

Functional diversity of snake locomotor behaviors: A review of the biological literature for bioinspiration

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Abstract

Organismal solutions to natural challenges can spark creative engineering applications. However, most engineers are not experts in organismal biology, creating a potential barrier to maximally effective bioinspired design. In this review, we aim to reduce that barrier with respect to a group of organisms that hold particular promise for a variety of applications: snakes. Representing >10% of tetrapod vertebrates, snakes inhabit nearly every imaginable terrestrial environment, moving with ease under many conditions that would thwart other animals. To do so, they employ over a dozen different types of locomotion (perhaps well over). Lacking limbs, they have evolved axial musculoskeletal features that enable their vast functional diversity, which can vary across species. Different species also have various skin features that provide numerous functional benefits, including frictional anisotropy or isotropy (as their locomotor habits demand), waterproofing, dirt shedding, antimicrobial properties, structural colors, and wear resistance. Snakes clearly have much to offer to the fields of robotics and materials science. We aim for this review to increase knowledge of snake functional diversity by facilitating access to the relevant literature.

KEYWORDS

biomechanics, functional morphology, gross anatomy, integument, limbless reptiles, multiarticular muscles, vertebral column

BACKGROUND AND PREMISE

Living organisms must overcome endless challenges as they interact with their environments. The central premise of bioinspired design is that human-engineered devices face many of the same problems as do organisms in the natural world, allowing us to explore the natural world for novel, efficient, and elegant solutions to these problems. Limbless terrestrial vertebrates represent a set of organisms with major potential to inform engineering design, and whose potential has so far been only partly realized. Despite the role of limbs in tetrapod diversification, an elongate body plan with reduced or

absent limbs has evolved more than 25 times in the reptile order Squamata (which includes snakes, other lizards, and amphisbaenians), and in an amphibian order called the Gymnophiona, or caecilians.^{1–3} Of those, snakes have achieved by far the greatest taxonomic and functional diversity, inhabiting nearly every imaginable terrestrial environment^{4,5} (Figure 1). They are especially adept at moving through cluttered, confined, and complex environments, including dense grass, underground burrows, weed-choked swamps, tangled branches, and coral reefs, among others,⁶ though some species have subsequently entered such uncluttered environments as dune seas or open ocean. Thus, limbless locomotion clearly has applications to robots and

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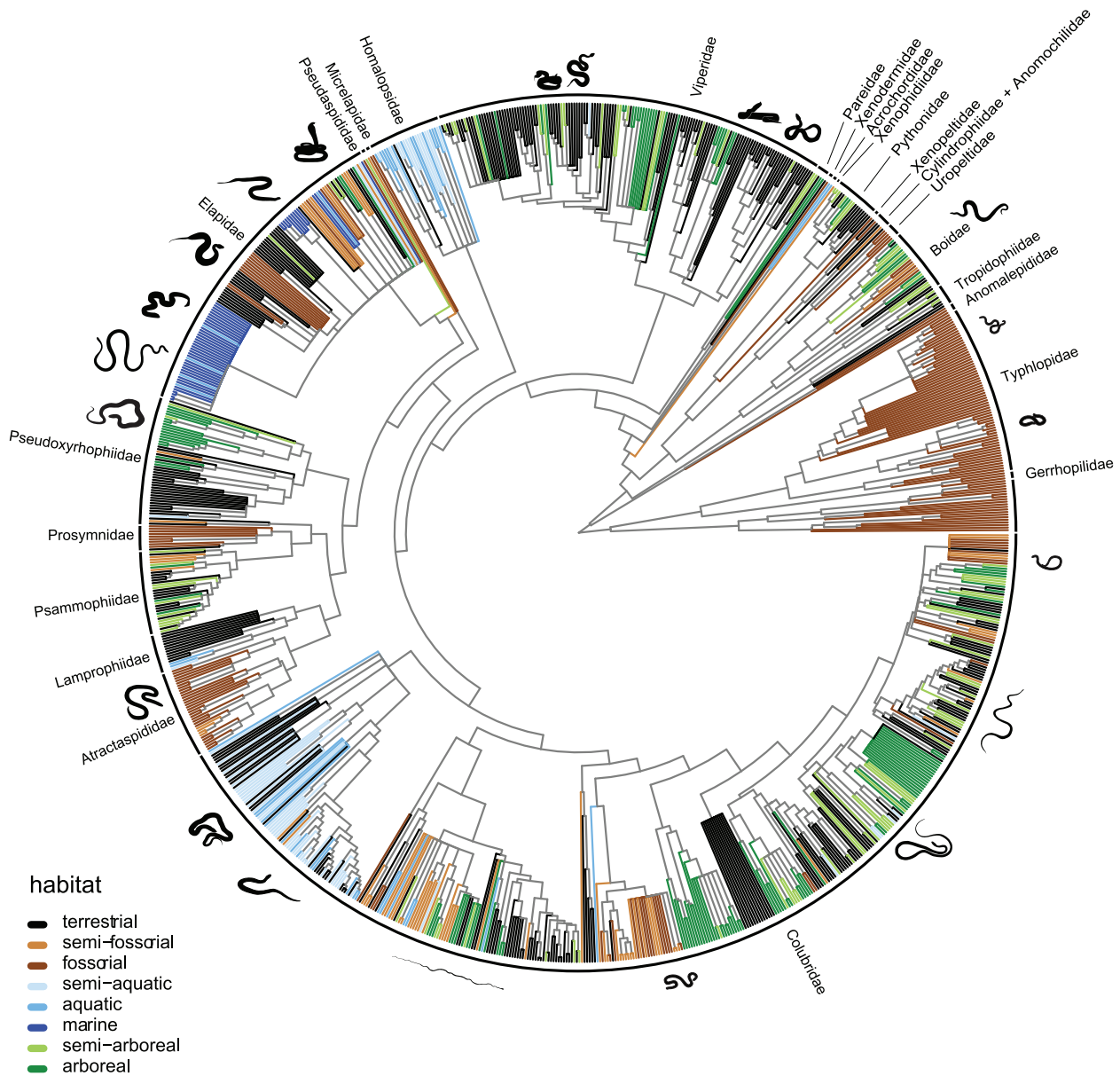


FIGURE 1 Phylogenetic tree showing snake habitat diversity. This phylogenetic tree displays habitat data for snake species representing 26 of 31 currently described families, with branch lengths proportional to time. It includes 1040 of the 4038 snake species listed in the December 2022 release of Reptile Database.⁴⁵ Habitat data were taken from field guides and monographs. The tree was pruned from Tonini et al.²⁹⁹ and plotted using the R package ggtree.³⁰⁰ Silhouettes not to scale and positioned near the branches representing their species; provided by authors J.L.T. and H.C.A., and phylopic.org users Ignazio Avella, Bill Bouton, V. Deepak, Guillaume Dera, T. Michael Keese, Blair Perry, Beth Reinke, Ferran Sayol, Alex Slavenko, Felix Landry Yuan, and Christina Zdenek (full license information provided in Table S1).

other devices designed to move through similarly cluttered, confined, and complex environments, including the natural ones that living snakes navigate so successfully, as well as human environments like building rubble after natural disasters, pipes or complex machines that need inspected or repaired, or even inside the human body for medical procedures.

In recent decades, scientists and engineers have taken inspiration from these functionally diverse animals to design snake-like robots and continuum robot arms for a variety of tasks. Most early work qualitatively mimicked snake body shape and/or movement, without the

benefit of quantitative data from live snakes (e.g., Refs. 7–10), and some of them departed from the snake body plan by inclusion of wheels or treads (e.g., Refs. 11 and 12); however, some exceptional early studies did verify mathematically derived theory with snake experiments.^{13–16} More recently, the application of data from live snakes has increasingly allowed snake-like robots to more effectively replicate a range of functions that snakes can perform but that remained outside the capability of robots.^{17–21} Despite these advances, snake-like robots still cannot replicate the versatility of living snakes, nor can they often achieve the same level of performance, leaving open many areas for future

multidisciplinary collaborations to push the boundaries of snake-inspired design.

Our goal in this review is to provide an overview of exciting aspects of snake biology that could provide inspiration for engineering design, and that might not be well-known to scientists and engineers who are not immersed in organismal biology. In so doing, we aim to provide a robust list of references on various topics for those aiming to dig deeper. Given the complexity of living organisms, we hope that this review will serve as a resource to anyone who endeavors to discern which biological aspects hold relevance to engineering challenges. Our goal is not to exhaustively review the existing literature on applications (e.g., snake-inspired robotics), as several such reviews exist.^{22–26} We wish instead to encourage scientists and engineers working on snake-inspired robots to continue incorporating relevant aspects of snake biology into their inspiration and design process, while also encouraging them to take inspiration from snakes for devices beyond snakebots.

