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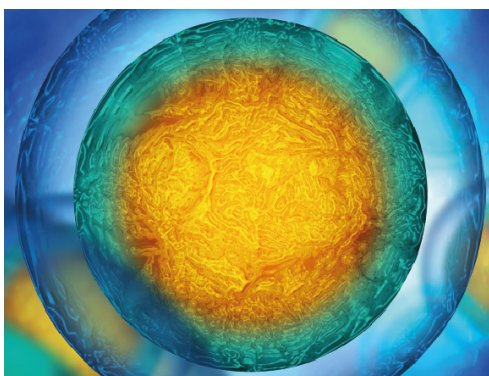
Lateral bending and buckling aids biological and robotic earthworm anchoring and locomotion

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PAPER

Lateral bending and buckling aids biological and robotic earthworm anchoring and locomotion

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Yasemin Ozkan-Aydin^{1,*} , Bangyuan Liu², Alexandra Carruthers Ferrero³,
Max Seidel^{3,4} , Frank L Hammond III²  and Daniel I Goldman³ 

¹ Department of Electrical Engineering, University of Notre Dame, Notre Dame, IN, United States of America

² George W. Woodruff School of Mechanical Engineering, Georgia Institute of Technology, Atlanta, GA, United States of America

³ School of Physics, Georgia Institute of Technology, Atlanta, GA, United States of America

⁴ Department of Mechanical and Industrial Engineering, Northeastern University, Boston, MA, United States of America

* Author to whom any correspondence should be addressed.

E-mail: yozkanay@nd.edu

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Abstract

Earthworms (*Lumbricus terrestris*) are characterized by soft, highly flexible and extensible bodies, and are capable of locomoting in most terrestrial environments. Previous studies of earthworm movement focused on the use of retrograde peristaltic gaits in which controlled contraction of longitudinal and circular muscles results in waves of shortening/thickening and thinning/lengthening of the hydrostatic skeleton. These waves can propel the animal across ground as well as into soil. However, worms benefit from axial body bends during locomotion. Such lateral bending and buckling dynamics can aid locomotor function via hooking/anchoring (to provide propulsion), modify travel orientation (to avoid obstacles and generate turns) and even generate snake-like undulatory locomotion in environments where peristaltic locomotion results in poor performance. To the best of our knowledge, lateral bending and buckling of an earthworm's body has not yet been systematically investigated. In this study, we observed that within confined environments, worms use lateral bending and buckling to anchor their body to the walls of their burrows and tip (anterior end) bending to search the environment. This locomotion strategy improved the performance of our soft-bodied robophysical model of the earthworm both in a confined (in an acrylic tube) and above-ground heterogeneous environment (rigid pegs), where present peristaltic robots are relatively limited in terradynamic capabilities. In summary, lateral bending and buckling facilitates the mobility of earthworm locomotion in diverse terrain and can play an important role in the creation of low cost soft robotic devices capable of traversing a variety of environments.

1. Introduction

Terrestrial animals have evolved strategies for effective propulsion and lift in complex terradynamic regimes using a diversity of structures [1, 2], including bodies [3–5], heads [6] and limbs [7–10]. For example, several animal groups travel through/on flowable substrates via undulatory propulsion that involves waves of body bends being propagated from head to tail [5, 6, 11, 12].

While many terrestrial locomotion studies focus on ground with rigid, flat, or homogeneous

characteristics (e.g. dry sand) [13, 14], movement in cohesive substrates is less explored [15–17]. Among terrestrial animals, earthworms provide an excellent experimental system to discover principles of terrestrial locomotion in cohesive soils [1, 18, 19] as well as diverse terradynamic regimes like heterogeneous clutter. Earthworms locomote within cohesive soils for many reasons, such as nesting, foraging, and surviving extreme environmental conditions (e.g. temperature, dryness etc) [18, 20]. They create tunnels of varying size and shape through soil burrowing and organic matter burial behaviors

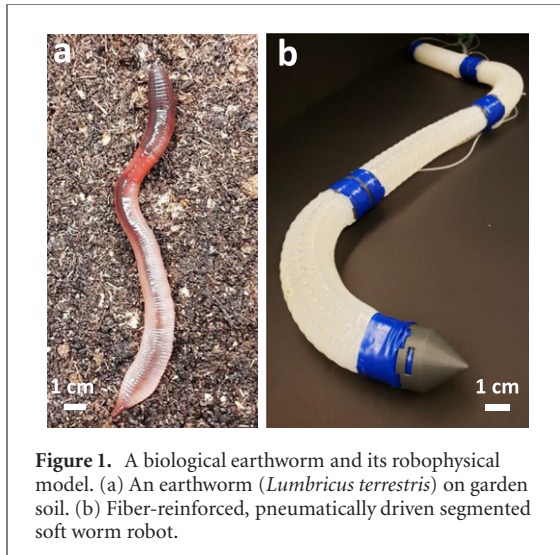


Figure 1. A biological earthworm and its robophysical model. (a) An earthworm (*Lumbricus terrestris*) on garden soil. (b) Fiber-reinforced, pneumatically driven segmented soft worm robot.

[21–24]. They locomote in confined spaces and underground tunnels largely via retrograde (a wave in the opposite direction to the movement) peristaltic gait where a transient substrate anchor is formed by the contraction of longitudinal muscles [1, 18].

The retrograde peristaltic gait that earthworms use to crawl within and on soil has been studied by many researchers [25–31]. These studies primarily focused on crawling in a straight line, however, natural environments in which the worms move have complex structures (e.g. differently sized and oriented tunnels, figure 2), require the worms to potentially use other types of movement.

The subterranean excavation ability of earthworms has inspired researchers to design earthworm-type robots [32–41], however, none of these robots burrow successfully in soil due in large part to high penetration forces and energy requirements [42, 43]. Instead of burrowing, these robots locomote in structured tunnels and on the surface by mimicking the peristaltic motion of the worm, where the segments can either elongate longitudinally or expand radially to form anchor points. This locomotion approach is useful if the radially extending segments can expand to fit the tunnel diameter; however, in most cases the segments cannot expand sufficiently due to the limited radial deformation. Moreover, being limited to pure peristalsis, robots cannot change their direction of movement, which reduces their mobility and maneuverability, especially in a heterogeneous environment.

