

LATERAL BENDING DURING LIZARD LOCOMOTION

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Summary

Lateral bending of the trunk during terrestrial, quadrupedal locomotion was analyzed in four species of lizards, using high-speed videography and computerized motion analysis. The focus of the analysis was whether lizards produce a standing or a traveling wave of bending in the trunk during locomotion. Lizards with well-developed limbs (*Cnemidophorus tigris* and *Dipsosaurus dorsalis*) exhibit a standing wave of lateral bending at low speeds, which is replaced by a traveling wave of bending as velocity increases. Lizards with diminutive limbs (*Gerrhonotus kingii* and *Eumeces multivirgatus*) exhibit a traveling wave of lateral bending, even at the lowest speeds recorded. These results are not consistent with the ideas that lizards produce a standing wave of lateral bending during locomotion or that amniote vertebrates have lost the ability to produce a traveling wave of lateral flexion due to a change in the central pattern generator that controls locomotion.

Introduction

Lateral bending of the trunk is a common aspect of locomotion in vertebrates (Blight, 1977; Roos, 1964; Avery *et al.* 1987). Waves of lateral flexion may be described as either traveling or standing. In a traveling wave, all points oscillate laterally, and maximum lateral displacement moves rostrocaudally through time along the body axis. In a standing wave, however, there is some point or points that do not move laterally, and all points on the wave reach their maximum lateral displacement at approximately the same time. The points of zero lateral displacement are 'nodes', and at least one node must be present in the trunk of an animal to define a standing wave. The absence of a node indicates a traveling wave.

Both the major types of fish swimming (i.e. anguilliform and carangiform) involve a traveling wave of lateral bending down the long axis of the body (Breder, 1926). The swimming movements of larval frogs (Wassersug and von Seckendorf Hoff, 1985; Soffe, 1991) and salamanders (Blight, 1976) also involve traveling waves of lateral bending. An initial report of lateral bending in terrestrial amphibians described a standing wave in the terrestrial locomotion of a newt (Roos, 1964). In a later study, however, it was shown that

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the lateral bending of many salamander species takes on a traveling wave pattern as speed increases (Edwards, 1976).

The lateral bending of lizards has been variously described as standing, traveling or as possessing attributes of both traveling and standing waves (Daan and Belterman, 1968; Peterson, 1984). The lack of conclusive evidence for traveling waves in the terrestrial locomotion of lizards has led to the hypothesis that amniote vertebrates have lost the ability to produce a traveling wave of lateral bending (Cohen, 1988; Bekoff, 1985). This loss has been attributed to a change in the central pattern generators controlling locomotion, and thus a major shift in the evolution of central pattern generators is believed to have occurred at the phylogenetic split between amphibians and reptiles (Cohen, 1988). Here new data are presented and previous data are re-evaluated to show that lizards can produce a traveling wave of lateral bending during terrestrial, quadrupedal locomotion.

Materials and methods

Four species of lizards from four families were studied. The lizard species used were chosen because they represent extremes of body form and locomotor types: *Dipsosaurus dorsalis* Baird and Girard (Iguanidae) and *Cnemidophorus tigris* Baird and Girard (Teiidae) have well-developed, muscular limbs and are capable of high sprint speeds (Belkin, 1961; Urban, 1965), whereas *Gerrhonotus kingii* (Gray) (Anguidae) and *Eumeces multivirgatus* (Hallowell) (Scincidae) have elongate bodies and diminutive, though functional, limbs. A salamander, *Ambystoma tigrinum* Green (Ambystomatidae), was included in the study because salamanders are known to produce standing waves of lateral bending at low speeds (Edwards, 1976).

Eight spots were painted down the dorsal midline of the animals, evenly spaced from the head to the level of the pelvic girdle. The animals were videotaped at 60 fields s^{-1} as they moved down a hardboard track, with the camera placed directly overhead. The animals were free to choose their own forward velocity, but sometimes were encouraged to move by lightly pinching the base of the tail by hand. Lizards were videotaped until they slowed considerably, so that a range of forward velocities was recorded for each lizard. Only slow (walking) speeds of the salamander were videotaped. A 1 cm grid was present on the track, from which aspect ratios and scaling factors were calculated. The x, y position for each point was digitized in each frame with a Peak motion-analysis system, such that the direction of forward movement was along the x -axis, and lateral movement was along the y -axis. Only video sequences in which the animal was moving in a straight line and at a constant speed were used for analysis.

