

# ONTOGENETIC SCALING OF BURROWING FORCES IN THE EARTHWORM *LUMBRICUS TERRESTRIS*

KIM J. QUILLIN\*

*Department of Integrative Biology, University of California, Berkeley, CA 94720-3140, USA*

\*Present address: 5705 Waterside Drive, Berlin, MD 21811, USA (e-mail: kquillin@shore.intercom.net)

*Accepted 20 June; published on WWW 22 August 2000*

## Summary

In hydrostatic skeletons, it is the internal fluid under pressure surrounded by a body wall in tension (rather than a rigid lever) that enables the stiffening of the organism, the antagonism of muscles and the transmission of force from the muscles to the environment. This study examined the ontogenetic effects of body size on force production by an organism supported with a hydrostatic skeleton. The earthworm *Lumbricus terrestris* burrows by forcefully enlarging crevices in the soil. I built a force-measuring apparatus that measured the radial forces as earthworms of different sizes crawled through and enlarged pre-formed soil burrows. I also built an apparatus that measured the radial and axial forces as earthworms of different sizes attempted to elongate a dead-end burrow. Earthworms ranging in body mass  $m_b$  from hatchlings (0.012 g) to adults (8.9 g) exerted maximum forces ( $F$ , in N) during active radial expansion of their burrows ( $F=0.32m_b^{0.43}$ ) and

comparable forces during axial elongation of the burrow ( $F=0.26m_b^{0.47}$ ). Both these forces were almost an order of magnitude greater than the radial anchoring forces during normal peristalsis within burrows ( $F=0.04m_b^{0.45}$ ). All radial and axial forces scaled as body mass raised to the  $2/5$  power rather than to the  $2/3$  power expected by geometric similarity, indicating that large worms exert greater forces than small worms on an absolute scale, but the difference was less than predicted by scaling considerations. When forces were normalized by body weight, hatchlings could push 500 times their own body weight, while large adults could push only 10 times their own body weight.

Key words: biomechanics, scaling, body size, hydrostatic skeleton, earthworm, ontogeny, burrowing, force, *Lumbricus terrestris*.

## Introduction

Animal skeletons perform a number of important mechanical functions: they provide postural support, re-extend shortened muscles (enabling reversible shape changes) and transmit forces from muscles to other parts of the organism and to the environment (enabling feeding and locomotion; for reviews, see Chapman, 1950; Currey, 1970; Trueman, 1975; Wainwright, 1988). Since skeletons function throughout the lifetime of animals, the ontogenetic scaling of skeletal function may have important implications for the life history, ecology and evolution of these animals (e.g. Peters, 1983; Calder, 1984; Werner and Gilliam, 1984; Carrier, 1996). The purpose of the present paper was to examine the ontogeny of skeletal force transmission in the hydrostatic skeleton of a soft-bodied organism.

Several studies have examined ontogenetic scaling of skeletal function in organisms with rigid, lever-like skeletons, namely vertebrates and arthropods (e.g. Garland, 1985; Marsh, 1988; Queathem, 1991; Katz and Gosline, 1992; Carrier, 1995; Hughes et al., 1995). However, the hydrostatic skeletons of soft-bodied organisms function by a different mechanism from lever-like skeletons. Hydrostatic skeletons are generally composed of a deformable body wall in tension surrounding

fluid and/or soft tissues in compression. Fluid in compression becomes pressurized; it is this pressure, rather than a rigid lever, that enables antagonism of muscles and stiffening of the organism (for reviews, see Chapman, 1958, 1975; Clark, 1964; Trueman, 1975; Kier and Smith, 1985; Wainwright, 1988). Since muscle forces are transmitted to other muscles and to the environment *via* the pressurized internal fluid, motions and forces in hydrostats are determined primarily by changes in the dimensions of the body segments themselves rather than changes in joint angles between segments. Diverse organisms from many phyla employ such a skeletal design. How does the ontogenetic increase in size of a hydrostatic skeleton affect its ability to transmit forces?

### *The scaling of burrowing forces in Lumbricus terrestris*

I chose earthworm burrowing as my experimental system to examine the ontogenetic scaling of force production in a hydrostat. *Lumbricus terrestris* is one of the largest of the temperate earthworms and has been studied often because of its abundance and agricultural importance (for reviews, see Darwin, 1881; Minnich, 1977; Edwards and Bohlen, 1996). *L. terrestris* grows by more than three orders of magnitude in

body mass from hatchling (0.01 g; K. J. Quillin, personal observation) to maturity (5–10 g; Lakhani and Satchell, 1970), providing a wide size range for the study of body size. Furthermore, earthworms are excellent burrowers (see Darwin, 1881). Several researchers have measured burrowing force in adult earthworms using flat glass bridges (Manton, 1965; Seymour, 1970), artificial burrows (Keudel and Schrader, 1999) and soil discs (McKenzie and Dexter, 1988a,b). Others have calculated force from measurements of internal pressure (Chapman, 1950; Newell, 1950). However, none of these studies measured burrowing force across an ontogenetic size range.

The earthworm *L. terrestris* lives in semi-permanent burrows and feeds primarily by pulling leaves into the burrows and secreting enzymatic saliva to digest them externally (e.g. Darwin, 1881; Arthur, 1965). This species also eats soil, but generally only when food is scarce or when it cannot otherwise penetrate compacted soil (Darwin, 1881; Evans, 1947; Arthur, 1965). Thus, burrows are generally created by ‘crevice burrowing’ (Seymour, 1970) rather than by ingestion. The anteriormost segments are first elongated axially, inserted into crevices in the soil and then expanded radially to enlarge the diameter of the crevice. After a burrow has been established, it is often maintained (sometimes for weeks or months; Evans, 1947) by radial compaction of the walls.

Many soft-bodied crawlers and burrowers use peristalsis to translate local shape changes into locomotion (e.g. earthworms, sea cucumbers, caterpillars, snails; Alexander, 1983; Trueman, 1975; Trueman and Jones, 1977; Elder and Trueman, 1980). Peristalsis occurs when waves of alternating contraction and relaxation of muscles move along a radially flexible tube (Heffernan and Wainwright, 1974). Typically, the radially expanded regions anchor the organism to the substratum while the radially contracted, axially elongated regions advance over or through the substratum. When the longitudinal muscles of an earthworm segment contract, the segment becomes shorter (along the anterior–posterior axis) and wider and can exert radial forces. When the circumferential muscles of an earthworm segment contract, the segment becomes longer and thinner and can exert axial forces. Waves of circumferential and longitudinal muscle contractions pass posteriorly along the constant-volume body segments as a worm crawls forward, forming retrograde waves (waves that move in the opposite direction to locomotion; Gray and Lissmann, 1938; Newell, 1950; for a review, see Trueman, 1975). Peristalsis is used both for crawling on the surface and for burrowing within the soil.

### Objectives

The objective of the present study was to determine how burrowing forces scale with body size during earthworm ontogeny. The first experimental goal was to measure axial and radial forces exerted by burrowing earthworms and to do so using an apparatus that simulates an actual soil burrow. If muscle properties are constant as a function of body size, geometrically similar organisms are expected to exert forces

that are proportional to body mass  $m_b^{2/3}$ , where  $m_b$  is body mass (e.g. Alexander et al., 1981; Alexander, 1985). This null hypothesis is derived from the observation that muscle force in vertebrates is proportional to the cross-sectional area of the muscle if peak muscle stress is constant (e.g. Close, 1972). Area scales as the square of length, or as  $m_b^{2/3}$  in geometrically similar organisms (e.g. Thompson, 1917). The ontogenetic scaling of muscle properties is unknown for earthworms, but the scaling relationship  $\text{force} \propto m_b^{2/3}$  is used as the null hypothesis in the present study. Thus, the corollaries to this null hypothesis are that force divided by weight scales as  $m_b^{-1/3}$  and force per area of application of force scales as  $m_b^0$ .

Quillin (1998) observed geometric similarity in earthworms across an ontogenetic size range. However, muscle area was not one of the variables measured. The second experimental goal of the present study was to measure the scaling of muscle area since it is a critical determinant of the scaling of force production. Finally, Quillin (1999) observed kinematic similarity in earthworms that were crawling on a surface, but the kinematic scaling of burrowing earthworms has not been examined. Since force and velocity tend to be inversely related, the third experimental goal of this study was to measure the scaling of burrowing kinematics to provide a context for the observed scaling of burrowing forces.

