

## AXIAL MUSCLE FUNCTION DURING LIZARD LOCOMOTION

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### Summary

It was recently reported that the epaxial muscles of a lizard, *Varanus salvator*, function to stabilize the trunk during locomotion, and it was suggested that this stabilizing role may be a shared derived feature of amniotes. This result was unexpected because it had previously been assumed that the epaxial muscles of lizards function to produce lateral bending during locomotion and that only in mammals and birds were the epaxial muscles active in stabilizing the trunk. These results and the inferences made from them lead to two questions. (1) Is the pattern of epaxial muscle activity observed in *V. salvator* representative of a basal lizard condition or is it a derived condition that evolved within lizards? (2) If the epaxial muscles do not produce lateral bending, which muscles do carry out this function? These questions were addressed by collecting synchronous electromyographic (EMG) and kinematic data from two lizard species during walking and running. EMG data were collected from the epaxial muscles of a lizard species from a basal clade, *Iguana iguana*, in order to address the first question. EMG data were collected from the hypaxial muscles of both *Iguana*

*iguana* and *Varanus salvator* to address the second question. The timing of epaxial muscle activity in *Iguana iguana* relative to the kinematics of limb support and lateral trunk bending is similar to that observed in *Varanus salvator*, a finding that supports the hypothesis that the epaxial muscles stabilize the trunk during locomotion in lizards and that this stabilizing role is a basal feature of lizards. Therefore, a stabilizing function of the epaxial muscles is most parsimoniously interpreted as a basal amniote feature. In both *Iguana iguana* and *Varanus salvator*, the activity of two of the hypaxial muscles, the external oblique and rectus abdominis, is appropriately timed for the production of lateral bending. This indicates that elements of the hypaxial musculature, not the epaxial musculature, are the primary lateral bending muscles of lizards.

Key words: *Varanus salvator*, *Iguana iguana*, electromyography, lizard, locomotion, epaxial muscles, hypaxial muscles, lateral bending.

### Introduction

The function of the axial musculature in vertebrate locomotion is of critical importance. For example, the axial muscles are the sole engines of the basal mode of vertebrate locomotion, swimming *via* lateral undulations of the trunk and tail. Undulatory swimming is retained in the majority of extant fishes, and both epaxial and hypaxial divisions of the axial musculature participate in bending the trunk (e.g. Jayne and Lauder, 1995). Salamanders also employ both epaxial (Frolich and Biewener, 1992) and hypaxial (Carrier, 1993) musculature in the production of lateral bending during undulatory swimming. During terrestrial locomotion (walking), however, activity of the hypaxial muscles of salamanders suggests that they are involved in stabilizing the trunk against some component(s) of the ground reaction force (Carrier, 1993). An electromyographic study of the hypaxial muscles of a lizard (the green iguana *Iguana iguana*) during walking led Carrier (1990) to conclude that these muscles function to stabilize the trunk during terrestrial locomotion in lizards as well. Historically, it

has been assumed that the epaxial muscles of lizards have a function similar to the epaxial muscles of salamanders; production of lateral bending during locomotion (e.g. Gasc, 1981). The emergent evolutionary scenario for the locomotor role of the axial muscles in lower vertebrates is as follows. The basal role of both epaxial and hypaxial muscles is lateral bending of the trunk. The movement of tetrapods to terrestrial habits was accompanied by a functional shift in the hypaxial muscles, which became stabilizers of the trunk in amphibians and retained this function in reptiles. The epaxial musculature of both amphibians and reptiles retains the basal vertebrate function of lateral bending of the trunk.