Here, we discover that earthworms use body undulation when moving in models of their natural environments. To date, several papers investigated the undulatory locomotion of limbless systems from mechanical modeling and control aspects [44, 45]. Most of these papers combine the undulatory locomotion of snakes with the peristaltic locomotion of worms [44–46]. Here, motivated by the locomotion capabilities of worms, we designed a robophysical

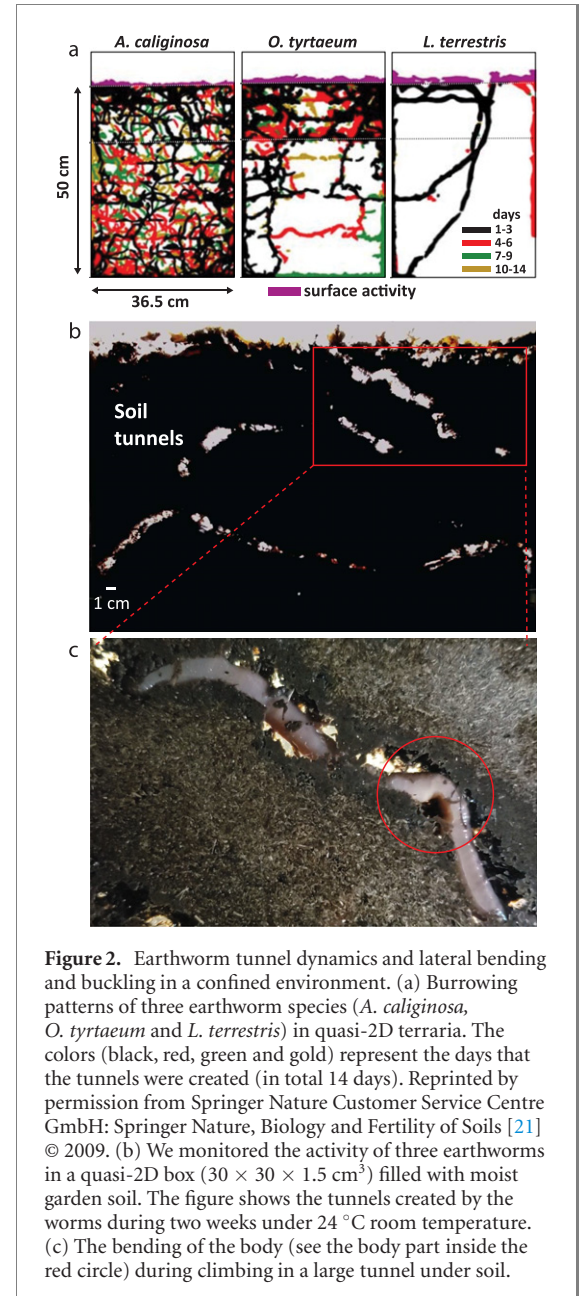


Figure 2. Earthworm tunnel dynamics and lateral bending and buckling in a confined environment. (a) Burrowing patterns of three earthworm species (*A. caliginosa*, *O. tyrtaeum* and *L. terrestris*) in quasi-2D terraria. The colors (black, red, green and gold) represent the days that the tunnels were created (in total 14 days). Reprinted by permission from Springer Nature Customer Service Centre GmbH: Springer Nature, Biology and Fertility of Soils [21] © 2009. (b) We monitored the activity of three earthworms in a quasi-2D box ($30 \times 30 \times 1.5 \text{ cm}^3$) filled with moist garden soil. The figure shows the tunnels created by the worms during two weeks under 24°C room temperature. (c) The bending of the body (see the body part inside the red circle) during climbing in a large tunnel under soil.

model of an earthworm (figure 1) whose soft elastomer segments can elongate longitudinally (for peristaltic motion) and also undulate in 2D space (for steering and anchoring). We systematically study how the earthworms control their shapes depending on the environment in which they locomote. We also study the performance of our robophysical model in similar environmental scenarios and show that the locomotion strategy (lateral bending and buckling) that worms use can be beneficial for controlling the locomotion of a pneumatically actuated soft segmented robot in tunnels and heterogeneous environments.

2. Methods and results

Several studies were performed to investigate the burrowing behavior of earthworms under soil [21, 24, 47]. Depending on the earthworm species,

worms create a network of horizontal and vertical tunnels in various sizes and orientations and use these tunnels for shelter and protection [21, 48, 49] (figure 2(a)).

Here, we focus specifically on how the worms locomote in their burrows using body undulation. In all experiments, we used a deep burrowing anecic species (*Lumbricus terrestris*) of earthworms [50]. Before systematically examining the benefits of worms' undulatory behavior, we first performed experiments in models of their natural environment, i.e. tunnels under soil, using quasi-2D terraria described in [51]. Each terrarium was built by two parallel sheets of glass ($30 \times 30 \text{ cm}^2$) and separated with 1 cm aluminum plates. We filled the terraria homogeneously with wet Magic Worm Bedding (moisture 80%) to construct a dark and moist model of their natural habitat.

Earthworms (10 worms, length = $26.95 \pm 6.18 \text{ cm}$, mass = $7.5 \pm 2.04 \text{ g}$) obtained from Carolina Biological Supply were maintained in Magic Worm Bedding (Magic Products Inc., WI, USA) and kept in an environmental chamber (15°C , a relative humidity of 30%). We placed three earthworms in each terrarium and covered the top of the boxes with aluminum foil to prevent the worms from escaping. We kept the boxes in the environmental chamber one week prior to the experiments to ensure that the worms adapted to the experimental soil. After the adaptation week, we recorded the burrow patterns and activity of the worms at room temperature (24°C) for a week. To stimulate the movement of the worms in their tunnels, we put organic fruit particles on the top of the box.

Figure 2(b) shows tunnels of the worms built in a week (see SI (<https://stacks.iop.org/BB/17/016001/mmedia>) movie-1 for timelapse video). We discovered that the worms employed body undulation (bending and buckling) of their flexible body segments to locomote in the tunnels. To quantify the occurrence of body undulation, we counted the frames that we observed body undulation (85 frames) during the first two days of the experiment (total 5760 frames) by focusing on the tunnel areas where the worms movement were clearly visible. We also recorded real-time video of the worms while moving in the tunnel. Figure 2(c) shows a snapshot from the experiments where the worm used lateral bending and buckling to anchor its body to the walls of the wide tunnel (SI movie-1).

