

KINEMATIC SCALING OF LOCOMOTION BY HYDROSTATIC ANIMALS: ONTOGENY OF PERISTALTIC CRAWLING BY THE EARTHWORM *LUMBRICUS TERRESTRIS*

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Accepted 22 December 1998; published on WWW 17 February 1999

Summary

This study examined the relationship between ontogenetic increase in body size and the kinematics of peristaltic locomotion by the earthworm *Lumbricus terrestris*, a soft-bodied organism supported by a hydrostatic skeleton. Whereas the motions of most vertebrates and arthropods are based primarily on the changes in the joint angles between rigid body segments, the motions of soft-bodied organisms with hydrostatic skeletons are based primarily on the changes in dimensions of the deformable body segments themselves. The overall kinematics of peristaltic crawling and the dynamic shape changes of individual earthworm segments were measured for individuals ranging in body mass (m_b) by almost three orders of magnitude (0.012–8.5 g). Preferred crawling speed varied both within and among individuals: earthworms crawled faster primarily by taking longer strides, but also by taking more strides per unit time and by decreasing duty factor. On average, larger worms crawled at a greater absolute speed than smaller worms ($U \propto m_b^{0.33}$) and did so by taking slightly longer strides

($l \propto m_b^{0.41}$, where l is stride length) than expected by geometric similarity, using slightly lower stride frequencies ($f \propto m_b^{-0.07}$) and the same duty factor ($df \propto m_b^{-0.03}$). Circumferential and longitudinal body wall strains were generally independent of body mass, while strain rates changed little as a function of body mass. Given the extent of kinematic variation within and among earthworms, the crawling of earthworms of different sizes can be considered to show kinematic similarity when the kinematic variables are normalized by body length. Since the motions of peristaltic organisms are based primarily on changes in the dimensions of the deformable body wall, the scaling of the material properties of the body wall is probably an especially important determinant of the scaling of the kinematics of locomotion.

Key words: biomechanics, scaling, size, hydrostatic skeleton, earthworm, ontogeny, locomotion, peristalsis, *Lumbricus terrestris*.

Introduction

The size of an animal is generally considered to be an important determinant of its locomotory behavior. For example, larger animals tend to have slower stride frequencies, wingbeat frequencies and tailbeat frequencies than smaller animals (for reviews, see Calder, 1984; McMahon and Bonner, 1983; Full, 1997). While a majority of the scaling studies on locomotion have compared adults of different species (mostly vertebrates and arthropods; e.g. McMahon, 1975; Heglund and Taylor, 1988; Full, 1997), only a few studies have examined the effect of ontogenetic increase in body size on locomotion, and these too have focused on organisms with jointed, lever-like skeletons (e.g. Marsh, 1988; Queathem, 1991; Carrier, 1995; Schepens et al., 1998). The purpose of the present study was to examine the ontogenetic scaling of locomotion by a hydrostatic skeleton.

Hydrostatic skeletons perform the same mechanical functions as the jointed skeletons of vertebrates and arthropods: they maintain posture, re-extend shortened

muscles (enabling reversible shape changes) and transmit forces from muscles to the environment (enabling feeding and locomotion) (for reviews, see Chapman, 1958; Currey, 1970; Trueman, 1975; Wainwright, 1988). Nonetheless, hydrostatic skeletons and jointed skeletons are qualitatively distinct as a result of differences in their mechanical design. Hydrostatic skeletons are generally composed of a deformable body wall in tension surrounding fluid and/or soft tissues under compression. Since fluid is incompressible, it becomes pressurized; it is this pressure, rather than a rigid lever, that enables antagonism of muscles and stiffening of the organism (as described, for example, by Wainwright, 1988).

Many soft-bodied crawlers and burrowers locomote using peristalsis (e.g. earthworms, sea cucumbers, caterpillars, snails; for reviews, see Alexander, 1983; Trueman, 1975; Elder and Trueman, 1980). Peristalsis occurs when waves of alternating contraction and relaxation of muscles move along the length of a radially flexible tube (Heffernan and

Wainwright, 1974). Typically, the radially expanded regions anchor the organisms to the substratum while the radially contracted regions advance over the substratum. Thus, the motions in hydrostats are based primarily on changes in the dimensions of the body segments themselves, rather than on changes in the joint angles between rigid body segments.

The most commonly used null hypothesis for kinematic scaling is the geometric similarity model of Hill (1950) which assumes (1) that geometric similarity is maintained among the animals to be compared, (2) that muscle stress (tension per cross-sectional area) is constant as a function of body size, and (3) that the work per stroke that a muscle can perform is proportional to muscle weight. Hill's model predicts that stride length is proportional to leg length and that stride frequency is inversely proportional to leg length, resulting in maximum speeds that are constant as a function of body size. Many empirical studies have tested Hill's (1950) model (e.g. Heglund et al., 1974; Pennycuik, 1975) and have generally observed that larger animals run more rapidly than smaller animals and that stride frequency decreases in proportion to the inverse square root of leg length rather than in proportion to the inverse of leg length. Alternative models have been proposed to account for the discrepancies between Hill's (1950) model and the data (e.g. static stress model and elastic similarity model; McMahan, 1973, 1975), allowing for changes in body geometry as a function of increasing size as well as changes in the scaling of muscle contractile properties (e.g. Marsh, 1988).

Overall, the existing scaling hypotheses do not necessarily provide a good framework for the study of scaling in hydrostatic skeletons. Unlike the case for jointed skeletons, the geometric similarity and static stress similarity models are not mutually exclusive for hydrostatic skeletons (Quillin, 1998). Also, while progress has been made in understanding the contractile properties and scaling of the cross-striated muscle of jointed skeletons, little is known about the scaling of the obliquely striated muscles found in most hydrostatic skeletons. Furthermore, the kinematics of peristalsis may be determined by neural control of the speed of the peristaltic wave along the body (e.g. Gray and Lissmann, 1938; Delcomyn, 1980). Since the scaling of neural mechanisms is poorly understood, the *a priori* prediction of the scaling of stride frequencies in hydrostats is difficult and may vary among organisms.

The goal of the present study was to use the ontogeny of the earthworm (*Lumbricus terrestris*) as a case study to examine the relationship between body size and the kinematics of peristaltic locomotion by a hydrostatic skeleton. *L. terrestris* provided a convenient experimental system because it was already known to grow isometrically and to maintain static and dynamic stress similarity during crawling (Quillin, 1998). The experimental approach was to measure the standard kinematic variables of locomotion (e.g. speed, stride length, stride frequency) and the shape changes and strain rates of individual segments over an ontogenetic size range. The results were then compared with a sampling of data for jointed skeletons to

outline some of the important similarities and differences between the scaling of kinematics in peristaltic hydrostatic skeletons *versus* limbed, jointed skeletons.

Materials and methods

Experimental animals

Earthworms *Lumbricus terrestris* L. provide an excellent experimental system to address the scaling of peristaltic locomotion in hydrostatic skeletons. These animals are relatively easy to maintain in the laboratory and have been studied prolifically because of their ecological and agricultural importance. *L. terrestris* grow 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 scaling. Furthermore, *L. terrestris* grow isometrically (Quillin, 1998), facilitating comparison of kinematics.

The present study focuses on the earthworms during their most observed and understood activity – surface crawling – although peristalsis is also used by this species to burrow. Most earthworm species are either geophagous (earth-eaters) or surface-feeders, but *L. terrestris* is both. As the common name 'night crawlers' suggests, earthworms feed on the surface at night, drawing leaves and other organic materials into their semi-permanent burrows and digesting them within (Darwin, 1881; Arthur, 1965; Satchell, 1967). The surface-crawling habit of *L. terrestris* is reflected in its morphology. For example, the bristle-like setae that provide traction for the radially expanded segments are present only on the ventral and lateral surfaces rather than uniformly around the circumference of the worm, as found in purely geophagous earthworms (Stephenson, 1930).