A recent electromyographic analysis of epaxial muscle function in a lizard (the water monitor *Varanus salvator*), however, concluded that the epaxial muscles are *not* involved in lateral bending of the trunk, but act to stabilize the trunk against the vertical component of the ground reaction force (Ritter, 1995). A stabilizing role for the epaxial muscles had

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previously been described only for mammals (Tokuriki, 1973a,b; Carlson *et al.* 1979; English, 1980; Thorstensson *et al.* 1982; Shapiro and Jungers, 1994) and birds (Gatesy and Dial, 1993). Given the apparent stabilizing role of the epaxial muscles in a lizard, Ritter (1995) suggested that this stabilizing function may be a basal feature of amniotes. Increased stability of the trunk may be important for attaining high speed during terrestrial locomotion, as it would allow animals to deal with the greater peak vertical forces that accompany increased speed (e.g. compare Figs 1 and 5 of Cavagna *et al.* 1977). Therefore, the proposed functional shift of the epaxial muscles from lateral bending of the trunk in amphibians to stabilization of the trunk in reptiles may represent a key innovation in the evolution of terrestrial locomotion in vertebrates (Ritter, 1995).

The goal of the present study is to investigate further axial muscle function during locomotion by evaluating function in a greater number of muscles and in an additional lizard species. *Iguana iguana* was chosen as a species for comparison with *Varanus salvator* because it is highly divergent from *Varanus salvator* (Estes *et al.* 1988) and these species are therefore expected to provide an indication of the diversity among lizards in axial muscle activity pattern. Also of importance is the fact that *Iguana iguana* is a member of a basal lizard taxon (Estes *et al.* 1988), and its pattern of axial EMG activity may be taken as more representative of the basal lizard pattern than that of *Varanus salvator*.

The generality of a stabilizing function of the epaxial muscles among lizards is addressed by testing epaxial muscle function in the green iguana (*Iguana iguana*). By testing the generality of the stabilizing function within lizards, we simultaneously evaluate the proposition that it is a basal feature of amniotes. For example, if the epaxial muscles of *Iguana iguana* function in lateral bending of the trunk, then we must conclude that the stabilizing role of the epaxial muscles of *Varanus salvator* is a derived feature that evolved within lizards and is therefore not a basal feature of amniotes. Conversely, if the epaxial muscles of *Iguana iguana* function in stabilization of the trunk, then we may conclude that the stabilizing role of the epaxial muscles is a likely basal feature of lizards, and parsimony would dictate that the stabilizing function is therefore a likely basal feature of amniotes. Therefore, investigation of epaxial muscle function in a lizard species from a basal clade provides information about the evolution of epaxial muscle function at two different phylogenetic levels; both within lizards as well as among the major clades of vertebrates.

Another goal of this study is to answer a question that logically follows the statement that the epaxial muscles of lizards do not produce lateral bending during locomotion; how is lateral bending produced? To investigate this question, EMGs were recorded from selected hypaxial muscles of both *Iguana iguana* and *Varanus salvator*.

## Materials and methods

### Animals

Lizards were housed communally (species were kept

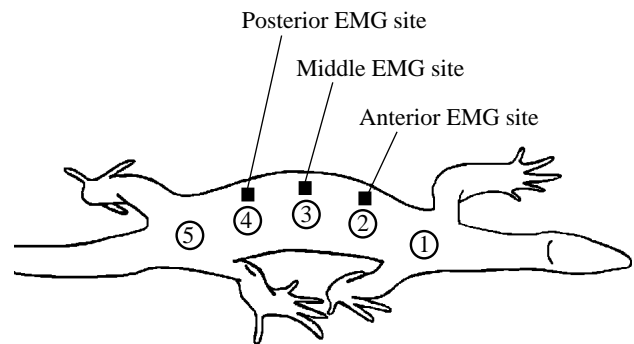


Fig. 1. Diagrammatic lizard trunk showing the placement of kinematic markers (numbered circles) and electromyography (EMG) electrodes (squares) for all animals used in this study (three *Iguana iguana* and three *Varanus salvator*). Bilateral implants were made at the middle EMG site. All animals had five kinematic markers glued to the dorsal midline. The middle trunk angle (subtended by points 2, 3 and 4) is used for all calculations in this study. All electromyographic data reported in this study are from electrodes implanted at the middle EMG site.

separate) in large pens (2 m×2 m×4 m), on a 12 h:12 h light:dark cycle that included full-spectrum light. The pens were maintained at 26 °C, and the lizards were allowed to thermoregulate behaviorally *via* heat lamps. Lizards were given free access to water. *Varanus salvator* Cantor were fed dead mice once per week. *Iguana iguana* L. were fed a mixture of greens every day. Two cadavers of each species were used for initial dissection of the axial muscles to facilitate electrode implantation and to provide a description of the muscles of interest. Electromyographic (EMG) and kinematic data from three individuals of each species are reported in this study. Snout–vent lengths (cm) and masses (g) of the three *Varanus salvator* were, respectively: 36, 900; 39, 960; 38, 1000. Snout–vent lengths (cm) and masses (g) of the three *Iguana iguana* were, respectively: 33, 1250; 35, 1400; 30, 1100.