2.1. Systematic animal experiments in confined space (undulation aided anchoring)

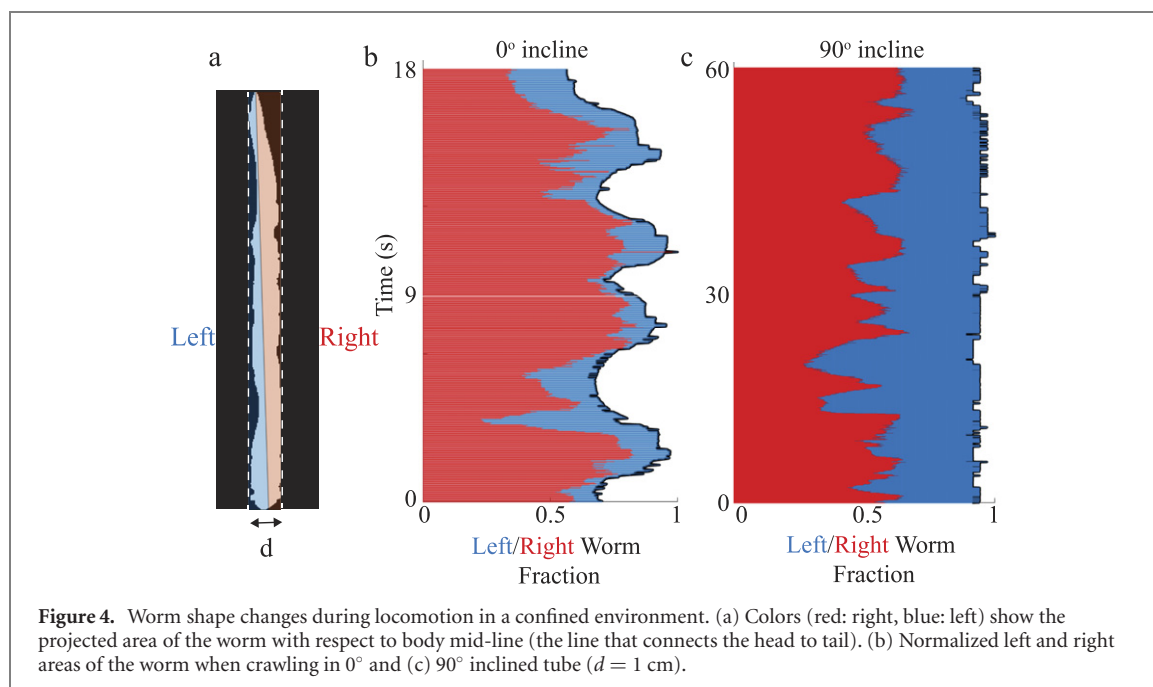
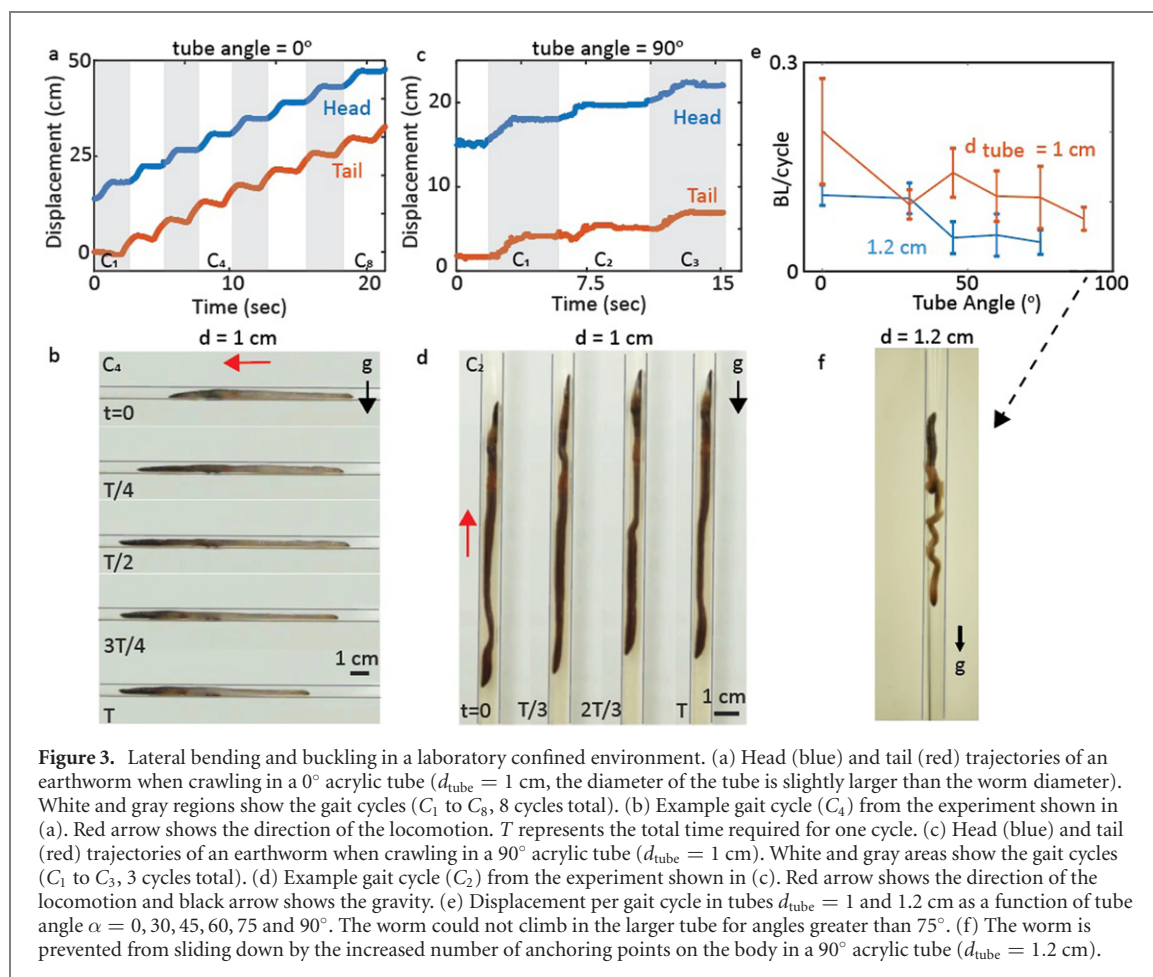
In this section, we seek to understand how earthworms change their locomotion strategies in tunnels depending on the tunnel size and orientation. As noted in the previous section, earthworms dig underground tunnels and spend much of their time

moving inside these tunnels. When the soil is compact, worms eat their way through and create compact, concentrated masses called castings [48, 52, 53]. These castings cement soil particles together to form stable tunnel walls [53]. However, these tunnels are not static structures, their width and compactness change as the worms move within [21, 24, 49]. To the best of our knowledge, no one has systematically studied how worms adapt their gaits, especially regarding body undulation, to move through tunnels of varying sizes and angles.

In the experiments, we allowed earthworms to crawl in two sizes of acrylic tubes ($d_1 = 1 \text{ cm}$, $d_2 = 1.2 \text{ cm}$, length = 1 m, $d_1, d_2 >$ worm diameter) while varying the tube angle from 0 to 90° with increments of 15° . Note that it is not entirely possible to compare the worm movement in soil tunnels and acrylic tubes due to mechanical differences between the two environments. For example, the soil is cohesive (deforms and holds its shape) while acrylic tubes are solid. The main reason for using acrylic tubes instead of soil in our experiments is to push worms to the limits of performance on a low friction surface and thus understand when and how undulatory and buckling control mechanisms are used in locomotion. Other reasons are: (1) worms are difficult to track in natural soil due to the color distribution and (2) we cannot control the width and angle of natural tunnels or keep these parameters constant during experiments. Acrylic tubes facilitate a clear view and simplify the change of environmental parameters (angle and width of the tunnels).

