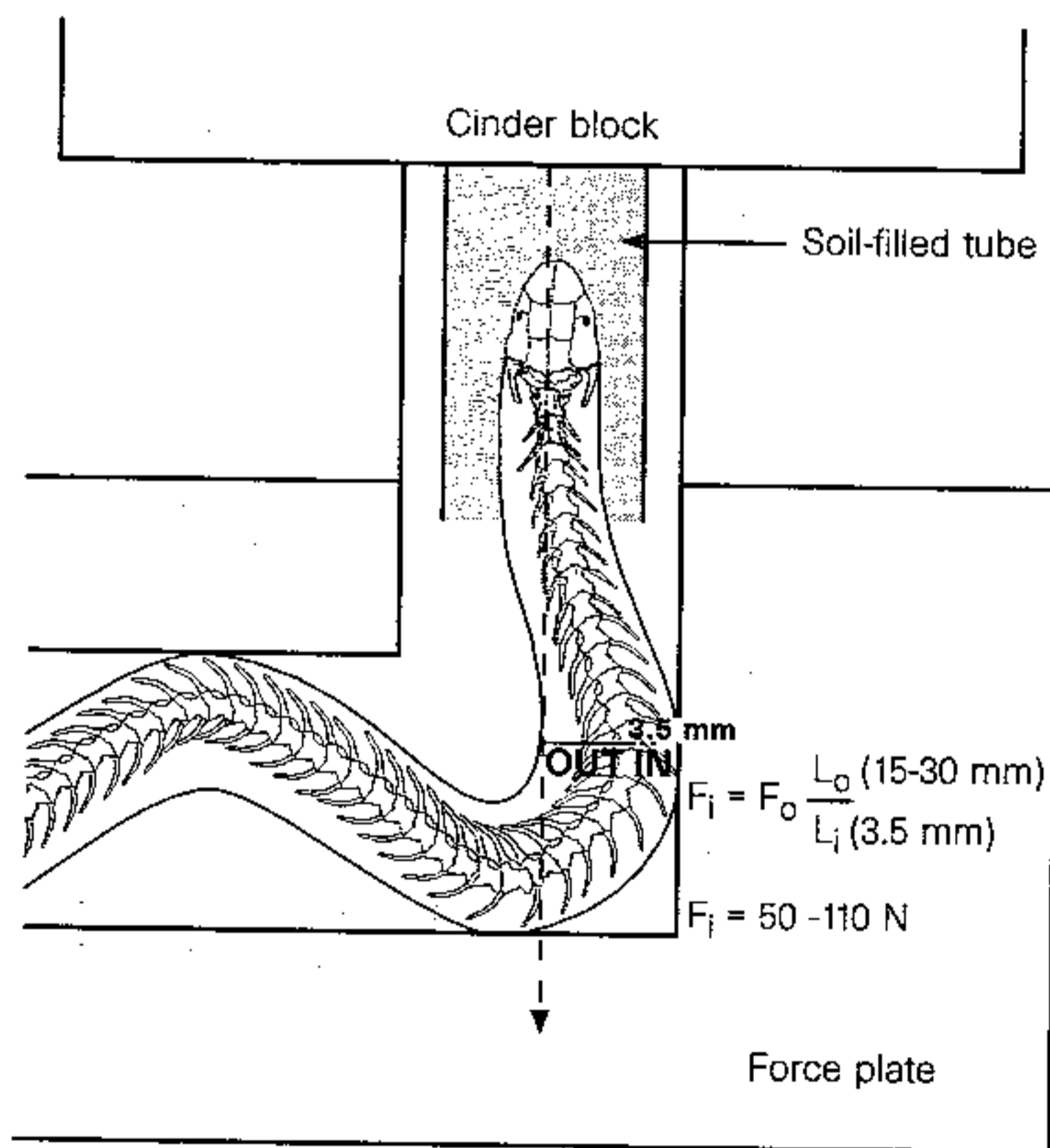


Figure 2 This diagram illustrates how forward force production in *Dermophis* was measured and how the contribution of the vertebral column and associated musculature (F_i) to total forward force (F_o) was estimated. Muscles of the vertebral column would have had to produce 440 N cm^{-2} of force to be able to account completely for the maximum thrust force measured.