### Video-taping

Video-taping was performed at 120 frames s<sup>-1</sup> with a Peak Performance Technologies high-speed video camera and video recorder. Lizards ran on a stationary trackway 0.6 m wide and 9.7 m long, with sides 0.6 m high. The middle 2.4 m of the trackway had an acrylic side-wall, the ‘working section’ of the trackway. The animals had sufficient trackway in front of and behind the working section to facilitate their movement at a constant speed while in the working section. The animal’s average forward speed was computed from movements of a kinematic marker glued to the dorsal midline at the level of the pectoral girdle (marker 1, Fig. 1). Trials chosen for analysis were those in which the animal moved in a straight line and the standard deviation of the speed of the animal in the working section was 10% or less of the average speed for that trial. A ‘locomotor trial’ encompassed the time during which the animal was visible in the working section of the trackway, which usually consisted of 2–3 locomotor cycles for a running

animal. A 1.8 m long mirror was suspended over the working section of the track, oriented at 45° to the horizontal, which permitted simultaneous lateral and dorsal views of the animal to be recorded. A light-emitting diode in the field of view was used to synchronize the video and EMG records.

#### *Kinematic analyses*

The techniques used for the kinematic analyses are after Ritter (1995). Briefly, kinematic analyses were performed using Peak Performance Technologies video analysis software (version 5) running on an IBM-compatible computer. Footfall events (time of placement and lift-off of all feet) were recorded from the video tapes. Both the amplitude and timing of lateral bending were calculated by manually digitizing the positions of 1 cm×1 cm reflective markers glued to the dorsal midline of the animal. Each animal bore five reflective markers, evenly spaced between the pectoral and pelvic girdle (Fig. 1). As the animals moved, any angle formed by the trunk in the horizontal plane oscillated above and below 180°. The amplitude of bending was recorded as the maximum resultant angles, which are the absolute values of the maximum deviations from 180°. Additionally, a given side of the trunk (left or right) may be described as oscillating between times of maximum concavity and maximum convexity. This is the convention used to report the times of maximum lateral trunk bending, and it is always reported relative to a kinematic or electromyographic event on the same (ipsilateral) side of the trunk.

#### *Electromyography*

Bipolar patch electrodes (Loeb and Gans, 1986) and sew-through electrodes (Betts *et al.* 1976) were used to record the activity of the transversospinalis (TS), longissimus dorsi (LD) and iliocostalis (IC) muscles of *Iguana iguana*, and from the rectus abdominis (RA) and external oblique (EO) muscles of both *Iguana iguana* and *Varanus salvator*. EMG data presented here for comparison from the TS, LD and IC muscles of *Varanus salvator* are from a previous study (Ritter, 1995). Individual animals were implanted with a mix of both electrode types, except for the TS muscle, which was only implanted with patch electrodes. As the study progressed, the sew-through electrodes were used increasingly, because of their simpler construction and the greater security of their implantation. A representative of each muscle was simultaneously implanted with both a patch and a sew-through electrode at least once during the study, so that a qualitative comparison of the resultant EMG signals could be made.

Both the patch and the sew-through electrodes were constructed from Dow Corning Silastic sheeting (500 µm thick) and Teflon-insulated, multi-stranded, stainless-steel wire (280 µm diameter, California Fine Wire Co.). Patch electrodes were approximately 4 mm×6 mm. The bared portions of the wires were approximately 1 mm long, and the bared wires were separated from each other by approximately 1 mm. Sew-through electrodes consisted of two parallel pieces of wire joined together at one end with an overhand knot. A short portion of each wire (approximately 1 mm long) was stripped

of insulation to form the electrode. This uninsulated portion of wire was approximately 5 mm from the knot in one wire, and approximately 7 mm from the knot in the other wire, so that the bared portions of the wires were separated from one another by approximately 1 mm.

