



SYMPOSIUM INTRODUCTION

Long Limbless Locomotors Over Land: The Mechanics and Biology of Elongate, Limbless Vertebrate Locomotion

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From the symposium “Long Limbless Locomotors: The Mechanics and Biology of Elongate, Limbless Vertebrate Locomotion” presented at the annual meeting of the Society for Integrative and Comparative Biology January 3–7, 2020 at Austin, Texas.

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Synopsis Elongate, limbless body plans are widespread in nature and frequently converged upon (with over two dozen independent convergences in Squamates alone, and many outside of Squamata). Despite their lack of legs, these animals move effectively through a wide range of microhabitats, and have a particular advantage in cluttered or confined environments. This has elicited interest from multiple disciplines in many aspects of their movements, from how and when limbless morphologies evolve to the biomechanics and control of limbless locomotion within and across taxa to its replication in elongate robots. Increasingly powerful tools and technology enable more detailed examinations of limbless locomotor biomechanics, and improved phylogenies have shed increasing light on the origins and evolution of limblessness, as well as the high frequency of convergence. Advances in actuators and control are increasing the capability of “snakebots” to solve real-world problems (e.g., search and rescue), while biological data have proven to be a potent inspiration for improvements in snakebot control. This collection of research brings together prominent researchers on the topic from around the world, including biologists, physicists, and roboticists to offer new perspective on locomotor modes, musculoskeletal mechanisms, locomotor control, and the evolution and diversity of limbless locomotion.

Serpents are too commonly looked down upon as animals degraded from a higher type; but their whole organisation, and especially their bony structure, demonstrate that their parts are as exquisitely adjusted to the form of their whole, and to their habits and sphere of life, as is the organisation of any animal which we call superior to them. It is true that the serpent has no limbs, yet it can outclimb the monkey, outswim the fish, out-leap the jerboa, and, suddenly loosing the close coils of its crouching spiral, it can spring into the air and seize the bird upon the wing; all these creatures have been observed to fall its prey.

—Sir Richard Owen (1866)

Introduction

Snakes have been the object of endless human fascination throughout history, figuring prominently in the mythology of almost every culture (Greene et al.

1997). Scientific observers since Aristotle have pondered their locomotion, particularly their remarkable proficiency at so many locomotor modes despite lacking legs (Owen 1866; Nussbaum 1985). While early descriptions of snake locomotion were remarkably astute (Owen 1866; Hutchinson 1879; Mosauer 1930, 1935; Nussbaum 1985), the advent of modern biomechanical techniques has allowed us to rapidly increase our understanding of limbless locomotion (Gray 1946; Gray and Lissmann 1950; Gans 1962; Jayne 1986, 1988a, 1988b; Gasc and Gans 1990).

As our knowledge of snake locomotion has grown, they have shown themselves to be particularly adept at locomotion in cluttered, confined, and complex environments where limbed animals (and limbed and wheeled devices) struggle. Lateral undulation (“slithering”) relies upon interactions with asperities in the environment to generate propulsive reaction

forces, turning what would be obstacles to limbed animals into propulsive “push points” (Gray 1946; Gray and Lissmann 1950; Jayne 1986; Kelley et al. 1997). Correspondingly, snakes slithering through densely cluttered environments increase their speed substantially with increasing obstacle density (until the obstacles become so dense as to confine and restrict movement; Kelley et al. 1997), while limbed organisms slow down with increasing obstacle density and unevenness (Sponberg et al. 2008; Collins et al. 2013; Parker and McBrayer 2016; Gast et al. 2019). Snakes also excel at motion through narrow, confined spaces such as tunnels using concertina and rectilinear locomotion (Lissmann 1950; Jayne 1986; Jayne and Davis 1991; Newman and Jayne 2018), aided by both their naturally low cross-sectional area relative to their mass and their ability to move their ribs to accommodate the narrow environment. Finally, snakes also excel at motion in mechanically complex environments such as on or beneath sand (Jayne 1986; Marvi et al. 2014; Sharpe et al. 2015; Astley et al. 2015), which can behave as a solid or fluid depending on subtle differences in loading mechanics (Maladen et al. 2009; Gravish et al. 2010; Li et al. 2010), or arboreal environments (Astley and Jayne 2007, 2009; Jayne and Riley 2007; Byrnes and Jayne 2012, 2014; Jayne et al. 2014; Mauro and Jayne 2016; Jorgensen and Jayne 2017), which require negotiating substrates that are often narrow, inclined, curved, compliant, and discontinuous, with secondary obstacles (Cartmill 1985; Astley and Jayne 2009; Jayne et al. 2014).