We calculated the average locomotion body length per gait cycle (BL/cyc) over several gait cycles defined with a body wave of expansion and elongation (peristalsis) which begins at the anterior end of the body and moves towards the tail. In each tube angle, we performed at least one experiment with four different animals. To induce movement of the worms in the tubes, we stimulated the animals at their tails using a pointed object. Some of the animals were unable to crawl even with stimulation. We did not include these experiments in our results (in a tube $d_1 = 1 \text{ cm}$, 8 of 42 trials and $d_2 = 1.2 \text{ cm}$, 5 of 30 trials were discarded).

At a 0° incline, in both tube sizes, the worms had their largest BL/cyc speeds (for d_1 : 0.20 ± 0.075 and d_2 : 0.11 ± 0.015). They had their lowest BL/cyc speeds for d_1 : 0.076 ± 0.016 at a 90° incline and d_2 : 0.04 ± 0.018 at a 75° incline but could still climb without significant slipping (figure 3(e)). We measured the shape changes of worms while climbing in a 0° and 90° inclined tube. In figure 4, we present how worms change their body shape (either by extending body length or bending their body left/right) during the locomotion. We used the midline (that connects the head to tail) as a reference line to calculate the percentage of body segments on each side of the body. We normalized the total body area at each time step with a maximum area obtained during each run.



Since we only focus on the pixel area, the left/right worm percentage also represents the length of the worm (value 1 is the maximum length of the worm for a given run). On level ground, the worms mostly used a peristaltic gait by extending and contracting (shortening) their body cyclically (figures 3(a) and (b)).

The shape of the body did not change from cycle to cycle (figure 4(b)). At higher inclination angles, such as 75° and 90° , body bending was more prevalent than at lower angles, providing extra anchoring points for forward locomotion and reducing the occurrences of slipping (figures 3(c) and (d)). When

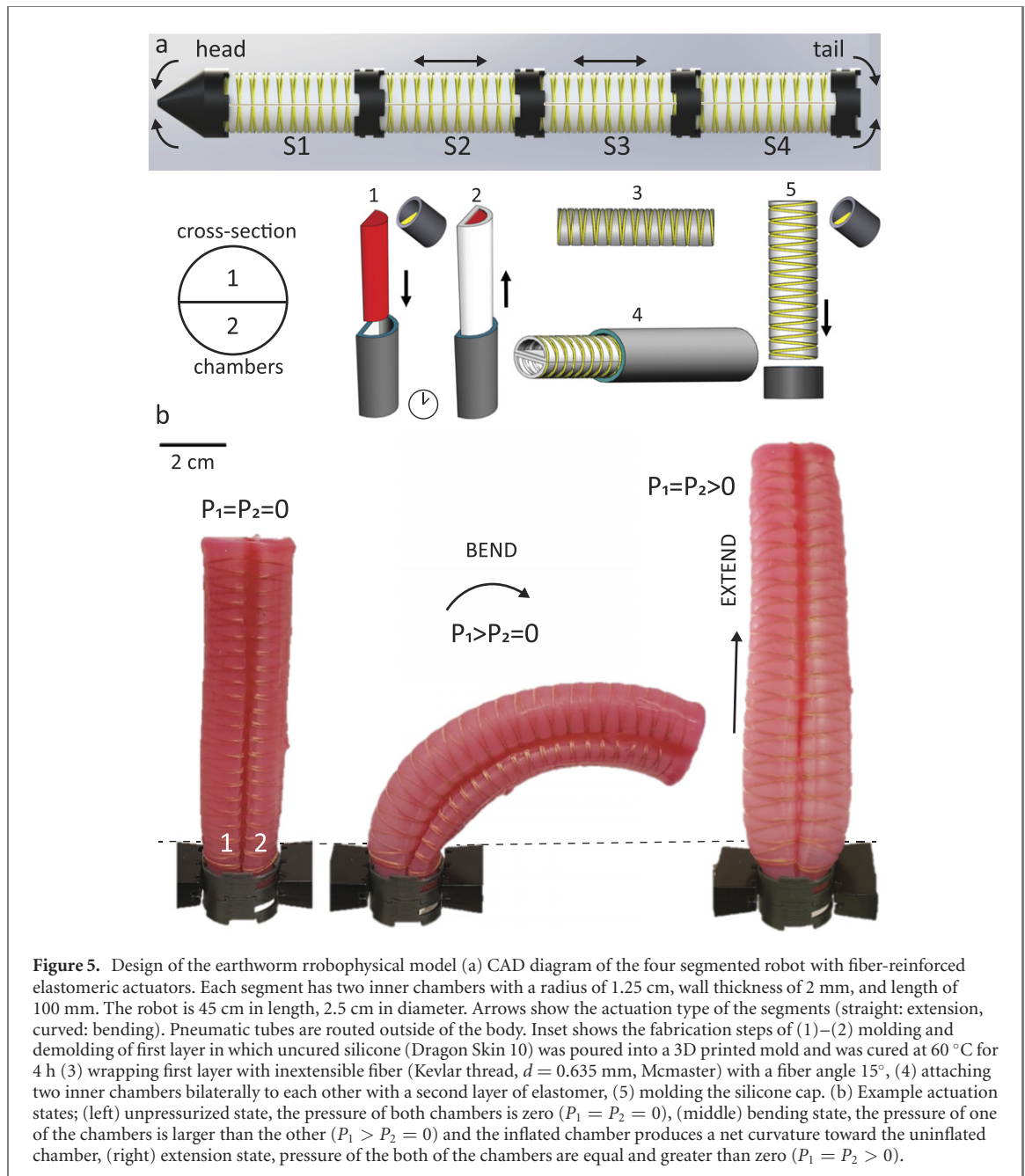


Figure 5. Design of the earthworm rrobophysical model (a) CAD diagram of the four segmented robot with fiber-reinforced elastomeric actuators. Each segment has two inner chambers with a radius of 1.25 cm, wall thickness of 2 mm, and length of 100 mm. The robot is 45 cm in length, 2.5 cm in diameter. Arrows show the actuation type of the segments (straight: extension, curved: bending). Pneumatic tubes are routed outside of the body. Inset shows the fabrication steps of (1)–(2) molding and demolding of first layer in which uncured silicone (Dragon Skin 10) was poured into a 3D printed mold and was cured at 60 °C for 4 h (3) wrapping first layer with inextensible fiber (Kevlar thread, $d = 0.635$ mm, McMaster) with a fiber angle 15°, (4) attaching two inner chambers bilaterally to each other with a second layer of elastomer, (5) molding the silicone cap. (b) Example actuation states; (left) unpressurized state, the pressure of both chambers is zero ($P_1 = P_2 = 0$), (middle) bending state, the pressure of one of the chambers is larger than the other ($P_1 > P_2 = 0$) and the inflated chamber produces a net curvature toward the uninflated chamber, (right) extension state, pressure of the both of the chambers are equal and greater than zero ($P_1 = P_2 > 0$).