Animals were anesthetized with an intramuscular injection of ketamine hydrochloride (150 mg kg<sup>-1</sup> for *Varanus salvator*; 120 mg kg<sup>-1</sup> for *Iguana iguana*). This was supplemented during the course of the surgery with one-third the initial dose, as needed. Small incisions were made overlying the intended site of implantation (Fig. 1). Both the TS and the LD are contained in distinct connective tissue sheaths. Incisions were made in these sheaths, the electrode was either placed between the muscle and the sheath (patch electrodes) or sewn through the muscle (sew-through electrodes), and the sheath was sutured closed. Because the IC was closely adherent to the overlying skin, a small 'pocket' was dissected between the skin and muscle to allow for electrode placement. In one *Iguana iguana*, electrodes were implanted in both the profundus and superficialis portions of the EO. Patch electrodes were placed on the surface of a muscle and were immobilized by suturing them to the underlying muscle fascia. Implantation of sew-through electrodes was performed using a cutting needle, so that the recording surfaces of the wires were embedded in the muscle and oriented parallel to the direction of the muscle fibers. Before implantation, the needle was passed through a small (approximately 2 mm×2 mm) piece of Silastic sheeting, forming a 'button' that reduced the risk of the knotted end of the sew-through electrode from pulling through the muscle (i.e. the button sat between the knot and the surface of the muscle). After the electrode had been sewn through the muscle, another small piece of Silastic sheeting was threaded down the wires and brought to rest on the muscle surface. A square knot was tied with the electrode leads and brought to rest against the Silastic sheeting, so that the Silastic sheeting sat between the knot and the surface of the muscle. The wire leads from the electrodes were passed subcutaneously to a single exit point on the dorsal midline at the level of the pelvic girdle and soldered into gold connector pins that were subsequently mounted in insulated Amphenol nine-pin plugs. Signals were transmitted *via* lightweight conductors (Cooner Wire) to Grass P511 amplifiers, amplified 5000 times and bandpass-filtered between 100 and 1000 Hz (the effective sampling rate was 0.5 kHz). The signals were stored on a Macintosh Quadra 700 computer (Labview software) or an IBM-compatible computer (Bioware software).

#### *Parameter calculation*

Quantification of the temporal relationship between lateral bending of the trunk and rear foot strike was accomplished by calculating the 'bending-footfall delay' (% cycle duration) = [(time of maximum concave curvature -  $t_r$ )/ $t_d$ ]×100, where  $t_r$  is the time of ipsilateral rear foot strike and  $t_d$  is the cycle duration (all in ms). Cycle duration is the elapsed time between  $t_r$  and the subsequent ipsilateral rear foot strike and was determined from the video tapes. A bending-footfall delay of

zero indicates that the trunk is maximally concave at the time of ipsilateral rear foot strike. Negative values indicate that maximal concavity occurs before rear foot strike, positive values indicate that maximal concavity occurs after rear foot strike. The middle trunk angle (see Fig. 1) was used to calculate maximum concave curvature. The effect of forward speed on the bending–footfall delay was evaluated by least-squares regression of bending–footfall delay *versus* forward speed data, using a single mean value of the bending–footfall delay calculated for each locomotor trial.

The times of onset and offset ( $t_{on}$  and  $t_{off}$ , respectively) of the axial muscles were expressed relative to several kinematic variables in order to test hypotheses of muscle function (see below). Two parameters were calculated to evaluate the relationship between axial muscle activity and rear foot support; relative EMG onset (%) =  $[(t_{on}-t_r)/t_d] \times 100$ , and relative EMG offset (%) =  $[(t_{off}-t_r)/t_d] \times 100$ . Two parameters were calculated to evaluate the relationship between axial muscle activity and lateral bending of the trunk: onset–bending delay (in ms) =  $t_{on}$  minus the time of maximum ipsilateral convex curvature; and offset–bending delay (in ms) =  $t_{off}$  minus the time of maximum ipsilateral concave curvature. The duration of muscle activity ( $t_{dur}$ ) was standardized as the relative EMG duration (%) =  $(t_{dur}/t_d) \times 100$ . In all cases, parameter values from left- and right-side muscles were pooled for regression analyses and calculations of means and standard errors.