SNAKE LOCOMOTOR MODES

For the better part of a century, biologists have canonically (if overly simplistically) recognized four modes of snake locomotion: lateral undulation, sidewinding, concertina, and rectilinear^{27–33} (Figure 2). Unfortunately, this categorization erases important variation within categories, some of which actually represent more than one distinct way of moving, and it also excludes a wide diversity of movement patterns not captured within the categories (see Ref. 34 for a review and discussion of this problem). Although this categorization may serve as a starting point for understanding limbless locomotion, a more nuanced and expansive view will help us to appreciate and more effectively study the full diversity of snake locomotor capabilities. Here, we will briefly describe the better-known modes of snake locomotion, point out some additional ways that snakes can move in a variety of situations, and then touch on some nonlocomotor behaviors that could inspire design.

Slithering: Lateral undulation plus vertical undulation

The most common locomotor mode used by limbless terrestrial vertebrates is lateral undulation, or slithering (Figure 2A). All snakes can use this mode of locomotion,²⁹ as can the other limbless terrestrial reptiles and amphibians, although the single term “lateral undulation” belies much kinematic and mechanistic diversity.^{3,32,35–39} During lateral undulation, the animal propagates a lateral bend down its body from head to tail, generating propulsive force by pushing on rocks, sticks, or other objects in the environment.^{27,29,40} As the animals undulate, they can selectively lift portions of their bodies’ bends to dynamically redistribute body weight in a way that enhances forward progress,⁴¹ implemented in robots as a sinus-lifting gait (see Refs. 42 and 43). Recent work has shown that snakes can also generate propulsive force via posteriorly propagating vertical bends, in a manner

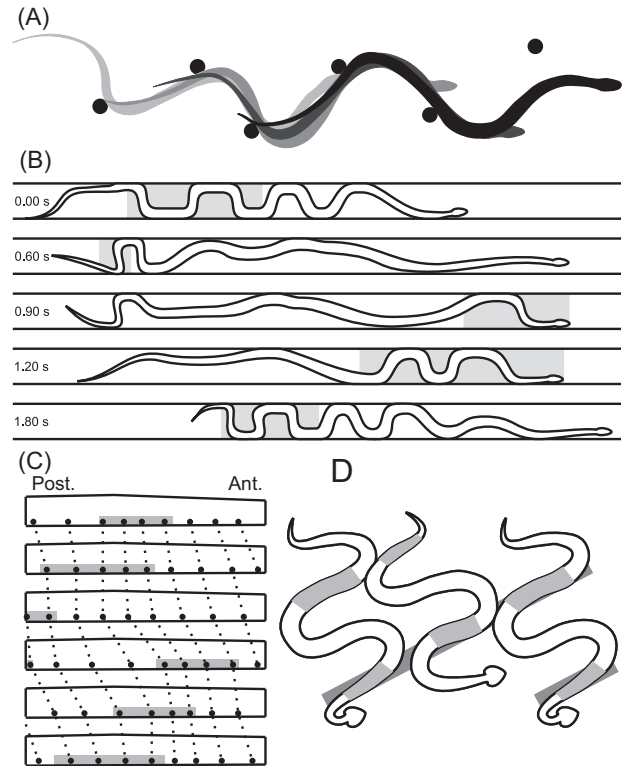


FIGURE 2 Diagram of several major snake locomotor modes. All image sequences depict a snake moving from left to right. (A) Slithering/lateral undulation, used in cluttered habitats. Posteriorly propagating bends press against objects in the environment to generate forward force. Darker outlines indicate later stages of the motion. (B) Tunnel concertina, showing extended, forward-moving body regions and flexed, static anchor regions. Gray indicates static body regions. The five vertically stacked concertina images represent five instants during a cycle, proceeding from top to bottom. Note that the term “concertina” also includes at least three additional kinematically different modes of locomotion, which can be used in various circumstances (see text). (C) Rectilinear, showing the lateral view of a body segment rather than the whole snake. Propagating regions of skin are lifted and moved anteriorly, then lowered, and retracted. Gray indicates static ground contact. The six vertically stacked images represent instants in time, proceeding from top to bottom. Dotted lines connect points on the body (black circles) at different moments in time as the snake progresses. (D) Sidewinding, used by several species in sandy deserts. Posteriorly propagating, offset waves of lateral bending combined with waves of vertical lifting and lowering produce propagating regions of static contact (gray) and lifted movement.

mechanistically similar to lateral undulation.³⁸ When provided a fully three-dimensional environment to move through, snakes will combine both lateral and vertical bending (often simultaneously), suggesting that this mode of locomotion is a fully three-dimensional behavior (“slithering”), with pure lateral and vertical undulation being artifacts of overly simplistic laboratory arenas.³⁹

Numerous authors have provided quantitative descriptions of lateral undulation,^{14,27,29,30,32,40,41,44,45} although some early descriptions erred in some aspects of the mechanics, and other authors have

investigated kinematics and muscle activity during lateral undulation for a variety of species.^{33,46–48} In most snakes, the pattern of bends tends to be irregular along the length of the body as the animal deforms itself to make contact with environmental push-points; however, some species might propagate very regular waveforms, exemplified by the sand-dwelling specialist *Chionactis occipitalis*.⁴⁸ Despite the energetic losses imposed by continuous sliding friction with the environment, metabolic measurements reveal equivalent caloric cost per meter in slithering snakes and limbed lizards of the same mass.⁴⁹

Swimming and floating

All snakes can likely swim via undulation.⁵⁰ Some species spend substantial portions of their lives in the water (Figure 1), including many in the family Homalopsidae^{51–55} and the colubrid subfamily Natricinae.^{56–60} The most specialized aquatic snakes include the Acrochordidae and certain marine members of the Elapidae, some of which have evolved tails with a pronounced paddle shape.^{61–65} A few studies have provided data on biomechanics and muscle activation patterns for snake undulatory swimming, also known as anguilliform swimming, which involves the propagation of a lateral traveling wave down the entire body, the amplitude of which increases from the head to the tail.^{46,66–72} Note that those looking to design an undulatory swimmer would do well to also examine the literature on other elongate animals, especially eels and lampreys; after all, the eel genus *Anguilla* lent its name to the term “anguilliform swimming.” Despite the superficial similarity of undulatory swimming and terrestrial lateral undulation, they differ in aspects of their kinematics and underlying muscle activity (for a detailed discussion, see Refs. 34 and 46). As for terrestrial lateral undulation, snakes show interesting variations in undulatory swimming. For example, species from at least two distantly related families can propagate a traveling wave in the reverse direction from normal (tail-to-head instead of head-to-tail) to swim backward, the sea snake *Hydrophis platurus*⁶¹ and the file snake *Acrochordus granulatus*.³⁴

Some species can float on top of water, no small feat given the extreme stability challenges of having an elongate form.⁷³ Aquatic species might assume a floating position with their heads positioned above their bodies, such that they could conceivably sense the environment around them more effectively than if they were actively swimming. Theoretical modeling has provided insight into potential mechanisms behind the maintenance of such a posture so that the principles of this behavior can eventually be applied to elongate aquatic robots.⁷³

Sidewinding

Like lateral undulation, sidewinding involves the propagation of a traveling wave from head to tail (Figure 2D). However, instead of sliding along the ground, a sidewinding snake maintains some sections of the body in static (or nearly static) contact with the ground while lifting other sections up and forward to new contact patches far-

ther ahead.^{29,33,74–76} Although motor control of sidewinding in living snakes remains an open question, sidewinding can be kinematically represented by combining vertical and lateral waves with a phase offset.^{18,77} As the waves propagate together, each point on the body is cyclically lifted from the substrate, moved forward, and placed into contact again, with subsequent points following at a slight lag.