In this study, a locomotor cycle is defined as beginning with a distinct footfall event and ending with the subsequent, identical footfall event. The minimum locomotor cycle duration reported here is 10 video fields (167 ms). Forward speed of the animals is converted to snout-vent lengths per second ($SVL s^{-1}$) to facilitate comparison between animals. The number of individual animals and total number of video sequences digitized per individual, respectively, are as follows: *Dipsosaurus* (3, 3); *Cnemidophorus* (2, 3); *Gerrhonotus* (3, 3); *Eumeces* (2, 3); *Ambystoma* (2, 4).

For initial analysis of the waveform produced by the animals, the lateral movement of the eight points along the body was described graphically. The lateral movement of points along the trunk was further analyzed by calculating the lateral velocity of each point, following similar analyses of fish swimming by Bainbridge (1963). The logical basis of the analysis is that a node, which experiences no lateral movement, will have zero lateral velocity. There are an infinite number of points along a wave which may be a node and, although it is unlikely that one would place a point precisely on the node, a graph of the lateral velocity of successive points along an animal's body will indicate the likelihood that a node exists between two points. As Bainbridge reasoned, a smooth curve that does not approach the x -axis makes the existence of a node unlikely.

The possibility that a standing wave occurs was further investigated as follows. 'Stick figures' for each video field were produced by connecting the eight points along the lizard's trunk. Stick figures from two fields that are separated in time by exactly half of a locomotor cycle are mirror images of one another. When these stick figures are superimposed, they intersect at that point along the body at which lateral excursion is minimal, which is here termed 'a point of minimum lateral excursion'. For example, if a locomotor cycle is ten video fields long, stick figures from video fields one and six will be mirror images of one another, and will intersect at a point approximately in the midline of the figure that is produced from superimposing all stick figures from that locomotor cycle. A node, and thus a standing wave, would be present if all of the points of minimum lateral excursion from a locomotor cycle occur within a narrow range along the trunk of the animal. In fact, it is the points of minimum lateral excursion that collectively produce the node. If, however, the points of minimum lateral excursion move along the long axis of the body through time, then no node exists and a traveling wave is present.

Results

Traveling waves of lateral bending are exhibited by all four lizard species analyzed in this study. There are, however, two important points to be made concerning the bending patterns. The first is that both *Dipsosaurus dorsalis* and *Cnemidophorus tigris* exhibit a standing wave pattern at the lowest speeds analyzed (1.6 and 2.5 SVL s^{-1} , respectively). As forward velocity increases, the lateral bending of both of these species takes on a traveling wave pattern. Both *Gerrhonotus kingii* and *Eumeces multivirgatus* exhibit a traveling wave of lateral bending at all speeds analyzed, their lowest speeds being 2.2 and 2.4 SVL s^{-1} , respectively. The second point is that the traveling wave of lateral bending apparent in *Dipsosaurus dorsalis* and *Cnemidophorus tigris* does not exhibit constant velocity or constant amplitude.

Locomotion at higher velocities

Graphs of lateral displacement (Fig. 1) show that during locomotion at high speeds all eight points along the trunks of all lizards studied experience lateral movement. Therefore, no nodes are present. The maximum lateral excursion of each point moves through time from anterior to posterior, giving further evidence that a traveling wave is propagated down the trunk (Fig. 1).