## Materials and methods

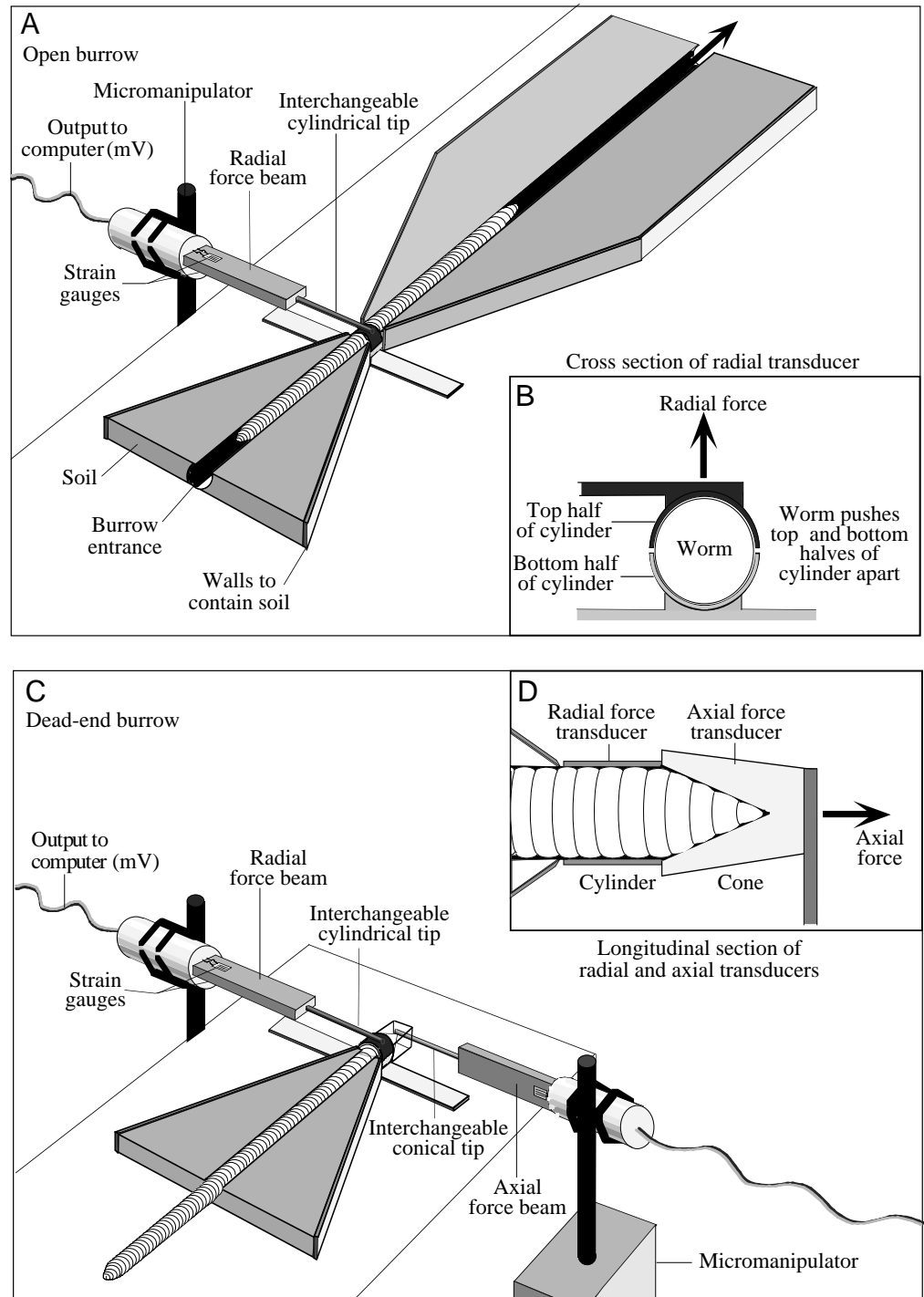
### Force-measuring apparatus

I designed the force-measuring apparatus to meet two requirements: (i) the use of soil burrows similar to those the earthworms experience in nature, and (ii) the use of interchangeable parts to accommodate earthworms varying by an order of magnitude in length and diameter. I designed the apparatus to operate in two configurations. The ‘open’ burrow configuration enabled the measurement of radial forces and burrowing kinematics as an earthworm crawled through a cylindrical soil burrow (Fig. 1A,B). The ‘dead-end’ burrow configuration enabled the simultaneous measurement of radial and axial forces as an earthworm attempted to penetrate the end of a dead-end soil burrow (Fig. 1C,D). These two configurations mimic the circumstances that earthworms of the species *Lumbricus terrestris* experience in their semi-permanent burrows in nature. Seven sets of parts were built to accommodate seven size classes of earthworm ranging from 0.012 to 8.9 g.

### Open-burrow configuration: measurement of radial forces and burrowing kinematics

The open-burrow configuration consisted of a short soil burrow (less than one body length) in series with a cylindrical force transducer and a long soil burrow (greater than one body length; Fig. 1A). I formed the burrows by packing soil around the outside of pipes and wires of known diameter (see below for soil properties). A Plexiglas lid served as the roof of the burrow and enabled observation of the earthworm within. The short length of the first burrow motivated the earthworms to

Fig. 1. Diagram of the force-measuring apparatus. Seven size classes of interchangeable parts were built to accommodate seven size classes of earthworm. (A) The open-burrow configuration measured the radial forces exerted by the different regions of an earthworm as it crawled through a pre-formed soil burrow (the burrow diameter is two-thirds of the maximum resting diameter of earthworm). A Plexiglas lid formed the roof of the burrow (not shown) so that the kinematics of the earthworm could be observed. (B) Radial force was measured by the top half of a cylindrical force transducer as the earthworm pushed its way through the burrow (inside diameter of cylinder = inside diameter of burrow). (C) The dead-end burrow configuration measured both radial and axial forces as an earthworm attempted to penetrate a barrier at the end of a pre-formed soil burrow. A Plexiglas lid formed the roof of the burrow (not shown). (D) Radial force was measured by the cylindrical force transducer and axial force was measured by a conical force transducer (in series with the burrow and radial cylinder; inside diameter of cone base = inside diameter of cylinder).



crawl forward through the force transducer. The long length of the second burrow motivated the earthworms to crawl completely through the force transducer before pausing at the end of the burrow, a typical behavior.

Each radial transducer tip consisted of a metal or Plexiglas cylinder whose length and inside diameter were the same as the inside diameter of the burrow (as determined by the outside diameter of the pipe or wire that was used to form the burrow). Each cylinder consisted of top and bottom halves (Fig. 1B).

Each top half was attached to a pipe that fitted over the stiff metal rod at the end of the Plexiglas force beam. Each bottom half was attached to a base for placement between the two burrows. As an earthworm passed through the cylinder and contracted its longitudinal muscles (causing the segments within the cylinder to expand radially), a radial force was exerted against the top half of the cylinder, causing the force beam to be deflected. The two strain gauges on the force beam (half-Wheatstone bridge) transmitted the deflection in

millivolts to LabVIEW software (Version 3.0.1; National Instruments, Austin, TX, USA) on a Gateway 2000 computer. Force data were collected at 10 scans  $s^{-1}$  at 22 °C in daylight; scanning at a higher rate did not influence the magnitude of the force peaks. I calibrated the force beam with weights at the beginning of each set of experiments to derive a conversion from millivolt output to newtons. The calibration data were all linear ( $r^2=0.999$  or better). Plexiglas force beams are sometimes subject to creep and can, therefore, show significant hysteresis. I cannot eliminate the possibility that hysteresis affected the shape of the force peaks during the experiment. However, the transducer re-zeroed itself between force peaks and I only measured maximum force, not the shape of the force curve. Therefore, I do not believe that the material properties of the force beam caused error in the force measurements.

I measured peak radial force for six replicates for each of 36 individuals ranging in mass from 0.012 to 8.9 g. I began collecting force data the instant that the anteriormost segment of the earthworm entered the transducer cylinder and terminated data collection either when the last segment entered the cylinder or when the earthworm stopped crawling part-way through. Using this method, I obtained the duration of crawling from the duration of the force recording. By measuring the length of earthworm that had passed through the cylinder during the duration of the force recording, I was able to calculate average crawling speed through the force transducer. I also used the force recording to determine the number of cycles of peristalsis that occurred during the duration of the trial, which enabled me to calculate stride frequency. I then calculated average stride length as the product of crawling speed and stride frequency. I also measured the entire length of the earthworm as it crawled through the transducer so that the ratio of total crawling length to resting body length (and thus the degree of body elongation) could be calculated; resting body length was calculated from body mass using the scaling relationship described by Quillin (1998). After each replicate, I repacked the burrow. I also re-zeroed the force transducer using a micromanipulator to place the top half of the radial transducer cylinder over the bottom half such that the two were barely touching and not prestressed. I ran the six replicates for each individual consecutively; there were no consistent trends in the peak force values over the course of the six replicates.

#### *Dead-end burrow configuration: measurement of radial and axial forces*

The dead-end burrow configuration consisted of a short soil burrow in series with a cylindrical radial transducer and a conical axial transducer (Fig. 1C). The burrow and radial transducer were assembled as described for the open-burrow configuration. Each axial transducer cone consisted of a clear Plexiglas block drilled with a conical hole (apex angle 37°) whose base diameter equaled the inside diameter of the burrow and radial transducer (Fig. 1D). The clear Plexiglas block enabled observation of the earthworm within the cone. Each cone was attached to a pipe that fitted over the stiff metal rod

at the end of the Plexiglas force beam. When an earthworm inserted its anteriormost segments into the cone and pushed forward in an attempt to advance, the force beam was deflected and its output was recorded by LabVIEW software. I measured peak radial force and peak axial force for four replicates for each of 37 individuals ranging in size from 0.012 to 8.9 g. I did not run the four replicates for each individual consecutively; three or four individuals were measured during each session, alternating individuals for each run to give the earthworms a rest between replicates (without a pause, earthworms often 'remembered' that the burrow was impenetrable and would not make a second attempt). I observed no trend in the peak force over the course of the four replicates. The axial force beam was calibrated as described for the radial force beam. The burrows and transducer tips were reset between replicates.

#### *Control experiment for burrow diameter*

The objective of this control experiment was to choose a ratio of earthworm diameter to burrow diameter for the scaling experiment that would maximize burrowing force while enabling replicate measurements. Peak radial force was measured as a 6.1 g earthworm (9.5 mm maximum resting diameter) crawled through the open-burrow apparatus configured with four different burrow diameters: 5.4 mm, 7.1 mm, 8.7 mm and infinite (a surface), which translated to burrow diameter to earthworm diameter ratios of 0.57, 0.75, 0.92 and infinity. Five replicates were recorded for each burrow configuration, and the order of the configurations was mixed (both starting and ending with the smallest diameter to ensure that the earthworm did not fatigue). Data were collected at 40 scans  $s^{-1}$  at 22 °C in daylight.

The earthworm exerted highest forces in the narrowest burrow (Kruskal–Wallis,  $P=0.01$ ; Fig. 2A). The earthworm also exerted the greatest number of radial pushes per run in the narrowest burrow in an apparent attempt to enlarge the burrow ( $P<0.001$ ; Fig. 2B). However, the earthworm crawled much more slowly in the narrow burrow ( $P<0.001$ ; Fig. 2C), often backing out after a very short distance of penetration and/or refusing to re-enter the burrow altogether. The earthworm did not change the extent of elongation of its body to accommodate different burrow diameter, as might be expected ( $P>0.10$ ; Fig. 2D). I chose to run the scaling experiments using a ratio of burrow diameter to earthworm diameter of 0.67, intermediate between the two smallest burrow diameters used in the control experiment. This burrow diameter enabled consistent measurement of near-maximal forces of earthworms that crawled through the burrow several times, enabling not only replicate measurements of force but also measurements of burrowing kinematics.