Early papers on sidewinding sometimes described sidewinding as a “rolling” motion, in large part because it leaves disconnected tracks in the sand that resemble the result if one were to roll a helix along the ground.^{27,75} More recent theoretical work has sometimes made use of this model, using an elliptical spiral to define a backbone curve.^{9,10} Although this model might be useful in certain specific circumstances, snake sidewinding locomotion is not correctly described as “rolling.” In a rolling system, an element of the rolling object (e.g., a portion of a tire or segment of a tank tread) undergoes a rotational transformation, which results in a reorientation of the element with respect to the world. If the rotational axis is horizontal (as in most such systems), the element will reorient such that the lowermost surface becomes uppermost and vice versa, as in a wheel. Furthermore, in true rolling systems, rotation will continue in the same direction until the original orientation has been restored. In contrast, aside from some minimal and transient tilting during lifting and lowering, the body segments of sidewinding snakes always retain the same orientation, and there is never a period in which the ventral surface of the snake is uppermost.

Several researchers have put forth models of sidewinding locomotion grounded in data from sidewinding snakes, which have allowed snakelike robots to more effectively replicate a range of functions that sidewinding snakes can perform, including ascending slopes, turning, and negotiating obstacles.^{17–20} Additional studies address a variety of additional questions related to sidewinding in living snakes, including muscular mechanisms,⁷⁸ maximal performance,^{79,80} the exceptionally low energetic cost,⁸⁰ among-species kinematic differences,^{33,81} within-species kinematic differences,⁸² scaling of kinematics with body size,⁸² and substrate effects on kinematics⁸³ (for a systematic review of the literature on sidewinding through 2019, see Ref. 84).

Contrary to the archetype of snakes as masters of confined and cluttered environments, sidewinding snakes maximize their potential in wide open spaces, although sidewinding does allow certain maneuvers as long as the environment does not become too cluttered.^{18,19} This mode of locomotion is strongly associated with viper species inhabiting several of the world’s deserts, likely because it provides a way for them to overcome the challenges associated with shifting sand. Vipers tend to have stout bodies relative to many other snakes,⁸⁵ and perhaps because of their body dimensions, vipers that attempt to use lateral undulation on sand tend to make little-to-no forward progress while wasting their effort pushing sand from side to side,⁴⁵ especially if the ground is sloped to any degree.¹⁷ Sidewinding, even a heavy-bodied snake can move relatively rapidly and efficiently across the sand and other shifting or smooth surfaces, including tidal mudflats and lab floors (for a review, see Ref. 84).

Unlike lateral undulation, sidewinding evidently cannot be performed by all snake species, and it has never been recorded for other elongate, limbless tetrapods.^{17,19,84} About a dozen viper species (not

all closely related) use sidewinding as a primary mode of locomotion when undisturbed in nature, and dozens of other species across the snake family tree can sidewind with varying degrees of proficiency when conditions elicit it.^{84,86} Some of the former have derived morphological features (e.g., muscle architecture⁸⁷ and skin nanostructure⁸⁸) hypothesized to improve sidewinding performance, potentially at the cost of reducing the performance of lateral undulation or other behaviors.

Jumping and cartwheeling

In the course of very fast sidewinding, a snake might generate enough impulse to propel itself from the ground, replacing one or more sidewinding cycles with leaps or jumps, or a snake might jump from a resting position after taking a pause during sidewinding.⁷⁶ Sometimes, an individual from a species not renowned for sidewinding might lunge or jump during an apparent attempt to sidewind as an escape behavior.^{89–92} During these jumps, snakes can become fully airborne. Jumping (also known as saltation) is not restricted to snakes among elongate tetrapods—it is considered a “characteristic behavior” of many members of Pygopodidae,⁹³ a family of geckoes that abandoned their famously sticky feet in favor of a snake-like body plan. Other limbless lizards have also been known to jump,^{94–96} as have amphisbaenians.^{97,98} Whereas jumping might lead to forward displacement, it does not necessarily do so, and jumping with no net displacement may serve the function of startling potential predators.^{93,95,98} Small individuals jump more readily than do large individuals in sidewinding South African horned adders (*Bitis caudalis*).⁷⁶ A recent preprint presents similar results for jumping in juvenile anacondas (*Eunectes murinus*), demonstrating that only small individuals jump.⁹⁹ The authors used mathematical modeling to demonstrate that as the snakes grow, their body weight eventually passes a threshold beyond which the muscles simply cannot generate enough torque to overcome gravity.

That inertia dominates jumping distinguishes it from most other modes of terrestrial snake locomotion, in which frictional forces tend to far outweigh inertial forces.⁴¹ As a result, one would expect allometric scaling relationships in jumping and the traits that enable it, unlike other locomotor modes, where isometric scaling (i.e., geometric similarity) means that differently sized snakes might largely be scale models.⁸²

Some old accounts present seemingly fantastical descriptions of “hoop snakes,” reputed to rapidly bound forward in a cartwheeling motion (e.g., Ref. 100). One could be forgiven for dismissing these as the product of overactive imaginations. Astoundingly, though, at least a couple of species really can jump so vigorously that they cartwheel themselves away from perceived danger with truly shocking rapidity, alternating between airborne and ground contact phases.^{101,102} This movement is also notable for its incorporation of rolling, an extremely rare form of movement by animals in contrast with its ubiquity in engineered systems. This impressive locomotor feat clearly deserves additional attention.

Concertina locomotion

Concertina locomotion is an extremely common and kinematically diverse mode, despite being both slow and metabolically expensive.^{33,34,49,103} In the broadest sense, snakes perform concertina using a combination of static anchoring points with the substrate interspersed with moving regions which use axial bending and straightening to move portions of the body forward (Figure 2B); these regions typically propagate posteriorly and are quite large, with snakes rarely if ever having more than three regions (one static and two moving or vice versa) on the body at any given time.^{33,34,104–106} Typically, a posterior anchor section will grip the substrate, while the anterior body extends until it establishes a new grip. With the anterior gripping section established, an increasingly large section of the body will be pulled forward into the anterior static contact region as it is released from the posterior static contact region. Initiation of a new cycle of forward movement at the anterior may or may not begin before the end of the tail has become static. Thus, any given point on the body is cyclically statically anchored, moved forward, then anchored again.^{33,34}

However, beyond the generalized description, concertina varies tremendously, and it may be the most kinematically diverse mode of snake locomotion.³⁴ Snakes can use concertina in a wide range of habitats, including traversing tunnels of variable diameter and slope, branches of variable diameter and slope, and flat surfaces which either lack suitable contacts for slithering or in which those contacts are too weak to withstand the forces needed without yielding.^{33,34,104–106} The fundamental mechanics of concertina must differ depending on the environmental context. The static anchoring may be achieved in a tunnel by laterally flexing the body outward to form bends which brace against the walls (termed “tunnel concertina”), or on a flat surface by simply anchoring via static friction (termed “flat-surface concertina”).^{33,34} It may be achieved in at least two separate ways in arboreal settings: through a combination of lateral and ventral flexion to grip the sides of a tree branch or trunk, or by helically spiraling the body around a tree trunk.^{34,104,105} The precise kinematics are similarly variable. Bends may be propagated down the body as in slithering,¹⁰⁴ or may be straightened and reformed with each cycle, not necessarily at the same points on the body.^{33,34} The pattern of bending varies with environment, species, and even from cycle to cycle.^{33,34,104–106} The distance moved per cycle may measure less than 2% to over 20% of body length.^{33,34,104,105} Active use of the scales may help prevent slipping.¹⁰⁷

The distribution of various versions of concertina across the snake family tree remains largely unknown, aside from knowledge of its general presence in most snakes.^{32–34} Beyond snakes, concertina is best known in amphisbaenians, a group of burrowing squamate reptiles, and in a largely subterranean order of amphibians called the caecilians.^{35,37,108,109} These groups add additional richness to concertina biomechanical diversity, as some of them can perform a rather different version that has been called “internal concertina,” enabled by loose skin.^{35,37,108} Although concertina has not been documented for many groups of nonsnake limbless lizards, it is not completely unknown in these groups; it has been reported that some Australian skinks use

concertina when traveling through a pegboard at low speeds, though the species was/were unspecified and a detailed paper was never published.³² Concertina's versatility comes at a steep metabolic cost: it is far more metabolically expensive than any other known mode of snake locomotion, which leads to very poor endurance.^{49,103} This cost may result from the high forces produced during anchoring, which causes concertina to reach 5x the minimum gripping force necessary to counteract gravity during vertical climbing.^{107,110}

Rectilinear locomotion

Rectilinear locomotion is a peculiar and distinctive mode of snake locomotion, in that it is the only one which does not rely on bending the body axis,^{34,111} nor even on the motion of skeletal elements.¹¹² Instead, rectilinear locomotion is achieved by cyclic motion of the ventral skin, each segment of which is lifted clear of the substrate, moved forward (relative to both the static substrate and the snake's body), placed into static contact with the substrate, and then retracted relative to the body, with minimal slip relative to the substrate.^{34,111,112} (Figure 2C). Each cycle of motion propagates posteriorly, resulting in traveling waves of lifted movement and static contact that generate propulsive force against the substrate.^{34,111,112} Although early researchers postulated rib motion as a driving mechanism, much like the legs of a millipede, X-ray videography showed that during rectilinear locomotion, a snake's body translates forward with no obvious movement of skeletal features relative to each other.¹¹²

Instead, the motion is powered by two muscle groups that connect the ribs to the ventrolateral edge of the skin (the costocutaneous superior and inferior), plus cutaneous muscles.^{111,112} The resulting locomotion is far slower than any other mode,^{27,34,112} though precisely why remains unknown. Similarly unknown are the metabolic cost of transport, endurance, responses to environmental variation, and frequency and circumstances of use in the wild.