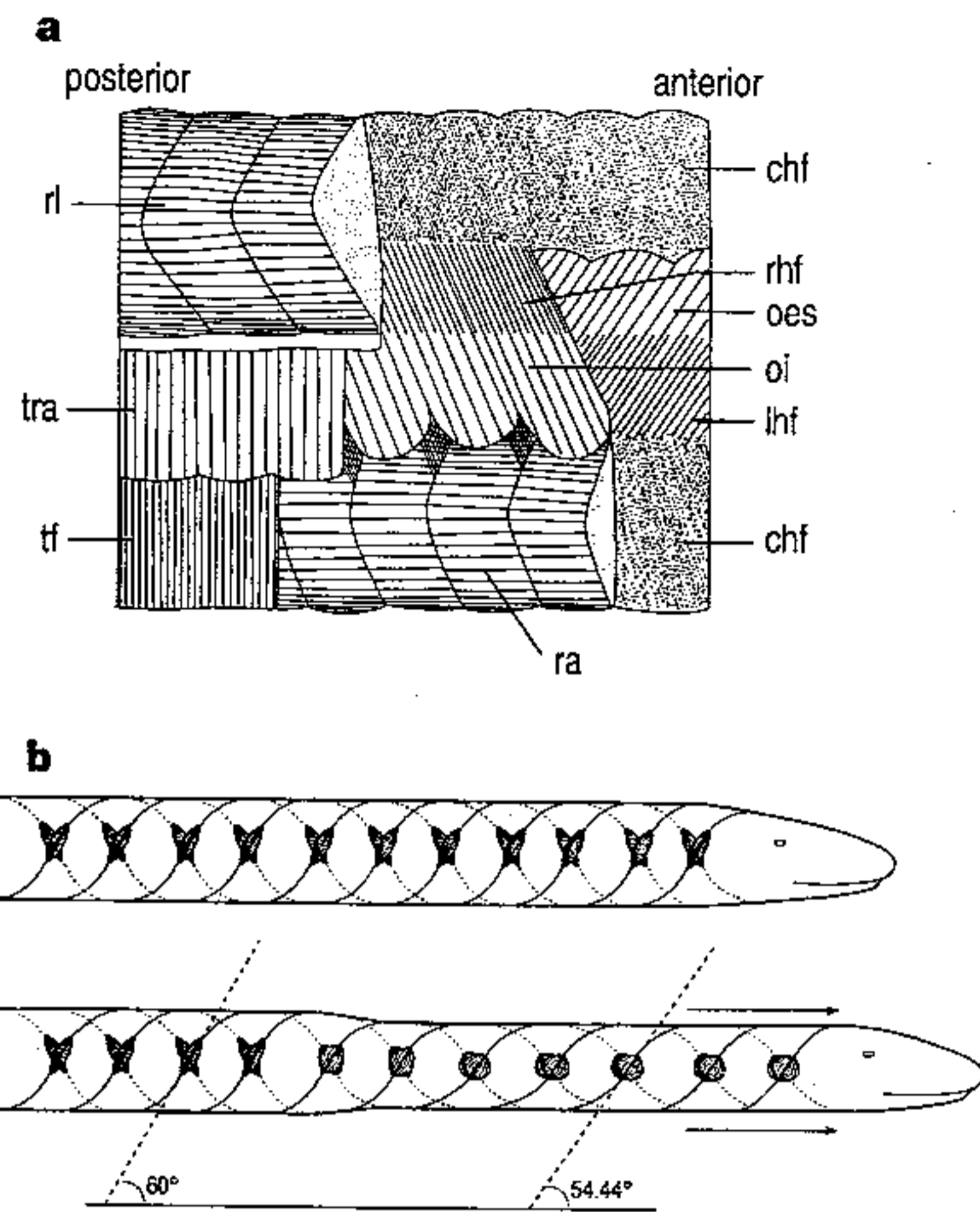


Figure 3 a, Anatomy of the left body wall of *Dermophis mexicanus* from an internal perspective. The layers are depicted from deepest (closest to the viscera) to most superficial (closest to the skin) from left to right. chf, crossed helical fibres; lhf, left-handed helical fibres; oes, m. obliquus externus superficialis; oi, m. obliquus internus; ra, m. rectus abdominus; rhf, right-handed helical fibres; rl, m. rectus lateralis; tf, transverse fibres; tra, m. transversus. **b**, Depiction of current working model of *Dermophis* concertina locomotion and burrowing. The entire helix is placed under tension by internal pressure generated by the transversus muscle. As the obliquus muscles place tension on parts of the helix, it shifts from its resting position of approximately 60° to the long axis of the body, towards 54.44° . As the helix extends, the now rigid outer body wall pushes on the head and aids the vertebral column musculature in generating forward directed force.