#### *Control experiments for soil properties*

The two most important properties of a given soil in determining penetration resistance are soil bulk density and water content (Campbell and O'Sullivan, 1991). The objective of the soil control experiments was to choose a soil bulk density and a soil moisture level that would maximize force



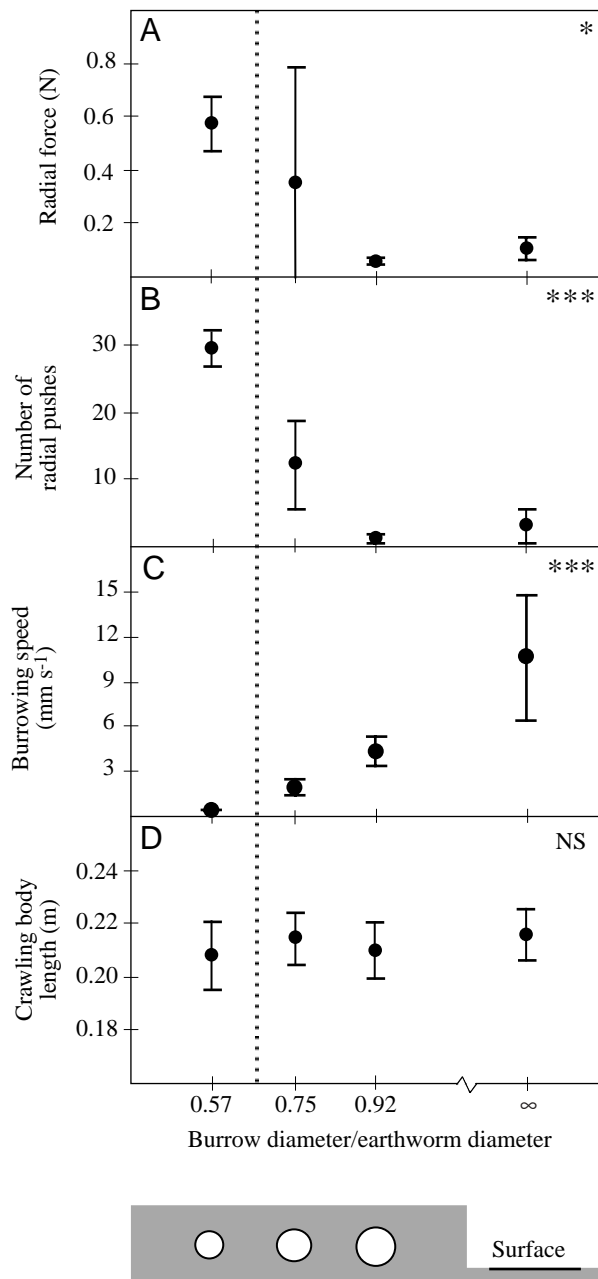


Fig. 2. Burrow diameter controls. Peak radial burrowing force and crawling kinematics were measured as an earthworm (6.1 g; maximum resting diameter 9.5 mm) crawled through the open-burrow apparatus configured with four different burrow diameters ( $N=5$  for each diameter). The infinite configuration was a flat surface. (A) The earthworm exerted greatest radial force in the smallest burrows (Kruskal–Wallis,  $P=0.01$ ). (B) The earthworm also made the greatest number of attempts to enlarge the smallest burrows radially ( $P<0.001$ ). (C) However, the smaller the burrow, the slower the earthworm progressed through the burrow ( $P<0.001$ ). (D) The earthworm did not adjust its body length to accommodate different burrow diameters ( $P>0.10$ ). The dotted line represents the ratio of burrow diameter to maximum resting earthworm diameter chosen for the scaling experiment (0.67). The error bars represent 95% confidence intervals. \* $P<0.05$ ; \*\*\* $P<0.001$ ; NS, not significant.

production by earthworms. In general, animals exert greatest forces when they experience greatest mechanical resistance to force production. Therefore, I hypothesized that earthworms would exert greatest forces when the soil bulk density (mass of solid fraction per total volume of soil) was highest and when the soil moisture was at a level that maximized soil cohesion (which resists deformation). These values depend on the structure and chemistry of the soil used (Campbell and O'Sullivan, 1991) and could not, therefore, be calculated *a priori*. The soil used was a clay loam (28% clay, 35% sand, 37% silt,  $\pm 5\%$ ) in the Tierra soil series (fine, montmorillonitic thermic mollic Palixeralf), collected in Berkeley, CA, USA. I removed the roots and pebbles and dried the soil in a drying oven at  $65^\circ$  for 1–3 days. Drying enabled isolation of the solid fraction so that soils of known bulk density and soil moisture could be mixed. The drying and rewetting of soils changes their tensile strength (Whiteley et al., 1981), but new soil was mixed prior to each experiment to maintain consistency in soil properties among experiments.

#### Soil bulk density control

I measured peak radial force as a 6.1 g earthworm crawled through the open-burrow apparatus configured with three soil bulk densities:  $660 \text{ kg m}^{-3}$  (as loosely packed as possible while maintaining shape of burrow; large air spaces),  $980 \text{ kg m}^{-3}$  (moderately packed; small air spaces) and  $1300 \text{ kg m}^{-3}$  (tightly packed; minute air spaces). The soil bulk densities were achieved by measuring the volume of the space to be occupied by the soil (volume within retaining walls minus volume of burrow; Fig. 1) and calculating the number of grams of water and soil needed to create the desired bulk densities in that volume. All three treatments had the same soil moisture content ( $0.21 \text{ g water g}^{-1}$  dry soil) and the same ratio of burrow diameter to maximum resting earthworm diameter (0.67). I placed the soil into the apparatus until it was visually homogeneous; earthworm burrowing forces were sufficiently variable that high precision in bulk density homogeneity was not deemed necessary. Five replicate force measurements were recorded for each soil bulk density. Data were collected at  $40 \text{ scans s}^{-1}$  at  $22^\circ\text{C}$  in daylight. Peak radial force increased with soil bulk density, but the increase was not statistically significant (Kruskal–Wallis,  $P>0.10$ ) (Fig. 3A). Nonetheless, the maximum soil bulk density,  $1300 \text{ kg m}^{-3}$ , was chosen for the scaling experiment.

#### Soil moisture control

Soil water content was defined on a mass basis ( $\text{g water g}^{-1}$  dry soil). I measured peak radial force as a 6.1 g earthworm crawled through the open-burrow apparatus configured with three soil moistures:  $0.15 \text{ g g}^{-1}$  (crumbly and incohesive),  $0.21 \text{ g g}^{-1}$  (moist and cohesive) and  $0.27 \text{ g g}^{-1}$  (muddy). All three treatments had the same soil bulk density ( $1300 \text{ kg m}^{-3}$ ) and the same ratio of burrow diameter to maximum resting earthworm diameter (0.67). Five replicate force measurements were recorded for each soil moisture. Data were collected at  $40 \text{ scans s}^{-1}$  at  $22^\circ\text{C}$  in daylight. Peak

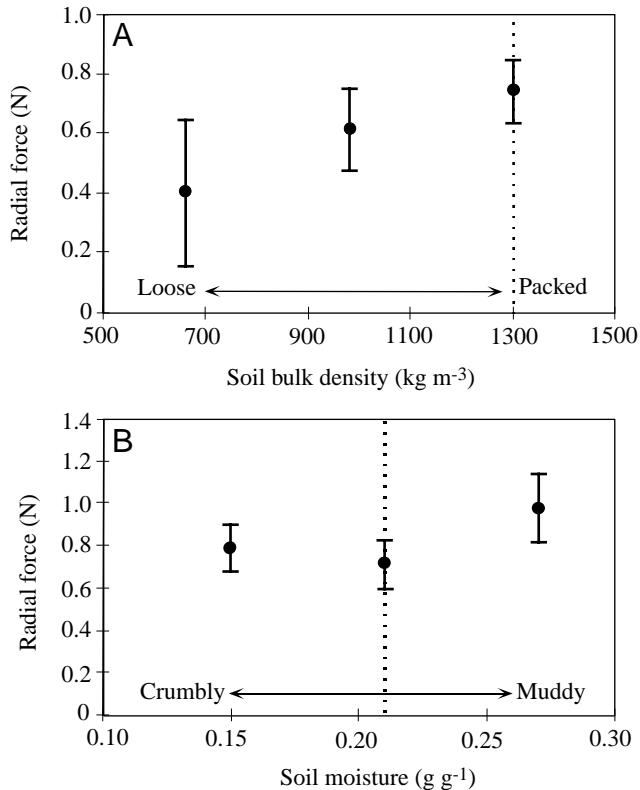


Fig. 3. Soil property controls. Peak radial force was measured as an earthworm (6.1 g) crawled through the open-burrow apparatus configured with soils of different properties. (A) The apparent increase in force as a function of soil bulk density was not statistically significant (Kruskal–Wallis,  $P>0.10$ ). (B) Force did not change as a function of soil moisture content (Kruskal–Wallis,  $P>0.10$ ). The dotted lines represent the properties chosen for the force scaling experiment. The error bars represent 95% confidence intervals ( $N=5$ ).

burrowing force did not change as a function of soil moisture (Kruskal–Wallis,  $P>0.10$ ) (Fig. 3B). This result agrees with the observation by Rushton (1986) that burrow lengths of *L. terrestris* did not significantly correlate with soil moisture content of sample soil blocks. Therefore, the intermediate value  $0.21 \text{ g g}^{-1}$  was chosen for the scaling experiments. The soil was exposed to the air intermittently between measurements. The surface of the soil was misted occasionally with water to counteract evaporation, especially in the apparatus assembled for the very small earthworms. These small fluctuations in soil moisture probably had a negligible effect on the force measurements since the soil moisture control experiment demonstrated that similar force measurements were acquired over a great range of soil moisture content.

#### Experimental animals

Earthworms (*Lumbricus terrestris* L.) ranging in mass from 0.3 to 8.9 g were obtained from Idaho (Loch Lomond Bait, San Rafael, CA, USA) and maintained in the dark at  $6^\circ\text{C}$  in Magic Worm Ranches using Magic Worm Bedding and Magic Worm

Food (Magic Products Inc., Amherst Junction, WI, USA). The mature earthworms reproduced in captivity, producing many cocoons. Six of these cocoons hatched, extending the size range down to 0.012 g. Seven size classes of earthworm were chosen for the scaling experiment on the basis of available earthworm sizes and available metal pipe and wire diameters (used to form the burrows), the goal being to maintain a ratio of burrow diameter to maximum resting earthworm diameter of 0.67. The target masses were 0.015, 0.050, 0.20, 0.40, 1.5, 4.5 and 8.0 g. Earthworm mass varied considerably between measurements as a result of the increase and/or decrease in gut contents and body hydration during the day of the experiment. The body mass of each individual was measured to two significant figures on a Mettler balance at least four times: once before measurement of burrowing force, once after measurement of burrowing force and on two other occasions within a few hours before or after the force measurements. The mean mass of each individual was calculated, and an attempt was made to keep this mean within 10% of the target mass (the mass of an individual earthworm could fluctuate by 20% during the day).