#### Analysis of muscle function

Two functional hypotheses were tested for each axial muscle: (1) that the muscle produces lateral bending of the trunk during locomotion, and (2) that the muscle functions to stabilize the trunk. These hypotheses were tested using the calculated parameters (described above) to determine whether EMG events and kinematic events were coupled. The presence of coupling was taken as indicative of a functional relationship between EMG events and kinematics, while the absence of coupling was taken as indicative of the lack of a functional relationship. Here, two events are considered to be coupled if an invariant temporal relationship exists between the two events over the range of forward speeds for which data were recorded. The determination of an invariant *versus* a variable temporal relationship was carried out by regressing the calculated parameters against speed (Fig. 2). A significant regression (Fig. 2B,C) indicates a variable temporal relationship and, therefore, a lack of coupling between the kinematic and electromyographic events. Conversely, the lack of a significant regression (Fig. 2A,D) indicates an invariant temporal relationship and, therefore, the presence of coupling between the kinematic and electromyographic events.

The onset– and offset–bending delays were used to test the lateral bending hypothesis, because they describe the temporal relationship between muscle activity and lateral trunk bending. For example, the finding of a significant regression between onset–bending delay and speed would indicate a lack of coupling between muscle EMG onset and maximum trunk

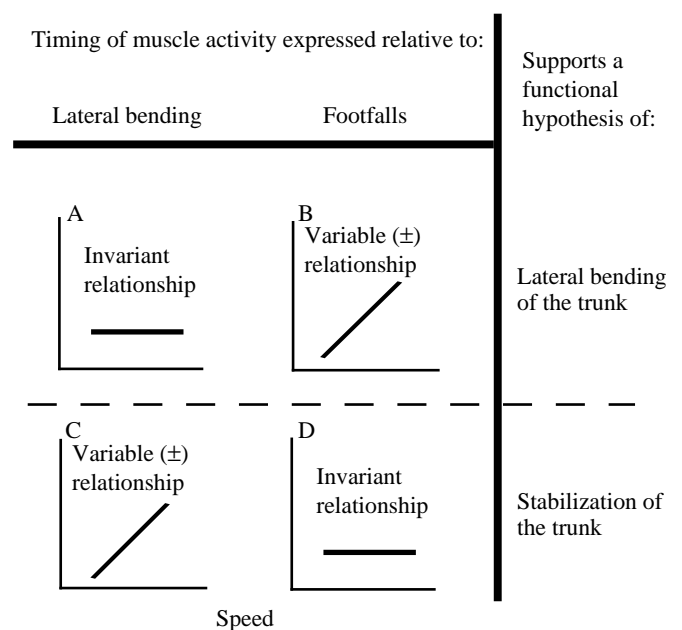


Fig. 2. A summary of the analysis of axial muscle function performed in this study. Timing of muscle activity (muscle EMG onset and offset) is expressed relative to kinematic events that describe lateral bending of the trunk or rear footfall. These calculated parameters are then regressed against speed. The lack of a significant relationship (A,D) indicates an invariant relationship between muscle activity and kinematics, indicating that muscle activity and kinematics are coupled. If muscle activity is coupled to lateral bending (A), this supports the lateral bending hypothesis for this muscle. If muscle activity is coupled to footfalls (D), this supports the stabilization hypothesis for this muscle. Since lateral bending and footfalls are *not* coupled (see Results), the activity of a given muscle should be coupled to one set of kinematic variables, but be uncoupled to the other. That is, either A and B or C and D should co-occur.

curvature, indicating that the muscle whose EMG onset times were used in the calculations is not involved in lateral bending of the trunk. The times of relative EMG onset and offset were used to test the stabilization hypothesis, because they describe the temporal relationship between muscle activity and rear limb support, and it is during limb support that the trunk would require stabilization against the ground reaction force.