As earthworms crawl forward, waves of circumferential and longitudinal muscle contractions pass posteriorly along their constant-volume body segments, forming retrograde waves (waves that move in the opposite direction to locomotion; Gray and Lissmann, 1938; for a review, see Trueman, 1975). When the longitudinal muscles of a segment contract, the segment becomes short (along the anterior–posterior axis) and wide, and the setae extend so that the segment can anchor against the substratum. When the circumferential muscles of a segment contract, the segment becomes long and thin and the setae retract so that the segment can advance over the substratum. These waves of muscle contraction result in a pulsatile form of locomotion, as described for adult earthworms by many authors (e.g. Gray and Lissmann, 1938; Chapman, 1950; Keller and Falkovitz, 1983).

A complete ontogenetic size range of earthworms (0.012–8.5 g) was maintained at 6 °C in Magic Worm Ranches using Magic Worm Bedding and Magic Worm Food (Magic Products Inc., Amherst Junction, WI, USA). The 0.3–8.5 g size range was obtained from Idaho (Loch Lomond Bait, San Rafael, CA, USA). Several adults reproduced in captivity, producing 0.012–0.03 g hatchlings. The intermediate size range (0.03–0.3 g) originated from Canada (Berkeley Bait, Berkeley,

CA, USA) but was maintained in the same Magic Worm Ranches as the earthworms from Idaho.

Crawling kinematics

The kinematics of crawling of earthworms and of other peristaltic hydrostats can be described by the same variables that describe the kinematics of legged locomotion. One cycle of peristalsis is equivalent to one stride (which, for a human equals one complete cycle of a leg, or two steps). The stride length of a hydrostat is the distance traveled during one cycle of peristalsis. The stride period is the duration of one stride, which for an earthworm can be divided into two parts: the

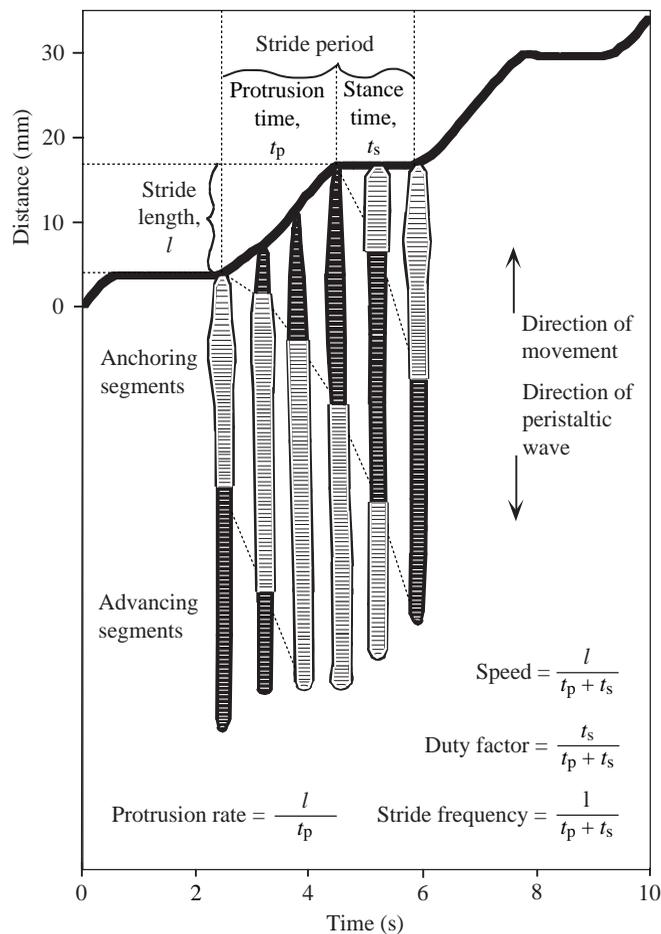


Fig. 1. Definitions of kinematic variables used to describe peristaltic crawling by earthworms. The continuous trace shows the distance traveled by the anteriormost segment of the earthworm as a function of time. One complete stride begins at the initiation of protrusion by the anteriormost segment and ends just prior to the initiation of a subsequent protrusion. Usually only one wave each of circumferential and longitudinal muscle contraction passes posteriorly (indicated by hatched lines) along the length of the earthworm during one stride. Longitudinal muscles are contracted in the anchoring segments, while circumferential muscles are contracted in the advancing segments. Crawling speed, duty factor, stride frequency and protrusion rate are all calculated from three independent variables: stride length (l), protrusion time (t_p) and stance time (t_s).

protrusion time when the segments are advancing over the substratum, and the stance time when the segments are anchored against the substratum. Since *L. terrestris* has approximately 145 segments which advance and anchor at different times during the stride, the present study focused on the protrusion time and stance time of the anteriormost segment for simplicity. All other kinematic variables, such as crawling speed, stride frequency and duty factor, were calculated from the three independent variables: stride length, protrusion time and stance time, as illustrated in Fig. 1.

The kinematics of earthworms crawling was measured at the earthworms' preferred crawling speeds; earthworms do not perform well on treadmills and there is no convenient 'physiologically equivalent' speed such as the speed of the trot-gallop transition as used in vertebrate studies (e.g. Heglund and Taylor, 1988). Earthworms were placed in a moist fabric trough at 22 °C and filmed at 60 Hz using a Sony HandyCam (CCD-TR101) connected to a Panasonic (AG-6300) VHS video recorder. A time/date generator (Panasonic WJ-810) marked each frame with the time in hundredths of a second. The trough was used to encourage the earthworms to crawl in a straight line, and the width of the trough was adjusted to the width of each worm to maximize traction by the ventral and lateral setae and therefore to minimize backslipping and lateral undulation. When traction was sufficient, neither backslipping nor lateral undulation occurred; however, to eliminate the small effect of backslipping when it did occur, stride length was measured from the point where the anteriormost segment began to extend forward to the point where maximum distance was achieved before backslipping (Fig. 1). Stride length was measured from the video recordings to the nearest 1 mm for all but the smallest worms, for which stride length was measured to the nearest 0.1 mm. Stride period was measured to the nearest 0.1 s from the frame in which the anteriormost segment began to elongate in one stride to the frame in which it began to elongate in the next. Mean speed was calculated by dividing mean stride length by mean stride period for 22 cycles of peristalsis (acquired from 3–4 bouts of continuous crawling). The duty factor of the anteriormost segment was calculated as the ratio of time this segment was not moving forward (stance time) to the total stride period (protrusion time + stance time). The protrusion rate of the anteriormost segment was calculated by dividing the stride length by the protrusion time. All the measured and calculated kinematic variables are defined in Fig. 1.

Individual earthworms of all sizes varied their speed during bouts of crawling. Therefore, it was possible to determine whether earthworms of different sizes crawled faster by increasing stride length or by increasing stride frequency, i.e. whether small and large earthworms used the same mechanism to increase speed. The crawling speeds for each of the 22 strides for each individual were plotted as a function of stride length and stride frequency to acquire a regression coefficient for the relationship between the latter variables and speed for each individual (see, for example, Berrigan and Lighton, 1993). The regression coefficient for each individual was then

plotted as a function of body mass to test whether the mechanism of changing speed changed as a function of body mass.

Segment shape changes

Material deformations are typically indicated by strain (ϵ =change in length/original length), but extension ratios (λ = ϵ +1) are sometimes used by engineers to make calculations on materials that extend by more than 10% (e.g. Wainwright et al., 1976). Although the earthworm body wall extends by more than 10%, strains were used in the present study rather than extension ratios for convenience and to facilitate distinguishing between extensions (positive values) and contractions (negative values).

Earthworms lack the distinct regional specialization of many other segmented animals such as arthropods and vertebrates, but some regionalization does occur. Two segments were chosen for the comparison of body wall strains and strain rates to assess the effects, if any, of this regionalization on the function of the hydrostatic skeleton. Segment 15 lies in the anterior region of the worm where segments are relatively long and wide. Segment 50, in contrast, lies in the relatively homogeneous midregion of the worm, where segments are relatively narrow and short.