While rectilinear locomotion is commonly associated with large, heavy-bodied species such as many pythons, boas, and vipers, most terrestrial species seem to have at least some capacity for it,^{27,32,34,113,114} even if only used in a portion of the body in combination with other modes. Rectilinear locomotion is also seen in amphisbaenians (a clade of predominantly limbless squamates), which can use it to move both forward and backward.^{30,32,115} However, presence/absence or relative use across species has not been systematically tested. We also lack data on other aspects of rectilinear locomotion, including whether high body mass per unit length might be an advantage for this mode or merely a disadvantage for other, faster modes.

Burrowing

Although many snakes will use pre-existing burrows or push their way through leaf litter, a few clades specialize in excavating their

own tunnels. These burrowing (or fossorial) snakes appear throughout the snake family tree (Figure 1). The largest such group are the five families commonly known as blind snakes, most of which are each other's closest relatives: Typhlopidae, Leptotyphlopidae, Xenotyphlopidae, Gerrhopilidae, and Anomalepididae. Among the rest of the snakes, many members of the families Uropeltidae, Atractaspididae, and Calamariinae have fossorial or semi-fossorial habits, along with various other species spread throughout the phylogeny. Not alone in their proclivity for adopting a subterranean lifestyle, snakes share the underground realm with other elongate, limbless tetrapods that burrow in soil or sand, including various lizards,¹¹⁶⁻¹¹⁹ amphisbaenians,^{97,120} and caecilians.^{121,122} These species might inspire the design of machines that need to excavate tunnels and/or move through subterranean environments.

Fossorial species must overcome many challenges. These include the requirement of generating high forces when burrowing in soil, which could be compacted and/or contain obstacles like rocks and roots, a task that they might accomplish with either a rigid, reinforced skull or with more kinetic skulls where the parts might be independently mobile, and perhaps also with derived trunk morphology.^{37,123-129} High forces combined with rough particles induce substantial abrasion. Some species burrow in sand or other granular media, which impose specific challenges due to their mix of solid-like and fluid-like properties, and which, like many other substrates, can pose different problems when wet than when dry.¹³⁰⁻¹³⁵ Underground, animals must contend with reduced visibility, which creates a need to sense the environment through tactile or chemical cues, or detection of vibrations propagated through the substrate.¹³⁶⁻¹³⁸ They must also resist the infiltration of dirt or sand into the body, which they may overcome through derived anatomical features or behavior.^{139,140} Some aquatic snakes (especially in the family Homalopsidae and colubrid subfamily Natricinae) burrow into the muddy or rocky bottoms or banks of their watery habitats, likely facing very particular problems associated with aquatic burrowing.^{54,59,60} Meanwhile, in the driest of Earth's biomes, certain dune-dwelling vipers move their ribs in a way that lets them sink into the sand, termed "vertical burrowing."¹⁴¹

The study of burrowing has posed logistical challenges. Subsurface animals cannot be seen, although imaging via X-ray video has made it possible to study some burrowing organisms. Additionally, the mechanics of burrowing through mud remains a particularly open question, likely due to the difficulty of experimental preparations involving damp or wet media. Several studies have shed light on the mechanics of aquatic and mud burrowing in elongate invertebrates,¹⁴²⁻¹⁴⁵ although size differences likely lead to very different mechanical environments for most of these species compared to snakes; a few studies have examined the mechanics of aquatic burrowing in eels,^{146,147} which we would expect to be more similar to snakes. Recent technological advances combined with clever experimental setups should provide opportunities for researchers to make major progress in the study of fossorial snake locomotion in the coming years.

Climbing, cantilevering, and gliding

Arboreal environments challenge animals to move on branches and trunks that vary in diameter, incline, flexibility, and surface texture, while also contending with secondary branches and vegetation both emerging from and impinging into a desired path as well as gaps between supports of highly variable distances.¹⁴⁸ Failure imposes a high cost, with larger animals facing potentially disastrous falls.¹⁴⁸ Although small animals may not face certain doom from ground impact,¹⁴⁹ falling still causes them to risk predation and expend energy while returning to the trees.

Branch diameter and secondary branching have starkly different consequences for snakes compared to limbed taxa as they move through the canopy. Limbed taxa move more rapidly on larger branches, as these branches more closely resemble the ground and ameliorate various problems of balance on narrow supports, regardless of whether the large branches have secondary branches emerging from them¹⁵⁰ or not.^{151–157} In contrast, snakes excel on secondary branches that impede the locomotion of limbed species,¹⁵⁰ reliably and rapidly performing slithering locomotion.^{105,158,159} The ability to generate propulsive force from vertical bends in addition to horizontal ones may provide a further advantage in cluttered habitats.³⁸ On larger diameters, snakes move more slowly, in part because they must engage a greater proportion of their bodies on lateral motion and gripping.^{104,159}

Ascending and descending pose challenges beyond those of translation through the canopy. Arboreal animals may, therefore, require special behavior and/or anatomy to either fight gravity (during the ascent) or work with it without tumbling downward (during the descent). For example, they might take advantage of surface roughness (as distinct from friction), although limbed versus limbless animals may use different strategies: just as many mammals or limbed lizards can use claws to interlock with the substrate, some snakes can form ridges in their ventral scales to allow slithering in many challenging situations (including on the underside of branches!).¹⁰⁵ Lab experiments with pegs (to simulate secondary branches) have demonstrated that while snake locomotion is impeded during an ascent compared to horizontal translation, the addition of pegs substantially increases speed and capability.^{104,105,158,159} Similarly, although downhill locomotion on surfaces lacking pegs can prompt unusual behaviors which resemble controlled sliding,¹⁰⁴ adding pegs allowed slithering and improved speed when descending perches.¹⁵⁸ Thus, taken as whole, the same arboreal environments which impede limbed taxa (narrow branches with many secondary branches) are beneficial to snakes, consistent with their general superiority in cluttered, confined, and complex habitats.

Bridging potentially large gaps presents a further challenge for arboreal animals. One common mechanism for both limbed and limbless species is simply reaching across, which typically allows either static stability or at least retaining an anchor in case of a mistake.^{148,160} In snakes, this behavior is known as “cantilevering,” and, when done slowly, it can be approximated as a cantilevered

beam problem,^{160,161} making it more amenable to analysis than more dynamic motions are.^{160,162} The ability to cantilever across gaps differs across species¹⁶³ depending upon the geometry of the musculoskeletal system^{164–166}; this fact in turn has led to significant insights into the musculoskeletal system (see the subsection on muscles below). A few species use more dynamic “lunging” behaviors, which allow them to cross slightly longer gaps than possible compared to cantilevering.^{160,162,167} Dynamic lunging behaviors might serve as the precursor for the most impressive gap-bridging mechanism among snakes: the gliding flight of snakes in the genus *Chrysopeled*.^{160,162,168,169} These remarkable snakes launch themselves from tall trees,¹⁶⁹ after which they use their highly mobile ribs to form an airfoil-like surface capable of generating lift.¹⁷⁰ During flight, they undulate their body to maintain control over their otherwise unstable posture.¹⁷¹ They have sufficiently mastered gliding control that they can turn during mid-glide to avoid obstacles.¹⁶⁸

Although many distantly related snakes have specialized in the tree-dwelling life (Figure 1), no limbless tetrapods outside of snakes have achieved arboreality to a comparable degree. Most limbless lizards are regarded as fossorial or terrestrial,¹⁷² though several species of pygopod geckoes are known to climb.^{173,174} The cause of the disparity in habitat diversity between snakes versus other limbless squamate reptiles remains unknown.