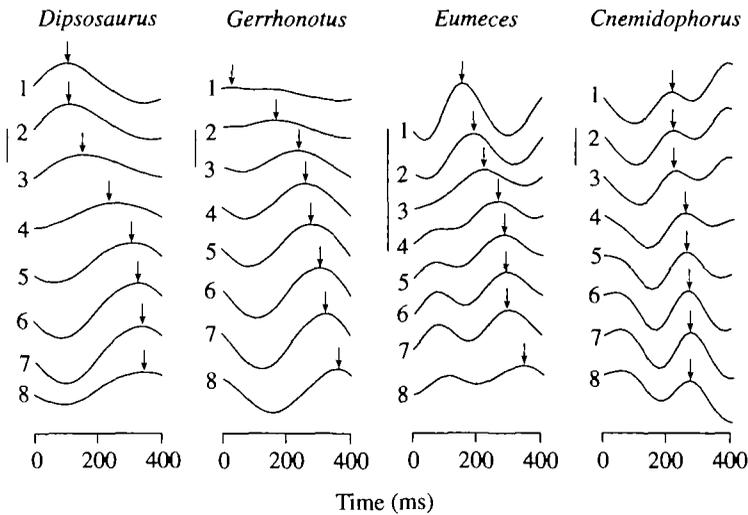


Fig. 1. Lateral excursion of eight points along the trunk of four lizard species. All eight points oscillate laterally and maximum lateral excursion of each point moves rostrocaudally through time in all four species. Point 1 is the snout. Point 2 is at the level of the pectoral girdle of *Dipsosaurus dorsalis*, *Gerrhonotus kingii* and *Eumeces multivirgatus*. Point 3 is at the level of the pectoral girdle of *Cnemidophorus tigris*. Point 8 is at the level of the pelvic girdle of all species. Scale bars, 1 cm. Arrows indicate times of maximum lateral excursion for each point along the trunk. Forward velocities ($\text{SVL} \cdot \text{s}^{-1}$) are as follows: *Dipsosaurus* 3.7, *Gerrhonotus* 4.5, *Eumeces* 3.1 and *Cnemidophorus* 5.9.

The lateral velocities of points along the trunks of all four lizard species indicate that the existence of nodes is unlikely (Fig. 2). None of the eight points shows zero lateral velocity, and no area between the eight points could drop to the x -axis without interrupting the smooth nature of the curves. *Gerrhonotus kingii* shows a pattern unlike that of the other three species. In this species, lateral velocity increases linearly with distance from the head to a point just anterior to the pelvic girdle, whereas in the other three species this variable is minimal near mid-trunk and increases towards both the head and the pelvic girdle (Fig. 2).

Effects of forward velocity on lateral bending

Both the superimposed stick figures (Fig. 3) and the graphs generated from these stick figures (Fig. 4) show the variability of the bending patterns produced by different species, as well as the effect of the forward velocity of the animals on the bending patterns. *Ambystoma tigrinum* (Fig. 3A) exhibits a typical standing wave pattern, with all the points of minimum lateral excursion occurring within a very restricted portion of the trunk (just posterior to the pectoral girdle in this case). Conversely, *Gerrhonotus kingii* (Fig. 3B) exhibits a traveling wave pattern, even at the lowest speed recorded, with the points of minimum lateral excursion showing regular movement in an anterior to posterior direction.

Variations of the standing and traveling wave patterns are shown by *Cnemidophorus tigris* and *Dipsosaurus dorsalis*. At the lowest velocity analyzed for *Cnemidophorus*

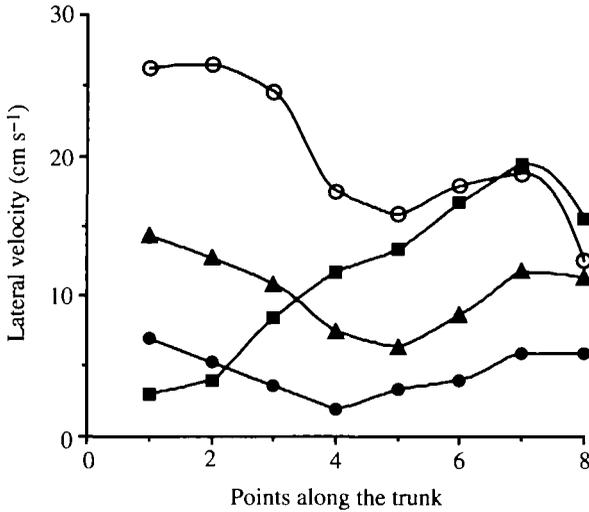


Fig. 2. Lateral velocity of eight points along the trunk of four lizard species. None of the points in any species exhibits zero lateral velocity. Velocity was calculated by measuring the distance between the maximum and minimum points of lateral excursion (twice the amplitude) and dividing that distance by the time between maximum and minimum. The points on the animals are identical to those in Fig. 1. Forward velocities (SVL s^{-1}) of the lizards are as follows: *Dipsosaurus* (filled triangles) 3.7, *Gerrhonotus* (filled squares) 4.5, *Eumeces* (filled circles) 3.1 and *Cnemidophorus* (open circles) 5.9.

tigris (2.5 SVL s^{-1}), the points of minimum lateral excursion move along the trunk in the first two successive video fields, but not in subsequent video fields (Figs 3C and 4). Although there is an initial movement of the points down the trunk, subsequent points are centered around the pectoral girdle, and the wave of bending is defined as standing. At an intermediate speed (3.7 SVL s^{-1}), *Dipsosaurus dorsalis* exhibits a bending pattern in which the points of minimum lateral excursion move in an anterior to posterior direction down the trunk, but move more slowly in mid-trunk (Figs 3D and 4). The points of minimum lateral excursion do not move in as regular a fashion as those of *Gerrhonotus kingii* (Fig. 3B), nor is the amplitude of bending seen in *Dipsosaurus dorsalis* as constant as that of *Gerrhonotus kingii*. The points of minimum lateral excursion do move from anterior to posterior, however, and the waveform is defined as traveling.