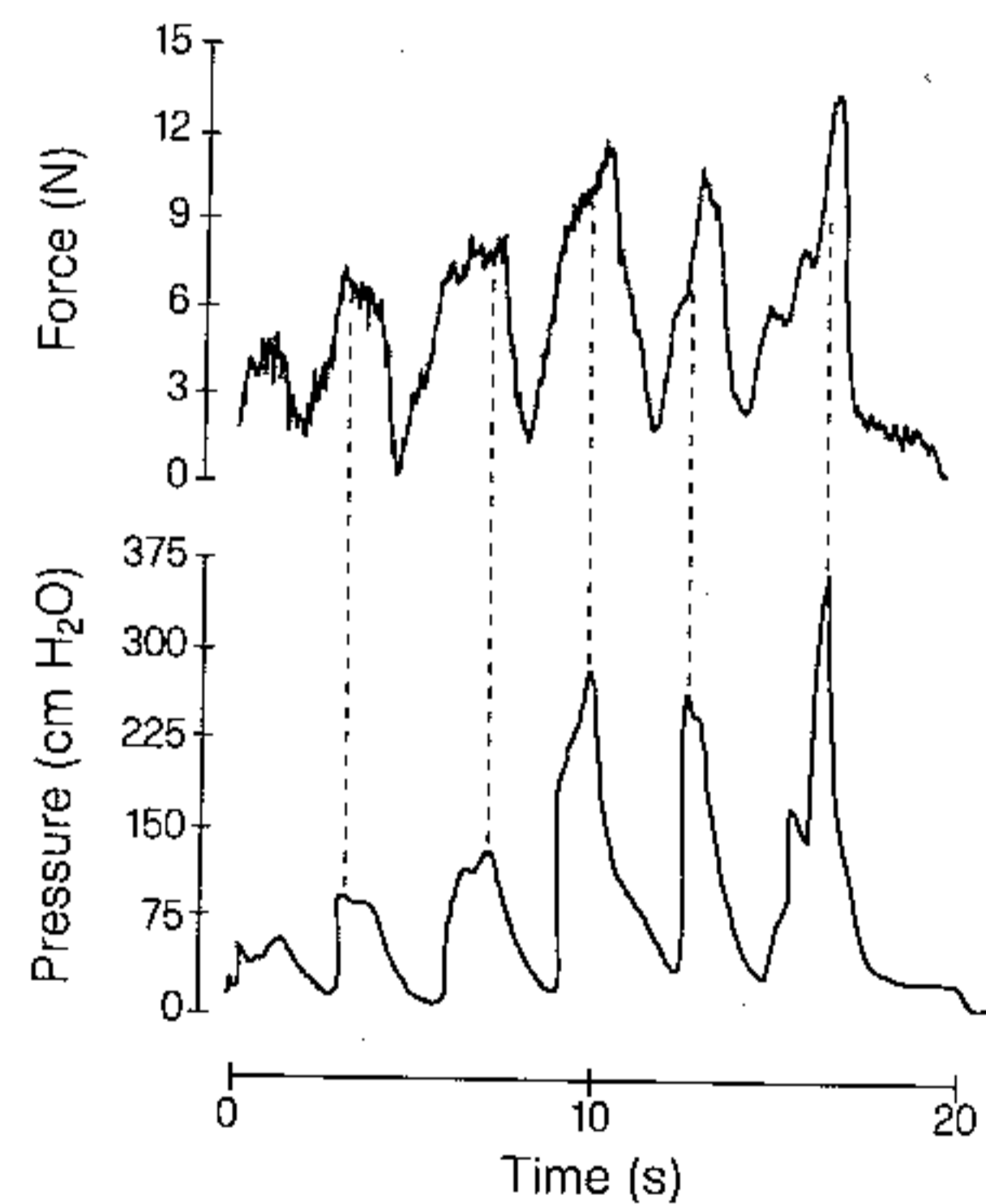


Figure 4 Two *Dermophis* were induced to burrow on the apparatus illustrated in Fig. 2. A fluid-filled catheter was surgically implanted in the pleuroperitoneal cavity so that pressure could be measured simultaneously. The maximum forces achieved by these individuals were less than those achieved before surgery, but a good correlation between pleuroperitoneal pressure and forward force was observed.