The role of substrate in snake locomotion

Whereas limbed locomotors primarily change gaits to modulate speed,^{175,176} snakes change the locomotor mode in response to features of their environment. Slithering snakes, for example, generate reaction forces by propagating body bends which press against suitably oriented features of the substrate, which in turn requires surface features of the appropriate geometry, friction, and orientation. The availability of more contact points allows snakes to increase overall speed during slithering, at least until the density becomes too confining.¹⁷⁷ In the absence of either pre-existing structures (e.g., grass, rocks, branches) or self-generated ones (piles of sand displaced by the body), the snake must resort to other locomotor modes, like a concertina or rectilinear.^{38,44,45,158} The environmental context of sidewinding contrasts strongly with that of lateral undulation, in that sidewinding requires sufficiently open spaces to accommodate the relatively wide path of their body.²⁹ Sidewinders whose path is blocked by obstacles can sometimes change their waveform to negotiate the obstacles, but they may also employ concertina locomotion to traverse these before resuming sidewinding.¹⁹ Concertina, in turn, is often associated with tunnels, although a tunnel's characteristics determine whether a snake uses concertina or some other gait. When presented with a rectangular tunnel with parallel walls and devoid of push points, snakes will perform concertina locomotion, but will immediately switch to slithering when encountering suitable contact surfaces in the form of a bend in the tunnel,⁴⁴ pegs,¹⁵⁸ or a vertical wedge.³⁸

Historically, many laboratory studies of animal and machine locomotion have necessarily used artificial surfaces (e.g., laboratory floors) as their testing environments. Flat, rigid, and smooth, such surfaces are not typically encountered in nature. Some snakes, particularly sidewinding specialists, may successfully negotiate these surfaces because their locomotor strategy for overcoming slipping on sand also mitigates slipping on vinyl or other such artificial surfaces.⁸³ Lacking the ability to sidewind, many species resort to either flat-surface concertina³³ or lateral undulation⁴¹ when placed on smooth, rigid surfaces. In this latter case, frictional anisotropy and lifting of certain body segments (sinus lifting) may allow some measure of forward progression,⁴¹ though with far more slipping and far less economy of motion than slithering in natural terrain; below a certain level of friction, snakes may simply become stuck. Observations of snakes moving despite slippage on roads and polished floors prompted a description of a gait called slide-pushing,^{31,32,178} which is no more a natural mode of snake locomotion than ice-skating is a natural mode of human locomotion. While such artificial conditions can be useful experimental perturbations to explore mechanics and control,^{41,83,88} the irrelevance to natural behavior means the results of such experiments should be used only with caution during the process of bioinspired design.

ADDITIONAL SNAKE BEHAVIORS

Lacking limbs, snakes rely on their elongate trunks for nearly all their behaviors, not just locomotion. As a result, they execute many tasks in a fundamentally different way from their limbed relatives, potentially providing a wealth of inspiration and data that applied scientists can translate into engineering design. We will not exhaustively review them here, given our main focus on locomotion, but we will provide some examples with a few references for anyone who wants to dig deeper.

Striking

Snakes can defend themselves against predators by striking as a deterrent, and many species strike to envenomate and/or capture their prey in terrestrial, arboreal, and aquatic environments. During a predatory strike, a venomous snake may either bite and release or bite and hold on until the venom takes effect, whereas a nonvenomous snake must progress to a prey subdual behavior after the initial strike. Several researchers have quantified biomechanics and performance metrics of snake strikes in a variety of contexts (e.g., Refs. 179–186). Striking behaviors can diverge widely across taxa. To give one somewhat bizarre example, snakes of the genus *Atractaspis*, which count “stiletto snakes” and “side-stabbing snakes” among their common names, can envenomate prey via a backward or sideways stab without even needing to open their mouths, allowing them to strike prey in tight spaces like burrows.¹⁸⁷ Recent research trends suggest that we will continue to learn substantially more about striking in the next few years. A bet-

ter understanding of snake strikes could inform a variety of engineering applications, including anything that requires accurate movement during rapid acceleration of complex, high degree-of-freedom systems.

Prey handling

Limbleless predators like snakes face particular challenges with respect to prey handling. One of the more famous, well-studied snake prey subdual methods is constriction, whereby a snake coils itself around a struggling prey with either the lateral or ventral surface contacting the prey, then applies pressure until the prey is incapacitated (e.g., Refs. 188–191). Most commonly observed in terrestrial contexts, constriction also serves in arboreal contexts where a snake may use the anterior half of its body for constriction, while the posterior body grips a branch to keep the snake suspended.^{192–194} Some species use derived behaviors and/or morphologies to overcome very particular challenges related to subduing certain prey, like members of the genus *Tantilla* (commonly called “centipede snakes” or “flat-head snakes”) that feed on elongate, venomous centipedes,¹⁹⁵ species in the Homalopsidae that rip apart crustaceans that would otherwise be impossible to swallow,¹⁹⁶ and egg-eating species that puncture eggs after swallowing to release their nutritious contents.^{97,197} Insights from the close study of snake prey handling could translate into a variety of object apprehension and manipulation tasks.

Prey ingestion

Among their most famous attributes, the kinetic heads characterizing most snakes allow them to swallow surprisingly sizeable prey.^{6,198} Once swallowed, large meals require the body cavity to expand and the skin to stretch to accommodate the bolus. During digestion, a snake might need to change its location, requiring it to overcome the locomotor challenges of added mass and a bulging body.^{199,200} We still have much to learn about how snakes overcome these challenges, but it does not seem like too much of a stretch to suggest that the answers might prove useful to elongate devices that “swallow” items for storage, transport, or other purposes.

Defensive displays

Despite all this discussion of snakes as predators, they also risk themselves becoming prey. To mitigate this risk, many species have evolved various defensive displays.²⁰¹ Some of the most spectacular examples come from the family Elapidae, including the hood display of cobras²⁰² and the mind-bending acrobatics of coral snakes,^{203,204} both of which are mimicked by harmless species that coexist with them. Display behaviors might pose idiosyncratic requirements on the muscles that actuate them (see discussion in Ref. 205). The biomechanics and control of these diverse behaviors certainly merit more attention.

Additional behaviors

Above, we reviewed some of the most iconic snake behaviors. This list is far from exhaustive: some species engage in wrestling/combat,^{206–208} at least one sea snake species can tie itself in knots, perhaps to clear the skin of ectoparasites,²⁰⁹ and some species generate sound by vibrating their tails, rubbing sections of their bodies together, or forcefully expelling air from their cloaca.^{210,211} A deeper dive into the snake literature reveals still more. This vast diversity of snake behaviors could have a similarly vast diversity of applications in bioinspired design.

INTERNAL MECHANISMS OF MOVEMENT

The diversity of behaviors described above must be produced via internal mechanisms. To truly understand organismal function, we must, therefore, complement our study of behavior with close examination of actuators, support systems, and surface interfaces. Knowledge of the anatomical and physiological underpinnings of animal behaviors may, in turn, promote the design of more efficient, more multifunctional, and/or generally better-performing engineered systems.

Muscles

Snakes' ability to perform the behaviors described above is ultimately contingent upon their actuator: muscles. As for any actuator, muscular function depends on both gross architecture (anatomy/morphology) and on its specific properties (physiology). Snake muscular anatomy shows a tantalizing mix of simplicity and complexity, potential adaptations and constraints, clever innovations, and puzzling mechanisms. Regarding simplicity, much of snake musculoskeletal anatomy is fundamentally metameric: the trunk consists of repeating segments, with each segment comprising a vertebra, its ribs, and one distinct muscle belly of every muscle type on each side of the body^{212–215} (Figure 3). Some snake species have slightly more than 100 segments, whereas others far exceed 300.^{216–218} Anatomy differs at either end of the snake, with vertebral shape accommodating different functions for the head and tail, and muscle spans changing as they approach the end of the vertebral column.^{216,217,219–221} The system's complexity comes from its predominantly multiarticular nature—while a few muscles connect one vertebra or rib to the adjacent one, most span several vertebral segments, overlapping with muscles of the same type in closely associated “bundles” running much of the length of the snake^{222–225} (Figure 3). The multiarticular span may be a modest three to five vertebrae for some muscles, but others may span dozens of vertebrae.^{87,205,218,222–225} Multiarticular spans range from entirely muscular to highly tendinous, and these proportions are known to vary across species based on descriptions.^{205,223–226} While some muscle–tendon units connect only to the relevant bones (or skin, in the case of the superior and inferior costocutaneous muscles), others show potential tendinous connections to adjacent muscles.²²⁵ These connections appear to vary among species,²²⁵ are difficult to trace

even for a skilled anatomist, and typically pass through fascial sheets which separate adjacent muscle groups (*pers obs.*), leaving it unclear whether substantial force or motion is transmitted between the muscles.