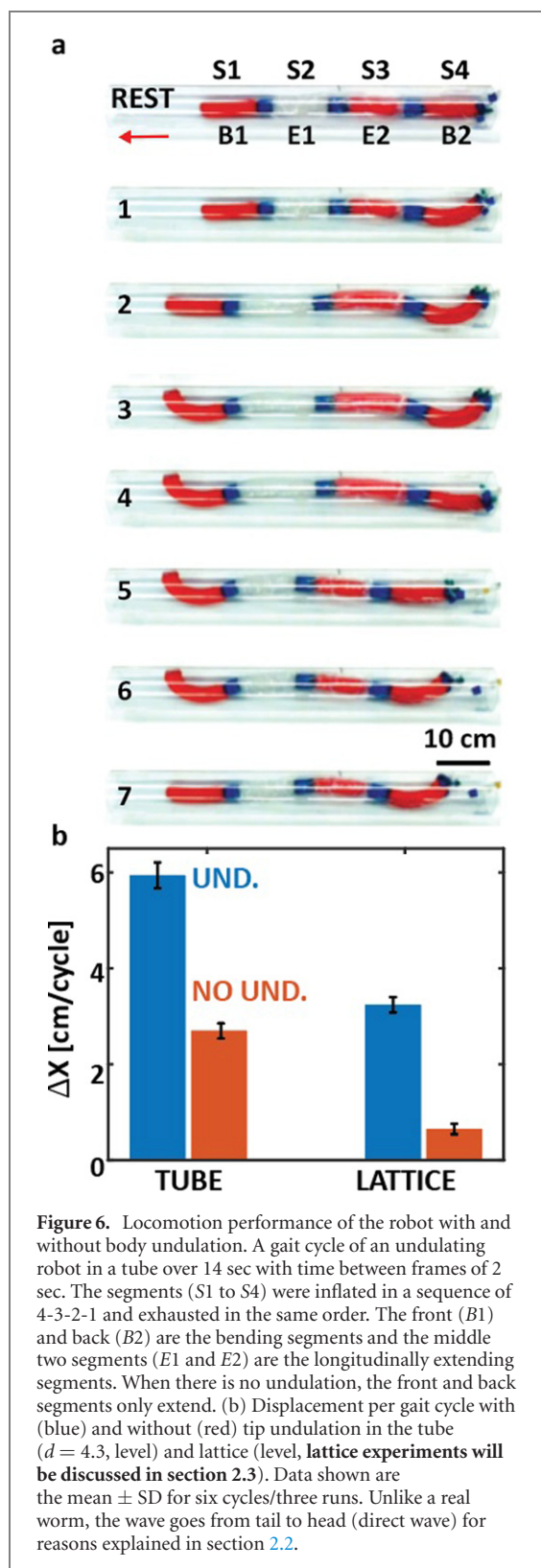
the worms crawled in a 90° tube, they attempted to keep the body length constant and undulated their body to balance body forces (figure 4(c)). This can be seen from figure 4(c) where the ratio of the red/blue areas changes during the run while the length of the body is relatively constant. In the larger diameter tube ($d_2 = 1.2$ cm) worms could not climb at 90°, however, they could maintain their position in the tube without slipping by buckling their body parts (figure 3(f), SI movie-2).

The lateral bending/buckling of the earthworms could be the result of the differential activity of longitudinal and circular muscles around the body which increases/decreases the length of worms. These length changes affect the body stiffness and cause buckling/bending under compressive load (under body weight) due to worms' thin geometry with

Table 1. The activation pattern of the segments (figure 5(a)) and displacement of the robot tip per cycle (cm/cycle) for different gait sequences. 1 and 4 are the bending segments, 2 and 3 are the extending segments. If the segment is a bending segment only one of its inner chambers is activated and if the segment is an extending segment both inner chambers are inflated at a time. The robot was tested in a tube ($d = 4.3$ cm). Data shown are mean \pm SD for six cycles/three runs. The last row (Gait-D) is generated greatest locomotor performance (see SI movie-4).

Gait	INFLATE	EXHAUST	cm/cycle
A	2-3-4-1	2-3-4-1	0.4 ± 0.3
B	2-3-4-1	4-3-2-1	3.3 ± 0.1
C	4-3-2-1	2-3-4-1	5.1 ± 0.6
D	4-3-2-1	4-3-2-1	7.0 ± 0.6

large aspect ratios. However, to the best of our knowledge, the level of stiffness generated by earthworms has not been studied. For biological and



neuromechanical insight as well as to develop engineering principles, it will be important in the future to conduct systematic investigation of the coordinated buckling/bending behavior of worms from material and structural perspectives.