that resemble horizontal inchworming to move through straight-sided tunnels. Stationary curves of the body are pressed against the walls of the tunnel to create static points from which the rest of the body can be pushed or pulled¹⁷. In order to determine if the pressure cycles were actively or passively generated, activity of the transversus muscle was also recorded electromyographically. The m. transversus was selected because it was the most easily accessed vertically oriented body-wall muscle and it was the most likely vertical muscle to be universally active during pressure increases. The electromyography revealed that increases in pressure were correlated with forward movement of the head and activity of the transversus muscle (Fig. 1).

In most limbless tetrapods, the longitudinally oriented musculature associated with the vertebral column powers forward movement¹⁸. However, the above observations led us to hypothesize that the vertically oriented muscles of the body wall were helping to power forward movement in *Dermophis* during concertina locomotion. This hypothesis was tested by measuring the maximum forward force the animals could generate and then calculating whether or not the vertebral musculature alone could produce this force. Two individuals were induced to push against a fixed vertical surface from within a channel that was anchored to a force plate (Fig. 2). Under these conditions, both individuals routinely generated 15 N of forward force and sometimes produced 20 N. Given the posture of the animals and the cross-sectional area of the muscles, we calculated that the longitudinal muscles of the vertebral column would have to generate at least 200 N cm^{-2} to account for the measured forces (Fig. 2); this is four times the maximum force per cross-sectional area measured previously in any vertebrate muscle¹⁹. Because the vertebral musculature alone could not produce these forward forces, we concluded that the vertically oriented muscles of the body wall must be assisting the vertebral muscles in powering forward movement.

The vertical muscles of the body wall could produce a forward-directed force by two different mechanisms. In the simpler, the body wall muscles would pressurize the body fluid by reducing body diameter. The pressurized fluid would then push directly on the skull to drive it into the substrate. A second mechanism involves

placing tension on a crossed helix of connective tissue surrounding a fluid-filled tube (in this case the pleuroperitoneal cavity) while the fluid is under pressure. When tension is placed on such a helix, it becomes rigid and changes shape until its constituent fibres are oriented at 54.44° , causing the tube to elongate¹³. In this second system, the rigid outer body wall would push the skull into the substrate. The two obliquely oriented body-wall muscles of *Dermophis* are continuous with a crossed-fibre array of tendons (Fig. 3a)^{3,4} that wind around the body cavity and are oriented approximately 60° to the long axis of the body when the animal is at rest. The completely vertical transversus muscle is in a position to increase body pressure globally (Fig. 3a) so that these obliquely oriented muscles can extend the helix locally (Fig. 3b). Thus, the anatomy of *Dermophis* is consistent with either of the proposed mechanisms.

In order to distinguish between these two mechanisms, we simultaneously measured forward force production and internal pressure in two individuals as they attempted to burrow (Fig. 4). These data allowed us to calculate whether or not the pressures generated in the pleuroperitoneal cavity were high enough to account directly for the forward forces (mechanism 1). The area of the back of the skull in the two *Dermophis* was approximately 1 cm^2 , and the pressures measured would produce only one-tenth of the forces measured on a surface of 1 cm^2 (Fig. 5). Thus, even with the help of the vertebral musculature, this simple mechanism cannot explain the forward forces measured in *Dermophis*. This leaves the second mechanism (extending helix pushing on the skull, Fig. 3b) as the most viable explanation for the data gathered.

The manner in which *Dermophis* changes shape during burrowing offers further evidence for the extending helix hypothesis. During burrowing, the body of *Dermophis* decreases in diameter only in the region between the point from where it pushes and the head. This is consistent with the idea that the helix, already stiffened by an increase in pressure generated throughout the body by the transversus muscle, is being extended locally by the oblique muscles. If global pressure changes were directly pushing on the skull, we would expect uniform changes in body diameter along the entire body.