#### Muscle area

Muscle area was measured from digital images acquired in a previous study (Quillin, 1998). The digital images show sagittal sections of 20 earthworms (*Lumbricus terrestris*) ranging in size from 0.16 to 7.5 g. The anesthetized earthworms were frozen in 95% ethanol chilled to  $-78^\circ\text{C}$  using cubes of dry ice. After 2–3 s, the earthworms were removed from the ethanol and cut sagittally with a razor blade to produce two lateral halves (Fig. 4). Images of these halves were captured using a high-resolution color video camera (Sony CCD-Iris SSC-C374) affixed to a Wild Heerbrugg dissecting microscope (model M5A). A RasterOps frame-grabber board was used to select individual video frames. In the present study, I used NIH Image software (Version 1.59) on a Power Macintosh 7100/80 to measure the cross-sectional area of circumferential muscle and the longitudinal area of longitudinal muscle in segments 15 and 50 (Fig. 4). Transverse sections of earthworms were not available for the measurement of the cross-sectional areas of longitudinal muscle. I chose segments 15 and 50 for the measurement of muscle area because these are relatively dissimilar segments. Segment 15 lies in the widest region of the worm near the anterior end, where segments are relatively long and wide and exert large forces on the burrow wall. Segment 50 lies in the relatively homogeneous midregion of the worm, where segments are narrower and shorter and less forceful. Muscle area was measured to the nearest  $0.01 \text{ mm}^2$ .

#### Allometric analysis

The exponential relationship between each of the measured variables and body mass is often expressed by the function  $y=am_b^b$  (Huxley, 1932), where  $m_b$  is body mass (g),  $y$  is the variable of interest,  $a$  is a constant and  $b$  is the mass exponent. The exponential relationships were analyzed by linear

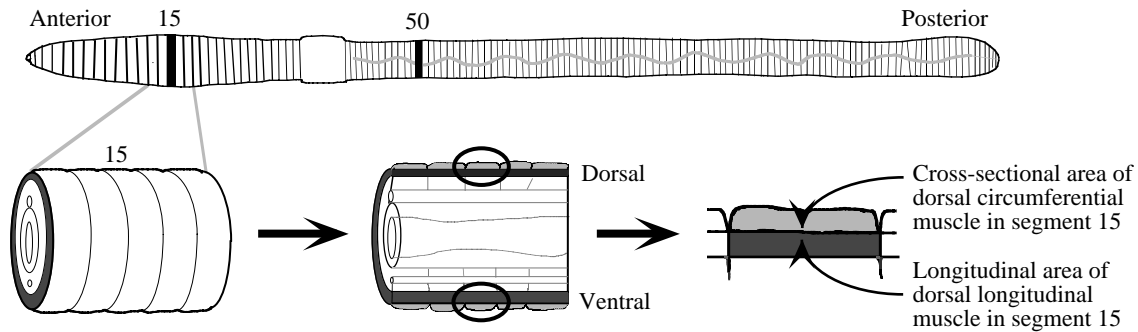


Fig. 4. Diagram illustrating the measurement of muscle area from sagittal sections made by Quillin (1998). The mean of the dorsal and ventral cross-sectional areas was calculated for circumferential muscle in segments 15 and 50. The mean of the dorsal and ventral longitudinal area was calculated for longitudinal muscle in segments 15 and 50. Transverse sections of earthworms were not available for the direct measurement of the cross-sectional area of longitudinal muscle.

regressions of log-transformed data, where the equation of the log-transformed allometric relationship is given by:

$$\log y = \log a + b \log m_b. \quad (1)$$

Ordinary regression analysis tends to underestimate the slope ( $b$ ) owing to the incorrect assumption that there is no measurement error in the  $x$  variate (Harvey and Pagel, 1991). The degree of underestimation of the slope may, however, be corrected using the reliability ratio ( $\kappa_{xx}$ ) as described by Fuller (1987),

$$\beta = b(\kappa_{xx})^{-1}, \quad (2)$$

where  $b$  is the attenuated slope as calculated by ordinary regression analysis and  $\beta$  is the corrected slope. For continuous variables, such as body mass, the reliability ratio is the correlation coefficient between two determinations of the same variable, one plotted on the  $x$  axis and one plotted on the  $y$  axis. I plotted the lowest body mass measurement against the highest body mass measurement for each of 25 individuals. Using the resulting correlation coefficient  $r$  ( $r = \kappa_{xx}$ ; Fuller, 1987), I corrected each slope to acquire the corrected slope  $\beta$ . The reliability ratio  $\kappa_{xx}$  calculated for body mass was 0.994; therefore, all regression slopes plotted as a function of body mass were increased by a factor of 1.006.

Student's  $t$  distribution was used to test the observed slopes against the hypothesized slopes, and analysis of covariance (ANCOVA) was used to compare observed slopes. All analyses were performed using Systat for Windows (Version 5) on a Power Macintosh 7100/80 computer.

## Results

### Individual force recordings

Individual earthworms of all sizes exhibited two distinct force-producing behaviors while burrowing through the open-burrow apparatus: (i) radial anchoring during forward peristaltic locomotion; and (ii) extreme radial expansion to enlarge the burrow, which required a pause in forward locomotion. The radial anchoring forces were represented by small sinusoidal fluctuations in the force record as the

earthworm passed through the cylindrical force transducer (Fig. 5A). These small forces were produced as waves of longitudinal muscle contraction (thus radial expansion) moved posteriorly along the length of the earthworm to establish purchase against the burrow wall for locomotion. The magnitude of the radial anchoring forces generally diminished along the length of the body. In contrast, the earthworm typically produced 1–3 spikes of force that were an order of magnitude greater than the anchoring forces. These forces occurred when the earthworms ceased crawling and contracted the longitudinal muscles of several segments simultaneously to enlarge forcefully the diameter of the burrow. These radial forces were exerted mostly by the relatively wide anteriormost 15–20 segments (out of a total of approximately 150 segments), regardless of the size of the earthworm. The maximum radial anchoring force ( $F_{R-anch}$ ) and the peak radial burrow-enlarging force ( $F_{R-enlg}$ ) were measured for each replicate for each individual.

The earthworms exerted both axial and radial pushes at the end of the dead-end burrow apparatus (Fig. 5B). The pattern of radial and axial force production varied both within and among individuals; sometimes the radial and axial force peaks were in phase, while at other times the radial and axial forces were out of phase. It is not a contradiction to have both forces peak at once; the radial force is produced by the segments within the radial force transducer only, while the axial force can be produced by the segments within or posterior to the radial and axial force transducers. Negative axial forces occurred either when the earthworm everted its pharynx and pulled back (as if to feed) or when suction resisted the removal of the earthworm's wet, conical 'nose' from the conical transducer. The maximum radial anchor force ( $F_{R-enlg}$ ) and the peak axial force ( $F_A$ ) were measured for each replicate for each individual.

### Scaling of burrowing forces

All burrowing forces increased as a function of body size, but significantly less than predicted by the null hypothesis. In the open-burrow apparatus, both the peak radial burrow-enlargement force ( $F_{R-enlg}$ ) and the radial anchoring force ( $F_{R-anch}$ ) scaled as  $m_b^{1/2}$  rather than the hypothesized  $m_b^{2/3}$

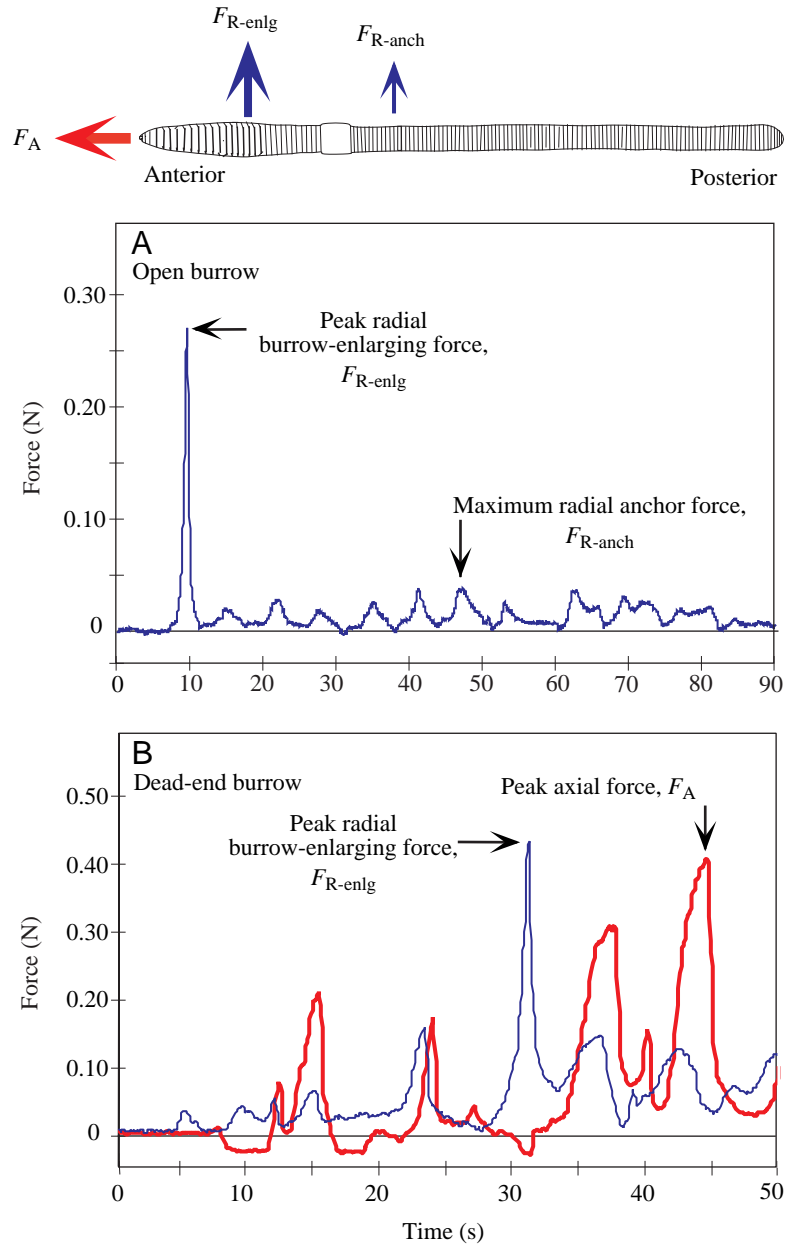


Fig. 5. Sample recordings of burrowing force as a function of time. (A) Radial force measured as an earthworm crawled through the open burrow. Peak radial burrow-enlarging forces ( $F_{R-enlg}$ ) occurred when the earthworm stopped forward progression and contracted the longitudinal muscles of several segments to expand radially, thereby enlarging the diameter of the burrow. Radial anchor forces ( $F_{R-anch}$ ) occurred during forward crawling when the segments were radially expanded for traction. (B) Simultaneous measurement of radial and axial ( $F_A$ ) forces when the earthworm attempted to penetrate a barrier at the end of the burrow.