The graphs derived from the superimposed stick figures facilitate comparison among species and within species at different velocities (Fig. 4). In these graphs, the y-axis shows the position of the points of minimum lateral excursion as a percentage of the snout-vent length of the four lizard species, and the x-axis is the video field in which the point of minimum lateral excursion occurs. It is important to note that, in this case, each 'field' actually represents two fields separated in time by exactly half a locomotor cycle (so the total number of fields in a locomotor cycle is double the number of points that make up a single line in Fig. 4). In both *Dipsosaurus dorsalis* and *Cnemidophorus tigris*, a standing wave of bending is present at the lowest velocity for which data are available. In both of these species, the node occurs at a point approximately 40% of snout-vent length, which corresponds to a point just posterior to the pectoral girdle. In contrast to

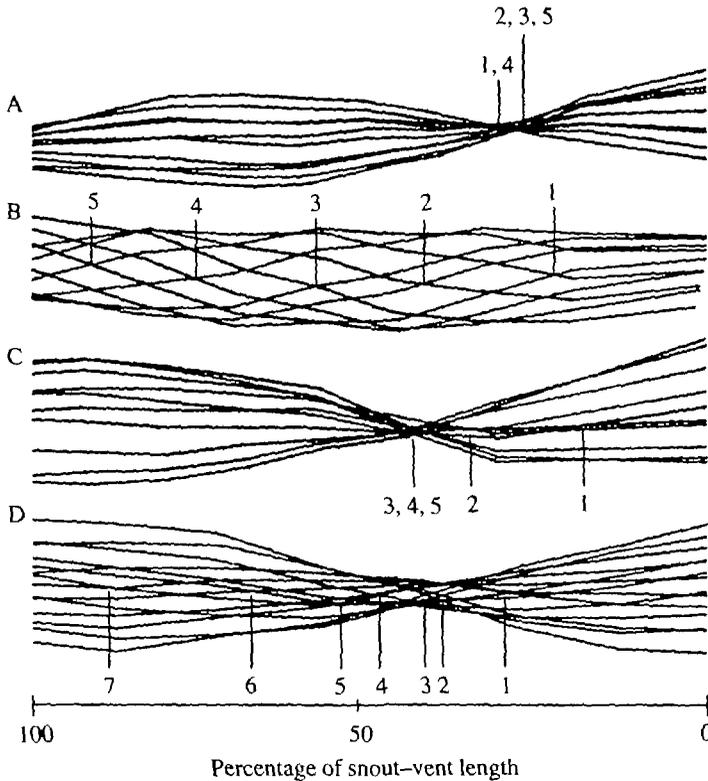


Fig. 3. Superimposed stick figures from digitized video fields. For the sake of clarity, not all of the stick figures from the locomotor cycle are shown, but the pattern of movement (or lack of movement) of the points of minimum lateral excursion is preserved. Numbered lines indicate points of minimum lateral excursion (see text for explanation of points of minimum lateral excursion). (A) *Ambystoma tigrinum* (0.5 SVLs^{-1}) exhibits a standing wave pattern with a node just posterior to the pectoral girdle. (B) *Gerrhonotus kingii* (2.2 SVLs^{-1}) exhibits a traveling wave pattern in which no node is present. This figure also shows the regular movement of points of minimum lateral excursion and the constant amplitude of the wave of bending. (C) *Cnemidophorus tigris* (2.5 SVLs^{-1}) shows a variation of the standing wave pattern. The first two points of minimum lateral excursion move along the trunk, but subsequent points are centered just posterior to the pectoral girdle. (D) *Dipsosaurus dorsalis* (3.7 SVLs^{-1}) shows a variation of the traveling wave pattern. The points of minimum lateral excursion move down the trunk, but the movement is slower in the mid-trunk, and the amplitude of the wave is not constant.

Dipsosaurus dorsalis and *Cnemidophorus tigris*, both *Gerrhonotus kingii* and *Eumeces multivirgatus* show a traveling wave pattern at all velocities for which data are available.