These data shed new light on the significance of some of the most divergent aspects of caecilian musculoskeletal anatomy. In order for the entire body to function as a hydrostatic system that generates pushing forces, the pleuroperitoneal cavity must be able to change length. This is impossible in most vertebrates, as the tissues that form the body cavity are tightly connected to the vertebral column. However, the specialized trunk anatomy of caecilians, with a loose connection of the skin and associated body wall musculature to the vertebral column, allows them to alter the length of the body cavity. This hydrostatic system appears to be more powerful than a vertebral-driven system, as burrowing snakes of the genera *Farancia*, *Eryx* and *Lococemus* are capable of generating only about 50% of force produced by a *Dermophis* with the same body cross-section (J.C.O'R., N. Kley, D.A.R. and A. P. Summers, unpublished results). In light of these new data, it seems likely that some of the oddest characteristics of caecilian musculoskeletal anatomy have changed little over the past 100 million years because they facilitate exceptional burrowing performance. □

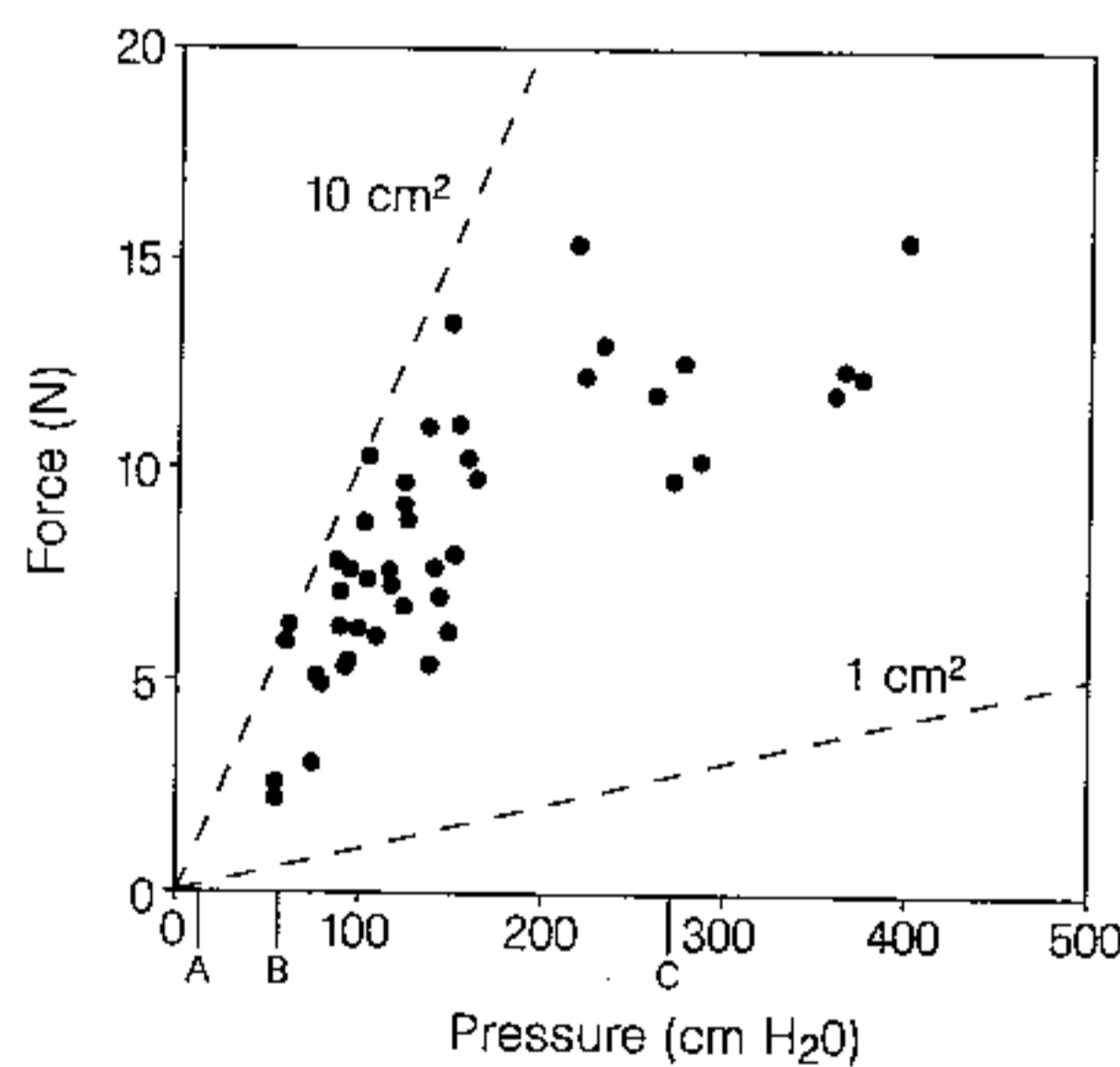


Figure 5 Peak pressure graphed against peak force for 45 thrusts for a single *Dermophis*. Peak pressures from a *Dermophis* at rest (A)¹⁶, a chuckwalla lizard (*Sauromalus obesus*) defensively inflated in a crack (B)²⁰, and a human performing the Valsalva manoeuvre (C)²¹ are included on the x-axis for reference. The dashed diagonal lines represent the force that would be produced on a given surface area as a function of the pressure on the x-axis using the equation pressure \times area = force.

Methods

Concertina locomotion experiments. After anaesthetizing specimens by immersing them in 0.2% methanesulphonate (MS222), an air-filled catheter (Intramedic polyethylene tubing, 1.14 mm internal diameter) was implanted in their vestigial left lung; the catheter was then attached to an Omega PX170-28DV pressure transducer. In two subjects, patch electrodes were implanted on the inner side of the m. transversus. The activity of the other two vertical muscles of the body wall (m. obliquus internus and m. obliquus externus) were not monitored due to the difficulty of securing electrodes to them and small number of individuals available for study. Patch electrodes were constructed

from Dow Corning Silastic sheeting (500 μm thick) and Teflon-insulated, multistranded, stainless-steel wire (280 μm diameter, California Fine Wire Co.). Individual patches were approximately 4 mm \times 4 mm. The bared portions of the wires were approximately 1 mm long, and the bared wires were separated from each other by approximately 1 mm. Animals were videotaped while performing concertina locomotion in a straight-sided Plexiglas channel. Movement of the head was digitized using Peak Performance 2DTM software and an IBM-compatible computer. Pressure and electromyograms were recorded using Bioware software and an IBM-compatible computer.