(Fig. 6A). The burrow-enlargement force was an order of magnitude greater than the radial anchoring force for individuals of all sizes. In the dead-end burrow apparatus, both the peak radial burrow-enlargement force ( $F_{R-enlg}$ ) and the peak axial force ( $F_A$ ) also scaled as approximately  $m_b^{1/2}$  rather than the hypothesized  $m_b^{2/3}$  (Fig. 6B). On average, the radial and axial forces were comparable in magnitude. The regression statistics for force as a function of body mass are summarized in Table 1.

When the force data were normalized by weight, the results indicated that large earthworms produced less force per newton body weight than small earthworms – even more so than expected by the null hypothesis. All four regressions scaled as approximately  $m_b^{-1/2}$  rather than the hypothesized  $m_b^{-1/3}$  (Fig. 7A). Likewise, when the force data were divided by the

projected area of application of the force (the plane area of the force transducer perpendicular to the direction of force), the resulting pressures ( $P$ ) decreased as a function of body mass ( $P \propto m_b^{-1/5}$ ) (Fig. 7B), whereas the null hypothesis predicted that large and small geometrically similar earthworms would exert the same pressures on their burrows. The regression statistics for force/weight and pressure are summarized in Table 1.

#### Scaling of muscle area

All four measures of muscle area scaled with a mass exponent greater than the 0.67 expected by geometric similarity (Fig. 8).

#### Scaling of crawling kinematics

Earthworms of different sizes were nearly kinematically



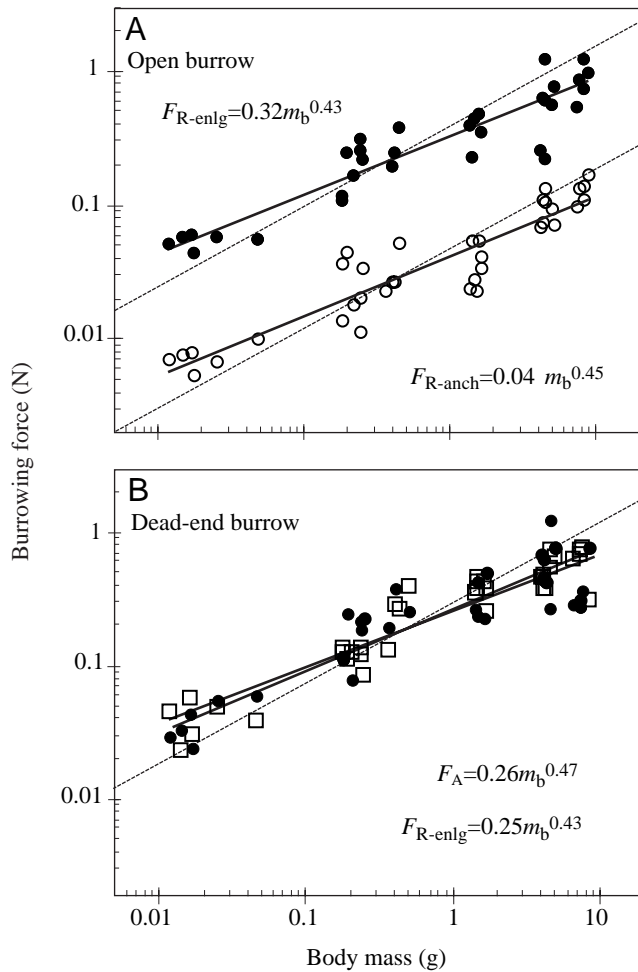


Fig. 6. Burrowing force plotted as a function of body mass ( $m_b$ ) on logarithmic coordinates. (A) Results of the open-burrow experiment. Radial burrow-enlarging forces  $F_{R-enlg}$  (●;  $N=33$ ) and anchor forces  $F_{R-anch}$  (○;  $N=36$ ) increased as a function of body mass, but less than expected by the null hypothesis (slope of dotted regression lines 0.67;  $P<0.001$ ). (B) Results of the dead-end burrow experiment. Radial burrow-enlarging forces (●;  $N=34$ ) and axial forces (□;  $N=37$ ) increased as a function of body mass, but less than expected by the null hypothesis (slope of dotted regression lines 0.67;  $P<0.001$ ). The regression statistics are listed in Table 1.

similar as they crawled through the open-burrow apparatus (Fig. 9). Relative crawling speed (body lengths  $s^{-1}$ ) varied within and among individuals, but overall did not differ as a function of body mass ( $t$ -test,  $P>0.10$ ). Similarly, relative stride length (stride length/body length) did not differ as a function of body size ( $P>0.10$ ). However, larger earthworms took fewer strides per second than small earthworms ( $P=0.007$ ) and used a slightly more elongated body posture (crawling body length/resting body length) than small earthworms ( $P<0.0001$ ). Burrowing earthworms crawl more slowly, take smaller steps and take fewer steps per time than earthworms crawling on a surface, but the scaling of these variables was similar on the surface and in burrows (Table 2).

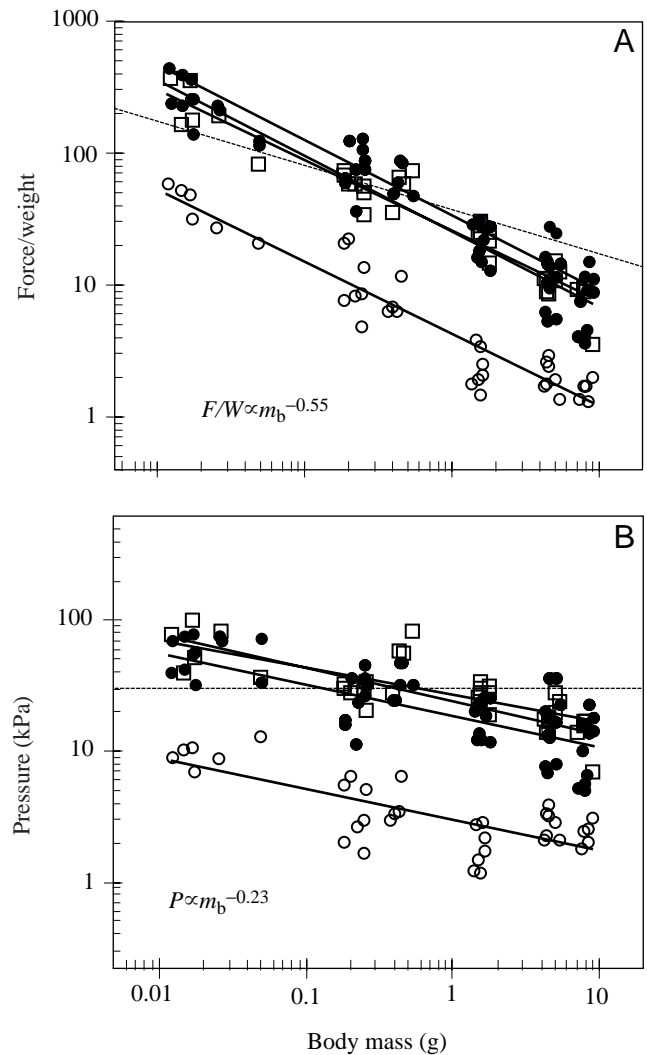


Fig. 7. (A) Burrowing force  $F$  normalized by body weight  $W$ , plotted as a function of body mass  $m_b$  on logarithmic coordinates. (B) Burrowing pressure  $P$ , the burrowing force normalized by area of application of force. The regression statistics are summarized in Table 1. ●, peak radial burrow-enlarging force; ○, peak radial anchoring force; □, peak axial force. The slopes of the hypothesized regression lines (dotted) are  $-0.33$  (A) and  $0$  (B).

## Discussion

### *The scaling of burrowing forces in earthworms*

The present study tested the null hypothesis that burrowing force is proportional to muscle cross-sectional area and therefore scales as  $m_b^{0.67}$ . This null hypothesis was rejected because pushing force scaled with a mass exponent of 0.45, which was significantly lower than the predicted mass exponent of 0.67. There are several factors that might be responsible for the observation that large worms push with lower force than predicted (or that small worms push with higher force than predicted): (i) muscle area might not increase isometrically with size; (ii) muscle stress might vary with body size; (iii) the mechanical advantage of the earthworm segments might change with body size; (iv) the burrowing kinematics of

Table 1. Summary of scaling relationships between burrowing forces and body mass

Variable $y$	Burrow	Symbol	$y=am_b^b$				
			$a$	$b$	95 % confidence intervals for $b$	Correlation coefficient	$P$
Force (N)	Open	$F_{R-enlg}$	0.32	0.43	$\pm 0.08$	0.86	<0.001
		$F_{R-anch}$	0.042	0.45	$\pm 0.04$	0.86	<0.001
	Dead-end	$F_{R-enlg}$	0.25	0.43	$\pm 0.09$	0.81	<0.001
		$F_A$	0.26	0.47	$\pm 0.06$	0.90	<0.001
Force/weight	Open	$F_{R-enlg}/W$	33.2	-0.58	$\pm 0.03$	0.92	<0.001
		$F_{R-anch}/W$	4.3	-0.56	$\pm 0.06$	0.90	<0.001
	Dead-end	$F_{R-enlg}/W$	25.6	-0.58	$\pm 0.04$	0.89	<0.001
		$F_A/W$	26.8	-0.54	$\pm 0.03$	0.93	<0.001
Pressure (kPa)	Open	$P_{R-enlg}$	14.5	-0.24	$\pm 0.05$	0.61	<0.001
		$P_{R-anch}$	1.9	-0.21	$\pm 0.16$	0.53	<0.001
	Dead-end	$P_{R-enlg}$	17.8	-0.24	$\pm 0.07$	0.52	<0.001
		$P_A$	25.8	-0.22	$\pm 0.08$	0.59	<0.001

$P$  values compare mass exponents ( $b$ ) with the null hypotheses:  $b=0.67$  for force,  $b=-0.33$  for force/weight and  $b=0$  for pressure.  $m_b$ , body mass (g); R-enlg, radial burrow-enlarging; R-anch, radial anchoring. A, axial; F, force; W, weight; P, pressure.