The shape changes of segments 15 and 50 of crawling earthworms were video-taped at 60 Hz using a Wild Heerbrugg dissecting microscope fitted with a Sony CCD-Iris (SSC-C374) high-resolution color video camera and a time/date generator (Panasonic WJ-810). The earthworms were placed on a wet, fabric-covered, movable board on the stage of the microscope so that individual segments could be kept in view despite the forward locomotion of the earthworm. RasterOps video capture software on a Power Macintosh 7100/80 computer

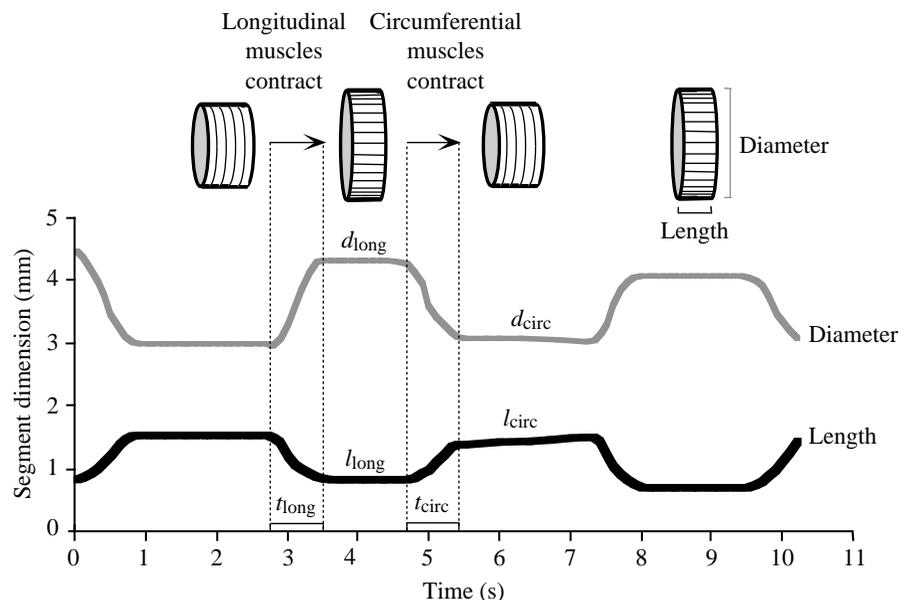
enabled the capture of individual video frames, and NIH Image software (version 1.59) enabled the measurement of the length and lateral diameter of the segments to the nearest 0.1 mm. A ruler was video-taped for calibration prior to the filming of each earthworm.

The segment dimensions of two individuals (0.3 g and 1.6 g) were measured at 10 ms intervals to characterize the precise shape of the curves describing segment length and diameter as a function of time. The curves revealed that there were discrete periods when little or no shape change occurred (Fig. 2). Therefore, the length and diameter of segments in subsequent individuals were measured only at the onset of a shape change and at the completion of a shape change. Maximum circumferential and longitudinal strains were calculated as the maximum shape changes that occurred during the protrusion phase of a step. This measurement convention resulted in positive longitudinal strains (axial elongation) and negative circumferential strains (radial shortening). Strain rates were calculated by dividing each maximum strain by the time it took the segment to change shape (see Fig. 2). Maximum strains were averaged over four cycles of peristalsis, and strain rates were averaged over two cycles of peristalsis. Since the circumferential and longitudinal locomotory muscles of earthworms are located directly under the thin cuticle and epidermis of the body wall, the shape changes observed in the segments approximate the length changes in the underlying muscles, providing an estimate of muscle length changes and contraction velocities.

Statistical analyses

The exponential relationship between kinematic variables and body mass can be expressed by the function $y=am_b^b$ (Huxley, 1932), where m_b is body mass in grams, y is the

Fig. 2. Sample record of shape changes of segment 15 during peristaltic crawling. The longitudinal strain was calculated by dividing the change in length of the segment ($l_{\text{circ}}-l_{\text{long}}$) by the length during maximum longitudinal muscle contraction (l_{long}). Likewise, the circumferential strain was calculated by dividing the change in segment diameter ($d_{\text{circ}}-d_{\text{long}}$) by the diameter during maximum longitudinal muscle contraction (d_{long}) (assuming that the cross-sectional shape of the segment does not change). The longitudinal and circumferential strain rates during circumferential muscle contraction were calculated by dividing the longitudinal and circumferential strains, respectively, by the time taken for the circumferential muscles to contract (t_{circ}). The longitudinal and circumferential strain rates during longitudinal muscle contraction were calculated by dividing the longitudinal and circumferential strains, respectively, by the time taken for the longitudinal muscles to contract (t_{long}). Strains were averaged over four cycles of peristalsis, while strain rates were averaged over two cycles of peristalsis.



variable of interest, a is a constant, and b is the mass exponent. The relationships between each of the measured variables and body mass were analyzed using linear regressions of log-transformed data, where the equation for 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 (κ_{xx}) as described by Fuller (1987):

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

where b is the attenuated slope as calculated using ordinary regression analysis and β is the corrected slope. For continuous variables, such as body mass, the reliability ratio is the correlation coefficient between two determinations of the same characteristic, one plotted on the x axis and one plotted on the y axis. The body masses of ten individuals were measured on separate days. The body mass from the first day was then plotted against the body mass from the second day for each individual to enable calculation of the correlation coefficient r ($r = \kappa_{xx}$; Fuller, 1987), and from this the corrected slope β . The reliability ratio κ_{xx} calculated for body mass was 0.995; therefore, all regression slopes plotted as a function of body mass were increased by a factor of 1.005. The reliability ratio calculated for crawling speed using the same method was 0.848; therefore, all regression slopes plotted as a function of crawling speed were increased by a factor of 1.18.

Student's t distribution was used to test slopes where the null hypothesis was $\beta=0$ or $\beta=1$. All analyses, including ordinary and multiple regression analyses, were performed using Systat for Windows (version 5). Values are presented as means \pm S.D.

Results

Variation in crawling speed within and among individuals

Worms of all sizes had the same tendency to increase their stride length in order to increase their crawling speed (slope $\propto m_b^{-0.004}$; $r^2 < 0.001$; $P > 0.10$; Fig. 3A), but smaller worms had a slightly greater tendency than larger worms to increase their stride frequency in order to increase their crawling speed (slope $\propto m_b^{0.16}$; $r^2 = 0.25$; $P = 0.003$; Fig. 3B). Thus, small and large earthworms used slightly different mechanisms to increase their speed. Earthworms of all sizes exhibited continuous rather than discrete changes in kinematics as they increased their speed over the range of speeds observed, i.e. they did not change 'gaits'.

Mean preferred crawling speed also varied among individuals of the same body size. Slow earthworms of all sizes either appeared lethargic (unresponsive to stimulation) or preoccupied with exploring the substratum for a burrow opening. Fast earthworms of all sizes were highly responsive to stimulation and locomoted readily rather than searching for

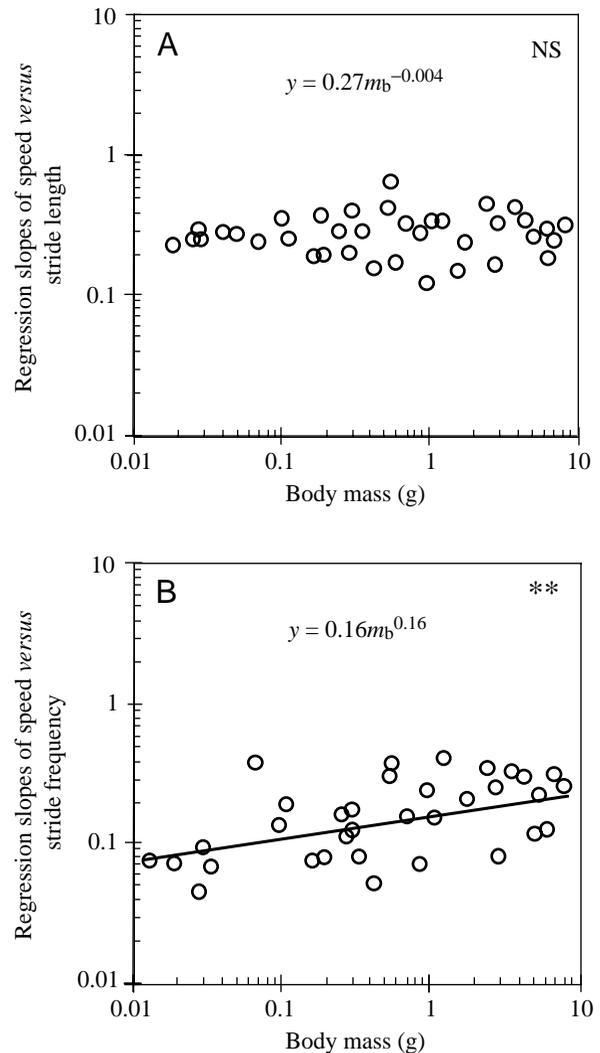


Fig. 3. Earthworms of different sizes do not differ greatly in their mechanism of changing speed. Each data point represents the slope of a linear regression of speed as a function of stride length (A) or stride frequency (B) for 22 cycles of peristalsis for an individual earthworm ($r^2 > 0.50$ for all regression slopes). (A) The relationship between crawling speed and stride length did not change as a function of body mass ($r^2 < 0.001$; $P > 0.10$). (B) The relationship between crawling speed and stride frequency increased only slightly as a function of body mass ($r^2 = 0.25$; $P = 0.003$), indicating only a small tendency for larger earthworms to increase their speed more by increasing their stride frequency than by increasing their stride length, compared with smaller earthworms. NS, not significant; ** $P < 0.01$.