To visualize better how the graphs were generated, one may compare the superimposed stick figures (Fig. 3) with specific lines in the graphs (Fig. 4). The line representing *Cnemidophorus tigris* moving at 2.5 SVLs^{-1} (filled squares of Fig. 4 for this species) was derived from a series of superimposed stick figures similar to that shown in Fig. 3C, in which the points of minimum lateral excursion initially move down the trunk, but then stop. The line representing *Dipsosaurus dorsalis* moving at 5.6 SVLs^{-1} (open squares of

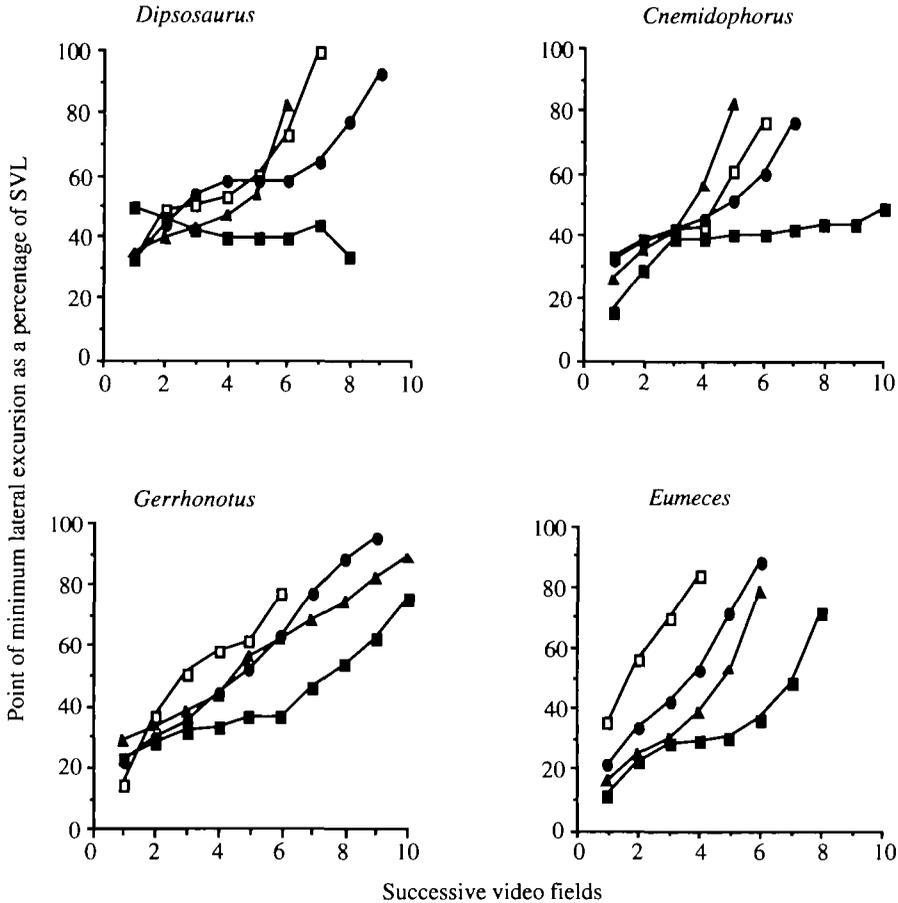


Fig. 4. Points of minimum lateral excursion as a percentage of snout-vent length for four species of lizards. Successive video fields are defined as follows: if a locomotor cycle is recorded in video fields 1–10, video field 1 (on the x -axis) is fields 1 and 6, field 2 (on the x -axis) is fields 2 and 7, and so on to field 5, which is fields 5 and 10. The presence of the traveling wave is velocity-dependent in *Dipsosaurus dorsalis* and *Cnemidophorus tigris*, while *Gerrhonotus kingii* and *Eumeces multivirgatus* show little difference in their waveforms at different velocities. Forward speeds of the animals ($SVL s^{-1}$) correspond to the symbols that make up the lines and are given in the following order: filled squares, filled circles, filled triangles, open squares. *Dipsosaurus* 1.6, 3.7, 4.6 and 5.6, *Cnemidophorus* 2.5, 5.9, 6.2 and 6.7, *Eumeces* 2.4, 3.1, 3.7 and 4.9, *Gerrhonotus* 2.2, 3.4, 4.5 and 5.9.

Fig. 4 for this species) was derived from a series of superimposed stick figures similar to those in Fig. 3D, in which the points of minimum lateral excursion move more slowly in mid-trunk than in either the anterior or posterior portion of the trunk. The lines connecting the filled triangles and filled circles of both *Gerrhonotus kingii* and *Eumeces multivirgatus* (Fig. 4) were derived from a series of superimposed stick figures similar to those in Fig. 3B, in which the points of minimum lateral excursion show a regular progression from anterior to posterior.