Axial muscle architecture shows clear signs of having evolved to accommodate the highly elongate body plans of some squamate reptiles, and within snakes, the limited available evidence points toward anatomical specialization for particular habits or behaviors. Across squamates, muscle groups are largely consistent in their presence but vary in the details of their anatomy.^{223–225} For example, the transversospinalis muscle group is always present, but within the transversospinalis group, various combinations of the individual muscles (spinalis, semispinalis, multifidus, interarticularis superior, and interneuralis) may be separated or fused depending on the species. Snakes differ from limbed squamates in several respects, including apparently greater differentiation between adjacent muscles, longer multiarticular spans, and longer tendinous portions of the muscle–tendon units.²²⁵ Other limbless squamates are diverse in their muscular anatomy, but overall they show greater similarity to snakes than to limbed squamates, particularly in terms of longer multiarticular spans, hinting at a functional benefit of longer spans for elongate body plans. Within snakes, one of the muscles known to play a role in locomotion, the semispinalis–spinalis, has been subject to detailed comparative analysis across a large number of species. Two studies showed that the span of this muscle–tendon unit evolves with respect to habitat, one of them conducted before the advent of modern phylogenetic comparative statistical methods²¹⁸ and the other conducted with phylogenetic comparative methods and a larger sample.⁸⁷ Arboreal species have extremely long spans hypothesized to improve cantilevering performance (a hypothesis later supported by mathematical modeling¹⁶¹), whereas sidewinding specialists have particularly short spans, hypothesized to provide the flexibility required to form the tight bends seen during sidewinding.^{87,218} Another study presented data on mass, cross-sectional area, and muscle–tendon unit length for three muscles (semispinalis–spinalis, longissimus dorsi, and iliocostalis) in a sample that included terrestrial, aquatic/semi-aquatic, and arboreal species; a phylogenetic test provided evidence that aquatic species have more massive semispinalis–spinalis muscles.²²⁷ Only in the last few years have functional studies begun to provide data supporting hypothesized mechanisms for some of the patterns revealed by comparative anatomical studies.

The functional consequences of snake muscular anatomy are straightforward in some aspects, such as lever arms. As in other vertebrates, a muscle's lever arm determines its relative contributions to torque about various axes of skeletal joints, while mediating the trade-off between force and motion. Although the lever arm approach assumes a single fulcrum, and hence most properly applies to monoarticular muscles, the intuition afforded by lever arms aligns with a more complex mathematical approach that explicitly accounts for distributed bending across the vertebral column in multiarticular systems²⁰⁵: muscles positioned dorsally or ventrally to the vertebral centra contribute to dorsiflexion and ventroflexion, respectively, with their contribution increasing with distance from the centra; muscles

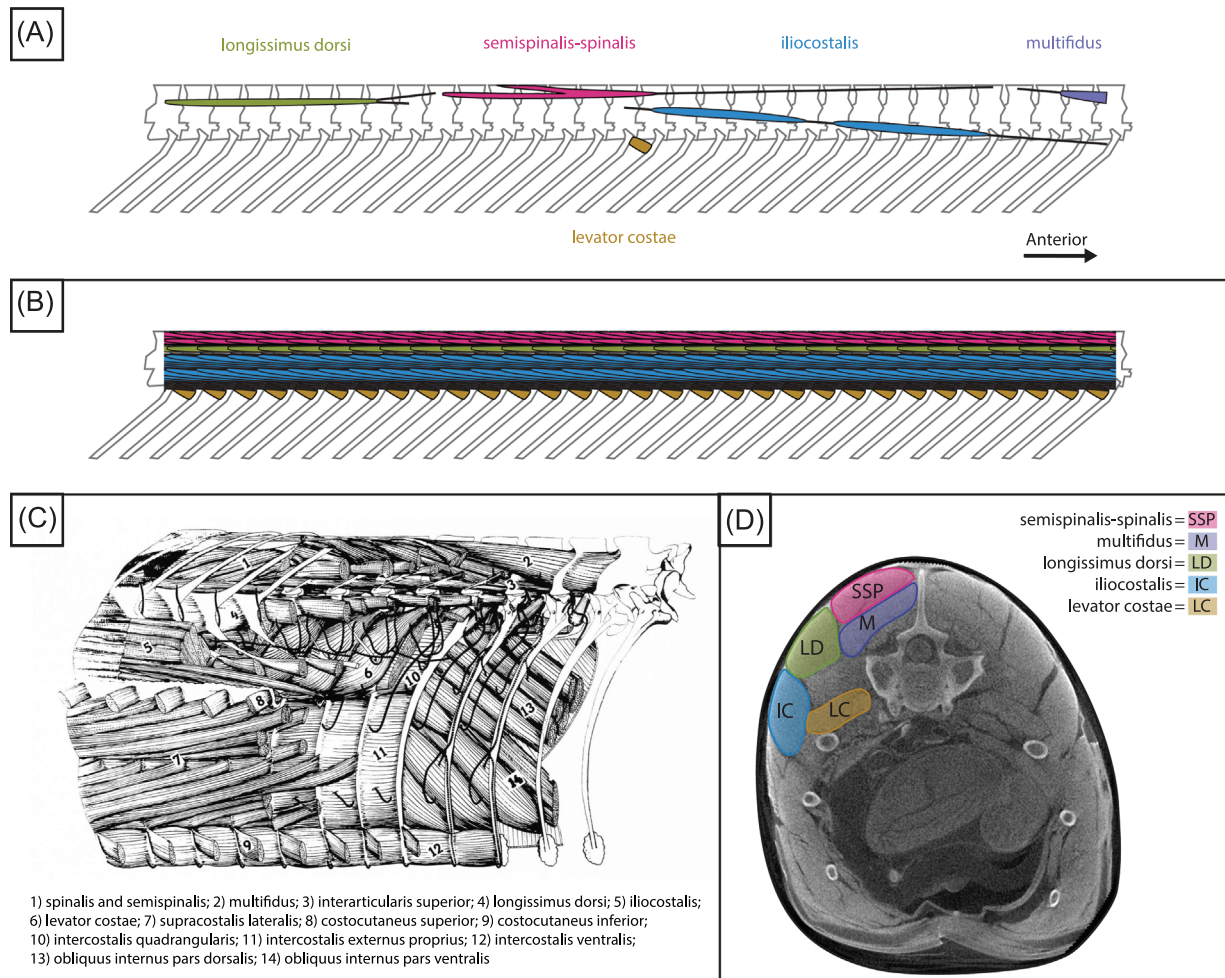


FIGURE 3 Diagrams showing five muscles in the corn snake *Pantherophis guttatus*. (A) A lateral view showing one of each type of muscle (modified slightly from Ref. 205). (B) A lateral view providing a better idea of snake anatomy. The trunk consists of repeating segments, with each segment comprising a vertebra, its ribs, and one distinct muscle belly of every muscle type on each side of the body. The multifidus is not visible because it is covered by more superficial muscles. (C) A detailed anatomical drawing of the axial musculature of the Saharan horned viper, *Cerastes cerastes* (reproduced from fig. 50 in Gasc,²²⁵ with permission from J.-P. Gasc). As in the upper panels, anterior is to the right. More superficial muscles are shown to the left, and deeper muscles are shown to the right. For anatomical drawings depicting the musculature for additional snake species, see Refs. 223–225. (D) A transverse section of a CT scan with the muscles outlined (reproduced from Ref. 205).

positioned more laterally have high lever arms for lateral flexion than do medially positioned muscles.