a burrow opening. When the three independent variables stride length, protrusion time and stance time were used in a multiple regression with crawling speed (body lengths s^{-1}) as the dependent variable, increased crawling speed was explained mostly by increased stride length (in body lengths, standardized coefficient = 0.90, $P < 0.001$) but also by decreased duration of the protrusion time and the stance time (both with standardized coefficients of -0.29 , $P < 0.001$). In other words, faster earthworms of a particular size had consistently longer

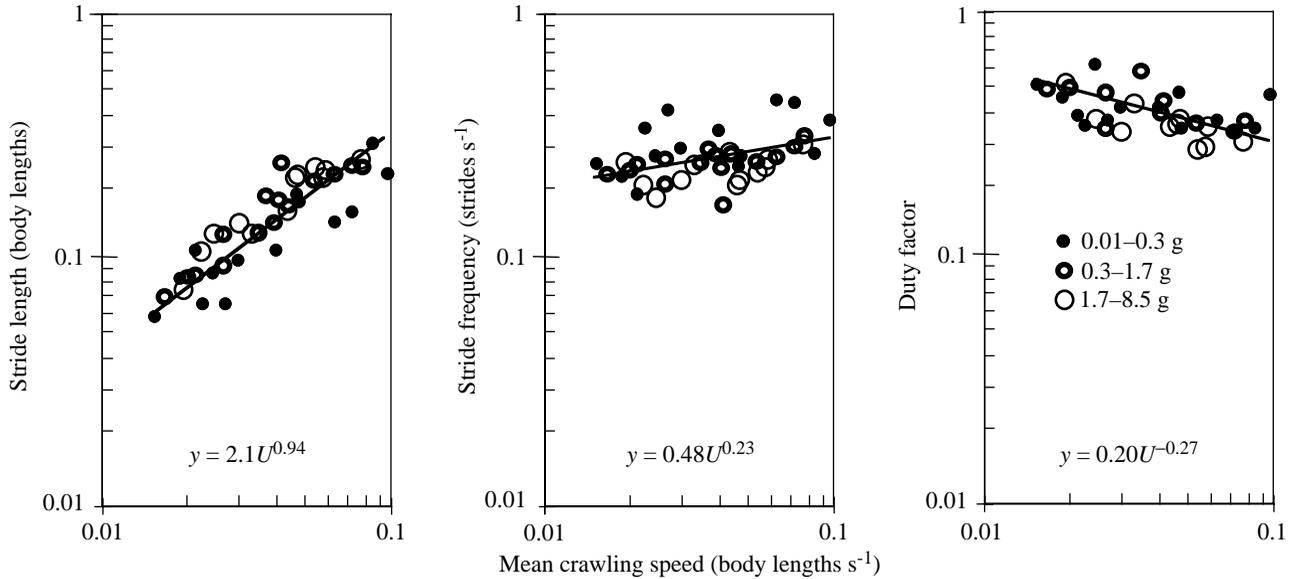


Fig. 4. The mean stride length, stride frequency and duty factor of each earthworm plotted as a function of that individual's mean crawling speed on logarithmic coordinates using normalized stride length and normalized crawling speed to control for body size ($N=41$). Fast earthworms tend to be faster than slow earthworms primarily because they have longer stride lengths ($r^2=0.79$; $P>0.10$ compared with a slope of 1.0), but also because they have higher stride frequencies ($r^2=0.18$; $P=0.002$ compared with a slope of zero) and lower duty factors ($r^2=0.33$; $P<0.001$, $N=35$, compared with a slope of zero). Different symbols are used to represent small, medium and large earthworms to facilitate visual comparison of sizes, but these groupings were not used in the statistical analysis.

stride lengths and only slightly higher stride frequencies than those of slower earthworms of the same size (Fig. 4).

Scaling of crawling kinematics

When the kinematic variables for each individual were plotted against body mass on logarithmic coordinates, some variables showed no relationship with body mass, while others changed with body mass. The regression statistics for the scaling of the kinematic variables are summarized in Table 1.

Stride length

Mean stride length scaled as $m_b^{0.41}$, which was greater than

the $m_b^{0.33}$ expected by isometry ($P=0.03$; Fig. 5A). Stride length normalized to body length scaled as $m_b^{0.07}$, which was significantly greater than a slope of zero ($P=0.04$). The mean normalized stride length was 0.16 ± 0.07 body lengths (mean \pm S.D.; $N=41$), indicating that earthworms advanced by approximately one-sixth of their body length per stride.

Stride frequency and duty factor

Stride frequency decreased slightly as a function of body mass, but duty factor showed no relationship with body mass. Stride frequency scaled as $m_b^{-0.07}$, which was significantly lower than a slope of zero ($P<0.001$; Fig. 5B). This scaling

Table 1. Summary of scaling relationships between kinematic variables and body mass

Variable y	$y=am_b^b$			Correlation coefficient
	a	b	95% confidence intervals for b	
Absolute crawling speed (mm s^{-1})	3.8	0.33	± 0.11	0.66
Normalized crawling speed (body lengths s^{-1})	0.037	0.001	± 0.05	0.0004
Absolute stride length (mm s^{-1})	15	0.41	± 0.05	0.81
Normalized stride length (body lengths)	0.15	0.07	± 0.07	0.10
Stride frequency (strides s^{-1})	0.25	0.07	± 0.04	0.37
Duty factor	0.38	-0.03	± 0.07	0.10
Absolute protrusion rate (mm s^{-1})	6.8	0.31	± 0.08	0.70
Normalized protrusion rate (body lengths s^{-1})	0.066	-0.02	± 0.06	0.005
Stance time (s)	1.6	0.04	± 0.22	0.06
Protrusion time (s)	2.5	0.10	± 0.08	0.49

m_b , body mass (g).