Discussion

The results of this study demonstrate that lizards of all four species exhibit a traveling wave of lateral flexion, at least at some velocities. The existence of the traveling wave at higher velocities in *Dipsosaurus dorsalis* and *Cnemidophorus tigris* is similar to results for salamanders, in which a standing wave present at lower velocities is replaced by a traveling wave as velocity increases (Edwards, 1976).

It is generally believed that lateral bending serves to increase the stride length of lizards. An increase in stride length may be accomplished by either a standing or a traveling wave. Since a traveling wave transmits force along its axis of progression, and a standing wave does not, one plausible hypothesis is that a traveling wave of lateral bending may not only increase stride length but also contribute propulsive force for locomotion. The force supplied for locomotion would be lessened in a standing wave, as the majority of the force developed by bending would be directed laterally. There is correlative data to support this idea, as those species with diminutive limbs (*Gerrhonotus kingii* and *Eumeces multivirgatus*) have a traveling wave of lateral bending even at the lowest speeds for which data are available. Perhaps in those species with shorter limbs the main function of lateral bending is shifted from increasing stride length to providing propulsive force for locomotion. Data correlating trunk curvature adjacent to the girdles and the presence or absence of a traveling wave with force production by the limbs will test whether lateral bending provides propulsive force during locomotion.

Earlier data and interpretations concerning lateral bending in lizards are inconclusive. A comparative study of several species (Daan and Belterman, 1968) reported that, although the bending of some species 'approximately approaches' a standing wave pattern, the bending of others could be described as either standing or traveling. *Chalcides ocellatus* is reported to produce traveling waves of lateral bending, and the authors state that 'In any case, only standing waves seem to occur in animals with strongly developed limbs' (Daan and Belterman, 1968). Data reported in this study do not support this statement. Both *Dipsosaurus dorsalis* and *Cnemidophorus tigris* possess well-developed limbs, and both species produce traveling waves of lateral bending at higher velocities.

A comparative study of three species of *Chamaeleo* (*C. dilepis*, *C. senegalensis* and *C. jacksoni*) and *Agama agama* reported that lizards produce a traveling wave which 'stands' at certain points along the body (Peterson, 1984). This statement appears to be based on the observation that the point of maximum curvature did not travel along the trunk with constant velocity: "Instead, it progresses rapidly through the stiff shoulder and hip regions, but 'stands' in the cervical, trunk and tail sections" (Peterson, 1984). However, the wave of curvature does not stand in these regions. Its velocity is reduced.

The same basic pattern is seen in the present study. At low velocities the points of minimum lateral excursion of both *Dipsosaurus dorsalis* and *Cnemidophorus tigris* move more slowly through the region of the pectoral girdle (e.g. Fig. 3D). Since the points of minimum lateral excursion are essentially points of inflection of the curvature in the animal's trunk, they may also be considered to be points of minimum curvature. The slowing of the points of minimum lateral excursion in the region of the pectoral girdle

implies that the point of maximum curvature also slows, approximately in mid-trunk. In those lizard species with well-developed limbs, the musculature associated with the limb girdles may have a greater influence on the movement of the wave of bending, causing the variation in both amplitude and speed of wave propagation seen in *Dipsosaurus dorsalis* and *Cnemidophorus tigris*.

Other studies, though not directly concerned with patterns of lateral bending, have stated that lizards produce a standing wave of lateral flexion during quadrupedal locomotion (Avery *et al.* 1987; Gans, 1975). Therefore, previous studies of lizards have not conclusively identified the wave of bending as standing or traveling, and the lack of a consensus has been interpreted as evidence for the existence of a standing wave (e.g. Cohen, 1988).

Based on previous data, it was suggested that a major transition in the central pattern generators controlling locomotion occurs at the phylogenetic split between amphibians and reptiles (Cohen, 1988). However, the kinematic data presented here do not support the idea that lizards have lost the ability to produce a traveling wave of lateral flexion and argue for conservation of the traveling wave pattern in amniotes, at least within reptiles.

It has been shown that a traveling wave of bending may be produced by either a standing or a traveling wave of muscular activation in swimming animals (Blight, 1976). Data on the pattern of muscle activity that produces the traveling wave of bending in lizards are needed to determine the neuromuscular basis of the kinematic patterns reported here. Work in progress on the rostrocaudal timing of electromyographic activity of the axial musculature of lizards will answer this question and add to our current knowledge of the role of the axial muscles during locomotion in vertebrates.

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