Table 2. Comparison of scaling results for burrowing (present study) and surface crawling (Quillin, 1999)

	Regression equation	$r^2$	$N$	$P^*$	Mass range (g)
Relative speed $U$ (body lengths $s^{-1}$ ) versus body mass (g)					
Burrowing	$U=0.007m_b^{-0.06}$	0.05	36	0.17	0.012–8.9
Surface crawling	$U=0.037m_b^{0.0006}$	<0.001	41	0.99	0.012–8.5
Relative stride lengths $l_s$ (body lengths) versus body mass (g)					
Burrowing	$l_s=0.04m_b^{0.03}$	0.04	36	0.26	0.012–8.9
Surface crawling	$l_s=0.15m_b^{0.07}$	0.10	41	0.04	0.012–8.5
Stride frequency $f_s$ ( $s^{-1}$ ) versus body mass (g)					
Burrowing	$f_s=0.16m_b^{-0.06}$	0.20	36	0.007	0.012–8.9
Surface crawling	$f_s=0.25m_b^{-0.07}$	0.37	41	0.00003	0.012–8.5

\* $t$ -test comparing the observed regression slope with a slope of zero.

small and large earthworms might be different; and (v) the resistance of the soil to deformation might depend upon the scale of the deformation.

#### The scaling of muscle area

The null hypothesis assumes that muscle cross-sectional area increases isometrically as a function of body size. Preliminary estimates of the scaling of circumferential and longitudinal muscle area as a function of body size (Fig. 8) indicate that muscle area increases at a greater rate than is expected by isometry. If muscle stress is constant, then a greater relative area of muscle in larger earthworms than smaller earthworms suggests that burrowing force would increase at a greater rate than predicted by isometry, not at a lesser rate as was observed in the present study. Thus, the allometric scaling of muscle area does not appear to account

for the observed trend in burrowing force as a function of body size.

#### The scaling of muscle stress

The null hypothesis assumes that muscle stress (the contractile force exerted per cross-sectional area of muscle) is independent of body size. The muscle stress of vertebrate striated muscle appears to change little as a function of body size when different species are compared and also when organisms of different ages within a species are compared (Close, 1972). The scaling of muscle stress in earthworm obliquely striated muscle is not known. However, since force decreases and relative muscle area increases as a function of body size, one testable hypothesis is that muscle stress decreases as a function of body size during earthworm ontogeny.

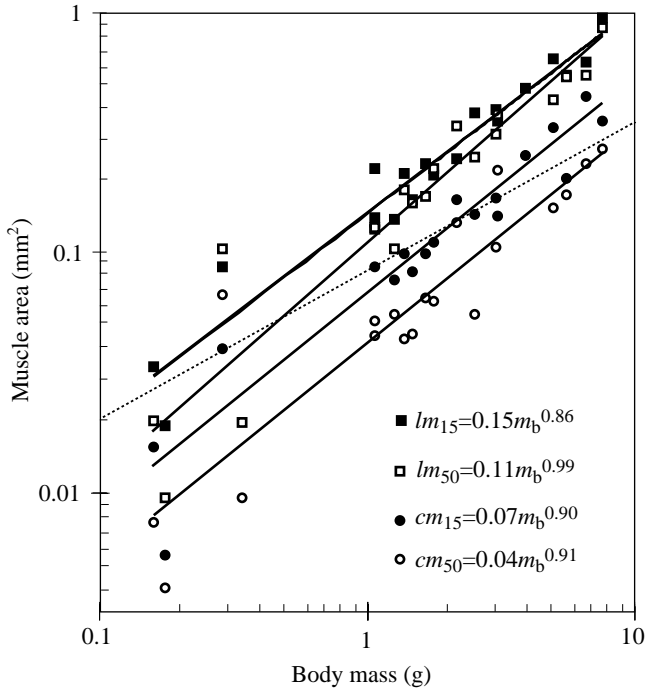


Fig. 8 Muscle area plotted as a function of body mass  $m_b$  on logarithmic coordinates ( $N=20$ ). The mean of the dorsal and ventral cross-sectional area for circumferential muscle ( $cm$ , see Fig. 4) is plotted for segments 15 ( $r^2=0.90$ ,  $P=0.006$ ) and 50 ( $r^2=0.81$ ,  $P=0.037$ ). The mean of the dorsal and ventral longitudinal area for longitudinal muscle ( $lm$ , see Fig. 4) is also plotted for segments 15 ( $r^2=0.94$ ,  $P=0.002$ ) and 50 ( $r^2=0.89$ ,  $P=0.001$ ). All slopes were significantly greater than expected by the null hypothesis (slope of dotted regression line 0.67).

#### The scaling of mechanical advantage

The muscle force transmitted to the environment will be proportional to the muscle stress only if the muscle cross-sectional area scales isometrically and the mechanical advantage of the system does not change as a function of body mass (because mechanical advantage =  $F_{out}/F_{in} = L_{in}/L_{out}$ , where  $F$  is the force and  $L$  is the lever arm; see Alexander et al., 1981; Biewener, 1989). Since mechanical advantage is determined by the geometry of the system, mechanical advantage is either implicitly or explicitly assumed to be constant as a function of body mass in geometrically similar organisms. Mechanical advantage has yet to be measured in hydrostatic skeletons that lack lever arms, but it is hypothesized that mechanical advantage is determined by the length-to-diameter ratio of constant-volume segments (see Chapman, 1950; Arthur, 1965; Kier and Smith, 1985). Earthworm segments grow with a constant length-to-diameter ratio (Quillin, 1998), suggesting that a change in mechanical advantage as a function of body mass does not account for the observed relationship between force and body mass. Although relative muscle area is not constant as a function of body mass, muscle area is a determinant of  $F_{in}$  rather than mechanical advantage *per se* (e.g. when the biceps of a bodybuilder atrophy, mechanical advantage stays constant, even though force production decreases).

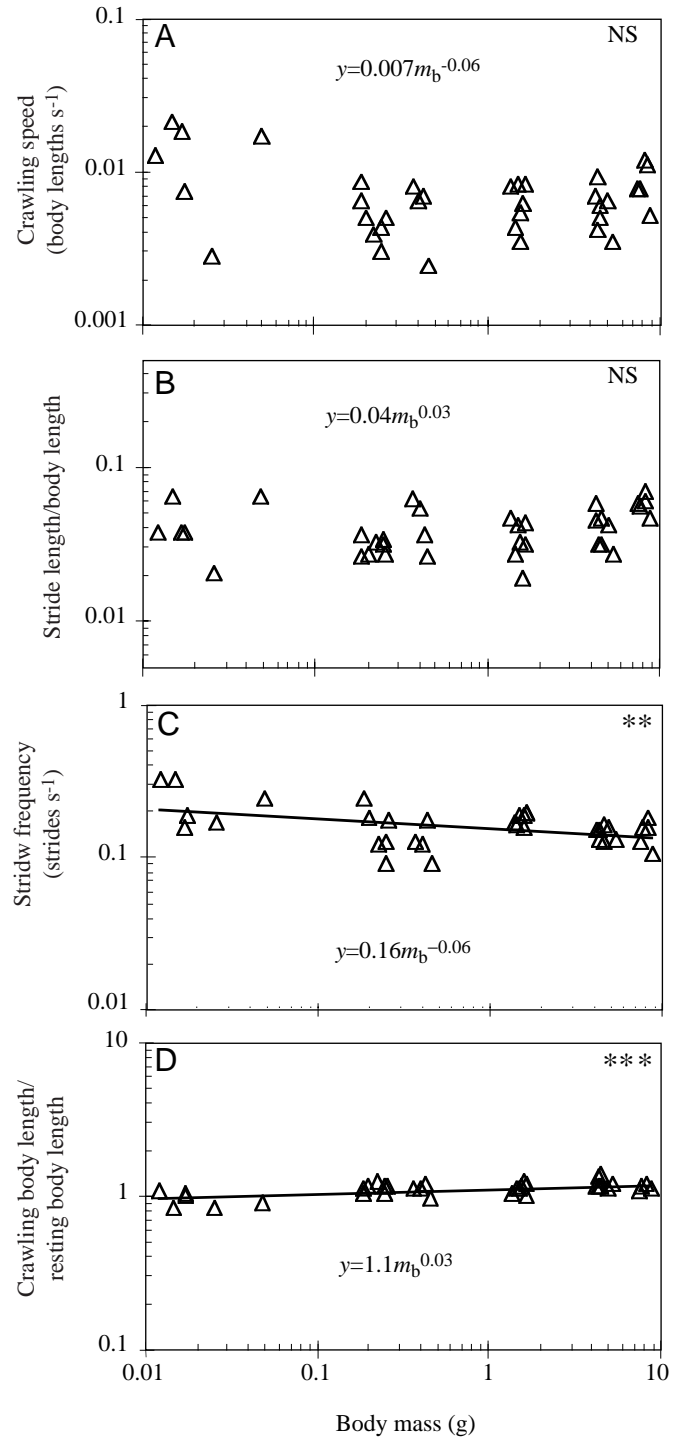


Fig. 9. Burrowing kinematics plotted as a function of body mass  $m_b$  on logarithmic coordinates ( $N=36$ ). Kinematics were observed through the Plexiglas lid of the open burrow apparatus. (A) Crawling speed, normalized to body length, was constant as a function of body mass ( $r^2=0.05$ ;  $P=0.17$ ). (B) Stride length, normalized to body length, was also constant as a function of body mass ( $r^2=0.04$ ;  $P>0.10$ ). (C) Stride frequency decreased slightly as a function of body mass ( $r^2=0.20$ ;  $P=0.007$ ). (D) The length of the crawling earthworm, normalized to resting length, increased significantly as a function of body mass ( $r^2=0.40$ ;  $P<0.0001$ ). \*\* $P<0.05$ ; \*\*\* $P<0.0001$ ; NS, not significant.