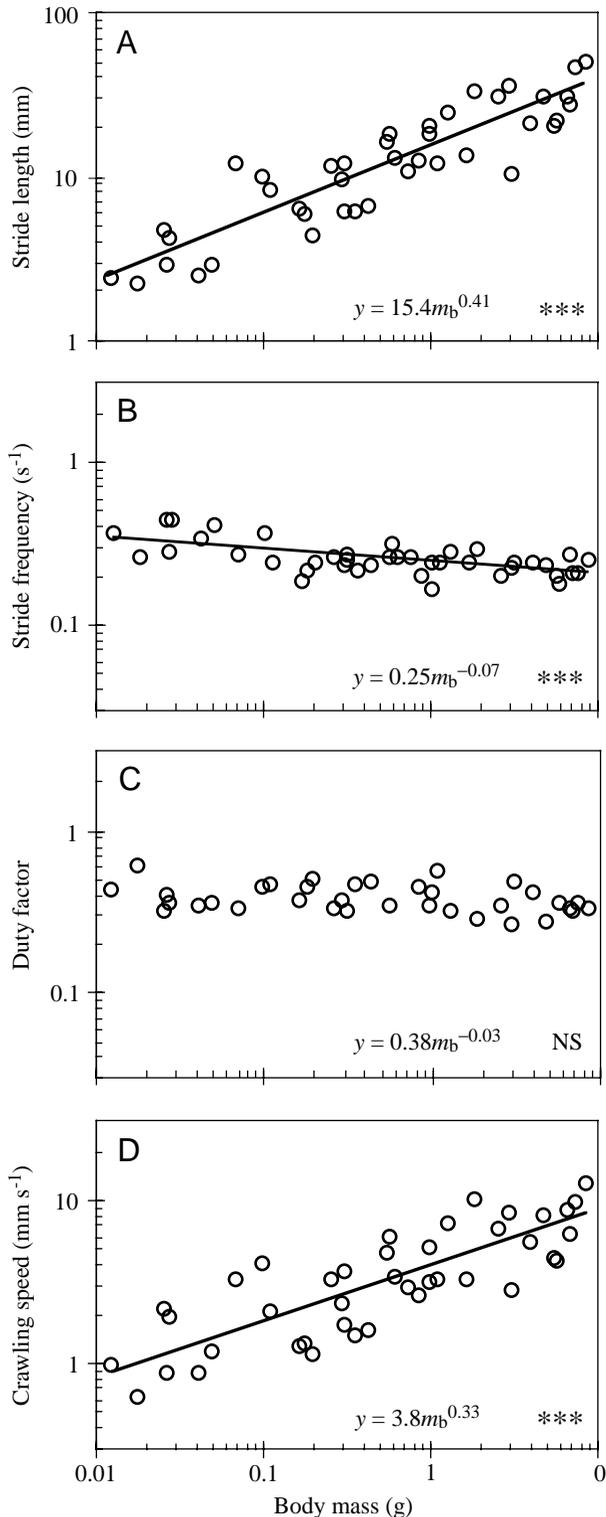


Fig. 5. Kinematic variables plotted as a function of body mass on logarithmic coordinates. (A) Stride length increased significantly as a function of body mass ($r^2=0.81$; $P=0.001$; $N=41$). (B) Stride frequency decreased slightly as a function of body mass ($r^2=0.37$; $P<0.001$; $N=41$). (C) Duty factor did not change as a function of body mass ($r^2=0.10$; $P=0.07$; $N=35$). (D) Crawling speed increased as a function of body mass ($r^2=0.66$; $P<0.001$; $N=41$). The regression statistics for all other kinematic variables are listed in Table 1. NS, not significant; $***P<0.001$.

result is best interpreted when the two components of stride frequency, the protrusion time and the stance time, are considered separately; the stance time was constant as a function of body mass ($t_s \propto m_b^{0.04}$; $P>0.10$) while the protrusion time increased with body mass ($t_p \propto m_b^{0.10}$; $P<0.001$), resulting in an overall increase in stride period as a function of body mass and, therefore, a slight decrease in stride frequency with body mass (Table 1). The mean stride frequency was $0.27 \pm 0.07\ s^{-1}$ (mean \pm s.d.; $N=41$), indicating that the mean duration of one stride was approximately 4 s. There was no significant relationship between duty factor (df) and body size ($df \propto m_b^{-0.03}$; $P=0.07$; Fig. 5C). The mean duty factor was 0.40 ± 0.08 ($N=35$), indicating that the earthworms spent approximately two-fifths of their stride period in the stance phase.

Speed

Absolute crawling speed U increased as a function of body mass ($U \propto m_b^{0.33}$, $P<0.001$; Fig. 5D), but relative speed (normalized to body length) showed no relationship with body mass ($U_r \propto m_b^{0.001}$, $P>0.9$). On average, earthworms crawled at a speed of 0.04 ± 0.02 body lengths s^{-1} (mean \pm s.d.; $N=41$), i.e. an average worm traveled one body length in 25 s. The normalized protrusion rate of the anteriormost segment showed no relationship with body mass, scaling as $m_b^{-0.02}$ ($P>0.6$). On average, the protrusion rate was 0.07 ± 0.03 body lengths s^{-1} ($N=35$), almost twice as fast as the mean crawling speed. Both the mean normalized crawling speed and the mean normalized protrusion rate were independent of body mass because the slight increase in protrusion time offset the slight increase in stride length as a function of body mass (Table 1).

Segment strains

Body wall strains were independent of body mass (Fig. 6). The strains for segments 15 and 50 were not significantly different from each other ($P>0.10$). Mean longitudinal strains were 0.63 ± 0.17 and 0.55 ± 0.14 (mean \pm s.d.) for segments 15 ($N=24$) and 50 ($N=19$), respectively, indicating that the segments elongated by approximately 60% during circumferential muscle contraction. Mean circumferential strains were -0.26 ± 0.06 and -0.24 ± 0.04 for segments 15 and 50, respectively, indicating that the segments narrowed by approximately 25% during circumferential muscle contraction.

Segment strain rates

Strain rates decreased only slightly as a function of body mass. During circumferential muscle contraction, the circumferential strain rate ($d\epsilon_c/dt$) decreased as a function of body mass ($d\epsilon_c/dt \propto m_b^{-0.09}$; $P=0.02$; Fig. 7A), resulting in longitudinal strain rates ($d\epsilon_l/dt$) that also decreased as a function of body mass ($d\epsilon_l/dt \propto m_b^{-0.14}$; $P=0.007$). However, when the longitudinal muscles contracted, the longitudinal strain rates did not change as a function of body mass ($d\epsilon_l/dt \propto m_b^{-0.06}$; $P>0.10$; Fig. 7B), resulting in circumferential

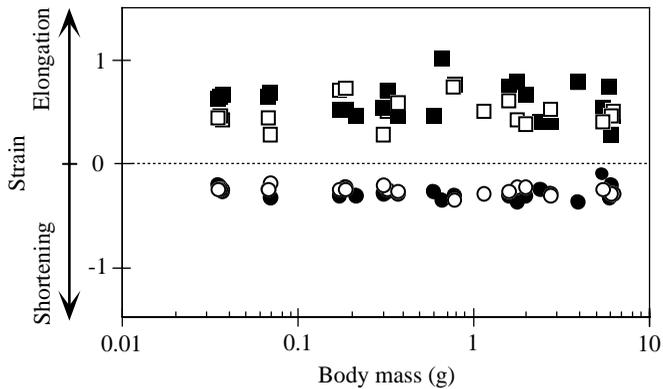


Fig. 6. Body wall strains in segments 15 (filled symbols, $N=24$) and 50 (open symbols, $N=19$) during crawling plotted as a function of body mass on logarithmic coordinates. Longitudinal strain (■; $r^2=0.03$) and circumferential strain (●; $r^2=0.02$) in segment 15, and longitudinal strain (□; $r^2=0.01$) in segment 50 did not change as a function of body mass ($P>0.10$). Circumferential strain (○; $r^2=0.23$) in segment 50 decreased only slightly as a function of body mass ($P=0.04$). The strains in segments 15 and 50 were not significantly different from each other ($P>0.10$). Strains were determined as shown in Fig. 2.

strain rates that were also independent of body mass ($d\epsilon_c/dt \propto m_b^{-0.04}$; $P>0.10$). During circumferential muscle contraction, the mean circumferential strain rate was $0.41 \pm 0.17 \text{ s}^{-1}$ and the mean longitudinal strain rate was $0.98 \pm 0.46 \text{ s}^{-1}$ (means \pm s.d.; $N=29$). During longitudinal muscle contraction, the mean longitudinal strain rate was $0.75 \pm 0.28 \text{ s}^{-1}$ and the mean circumferential strain rate was $0.58 \pm 0.25 \text{ s}^{-1}$. In summary, earthworms of all sizes shortened their segments at the same strain rate, but large earthworms elongated their segments slightly more slowly than did smaller earthworms.

Discussion

The present study sought to examine how the peristaltic locomotion of a hydrostatic skeleton scales as a function of body size during ontogeny. The results indicate that large earthworms crawl at a greater absolute speed than small earthworms, but at the same relative speed (in body lengths s^{-1}), and do so by taking slightly longer strides (relative to body length) at a slightly lower frequency. However, compared with the variation in kinematics both within individuals and among individuals of the same size, the normalized kinematic variables appear to be relatively constant as a function of body size. This point is demonstrated in a schematic summary comparing the kinematics of peristalsis in earthworms of the same size but at different crawling speeds (Fig. 8A) and of earthworms of different sizes at the same relative crawling speed (Fig. 8B).