Unsurprisingly, the benefits of limbless locomotion and the elongate, snake-like body plan have led to widespread convergence throughout animals. Within squamate reptiles alone, there are approximately two dozen independent convergences on an elongate, functionally limbless body form (Wiens et al. 2006), including within clades such as the armored Cordylids (*Chamaesaura* spp.) and even within Gekkota (Pygopodidae). Numerous fish species have converged upon an eel-like body plan (Mehta et al. 2010; Ward and Mehta 2010), and three lineages of Lissamphibians (thermal limitations preclude this body form in endotherms; Pough 1980). Many of these clades are quite ancient (Jenkins and Walsh 1993; Caldwell et al. 2015; Garberoglio et al. 2019), including three lineages of early tetrapods that became functionally limbless shortly after the origin of the tetrapod limb (Olson 1971; Andrews and Carroll 1991; Pardo et al. 2017). This astonishing number of convergences may make

the limbless, elongate body plan the most frequently converged-upon body plan in animals.

This frequency of convergence has given rise to a correspondingly high number of species, particularly within vertebrates. A brief survey of functionally limbless vertebrate taxa reveals an estimated 4300 species, only a few hundred behind the total of all non-flying mammals (Burgin et al. 2018; Uetz 2020). Indeed, when considered in proportional terms, terrestrial limbless species comprise 19% of all terrestrial vertebrates.

Despite this tremendous diversity of species and the functional benefits of the limbless body plan, our knowledge of the limbless locomotion is in its infancy. While earlier major works have laid the foundation (Mosauer 1932; Gray 1946; Gans 1962; Jayne 1986), there are still huge areas of unknowns. Fundamental properties such as the lever arms and contractile properties of the locomotor muscles are completely unknown and unexplored, as is the neural control of locomotion. As patchy as our knowledge of snake locomotion is, we know, still less about the locomotion of other limbless species. Indeed, searches on PubMed reveal that while walking and swimming generate tremendous numbers of hits (>73,000 and >19,000, respectively) and even flight generates almost 5000 hits, limbless locomotion (and various other, related queries) consistently return <400, indicating that despite comprising almost 20% of terrestrial vertebrates, limbless locomotion studies comprise <0.5% of the locomotion literature. Consequently, the articles in this symposium collection comprise ~2.5% of all scientific literature on the topic.

This collection of papers, arising from the first symposium of limbless locomotion ever held, includes contributions from many of the leading researchers in the field attempting to fill in some of these gaps and point us toward promising areas for exploration. These papers broadly fall along a spectrum from behavioral (locomotor modes and sensorimotor integration (Zamore et al. 2020; Jayne 2020; Tingle 2020)) through control of locomotion (Schiebel et al. Forthcoming; Kano and Ishiguro 2020; Fu et al. 2020) to locomotor mechanics and functional morphology (Astley 2020; Capano 2020; Redmann et al. 2020; Bergmann et al. 2020), though many papers straddle multiple categories. While snakes are both the most speciose and well-studied limbless vertebrates, a great deal of insight can come from other limbless taxa, with contributions on both limbless lizards (Bergmann et al. 2020) and eels

(Redmann et al. 2020). Finally, the exceptional locomotion abilities of limbless species have led to significant efforts to develop biomimetic snake robots (Walker et al. 2016). The high number of joints and interactions between the snakebot and substrate pose significant challenges to effective control but recent progress has been substantial, including decentralized control mechanisms (Kano and Ishiguro 2020).

Locomotor behavior

Limbless taxa use a wide range of locomotor modes, often in response to different environmental challenges (Mosauer 1932; Gray 1946; Gans 1975; Jayne 1986) but not all taxa are capable of all modes, nor is it always clear what exactly constitutes a distinct mode versus a variation on an existing mode. While the traditional understanding has divided terrestrial limbless locomotion into four broad modes (lateral undulation, sidewinding, concertina, and rectilinear), Jayne examines the recent data across species and environment to assess these divides (Jayne 2020). This overview shows a wide range of locomotor behaviors, some of which are difficult to place under traditional classifications, with implications for evolution, locomotor control and biomechanics, and habitat preferences (Jayne 2020). Among these modes, sidewinding has a particularly peculiar distribution across species. Traditionally regarded as being limited to a few viper species, as well as a homalopsid and nactricine water snake, the lack of data across many species makes it difficult to distinguish between multiple independent evolutions of sidewinding or simply lack of observations across most species (Tingle 2020). Tingle compiles the evidence from the literature and adds new experimental evidence to suggest that sidewinding and related behaviors are more common than previously appreciated (Tingle 2020).