Estimation of forward force produced by vertebral musculature. Forward force was measured using a custom-built force plate (Pharos Systems, Inc.) We estimated the maximum forward forces that could be generated by the caecilian's vertebral musculature based on the cross-sectional area of the vertebral musculature and the posture exhibited by the animals as recorded on video tape. The muscles along each side of the vertebral column are never active simultaneously during concertina¹⁸; thus the vertebral muscles act in series and have a maximum physiological cross-section equal to the cross-section of the musculature on one side. The cross-sectional area of one side of the vertebral musculature in the two individuals for which forward force data are available is $\sim 0.25 \text{ cm}^2$. The most liberal estimation of force production by the vertebral musculature assumes that the contraction of the vertebral musculature is isometric, a maximum isometric force production of 50 N per cm^2 of cross-section¹⁹, and an average mechanical advantage of 1. This calculation yields a figure for force production by the vertebral musculature of about 12.5 N. The maximum forward force of 18.7 N measured by us exceeds this by a substantial margin. Furthermore, in reality the vertebral column was bent throughout all burrowing attempts and the mechanical advantage was far less than 1. During sequences in which vertebral posture and forward force were measured simultaneously, the mechanical advantage of the vertebral musculature never exceeded 0.25. On the basis of these more realistic parameters, we estimate that the animals used in this study would have to generate over 400 N of force per cm^2 of muscle cross-section to achieve the maximum measured forward forces if only the vertebral muscles were used.

Calculation of potential force using hydraulic model. In a simple hydraulic system, the amount of force produced by a given pressure will be directly proportional to the area over which the pressure is applied. Applied over a surface area of 1 cm^2 , the approximate surface area of the back the head of the individuals used, the pleuroperitoneal pressures measured cannot account for the forward forces measured. For example, 100 cm $\text{H}_2\text{O} = 9,785 \text{ Pa}$ and 1 $\text{cm}^2 = 1 \times 10^{-4} \text{ m}^2$, thus the amount of force produced by 100 cm of H_2O on 1 $\text{cm}^2 = 9,785 \text{ Pa} \times (1 \times 10^{-4} \text{ m}^2) = 0.98 \text{ N}$. The same pressure would have to be applied over 10 cm^2 to produce the measured pushing forces (Fig. 5).

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