Two organisms are said to be 'kinematically similar' if all ratios of lengths, periods and speeds within one organism produce the same constants as the ratios of corresponding

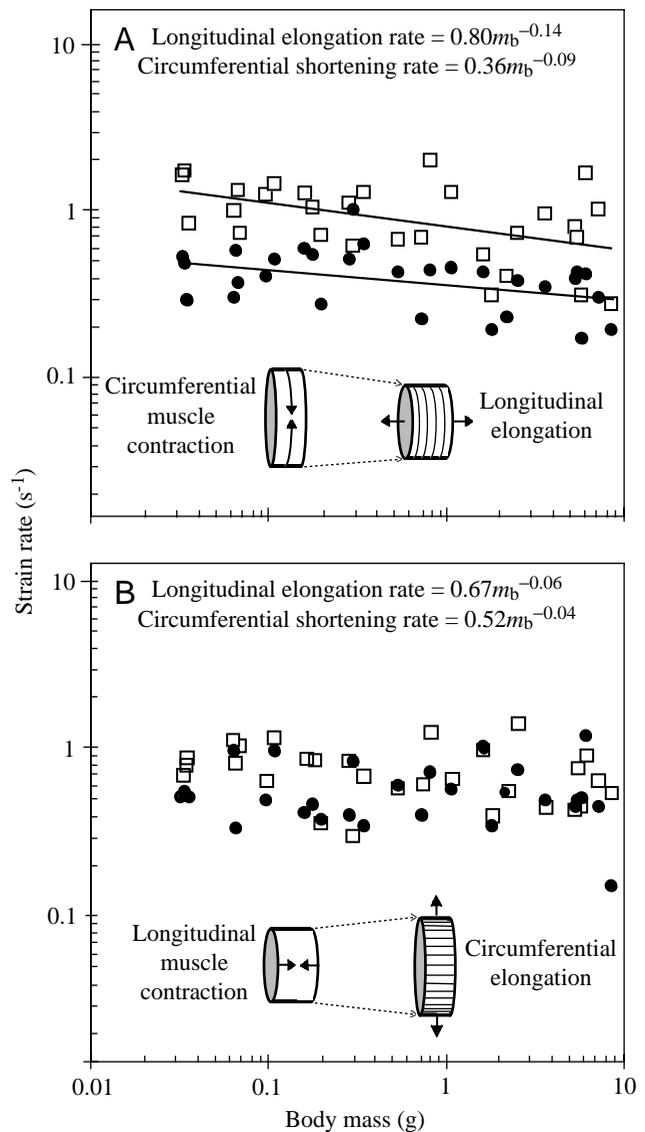


Fig. 7. Body wall strain rates in segment 15 during circumferential (A) and longitudinal (B) muscle contraction plotted as a function of body mass ($N=29$). (A) During circumferential muscle contraction, both the circumferential shortening rate (●; $r^2=0.18$; $P=0.02$) and the resulting longitudinal elongation rate (□; $r^2=0.24$; $P=0.007$) decreased slightly as a function of body mass. (B) During longitudinal muscle contraction, both the longitudinal shortening rate (□; $r^2=0.08$) and the resulting circumferential elongation rate (●; $r^2=0.03$) were independent of body mass ($P>0.10$). Overall, large earthworms elongate their segments slightly more slowly than small earthworms, but shorten their segments at the same rate. Strain rates were determined as shown in Fig. 2.

lengths, periods and speeds within the other (e.g. Daugherty and Franzini, 1997). Using relative stride length (stride length/body length) as an index of relative length, duty factor (stance time/stride period) as an index of relative period and the ratio of protrusion rate to crawling speed as an index of relative speed, peristaltic crawling appears to be kinematically similar for earthworms of different sizes.

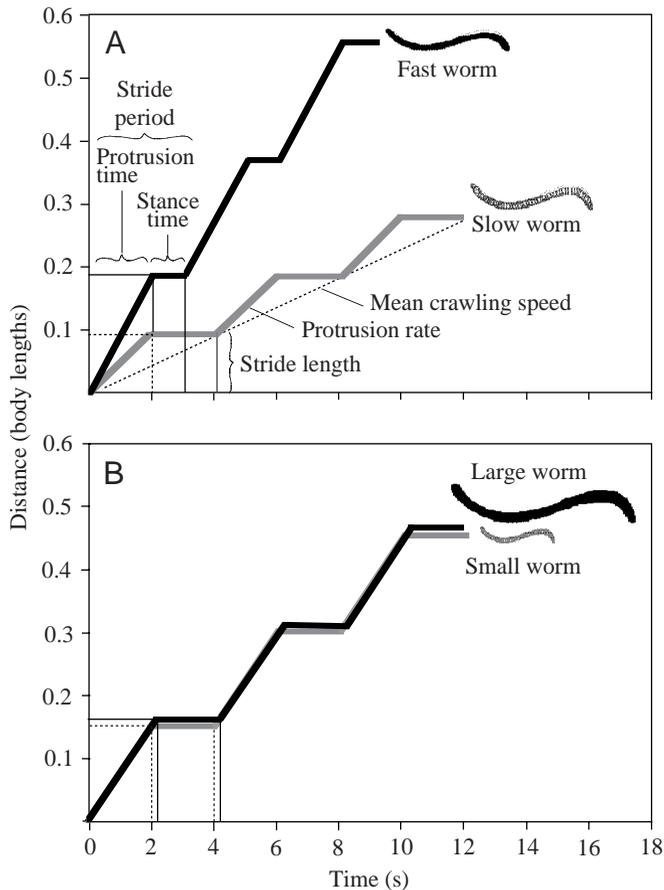


Fig. 8. Schematic summary of earthworm crawling kinematics. (A) Comparison of the average crawling kinematics of a fast worm and a slow worm of the same size. (B) Comparison of the average crawling kinematics of a large worm and a small worm at the same average speed ($\text{body lengths s}^{-1}$). Earthworms of the same size at different crawling speeds were kinematically more variable than earthworms of average speed but of different sizes. The time traces were modeled after Fig. 1 and were calculated on the basis of the speed and scaling relationships described in Figs 4 and Table 1, respectively. Fast earthworms derived their speed from large stride lengths and short stance phases, which resulted in high protrusion rates and low duty factors compared with slow earthworms. In contrast, average earthworms of different sizes were essentially kinematically similar.

Variation in crawling speed within and among individuals

Mean crawling speeds were calculated to compare earthworms of different sizes in this scaling study. However, speed varied greatly both within organisms and among earthworms of the same size, enabling a quantification of how earthworms change their crawling speed. Many investigators have examined how animals differing widely in size and mode of locomotion change their kinematics to accommodate different speeds. Overall, the mechanisms of changing speed vary both within individuals at different speeds and among species. For example, in many organisms with legs, an increase in speed is achieved primarily by increases in stride frequency at low speeds and primarily by increases in stride length at high

speeds (e.g. Heglund et al., 1974; Heglund and Taylor, 1988; Full, 1997).

Most hydrostatic species can increase both stride length and stride frequency in order to increase speed, but the relative contribution of each variable to increasing speed varies. For example, gypsy moth caterpillars (Casey, 1991) increase their crawling speed primarily by increasing their stride frequency, blowfly maggots (Berrigan and Lighton, 1993) increase their speed by increasing both their stride length and their stride frequency, and snails (Lissmann, 1945) and earthworms (present study) increase their speed by increasing their stride length more than their stride frequency. There are insufficient data to indicate why these different peristaltic organisms differ in their mechanisms of changing speed. For example, neither the occurrence of an unsegmented haemocoel (maggots, caterpillars and snails) *versus* a segmented coelom (earthworms) nor the use of direct peristaltic waves (waves that travel in the same direction as motion; maggots, caterpillars and snails) *versus* retrograde peristaltic waves (waves that travel in the opposite direction to locomotion; earthworms) correlate with mechanisms of increasing speed. One feature that is common among peristaltic locomoters is the absence of discrete gait transitions during increases in speed.