Control and perception

These locomotor behaviors are ultimately the product of neural control, both at the high level of initiating particular locomotor behaviors and the lower level modulation of these behaviors in response to environmental feedback, though little is known about any of these processes in snakes. Zamore et al. provide insight into the visual perception of a highly visually-oriented snake species, the gliding tree snake, and how this species manages the perceptual demands of its unusual aerial locomotion (Zamore et al. 2020). Looking within locomotor behaviors, Schiebel et al. use mathematical analysis of body curvature over time and reaction forces on

an obstacle to examine control in a sand specialist and a generalist (Schiebel et al. Forthcoming). They show that the sand-specialist uses a highly stereotyped waveform to maximize performance across uniform sand but often failed to generate propulsive force from the obstacle, while a generalist snake used aperiodic motions that resulted in lower performance on sand but were highly effective at generating propulsion from the obstacle (Schiebel et al. Forthcoming). Fu et al. tackled the under-examined area of vertical environmental structure, particularly how snakes tackle a vertical step (Fu et al. 2020). By using a combination of biological data and robotic modeling, they were able to discern the benefits of both body posture and body compliance in step traversal (Fu et al. 2020). Finally, Kano and Ishiguro discussed their previous work using a decentralized Tegotae-based control scheme that incorporates local environmental feedback to achieve exceptional replication of both snake kinematics and performance across multiple environments (Kano and Ishiguro 2020). This remarkable controller is capable of generating both lateral undulation and concertina locomotion purely in response to local environmental conditions (Kano and Ishiguro 2020).

Functional morphology

Neural control is crucial for effective locomotion but the neural signals must be translated into behaviors via the musculoskeletal system, and the properties of this system (and how it interacts with environmental physics) have a tremendous influence on the resulting behavior and performance (Tytell et al. 2011). Despite their superficially simple external morphology, limbless species display a wide range of varied morphologies, and the function of some universal structures is still not fully understood. Astley examines the consequences of the unique, highly multi-articular axial muscular system of snakes using mathematical tools from engineering, and finds that, for cantilevered gap bridging, the long tendons of arboreal colubroids confer a significant advantage in terms of performance (Astley 2020). Capano et al. expand beyond the vertebral column to consider the role of ribs in snake locomotion, particularly related to the dual demands of providing a deformable interface with the environment while also providing a firm structure for transmitting forces (Capano 2020).

Beyond snakes

While snakes have been the focus of most limbless locomotion research, they represent only a single clade, and tremendous insights can be gained from

studying other limbless and functionally limbless taxa. While snakes are a very old and highly derived clade with numerous specializations for locomotion, feeding, and prey capture (Kardong 1977; Gasc 1981; Gans 1983, 1986; Kardong and Bels 1998; Caldwell et al. 2015; Garberoglio et al. 2019), these are absent in most other independent evolutions of limblessness, making these taxa particularly informative about the early evolution of limb reduction and loss. Bergmann et al. examine the evolution of the vertebrae and kinematics in limbless lizards and a basal snake, showing widespread convergence (Bergmann et al. 2020). Stepping beyond tetrapods, Ward et al. examine the motion of eels during the migrations between the sea and freshwater, which are often blocked by dams, requiring terrestrial locomotion to cross (Redmann et al. 2020). Eels moving on level substrates used lateral undulation, while those moving on inclines switched to concertina, which has not previously been described in fish (Redmann et al. 2020).

Slithering into the future

These collected papers represent significant new progress in the field of limbless locomotion, and we hope that this will spur further interest into this sadly neglected field of study. In addition to these topics, many other aspects of limbless locomotion remain nearly or completely unknown, such as sensory feedback during locomotion, muscle contractile properties, consequences of scaling, and the frequencies of various modes during natural behavior. But these gaps in the literature, frustrating though they may be, represent tremendous opportunities for discovery, particularly relative to more well-studied systems. While the map of our biomechanical knowledge has many blank spaces, few present greater opportunity for exploration than the one labeled “Here Be Serpents.”

Funding

This symposium has been generously supported by the Society for Integrative and Comparative Biology, with financial contributions from the SICB Divisions of Comparative Biomechanics, Vertebrate Morphology, Animal Behavior, and Neurobiology, Neuroethology, and Sensory Biology. External funding was generously provided by grants from the Society for Experimental Biology and the Company of Biologists.

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