*The scaling of burrowing kinematics*

Quillin (1999) measured the scaling of kinematics of earthworms crawling on a surface and concluded that earthworms (0.012–8.5 g) were essentially kinematically similar. The kinematics of burrowing earthworms appear to scale similarly (Table 2), although the absolute magnitudes of crawling speed, stride length and stride frequency are higher in surface crawling than in burrowing. One statistically significant result was that larger earthworms tend to burrow with a more elongated body than smaller earthworms. For example, a 8.9 g worm burrows with a ratio of burrowing body length to resting body length of 1.13, whereas a 0.15 g worm burrows with a ratio of burrowing body length to resting body length of 0.83, a difference of 35%. Obliquely striated muscle tends to have a flatter force/extension curve than cross-striated muscle (Full, 1997) such that maximum force is not as highly dependent upon muscle strain. The length/tension curve for earthworm muscle generated by Hidaka et al. (1969) supports this generalization. However, their data suggest that a 35% change in muscle length may result in a comparable change in muscle tension. Thus, one testable hypothesis is that larger earthworms exert lower forces than expected because their muscles are working at a higher strain, where the ability to exert force is diminished.

*The scaling of soil properties*

Pores in soils can range in size over several orders of magnitude and generally constitute 30–60% of the volume of soil (Marshall and Holmes, 1988). Since pores are one important determinant of the mechanical properties of soil, the properties of soil are different at different scales (soil scientists use penetrometers of different sizes to measure the strength of soil at different scales; Campbell and O'Sullivan, 1991). Although either metal or Plexiglas served as the interface between the earthworms and the force transducers in the

present experiment, the scaling of soil properties may have had an indirect effect on the forces that the earthworms could exert (e.g. by affecting how well worms of different sizes could anchor in the soil burrow). This hypothesis remains to be tested and has important ecological implications.

*Maximum pushing pressures in Lumbricus terrestris compared with values in the literature*

A recent study reports maximum axial and radial pressures exerted by *L. terrestris* in Plexiglas tubes (Keudel and Schrader, 1999). The mean axial pressure of 51 individuals (unknown size) was  $46.26 \pm 2.95$  kPa (mean  $\pm$  S.E.M.) while the mean radial pressure of nine individuals (unknown size) was  $72.62 \pm 12.46$  kPa (mean  $\pm$  S.E.M.). The values of Keudel and Schrader (1999) are higher than those reported in the present study (Fig. 7; assuming that their individuals were large juveniles and/or adults). This difference may be due to the condition of the study animals (e.g. level of hydration) or to the method of force measurement (e.g. ratio of worm diameter to diameter of force transducer). Keudel and Schrader (1999) also observed that radial pressures were greater in magnitude than axial pressures, whereas the present data reported no difference. It is not clear whether the present study underestimated radial pressure, or whether Keudel and Schrader (1999) underestimated axial pressure. One methodological difference between the two studies concerns the shape of the depression against which the earthworms pushed axially. Keudel and Schrader (1999) used a rectilinear tip, whereas I used a conical tip. Since the prostomium of earthworms is very sensitive, this methodological difference may have had an effect on pushing pressure.

*Maximum forces in earthworms compared with other animals*

Soft-bodied organisms with hydrostatic skeletons generally

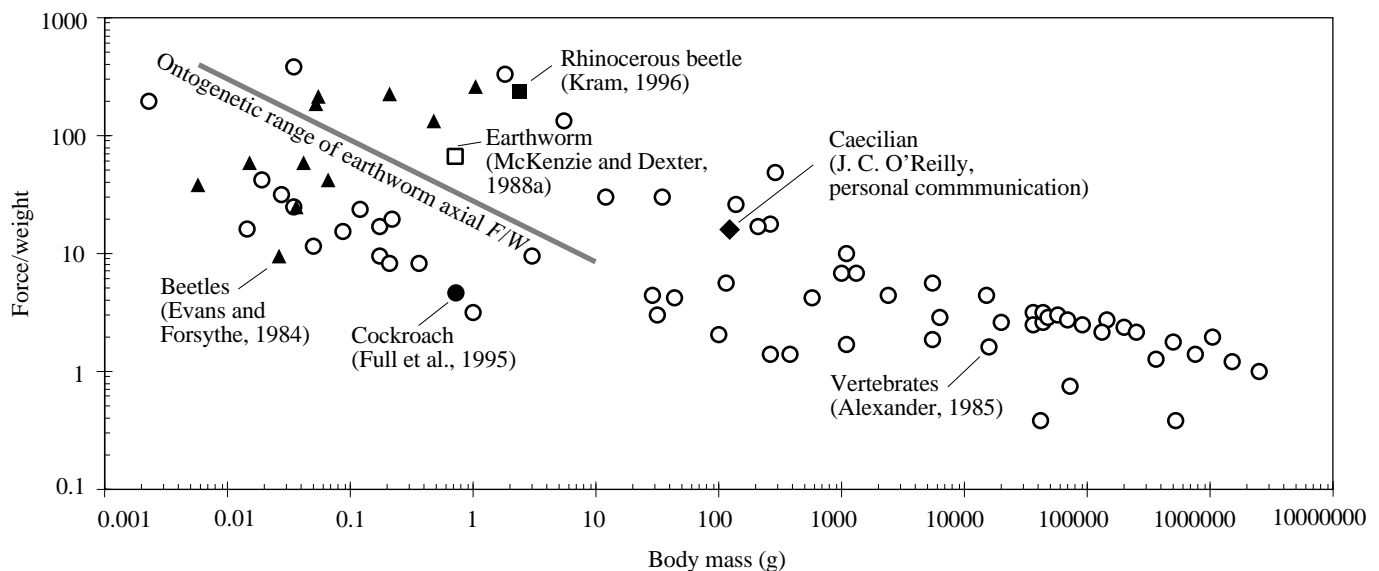


Fig. 10. Force/weight ( $F/W$ ) comparison for several species. See Fig. 7 for the data that produced the ontogenetic regression line for earthworm axial force/weight. The remaining data points are for adult organisms taken from the literature.



appear to move more slowly than their counterparts with rigid skeletons, with some notable exceptions (Maitland, 1992; Kier and Van Leeuwen, 1997; Brackenbury, 1997). Also, the cost of transport of organisms with hydrostatic skeletons appears to be higher than for arthropods of the same body mass (Casey, 1991; Berrigan and Lighton, 1993). How do forces exerted on the environment compare? The force/weight exerted by adult earthworms is intermediate compared with the force/weight exerted by wedging ground beetles (Evans 1977; Evans and Forsythe, 1984), righting cockroaches (Full et al., 1995) and load-carrying rhinoceros beetles (Kram, 1996) of similar size (Fig. 10). Compared with other hydrostatic skeletons, the burrowing forces of adult *Lumbricus terrestris* were smaller than those exerted by burrowing caecilians (legless amphibians) of twice the length (mass not provided, O'Reilly et al., 1997) and comparable in magnitude with the forces measured in a smaller earthworm, *Aporrectodea rosea* (McKenzie and Dexter, 1988a,b). Maximum forces vary widely, even among closely related species (Evans and Forsythe, 1984; Keudel and Schrader, 1999). Overall, it appears that force-generating ability depends upon the subtle mechanical design and ecological strategy of the organism (e.g. fast crawler *versus* forceful burrower), not whether the skeleton is hydrostatic or rigid.

Most scaling studies have focused on comparisons of adults of different species (e.g. Evans, 1977; Alexander, 1985; Biewener, 1989) rather than an ontogenetic size range. Of the ontogenetic studies, the measurements tend to be of performance variables such as sprint speed (Garland, 1985; Marsh, 1988), maximum jump distance (Queathem, 1991) and jump acceleration (Carrier, 1995). Inferences about forces can be made from these studies but, overall, there are few data for the comparison of ontogenetic force production in hydrostatic skeletons *versus* rigid skeletons.

#### Dynamic similarity

For two organisms of different sizes to be dynamically similar, the ratios of linear dimensions, velocities and forces must be the same (Daugherty and Franzini, 1997). Quillin (1998) determined that *Lumbricus terrestris* grows with geometric similarity, satisfying the first requirement for dynamic similarity. Quillin (1999) observed that *L. terrestris* maintains kinematic similarity while crawling on a surface, and the present study indicates kinematic similarity in burrowing as well, satisfying the second requirement of dynamic similarity. The present study has demonstrated that the ratios of one burrowing force (e.g. radial) to another burrowing force (e.g. axial) remain constant as earthworms grow. However, the ratio of burrowing force to gravitational force (weight) decreases as a function of body size. Burrowing force and weight are only two components of the total balance of forces on the burrowing earthworm (for the equation of motion of crawling earthworms, see Keller and Falkovitz, 1983), but the data on these two forces seem to suggest that earthworms do not possess dynamic similarity in burrowing.

In summary, larger earthworms exert greater absolute burrowing forces than smaller earthworms, but the difference

is less than expected on the basis of traditional scaling theory derived for jointed skeletons. Testable hypotheses explaining this discrepancy include: (i) that muscle stress decreases during ontogeny, (ii) that larger earthworms exert smaller forces than expected because their muscles work at larger strains, and (iii) that the scaling of soil properties affects the scaling of burrowing forces in earthworms. Earthworm forces fall within the range of forces observed for other animals of comparable mass, but there are few ontogenetic force regressions in other studies to provide comparison and contrast to the present study.