2.2. Confined space robot experiments

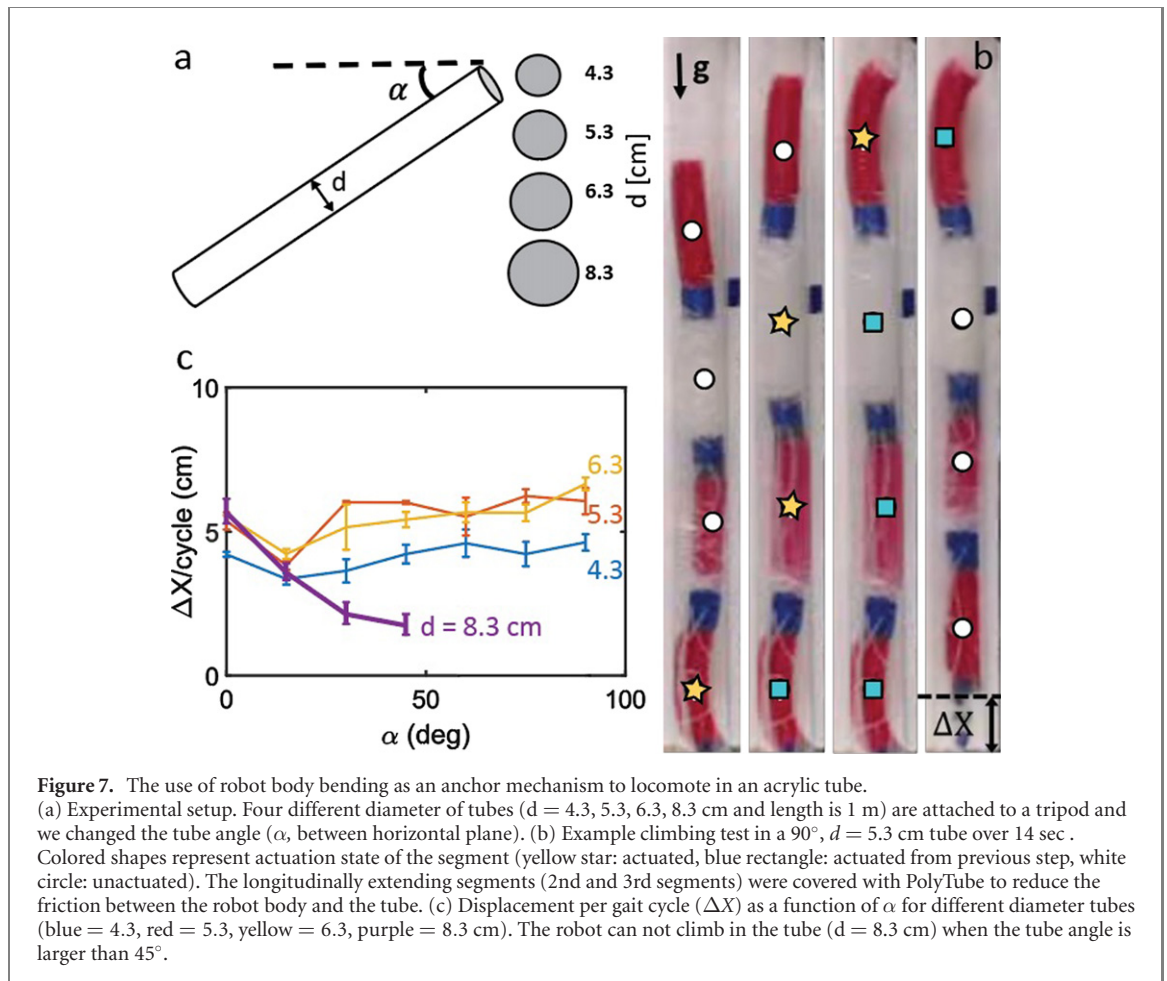
The animal experiments in confined environments revealed that successful locomotion of earthworms

depends on the execution of lateral bending and buckling which generate appropriate reaction forces from the environment. These observations encouraged us to develop a robophysical model of an earthworm whose mechanical design enables locomotion capabilities analogous to those of earthworms. The robot has a soft, flexible segmented body which can bend and extend with pneumatic actuation. In this section, we test our biological observation of the efficacy of buckling/bending in confined space locomotion through robophysical experiments in confined and heterogeneous environments.

Soft robot fabrication. We developed a worm robot by connecting four fiber-reinforced actuators in series (see figure 5(a)) using the methodology described in [54]; fabrication involves multi-step molding of elastomer materials along with cylindrical geometry. Each actuator consists of two half-cylinder elastomeric (Dragon Skin 10, smooth-on) inner chambers that have helical fibers (Kevlar thread) wound around the outside (see figure 5(a) for the details of the fabrication steps). These two inner chambers allow the segment to expand in directions with the lowest stiffness; i.e. the segment bends left/right when one of the chambers is inflated and extends longitudinally when both of them are inflated (see right panel of figure 5(b)). Our scheme differs from previous pneumatically driven soft elastomer earthworm robots in which anchoring is provided by radially expanding segments [35–38, 41, 55] in that we use undulation of the segment to anchor and steer the robot in complex environments.

The robot was assembled by attaching four actuators with 3D printed rigid connectors. We inserted straight barbed fittings (1/16" ID, McMaster-Carr) extended with Tygon PVC tubing (durometer 65A, 1/8" ID, 1/4" OD, McMaster-Carr) to the end of the actuators (at the side of connectors) and sealed it with Sil-Poxy glue (Smooth-On) for an air input. Silicone rubber tubings (durometer 50A, 1/32" ID, 1/16" OD, McMaster-Carr) were used to connect the actuators to an air source.

Control board. The robot was controlled via an Arduino Mega 2560 microcontroller, eight solenoid valves (NITRA, five-port, four-way, three-position, AutomationDirect), eight manual pneumatic regulators (Nitra, 4-57 adjustable range, AutomationDirect), and IRF540 MOSFET switch modules. Four-way, three-position solenoid valves allow the chambers to inflate, deflate, or hold the air pressure according to the desired activation pattern. We control the pressure of the chamber of each segment (total eight chambers) independently by using a network of pneumatic channels and Arduino-controlled solenoid valves. Each of the four segments could be pressurized from an external source (compressed air, 10–15 psi; 0.7–1 atm) that was connected to the robot via flexible tubing routed outside of the robot.



Gait generation. To model the peristaltic gait and lateral bending of earthworms, we use the first and last segments as anchoring/bending segments and the middle two segments as elongation segments. The middle two segments also have the same structure (with two inner chambers) as the anchoring/bending segments. We used two-chamber elongation segments instead of the one-chamber to eliminate any errors (such as uneven thickness of the elastomeric body) during the fabrication steps which causes varying degrees of undesired deformations under the same pressure. The two-chamber design allows us to adjust the maximum pressure of the segments individually, which provides symmetrical straight elongation.

The gaits were empirically determined by actuating the segments with different sequences. Table 1 shows the four samples from the set where the displacement/cycle changes from minimum (0.4 ± 0.3 cm) to maximum (7.0 ± 0.6 cm). The fastest locomotion (with 7 ± 0.6 cm/cycle) we observed was generated by inflation of segments 4-3-2-1 followed by exhausting them in the same order (table 1, Gait-D). We used Gait-D throughout the paper. Note that the wave of expansion and lateral bending propagated from the tail to the head in the case of Gait D in table 1, which is opposite to real earthworms. This is because of mechanical differences between worms and our robot. For

example, earthworms have segmented hydrostatic skeletons filled with fluid [18, 26, 52]. The volume of each segment is constant [18, 56, 57]. Each segment has longitudinal and circular muscles that enable the worm to actively control the diameter and length of the segment [18, 26]. However, in our robot, the volume of the segments is not constant and increases with the applied pressure. Also, our fiber-reinforced elastomeric design allows segments to either elongate longitudinally with a minimal radial extension or bend to the left/right.

In Gait-D, a cycle begins from the rest state (all the segments are deflated). Pressurization of one of the chambers of segment 4 (S4) bends the robot's back to the left/right ($\sim 60^\circ$) and anchors the body to avoid sliding backward. Then the middle segments (S3 and S2) elongate (by pressurizing both of the inner chambers) to provide forward displacement while keeping S4 inflated; finally pressurization of S1 bends the tip of the robot and establishes an anchoring point at the front to propel the back of the robot forward when all of the segments (S2, S3, and S4) are deflated. The mean \pm SD (standard deviation) values of the displacements per cycle for other gait sequences are given in table 1 (SI movie-4).