Despite recent advances, many aspects of functional morphology in multiarticular muscles remain poorly understood. For example, the impact of variation in the tendinous versus muscular proportion of the multiarticular span has been the focus of only a single theoretical study, which examined the consequences of multiarticularity during cantilevered gap bridging.¹⁶¹ Although multiarticularity allows a single muscle to apply torque across multiple joints, a multiarticular system can outperform a monoarticular one of the same muscle mass only through the presence of a substantial tendinous portion.¹⁶¹ As usual, a trade-off arises: when the proportion of the span occupied by the tendon increases, greater muscle strain (i.e., muscle length change as a fraction of resting muscle length) and higher strain rate are required for a given movement.^{161,228} Our understanding of the functional consequences of multiarticular muscle architecture will improve through

increased scientific efforts toward both phylogenetic comparative and functional studies, which strongly complement each other. Increased effort toward comparative studies (in the vein of^{87,218} for muscles beyond the semispinalis-spinalis) will provide data on anatomical diversity to fuel functional studies. The results of functional studies (in the vein of^{161,205}) will help explain evolutionary patterns revealed by comparative studies while also providing an avenue for applied scientists to translate biological diversity into societal benefit.

As with any actuated system, biological or mechanical, below the level of gross structure lie the properties of the actuators themselves. These are crucial for understanding the mechanical capabilities of the system. Yet, here we face an acute lack of data. Contractile physiology is unknown for the vast majority of snake muscles, with the sole exception of the costocutaneous superior and inferior.^{229–234} These muscles, most directly involved in rectilinear locomotion, display a mix of twitch fibers with properties fairly typical to most vertebrate

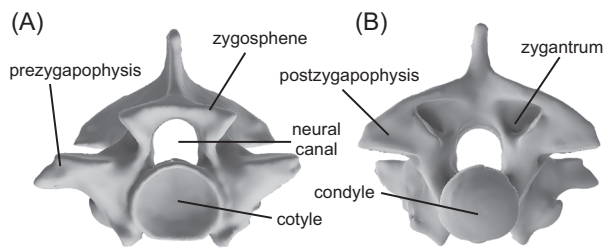


FIGURE 4 Vertebral morphology. Example snake vertebra from *Pantherophis guttatus*, based on μ CT scans. (A) Anterior view. (B) Posterior view. Note the ball-and-socket configuration of the cotyle/condyle, the overlapping and nearly horizontal pre- and post-zygapophyses, and the prominent zygosphene/zygantrum joint above the neural canal. Figure from Ref. 246.

muscles^{231,232,234} and much slower tonic fibers.^{229,230,233,234} To what extent these twitch properties are representative of other snake muscles remains unknown. Since vertebrate muscles vary widely, particularly with respect to time-dependent properties such as activation and deactivation rates and peak speed and power,^{235,236} it is difficult to infer how muscle properties affect movement. Moreover, the effects of temperature on performance suggest the effects of these time-dependent properties are substantial.^{56,237–240}

Skeletal system

The muscular system acts via the skeleton to produce overall body deformations. For locomotion, these can broadly be broken down into (1) motions of the vertebral column, generating torques and the overall path of the snake's body, and (2) motions of the ribs, which, together with the skin, modify contact mechanics between the snake's body and the environment. However, the mechanics of this system are very poorly understood. While lever arms are known for one species,²⁰⁵ these were calculated relative to the centroid of the vertebral condyle, whose morphology would be expected to have consequences on motion between pairs of vertebrae. We know that adjacent cotyle/condyle pairs form ball-and-socket joints (Figure 4) with synovial (fluid-lubricated) articulations that reduce resistance to movement.^{241,242} Vertebral shape, including condyle dimensions, has been the subject of only one large-scale comparative investigation in snakes.²¹⁶ It found that vertebral shape largely reflected family relationships, with very slight evidence of shape adaptation to particular habitat associations; however, it used only two-dimensional data and preceded the advent of phylogenetic comparative statistical methods by several decades,²⁴³ so studies using more modern methods may reveal previously hidden relationships. Although the cotyle/condyle pairs form the joint about which rotation happens, other vertebral features have functional importance (see Figure 4 for images of vertebral morphology based on μ CT scans). Snake vertebrae have distinctive features called the zygosphene and zygantrum that articulate with each other above the neural canal; the zygosphene–zygantrum

articulation is absent or minimal in all other extant vertebrates, including other limbless squamates, although it has been described in mosasaurs.^{244,245} The zygosphene–zygantrum articulation was originally postulated to prevent intervertebral twisting or torsion around the body axis,²⁴⁴ but subsequently was found to function more as a bony limit on range of motion that prevents disarticulation of the pre- and post-zygapophyses (a vertebral feature found across extant tetrapods), and thus only indirectly preventing torsion (because the pre- and post-zygapophyses serve to prevent torsion).²⁴⁶

Snake ribs execute significant motion in threat displays like cobra hooding,²⁰² and in specialized locomotion like gliding¹⁶⁸ and displacement of sand during vertical burrowing.¹⁴¹ They also perform more subtle (but more crucial) motion during breathing.^{247,248} Despite the potential role of rib motions in modulating contact during locomotion, very little is known about how they move during locomotion.²⁴⁹ Based on external observation, snakes moving through complex terrain seem to display significant deformation of the overall body shape, and preliminary X-ray cineradiography shows substantial rib movement accompanying this deformation (*unpublished data*). Conversely, the biarticular joints of snake ribs seem to allow a passive “bracing” mechanism, which could be advantageous for preventing movement during exertion of high forces.²⁴⁹ Given the potentially substantial and varied roles of ribs during snake locomotion, they clearly represent a structure worthy of far greater functional study.

The skull can also play a role during certain types of snake locomotion (see Wake's 1993 book chapter for a nice discussion on “the skull as a locomotor organ” across vertebrates, which includes mechanical roles and sensory roles¹²⁴). Its role manifests most obviously during burrowing, when it might act as a wedge or a shovel, experiencing high forces as it contacts the substrate. Given the clear importance of the skull for burrowing, a comparative dataset combining anatomy and locomotor behavior in a biomechanics framework could shed light on the mechanisms behind effective and efficient burrowing, which might vary with organism size and substrate characteristics. The skull also matters for aquatic species. Head shape affects hydrodynamic forces involved in underwater striking,^{181,250,251} and it is reasonable to expect that head shape could also matter for swimming. The relationship between skull anatomy and swimming biomechanics remains another area open for future study. For both burrowing and swimming, the individual elements of the skull and connections between them would be worth examining in addition to the overall shape.

Integument

As snakes move through the environment, the outer layer of skin maintains contact with the substrate, necessitating adaptations for efficient movement. Unlike most other animals, which make only static contact with the substrate during terrestrial locomotion, snakes can use both static and sliding contact. That their integument manages the very different functional challenges of static versus sliding contact, and in addition to all of its other roles, makes it a potentially instructive model for bioinspired design.

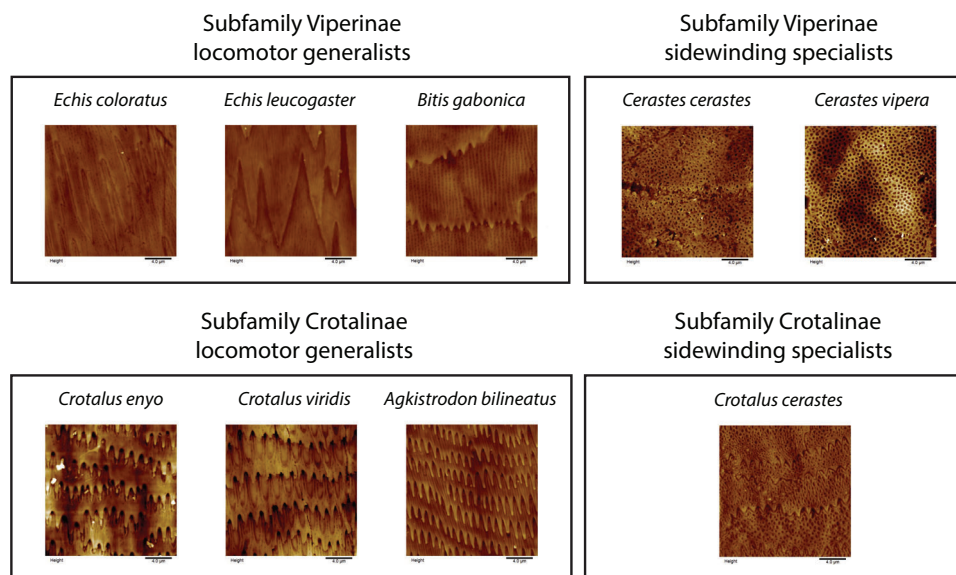


FIGURE 5 Skin microstructure in a few representative viper species. Ventral scale microstructure in some representative species of two subfamilies within the viper family (top row: Viperinae; bottom row: Crotalinae). Images produced using atomic force microscopy (AFM); courtesy of Tai-De Li. Species in the left column are terrestrial locomotor generalists, likely employing lateral undulation and rectilinear locomotion as their major locomotor modes during regular activities (but note the dearth of detailed information on locomotor preferences in natural habitats for most snake species). Species in the right column are three of the 12 species known to regularly use sidewinding locomotion.^{84,86} For an analysis of the functional consequences of these microstructures for sidewinding versus lateral undulation, see Rieser et al.⁸⁸