The effect of body size on the kinematics of locomotion

Central to this and similar studies is the question: which kinematic variables will be constant between small and large locomoting animals and which variables will necessarily change as a function of body size? That the earthworms are 'kinematically similar' indicates that the mean relative lengths, periods and speeds are constant, but this description does not indicate how lengths, periods and speeds will scale in absolute terms. Several scaling models have enabled predictions of kinematic variables in absolute terms, the three main models being geometric similarity, elastic similarity and static stress similarity. The main assumption of the geometric similarity model is that large and small animals have the same physical proportions. The elastic similarity model assumes that elastic deformations of large and small structures are the same when they are loaded by their own weight. Finally, the static stress similarity model assumes that the magnitude of maximum stress (force/cross-sectional area) is the same in large and small structures (modeled as beams) loaded by their own weight. McMahon (1975) reviewed the scaling predictions made by these models for several kinematic variables in the context of terrestrial vertebrates at the trot-gallop transition (Table 2).

The scaling results from the present study are not consistent with the geometric similarity predictions (Table 2), even though earthworms grow with geometric similarity (Quillin, 1998). The results do, however, approximate the predictions of the static stress similarity model, and earthworms have previously been observed to scale with static stress similarity (Quillin, 1998; the geometric similarity and static stress similarity models are not mutually exclusive for hydrostatic skeletons). To understand these results, we must consider the qualitative differences between the locomotion of organisms

Table 2. Summary of predictions made by three scaling models for the relationship between three kinematic variables and body mass in terrestrial quadrupeds (McMahon, 1975) compared with results from the present study

	Speed, U	Stride length, l	Stride frequency, f
Geometric similarity	$U \propto m_b^0$	$l \propto m_b^{0.33}$	$f \propto m_b^{-0.33}$
Elastic similarity	$U \propto m_b^{0.25}$	$l \propto m_b^{0.37}$	$f \propto m_b^{-0.12}$
Static stress similarity	$U \propto m_b^{0.40}$	$l \propto m_b^{0.40}$	$f \propto m_b^0$
Earthworm peristalsis	$U \propto m_b^{0.33 \pm 0.11}$	$l \propto m_b^{0.41 \pm 0.05}$	$f \propto m_b^{-0.07 \pm 0.04}$

m_b , body mass.

with jointed skeletons and the peristaltic locomotion of organisms with hydrostatic skeletons. These differences will be discussed below in terms of the scaling of speed, stride length and stride frequency.

The scaling of speed

Hill (1950) predicted that geometrically similar animals of all sizes would run, fly or swim at approximately the same speed. In general, however, larger individuals locomote faster than smaller individuals when species are compared (e.g. Heglund and Taylor, 1988; Garland, 1983; Full, 1997). When ontogenetic size ranges are considered, the scaling of speed is less consistent. For example, maximum sprint speed is proportional to $m_b^{0.34}$ during the ontogeny of the lizard *Stellio stellio* (Huey and Hertz, 1982), but sprint speed changed little during the ontogeny of the lizard *Dipsosaurus dorsalis* (Marsh, 1988). Other ontogenetic studies of terrestrial quadrupeds have observed intermediate values for the scaling of speed (e.g. Garland, 1985; Zani and Claussen, 1994). The observed variation in ontogenetic scaling among terrestrial vertebrates may be attributed to the importance of other variables besides body size, such as changing body proportions (e.g. Garland, 1985) and life history strategy (e.g. precocial *versus* altricial development; Carrier, 1996).

Speed is generally presumed to be under high selective pressure since most organisms are either predators themselves or must escape from predators – both as juveniles and as adults. However, selection for rapid crawling speed is probably not very important for most peristaltic organisms because they tend to use non-peristaltic mechanisms to locomote rapidly or attempt to evade the notice of predators altogether (e.g. by crypsis). For example, the hydrostatic larvae of arthropods tend to crawl slowly compared with similarly sized arthropods with jointed skeletons (Casey, 1991; Berrigan and Lighton, 1993), but have been observed moving rapidly by non-peristaltic mechanisms such as jumping (Maitland, 1992) and rolling (Brackenbury, 1997).

Some hydrostatic organisms do move rapidly using peristalsis, but only for short periods and distances. For example, tube-dwelling polychaetes can disappear into their tubes with lightning speed (e.g. Buchsbaum et al., 1997). Likewise, the first line of defense of earthworms is probably

their subterranean habitat (Minnich, 1977), and earthworms can retreat rapidly into their burrows from the surface (although earthworms have many subterranean predators as well; for a review, see Edwards and Bohlen, 1996). The present study examined the scaling of the preferred crawling speed of earthworms since this was the most observable and repeatable measure of their performance. However, maximum speeds during earthworm escape (for example, when they retreat into their burrows from the surface) may be important and may scale differently from preferred crawling speed. There are insufficient data on the *in situ* activities of juvenile earthworms for comparison with adults, so there is little basis for a statement about the importance of speed throughout the ontogeny of *Lumbricus terrestris*. That the preferred crawling speed of earthworms scaled in proportion to body length (Fig. 5; Table 1) may be merely a consequence of the scaling of stride length and stride frequency.

The scaling of stride length

Stride length represents the horizontal distance traveled by an organism during one stride. In terrestrial legged vertebrates and arthropods, stride length is limited primarily by leg length and by the joint angles between rigid leg segments, in addition to other variables such as the pattern of cycling of the legs (e.g. McMahon, 1975). Interspecific studies of mammalian quadrupeds have observed that stride length is proportional to $m_b^{0.38}$ (e.g. Heglund et al., 1974; Heglund and Taylor, 1988), consistent with the elastic similarity model (Table 2). When adults of different arthropod species are compared, stride length scales nearly as predicted by geometric similarity ($m_b^{0.33}$; Full, 1997). Ontogenetic studies generally assume that stride length scales in proportion to leg length, which is sometimes (e.g. Marsh, 1988), but not always (see Garland, 1985), the case.

What determines stride length during peristalsis? Earthworm stride length (l) is determined by the sum of the longitudinal extensions of each segment in the protrusion phase of a stride (assuming that traction is sufficient to prevent backslipping; Fig. 1):

$$l = \sum_{i=0}^n \Delta l_n, \quad (3)$$

where n is the number of segments engaged in anterior protrusion and Δl_n is the longitudinal extension of each of the n segments (Alexander, 1982; Pearce, 1983). For unsegmented hydrostats, the same reasoning applies, but to body regions rather than to discrete segments.

First, what determines the number of segments engaged in anterior protrusion? In the case of the earthworm *Lumbricus terrestris*, segment number and resting segment proportions are constant as a function of body mass (Quillin, 1998), and segment strains are constant as a function of body mass (Fig. 6, assuming that all segments scale in the same way as segments 15 and 50). Therefore, earthworms of all sizes appear to engage roughly the same number of segments in the protrusion phase

of a stride (only slightly more in large earthworms). If neural control is responsible for determining the number of segments engaged in the protrusion phase of each stride, then this aspect of neural control appears to be conserved during the ontogeny of earthworms.

Second, what determines the longitudinal extension of each segment? Both structural and material properties may limit the longitudinal extension of segments. Structural properties are determined in part by the geometry of the skeleton. For example, in earthworms, shape changes are constrained by the constant volume of fluid within each segment (Newell, 1950); extreme shape changes cannot occur because the internal volume would have to decrease to accommodate them (see Clark and Cowey, 1958), and coelomic fluid can neither escape nor be compressed during normal locomotion. Since both the proportions and internal pressures of earthworm segments are constant as a function of body mass (Quillin, 1998), the limitations on segment shape changes (and therefore stride length) due to the geometry of the skeleton are probably comparable for small and large earthworms.

The second variable that may limit the longitudinal extension of each segment is the material properties of the body wall. Like most pliable tissues such as skin and passive muscle (e.g. Vincent, 1990), earthworm body wall offers little resistance to being stretched at low strains, but great resistance to stretching at high strains. Active muscles also resist extension. Many hydrostatic skeletons possess obliquely striated (rather than cross-striated) skeletal muscles whose fibers are more extensible and can exert force over a larger length range than in cross-striated muscle (e.g. Hidaka et al., 1969; Miller, 1975; Tashiro, 1971; see Milligan et al., 1997; Burr and Gans, 1998), allowing for the remarkable extensions that are observed in many hydrostatic skeletons. The scaling of the passive and active material properties of the hydrostat body wall (earthworm or otherwise) has not been determined directly. However, since the earthworm *Lumbricus terrestris* shows geometric similarity and dynamic stress similarity during crawling (Quillin, 1998), and since body wall strains are constant as a function of body mass during crawling (Fig. 6), I predict that earthworm body wall stiffness (i.e. resistance to extension) is constant as a function of body mass. This scaling result would help to explain the isometric scaling of relative stride length as a function of body mass (Fig. 8B).