We next demonstrated that without changing the gait sequence, the locomotion performance decreased when we did not use undulatory motion (i.e when

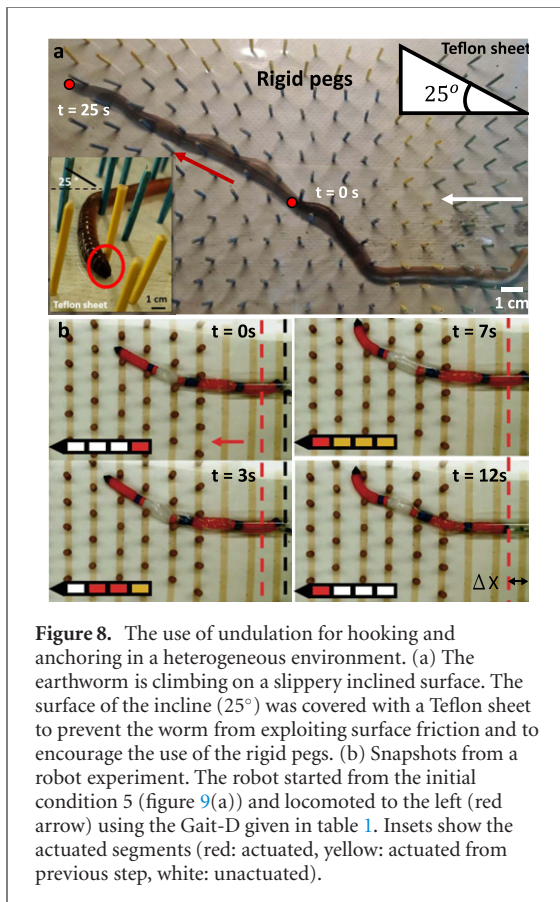


Figure 8. The use of undulation for hooking and anchoring in a heterogeneous environment. (a) The earthworm is climbing on a slippery inclined surface. The surface of the incline (25°) was covered with a Teflon sheet to prevent the worm from exploiting surface friction and to encourage the use of the rigid pegs. (b) Snapshots from a robot experiment. The robot started from the initial condition 5 (figure 9(a)) and locomoted to the left (red arrow) using the Gait-D given in table 1. Insets show the actuated segments (red: actuated, yellow: actuated from previous step, white: unactuated).

segments 1 and 4 also were only used as elongation segments). In these experiments, using Gait-D, we performed two sets of experiments in an acrylic tube ($d = 4.3$ cm) and a hexagonal lattice comprised of rigid pegs (cylindrical corks, see figure 9, lattice experiments will be discussed in section 2.3) with and without cyclic body undulation. In both environments, gaits that used body undulation (5.94 ± 0.27 cm in the tube, 3.24 ± 0.16 cm in the lattice) outperformed those without body undulation (2.7 ± 0.16 cm in the tube, 0.65 ± 0.11 cm in the lattice). Figure 6(a) shows a gait cycle of an undulated robot when crawling in a tube. Note that, when inflated, the diameter of the segments can increase up to 50% of its neutral diameter, which we used to anchor to the body in the absence of undulation. Data shown in figure 6(b) are the mean \pm SD for six cycles/three runs with and without body undulation.

Systematic robophysical study of locomotion in tunnels. We next systematically tested the effect of both gait and substrate properties on locomotor performance. Earthworms actively control the friction by extracting/retracting setae around the body [18, 26]. The setae are retracted during the circular contraction period (elongation), which reduces the friction [18]. Moreover, many earthworms secrete mucus (coelomic fluid) as a lubricant to help them move more easily through the soil [58]. During our robot experiments, we observed that when the friction between the elongation segments and the

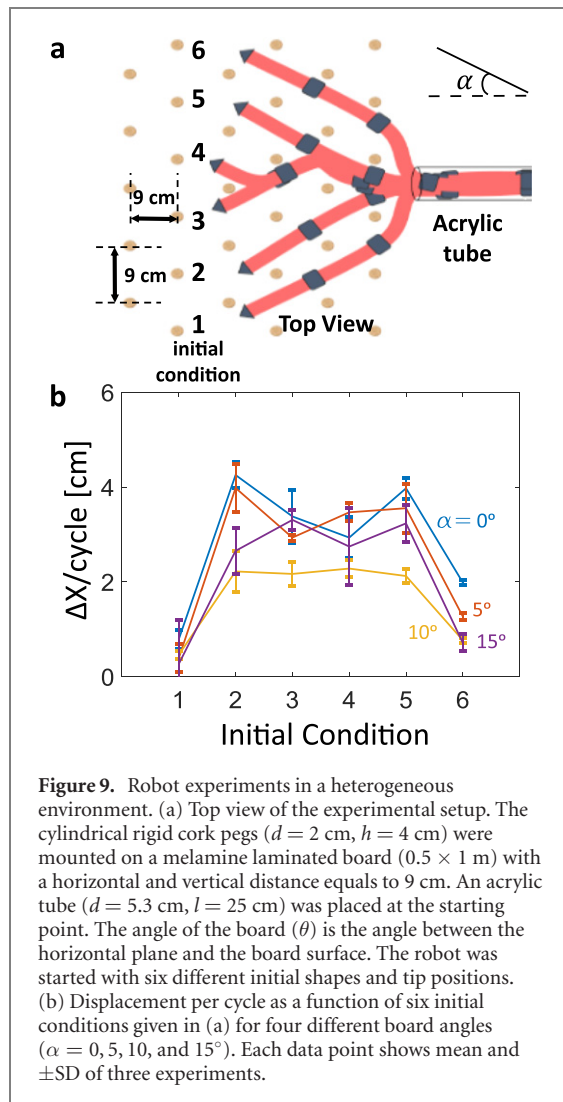
surface was high, the robot could not overcome friction and would slide back, or undesired body buckling occurred. Although we do not control the friction of the robot's surface actively (as can earthworms), when we covered the middle two segments with a Polytube, we reduced the friction by approximately 40% and obtained a 40% increase in the tube climbing performance. Note that, this friction reduction method differs from the method that uses unidirectional spikes to prevent backward slipping [41, 45, 59]. In our robotic worm, the bending of the first and last segments provides anchoring and prevents slipping.