This research was supported by a NSF Graduate Research Fellowship, a University of California at Berkeley Frankhauser Fellowship and a Sigma Xi Grants-in-Aid of Research to K.Q. by NSF Grant 92-20525 to M. Koehl and R. Keller and by ONR Grant 444095-23068 to M. Koehl. I am grateful to M. Koehl for helpful discussion and advice, to G. Wang for assistance with the force experiments and to R. Amundsen for his help in classifying the soil. I am also grateful to M. Koehl and R. Kram for critical reading of this manuscript and to the members of the biomechanics group at the University of California at Berkeley for their insights and suggestions.

#### References

- Alexander, R. McN. (1983). *Animal Mechanics*. Second edition. Oxford: Blackwell Scientific Publications.
- Alexander, R. McN. (1985). The maximum forces exerted by animals. *J. Exp. Biol.* **115**, 231–238.
- Alexander, R. McN., Jayes, A. S., Maloiy, G. M. O. and Wathuta, E. M. (1981). Allometry of the leg muscles of mammals. *J. Zool., Lond.* **201**, 135–152.
- Arthur, D. R. (1965). Form and function in the interpretation of feeding in lumbricid worms. *Viewpoints Biol.* **4**, 204–251.
- Berrigan, D. and Lighton, J. R. B. (1993). Bioenergetic and kinematic consequences of limblessness in larval Diptera. *J. Exp. Biol.* **179**, 245–259.
- Biewener, A. A. (1989). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**, 45–48.
- Brackenbury, J. (1997). Caterpillar kinematics. *Nature* **390**, 453.
- Calder, W. A. (1984). *Size, Function and Life History*. Cambridge, MA: Harvard University Press.
- Campbell, D. J. and O'Sullivan, M. F. (1991). The cone penetrometer in relation to trafficability, compaction and tillage. In *Soil Analysis: Physical Methods* (ed. K. A. Smith and C. E. Mullins), pp. 399–429. New York: Marcel Dekker, Inc.
- Carrier, D. R. (1995). Ontogeny of jumping performance in the black-tailed jack rabbit (*Lepus californicus*). *Zoology (Jena)* **98**, 309–313.
- Carrier, D. R. (1996). Ontogenetic limits on locomotor performance. *Physiol. Zool.* **69**, 467–488.
- Casey, T. M. (1991). Energetics of caterpillar locomotion: biomechanical constraints of a hydraulic skeleton. *Science* **252**, 112–113.
- Chapman, G. (1950). On the movement of worms. *J. Exp. Biol.* **27**, 29–39.
- Chapman, G. (1958). The hydrostatic skeleton in the invertebrates. *Biol. Rev.* **33**, 338–371.

- Chapman, G.** (1975). Versatility of hydraulic systems. *J. Exp. Zool.* **194**, 249–270.
- Clark, R. B.** (1964). *Dynamics of Metazoan Evolution*. Oxford: Clarendon Press.
- Close, R. I.** (1972). Dynamic properties of mammalian skeletal muscles. *Physiol. Rev.* **52**, 129–197.
- Currey, J. D.** (1970). *Animal Skeletons*. New York: St Martin Press.
- Darwin, C.** (1881). *The Formation of Vegetable Mould through the Action of Worms, with Observations of their Habits*. London: Murray.
- Daugherty, R. L. and Franzini, J. B.** (1997). *Fluid Mechanics with Engineering Applications*. Seventh edition. New York: McGraw-Hill.
- Edwards, C. A. and Bohlen, P. J.** (1996). *Biology and Ecology of Earthworms*. New York: Chapman & Hall.
- Elder, H. Y. and Trueman, E. R.** (1980). *Aspects of Animal Movement*. Cambridge: Cambridge University Press.
- Evans, A. C.** (1947). A method of studying the burrowing activities of earthworms. *Annu. Mag. Nat. Hist.* **14**, 643–650.
- Evans, M. E. G.** (1977). Locomotion in the Coleoptera Adephega, especially Carabidae. *J. Zool., Lond.* **181**, 189–226.
- Evans, M. E. G. and Forsythe, T. G.** (1984). A comparison of adaptations to running, pushing and burrowing in some adult Coleoptera: especially Carabidae. *J. Zool., Lond.* **202**, 513–534.
- Full, R. J.** (1997). Invertebrate locomotor systems. In *The Handbook of Comparative Physiology* (ed. W. Dantzler), pp. 853–930. Oxford: Oxford University Press.
- Full, R. J., Yamauchi, A. and Jindrich, D. L.** (1995). Maximum single leg force production: cockroaches righting on photoelastic gelatin. *J. Exp. Biol.* **198**, 2441–2452.
- Fuller, W. A.** (1987). *Measurement of Error Models*. New York: John Wiley & Sons.
- Garland, T., Jr** (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolorus nuchalis*. *J. Zool., Lond. A* **207**, 425–439.
- Gray, J. and Lissmann, H. W.** (1938). Studies in locomotion. VII. Locomotory reflexes in the earthworm. *J. Exp. Biol.* **15**, 506–517.
- Harvey, P. H. and Pagel, M. D.** (1991). *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Heffernan, J. M. and Wainwright, S. A.** (1974). Locomotion of the holothurian *Euapta lappa* and redefinition of peristalsis. *Biol. Bull.* **147**, 95–104.
- Hidaka, T., Kuriyama, H. and Yamamoto, T.** (1969). The mechanical properties of the longitudinal muscle in the earthworm. *J. Exp. Biol.* **50**, 431–443.
- Hughes, P. M., Rayner, J. M. V. and Jones, G.** (1995). Ontogeny of ‘true’ flight and other aspects of growth in the bat *Pipistrellus pipistrellus*. *J. Zool., Lond.* **235**, 291–318.
- Huxley, J. S.** (1932). *Problems of Relative Growth*. Oxford: Oxford University Press.
- Katz, S. L. and Gosline, J. M.** (1992). Ontogenetic scaling and mechanical behavior of the tibiae of the African desert locust (*Schistocerca gregaria*). *J. Exp. Biol.* **168**, 125–150.
- Keller, J. B. and Falkovitz, M. S.** (1983). Crawling of worms. *J. Theor. Biol.* **104**, 417–442.
- Keudel, M. and Schrader, S.** (1999). Axial and radial pressures exerted by earthworms of different ecological groups. *Biol. Fert. Soils* **29**, 262–269.
- Kier, W. M. and Smith, K. K.** (1985). Tongues, tentacles and trunks: The biomechanics of movement in muscular hydrostats. *J. Linn. Soc.* **83**, 307–324.
- Kier, W. M. and Van Leeuwen, J. L.** (1997). A kinematic analysis of tentacle extension in the squid *Loligo pealei*. *J. Exp. Biol.* **200**, 41–53.
- Kram, R.** (1996). Inexpensive load carrying by rhinoceros beetles. *J. Exp. Biol.* **199**, 609–612.
- Lakhani, K. H. and Satchell, J. E.** (1970). Production by *Lumbricus terrestris* (L.). *J. Anim. Ecol.* **39**, 473–492.
- Maitland, D. P.** (1992). Locomotion by jumping in the Mediterranean fruit-fly larva *Ceratitis capitata*. *Nature* **355**, 159–160.
- Manton, S. M.** (1965). The evolution of arthropodal locomotory mechanisms. Part B. Functional requirements and body design in Chilopoda together with a comparative account of their skeleto-muscular systems and an appendix on a comparison between burrowing forces of annelids and chilopods and its bearing upon the evolution of the arthropodal haemocoel. *J. Linn. Soc.* **45**, 251–361.
- Marsh, R. L.** (1988). Ontogenesis of contractile properties of skeletal muscle and sprint performance in the lizard *Dipsosaurus dorsalis*. *J. Exp. Biol.* **137**, 119–139.
- Marshall, T. J. and Holmes, J. W.** (1988). *Soil Physics*. Second edition. Cambridge: Cambridge University Press.
- McKenzie, B. M. and Dexter, A. R.** (1988a). Axial pressures generated by the earthworm *Aporrectodea rosea*. *Biol. Fert. Soils* **5**, 323–327.
- McKenzie, B. M. and Dexter, A. R.** (1988b). Radial pressures generated by the earthworm *Aporrectodea rosea*. *Biol. Fert. Soils* **5**, 328–332.
- Minnich, J.** (1977). *The Earthworm Book*. Emmaus, PA: Rodale Press.
- Newell, G. E.** (1950). The role of the coelomic fluid in the movements of earthworms. *J. Exp. Biol.* **27**, 110–121.
- O’Reilly, J. C., Ritter, D. A. and Carrier, D. R.** (1997). Hydrostatic locomotion in a limbless tetrapod. *Nature* **386**, 269–271.
- Peters, R. H.** (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- Queathem, E.** (1991). The ontogeny of grasshopper jumping performance. *J. Insect Physiol.* **37**, 129–138.
- Quillin, K. J.** (1998). Ontogenetic scaling of hydrostatic skeletons: geometric, static stress and dynamic stress scaling of the earthworm *Lumbricus terrestris*. *J. Exp. Biol.* **201**, 1871–1883.
- Quillin, K. J.** (1999). Ontogenetic scaling of peristaltic crawling in the earthworm *Lumbricus terrestris*. *J. Exp. Biol.* **202**, 661–674.
- Rushton, S. P.** (1986). The effects of soil compaction on *Lumbricus terrestris* and its possible implications for populations on land reclaimed from open-coal mining. *Pedobiologia* **29**, 85–90.
- Seymour, M. K.** (1970). Skeletons of *Lumbricus terrestris* L. and *Arenicola marina* (L.). *Nature* **228**, 383–385.
- Thompson, D. W.** (1917). *On Growth and Form*. Cambridge: Cambridge University Press.
- Trueman, E. R.** (1975). *Locomotion in Soft-bodied Animals*. London: Edward Arnold.
- Trueman, E. R. and Jones, H. D.** (1977). Crawling and burrowing. In *Mechanics of Energetics and Locomotion* (ed. R. McN. Alexander and G. Goldspink), pp. 204–221. London: Chapman & Hall.
- Wainwright, S. A.** (1988). *Axis and Circumference*. Cambridge, MA: Harvard University Press.
- Werner, E. E. and Gilliam, J. F.** (1984). The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15**, 393–425.
- Whiteley, G. M., Utomo, W. H. and Dexter, A. R.** (1981). A comparison of penetrometer pressures and the pressures exerted by roots. *Plant and Soil* **61**, 351–363.