The snake integument is characterized by rigid overlapping scales with soft interconnections.²⁵² Zooming in on the outermost surface, many studies have documented micro- and nanostructures (e.g., Refs. 253–257), which have garnered attention for their influence on the skin's frictional properties (see Figure 5 for atomic force microscopy scans of ventral scales for several viper species). Several studies have focused on their role in producing frictional anisotropy, or directional dependence of friction coefficient, which facilitates sliding contact in the forward direction during slithering.^{88,258–264} However, snakes move in many ways and frictional anisotropy may only be beneficial for certain modes of locomotion that involve sliding contact in a single direction, especially slithering. In contrast, sidewinding requires static (or nearly static) contact with the ground, such that nanostructures promoting isotropy (the same friction coefficient in all directions) enhance sidewinding performance at the expense of lateral undulation⁸⁸ (Figure 5). Beyond friction, a few studies have examined additional mechanical properties of snake skin, such as strength and stiffness, that have functional importance for at least some locomotor behaviors.^{264–268} As with many topics in snake biology, the existing literature provides interesting glimpses into structure and function, yet the mechanical properties of snake skin remain a wide-open area for future study.

Some trade-offs resulting from skin properties (like structural isotropy/anisotropy) might be inevitable, but snakes may have morphological or behavioral strategies to potentially mitigate trade-offs. For example, snakes can increase friction by actuating their scales, an impressive ability that lets them accomplish such difficult locomotor feats as vertical climbs and concertina on steep inclines.^{107,269} This ability has clear applications for improving the performance of snake-

inspired robots, and it could also apply to any other device that might need to modulate its friction for gripping in different contexts.

The abrasive nature of terrestrial locomotion, especially of modes involving sliding contact with environmental surfaces, imposes the requirement that skin be either resistant or resilient to wear. Researchers have taken an interest in snake skin as a potential source of inspiration for abrasion-resistant surfaces.^{259,270,271} In the face of wear, injury, birth, and growth, periodic shedding of the skin (ecdysis) provides an avenue for renewal.^{272–275} Although implementation might be tricky, engineers could take inspiration from snakes to incorporate a shedding process for machines that operate in areas where humans cannot frequently service them.

Like many (perhaps most) biological structures, snake skin must perform a multitude of functions. Although this review focuses on locomotion, some of those additional functions merit attention, especially in the context of potential applications. Features of snake skin have already been translated to the design of textured surfaces for reducing friction²⁷⁶ and preventing microbial growth.²⁷⁷ In the area of yet-to-be-tapped potential, burrowing snakes of the family Uropeltidae (commonly called “shield-tail snakes”) have magnificently smooth skin with remarkable dirt-shedding abilities.^{278,279} Humans might do well to learn from them, given the trouble that dirt encrustation can cause for solar panels and other engineered devices.²⁸⁰ As another example, snake skin micro-ornamentation can provide waterproofing while still allowing flexibility for movement.²⁸¹ Microstructures can also be influential in enhancing color (i.e., structural colors), which can play a role in camouflage and thermoregulation.^{257,282,283} Moving on to the sensory realm, the skin can harbor structures that help snakes perceive the world around them, like the mechanoreceptors found in some sea

snakes.^{284–286} The list of skin functions continues on, well beyond our ability to provide a comprehensive review here. The properties that enable these diverse functions in nature could serve to inspire many future innovations.

CONTROL

To produce any functional outcome, the musculoskeletal system requires control. At the lowest level, control consists simply of the activation/deactivation patterns of muscles, which have been described for several muscles during several modes of snake locomotion, including terrestrial lateral undulation, undulatory swimming, sidewinding, tunnel concertina, rectilinear locomotion, and arboreal cantilevering.^{46,78,111,166} Those muscles show activity patterns consistent with the anatomical positions and lever arms.²⁰⁵ The role of multiarticularity in control remains unclear, particularly since the motor patterns of snakes engaging in terrestrial lateral undulation and swimming are surprisingly similar (though not identical) to those of eels moving terrestrially and swimming, despite eels having dramatically different muscular anatomy.^{46,287–289} Without muscle physiology data, we cannot extrapolate from activity patterns to force generation.

The higher-level control, which determines the signals sent to muscles, remains a mystery for locomotion in living snakes. Although numerous control schemes have been used in robotic snakes,^{14,19,24,42,290,291} no comparable experiments have ever tested these mechanisms in biological snakes. Because coordination of a huge number of degrees of freedom is the principal challenge of snakes (and snake robots), higher-level control in living snakes represents an avenue of inquiry with tremendous potential.

FINAL THOUGHTS

Snakes clearly have much to offer to the fields of robotics and materials science. They perform an impressive range of locomotor modes that snakelike robots have begun to imitate and that should continue to provide inspiration and control mechanisms for a long time to come. Most recognized as a model for navigating cluttered environments like rubble, tunnels, and large machines, they also show us how an elongate form can cover long distances through wide open expanses of sand or mud, navigate arboreal environments, maneuver in aquatic environments, and more. Such behaviors such as climbing, constriction, and prey handling have clear applications for gripping in robotic arms or other machines. Their complex multiarticular musculoskeletal system offers lessons for actuation, while the skin of various species offers a multitude of useful properties, from water resistance to dirt shedding to stretchiness to antimicrobial action.

In drawing inspiration from snakes or any other organism, certain considerations can allow scientists to maximize the value-added factor of the “bioinspiration” part of the process. One set of considerations results from the reality that organisms and machines face some of the same constraints while differing deeply with respect to others. For

example, scaling presents a universal or near-universal consideration: two organisms or objects that are scale models of each other might maintain geometric similarity at different sizes, but they will differ in other important properties like surface-area-to-volume ratio, forces experienced during locomotion, and cost of transport. Limbless terrestrial locomotion may have advantages over limbed locomotion in this respect. Whereas inertial forces dominate limbed locomotion, such that geometric and temporal variables must be adjusted with size to maintain a constant ratio between dominant forces,^{292,293} frictional forces dominate most limbless terrestrial locomotor modes, such that kinematics may be maintained or change only minimally in differently sized locomotors.⁸² Trade-offs arising from laws of physics, like the force-velocity trade-off in lever systems, represent another universal consideration for organisms and machines.

Perhaps the sharpest divide between organisms and machines results from the fact that machines are designed, whereas organisms arise through the processes of development (on the individual level) and evolution (of populations, species, and higher-level taxa). As a result, organisms face developmental and phylogenetic constraints that need not factor into design decisions for machines.^{294–297} In many cases, organisms evolve adaptations (or exaptations²⁹⁸) that brilliantly fill the need at hand. In other cases, engineers can produce something better because they have the luxury of designing from scratch.

We would not be surprised if researchers continue discovering exciting behaviors that expand our understanding of snake locomotor capabilities. Research on snake locomotion has historically lagged behind research on walking, swimming, and flying despite the magnificent functional diversity of snakes and their potential for bioinspiration.² As more researchers from a variety of fields direct their attention to snake locomotion, we expect major advances in our collective understanding of the mechanisms of snake movement. Some areas for future efforts include deepening our biomechanical knowledge of most locomotor modes (some of which have never been the subject of biomechanical study); shedding light on the motor control/neuromechanics of snake locomotion, including sensory feedback; and strengthening our (currently almost nonexistent) understanding of locomotor biomechanics and the factors that influence locomotor choices in free-living snakes. Between technological advances and the increasingly multidisciplinary nature of research collaborations, we envision a bright future for increasingly effective bioinspired design based on strong engagement with organismal biology.

AUTHOR CONTRIBUTIONS

J.L.T., K.L.G., and H.C.A. contributed to conceptualization, original draft preparation, and review and editing. J.L.T. and H.C.A. contributed to visualization, supervision, project administration, and funding acquisition.

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COMPETING INTERESTS

The authors have no competing interests.

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