We first performed experiments in four acrylic tubes with diameters $d_1 = 4.3$, $d_2 = 5.3$, $d_3 = 6.3$, $d_4 = 8.3$ cm which are 1.7, 2.1, 2.5 and 3.3 times larger than the robot diameter and changed the tube angle from 0 to 90° in increments of 15° (figure 7(a)). In all experiments we used the Gait-D described in the previous section. Figure 7(b) shows snapshots from one of the experiments where the robot climbed in a tube ($d = 5.4$ cm, $\alpha = 90^\circ$, SI movie-5). As seen in figure 7(c), the robot performed similarly for all tube angles (5.06 ± 0.95 cm/cycle) until the tube diameter 6.3 cm for all tube angles without any significant reduction in performance. The lateral bending guarantees that the robot can climb up the tube steadily without slipping or falling. However, in the large tube ($d = 8.3$ cm) the mean displacement/cycle decreased from 5.72 ± 0.42 cm to 1.78 ± 0.36 cm as the tube angle was changed from 0 to 45° . After 45° the robot was unable to apply enough lateral force required to overcome the robot weight (200 gr.) during the climbing process, and it slid backwards.

2.3. Heterogeneous environment animal experiments (undulation aided grabbing)

In previous sections, despite differences in gait dynamics in biological worms and the robophysical model, body bending and buckling conferred benefits in both systems in natural and laboratory confined environments. Given these locomotion benefits we next examined how the worms actively control the body shape when they encounter obstacles.

As a model of surface heterogeneity, we studied worms as they crawled through an inclined (25°) surface ($l = 40$, $d = 24$ cm) covered with regularly distributed rigid pegs ($h = 1.5$ cm, $d = 3$ mm, figure 8(a)). To encourage worms to use the pegs instead of surface friction, we covered the surface of the test area with a low friction material (Teflon sheet). Figure 8(a) shows an example of combined time-lapse images of a worm while climbing through the obstacle course for 25 s (SI movie-3). Rather than continuing to travel through the incline in a straight line, the worms searched the environment, grabbed the pegs by bending their body (especially the tip) and used pegs as anchor points to assist movement (8 animals, 3 trials each).



2.4. Heterogeneous environment robot experiments

To show that our earthworm robot also can benefit from lateral bending and buckling in a heterogeneous environment, we next performed systematic robophysical tests in a scaled lattice (SI movie-5). The obstacle-aided locomotion strategy of snakes has encouraged the design of several snake-like robots that can navigate through rigid pegs or walls by pushing against them [60–62]. Here, we use a similar heterogeneous environment model analogous to our biological experiments and to environments generated to test robots previously [60, 61]—cylindrical rigid cork pegs are mounted on a melamine laminated board in the form of a vertical hexagonal lattice (figure 8(b)). To provide an initial anchoring point at the back we used an acrylic tube at the middle of the setup of length approximately one segment length and initiated the robot from six different initial configurations as shown in figure 9(a). We also changed the angle of the surface (α) with respect to the ground from 0 to 15° with an increment of 5° to demonstrate that lateral bending and buckling was beneficial in an inclined heterogeneous environment. Using Gait-D, we performed three experiments

for each initial condition and measured the displacement per cycle. Figure 8(b) shows snapshots from one of the experiments ($\alpha = 0^\circ$) where the robot used pegs for holding points while locomoting within the obstacles. The robot performed similarly (2.33 ± 1.25 cm/cycle) for all the surface angles (0 to 15°) when it started from the initial conditions 2 to 5 (figure 9(b)). The open loop tip bending allowed the robot to overcome the obstacles without any sensory feedback and complex control methods. However, if the relative angle between segments three and four was larger than 45° , which occurred when the robot started from initial conditions 1 and 6, the buckling of the extending segments prevented the robot from moving forward.

3. Conclusions

In this paper, we studied lateral bending and buckling of earthworms in confined and heterogeneous environments, which, to the best of our knowledge, has not been studied before. In addition to crawling using peristalsis in a straight line, on a variety of surfaces the worms also changed the shape of their long, slender bodies by bending or buckling laterally. We showed with systematic laboratory experiments that lateral bending/buckling helped prevent the earthworms from slipping while climbing in confined environments (different size inclines (0 to 90°)) such as under soil tunnels and utilized locomotion in heterogeneous environment by creating extra support points.

The locomotion mode of worms in confined environments resembles that of concertina locomotion of snakes used to crawl through tunnels or narrow passages [63–66]. Depending on the size of a tunnel, a snake body forms a series of curves and presses against the wall of the tunnel to compensate for the sliding friction. As the cross-section of the tunnel decreases the number of curves exhibited by the body increases [67]. When the tunnel is sufficiently narrow, snakes use a gait called rectilinear locomotion to propel themselves in a straight line, similar to earthworm peristaltic gait [68]. In contrast to snakes, earthworms mostly use a peristaltic gait [26] without bending or buckling their bodies on level ground and narrow tunnels; as the locomotion task became more challenging (e.g. locomotion on inclined slippery surface), worms employed buckling/bending behaviors.

Other limbless animals like snakes utilize irregularities in the terrain and self-deform in response to terrain contacts [67, 69–71], which is referred to as obstacle-aided locomotion. The body waves form support points and firmly press against the wall of the channel or objects in the environment, and the resulting forces propel the snake forward. This behavior is similar to what we observed in worms when they locomoted in tunnels and heterogeneous environments with a small difference that worms use tip bending

frequently while snakes bend body parts and do not typically use the head.

Soft robots possess the benefit of having flexible bodies that promote robustness during locomotion while maintaining animal-like motion characteristics. To test the performance benefits of lateral bending and buckling revealed by the biological worms, we built a robo-physical model of an earthworm with a segmented soft body that can laterally bend and elongate. Despite differences in actuation mechanism (i.e. the robot used minimal radial expansion with a direct wave of lateral bending while the worms use a retrograde wave of peristaltic expansion/contraction and lateral buckling) systematic robo-physical experiments revealed that an open-loop body undulation strategy helped propel the robot in complex environments similar to worms. The robot could climb in a vertical tube that was more than three times larger than its diameter and navigate through obstacles without any external or internal sensing.

For advanced applications of autonomous robots, such as search-and-rescue operations and sub-surface soil exploration and monitoring, robots must move through rough terrain with an ability to control their deformation and sense the environment [72]. We hypothesize that the already impressive autonomy and motion performance of our simple and robust open-loop controlled robot can be further enhanced by the integration of soft sensors with a closed-loop controller. Our recent study [73] has shown that soft, stretchable nanocomposite strain sensors integrated with the robot body are a promising technique to enable feedback-controlled locomotion in complex and dynamic terrestrial environments.

Author contributions

YOA and BL fabricated the robot; YOA designed the robot and animal experiments; YOA and ACF performed animal experiments; YOA and MS performed the robot experiments; YOA, FLH and DIG wrote the paper; FLH and DIG guided the overall research program.

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Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

ORCID iDs

Yasemin Ozkan-Aydin  <https://orcid.org/0000-0003-4593-2146>

Max Seidel  <https://orcid.org/0000-0002-3677-7079>

Frank L Hammond III  <https://orcid.org/0000-0002-1634-7573>

Daniel I Goldman  <https://orcid.org/0000-0002-6954-9857>

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