However, the resistance of materials to extension may depend not only on the extent of deformation but also on the rate of deformation of the material; many of the extensible tissues of soft-bodied organisms are more stiff when pulled rapidly than when pulled slowly (i.e. they are viscoelastic; Wainwright et al., 1976; Vincent, 1990). Data from the present study indicate that the body wall strain rate changed little as a function of body size in earthworms (Fig. 7). Since strains were constant as a function of body size, the strain rate data provide further evidence that the time-dependent material properties of the earthworm body wall may change little as a function of body size. This is an important area of further research, especially since Keller and Falkovitz (1983) observed

in their mathematical model of earthworm crawling that the rate of change of tension in the body wall was an important variable limiting the ultimate speed of peristalsis.

The measurement of the scaling of dynamic strains in the earthworm body wall enabled the testing of a 'dynamic strain similarity' hypothesis. Note, however, that the dynamic strain similarity hypothesis as introduced by Rubin and Lanyon (1984) examined the strains in bones of locomoting vertebrates to calculate bone stresses rather than to observe the shape changes of the bones *per se* (i.e. it was essentially a 'dynamic stress similarity' hypothesis, proposing that the peak stresses experienced by the skeletons of actively locomoting animals are constant). Dynamic strain similarity, in the literal sense, is especially applicable to hydrostatic skeletons because the shape changes of a hydrostat body wall tend to be considerable (e.g. two orders of magnitude greater in earthworm body wall than in bone) and themselves constitute the kinematics of locomotion in soft-bodied organisms.

The scaling of stride frequency

Hill (1950) observed that large animals tend to locomote using slower stride frequencies, wingbeat frequencies and tailbeat frequencies than smaller animals and predicted that frequency would be proportional to $m_b^{-0.33}$. In general, stride frequency does decrease with an increase in body size when species are compared, but less than predicted by Hill (1950) (on average, $f \propto m_b^{-0.16}$ for vertebrates, calculated from data in Table 3 in Drucker and Jensen, 1996; on average, $f \propto m_b^{-0.25}$ for invertebrates, calculated from data in Table 12.2 in Full, 1997). Hill (1950) believed that the natural frequency of movements was determined primarily by the intrinsic contractile properties of muscles, rather than by neural control. Muscle contraction studies have generally shown that larger vertebrate muscles contract more slowly in absolute terms than smaller muscles, even during ontogenetic increases in size (e.g. Archer et al., 1990; Bennett et al., 1989; Marsh, 1988; Richard and Wainwright, 1995). However, when the scaling of muscle contraction velocity and of stride frequency are measured in the same study, the scaling exponents may or may not correlate. For example, muscle contraction velocity is correlated with foot contact time rather than with stride frequency in some terrestrial vertebrates (see Kram and Taylor, 1990; Rome, 1992).

The scaling of muscle properties is not known for obliquely striated muscle. However, if the shortening rate and elongation rate of earthworm segments (Fig. 7) can be used as a metric of the contraction velocities of the longitudinal and circumferential muscles, respectively, then data from the present study suggest that muscle contraction velocity scales with a similar mass exponent as stride frequency (Fig. 5). However, each muscle group is only active for a small fraction of the stride period; the circumferential muscles contract at the beginning of the protrusion phase and the longitudinal muscles contract at the beginning of the stance phase (see Figs 1, 2), so the rough correspondence between the scaling of estimated contraction velocities and stride frequency may not be meaningful.

What are the kinematic determinants of stride frequency in a hydrostatic skeleton? In peristaltic organisms, stride frequency is determined by the speed of the peristaltic wave along the length of the organism (Alexander, 1982) and by the time between initiations of waves. Peristaltic waves are a classic example of rhythmic behaviors that are generally controlled by the central nervous system (by neural 'oscillators') but may in some cases be strongly influenced by sensory feedback (see Delcomyn, 1980). Indeed, in earthworms, the nerve cord of an adult earthworm exhibits an electrical rhythm whose frequency is identical with that of the muscular rhythm during normal peristalsis (Gray and Lissmann, 1938). This evidence suggests that the electrical rhythm of the nerve cord may be responsible for determining the wave speed, which is an important determinant of stride frequency. Preliminary data for the scaling of stride frequency in burrowing earthworms suggest that stride frequency is lower in magnitude during burrowing than during surface crawling, but that stride frequency scales with a similar exponent during both activities (a very slight decrease with body size; K. J. Quillin, unpublished results). This evidence suggests that the wave speed varies according to the external resistance to crawling, but that the scaling of stride frequency is conserved. Therefore, if neural control is an important determinant of stride frequency, then the scaling of neural control itself is complex and responsive to mechanosensory feedback.

The scaling of stride frequency may also be examined in terms of energetics (e.g. Strang and Steudel, 1990). The musculoskeletal systems of many animals operate mechanically as pendulum and/or spring-mass systems that operate most efficiently, from a metabolic standpoint, at natural frequencies determined in part by size (for a review, see McMahon, 1984). In hydrostatic organisms, viscous damping is certain to be more important than for jointed skeletons owing to fluid flow within the deforming body. Thus, natural frequency may not be as important a determinant of stride frequency in peristaltic organisms as expected for some jointed skeletons. Peristaltic locomotors tend to have a high cost of transport compared with their jointed-skeleton counterparts (e.g. Casey, 1991; Berrigan and Lighton, 1993; for a review, see Full, 1997). Cost of transport may provide an upper limit to stride frequencies in hydrostats, but the scaling of cost of transport is not known for peristaltic locomotors.

In summary, the ontogenetic scaling of earthworm peristalsis was used as an experimental system to examine how hydrostatic skeleton function may scale in comparison with the function of jointed skeletons. It is evident from a review of the literature on jointed skeletons that no one quantitative scaling 'rule' applies to the kinematics of all jointed skeletons; even the few existing ontogenetic studies of jointed skeletons have revealed considerable variation in the scaling of kinematics among similar organisms. Likewise, there is probably no one quantitative scaling 'rule' that applies to all hydrostatic skeletons that locomote by peristalsis. The hydrostatic skeletons of soft-bodied organisms are diverse in structure,

material composition, neural control, functional role and evolutionary history. One fundamental difference between jointed skeletons and hydrostatic skeletons is that the motions of most jointed skeletons are derived primarily from changes in the joint angles between rigid segments, whereas the motions of most hydrostatic skeletons are derived primarily from changes in the dimensions of the body segments themselves. It is intuitive, then, that the material properties of the body wall would play an especially important role in determining the scaling of peristaltic crawling in hydrostatic skeletons. A previous study (Quillin, 1998) concluded that the earthworm *Lumbricus terrestris* scales with geometric similarity as well as static and dynamic stress similarity. The present study further concludes that the crawling of *L. terrestris* is kinematically similar when the motions are normalized by body length (the un-normalized values scale closely to the predictions made by the static stress similarity model derived for jointed skeletons) and that the motions approximate dynamic strain similarity. Overall, the active and passive time-dependent material properties of the body wall are probably the most important determinants of the scaling of kinematics in peristaltic organisms.

This research was supported by an N.S.F. Graduate Research Fellowship, a University of California at Berkeley Frankhauser Fellowship, and a Sigma Xi Grants-in-Aid of Research to K.Q., by N.S.F. Grant 92-20525 to M. Koehl and R. Keller and by O.N.R. Grant 444095-23068 to M. Koehl. I am especially grateful to M. Koehl for helpful discussion and advice, and to the members of the biomechanics group at the University of California at Berkeley for their feedback. M. Koehl, M. Martinez, R. Kram and two anonymous reviewers provided valuable critiques of this manuscript.

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