## Results

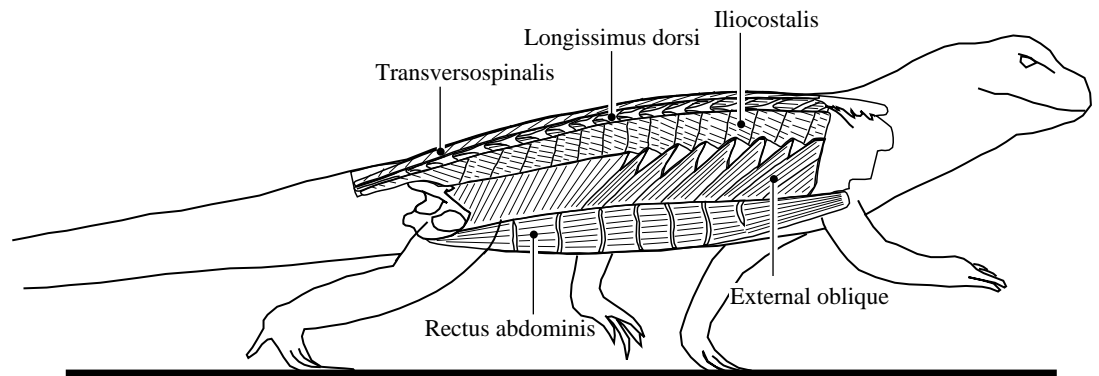
### Anatomy

The following description of the axial muscles is based on gross dissections performed as part of this study (Fig. 3). A more detailed treatment of the axial musculature of lizards, in general, may be found in Gasc (1981) and of *Iguana iguana*, in particular, in Carrier (1988).

### Epaxial muscles of *Iguana iguana*

The iliocostalis (IC) muscle occupies a dorso-lateral position on the trunk and is composed of broad, flat sheets of muscle fascicles that span only one vertebral segment. A given muscle

Fig. 3. A diagrammatic representation of some of the superficial axial muscles of *Iguana iguana*. Modified from Carrier (1990).



fascicle inserts onto the posterior aspect of a rib *via* a broad aponeurosis and originates from the aponeurosis of insertion of the next most posterior IC fascicle. The muscle fascicles have a slight lateral orientation as they course from posterior to anterior.

The longissimus dorsi (LD) muscle is medial to the IC muscle. The individual muscle fascicles of the LD arise tendinously from the post-zygapophysis of a vertebra and course anterolaterally. The fleshy belly of an LD fascicle is distinct and is approximately two vertebral segments long. The tendon of insertion divides so that a medial and a lateral tendon of insertion are formed. The lateral tendon contributes to the broad connective tissue sheet that separates the IC and LD muscles and also fans out to insert into the prezygapophysis of a vertebra and the proximal portion of the rib that articulates with that vertebra. The medial tendon of the LD contributes to the thick sheet of connective tissue that covers the mid-dorsal aspect of the body axis and has no direct connection to any bony structure. From origin to insertion, a fascicle of the LD muscle crosses 4–5 vertebral segments.

The most medial of the epaxial muscles, the transversospinalis (TS) muscle, is the most internally complex of the epaxial group and is composed of muscle fascicles that span adjacent vertebrae. The main divisions of the TS are the multifidus, spinalis and semispinalis fascicles. The most medial and deepest of these is the multifidus. Only patch electrodes were used to record from the TS, and it is unlikely that recordings were made from these deepest fascicles. The fascicles of the spinalis are lateral and dorsal to the multifidus. They originate on the post-zygapophyseal wing of a vertebra, course in a posteromedial direction, and insert *via* a discrete tendon onto the neural spine of a vertebra four segments posterior. The semispinalis is the most lateral and superficial of the muscle fascicles of the TS. Fascicles of the semispinalis originate from the post-zygapophyseal wing of a vertebra, course anteromedially, and insert by a strong tendon onto the neural spine of a vertebra four segments anterior. The patch electrodes were in direct contact with the semispinalis portion of the TS, although they may also have recorded activity from the spinalis.

#### *Hypaxial muscles of Iguana iguana and Varanus salvator*

The rectus abdominis (RA) muscle lies just beneath the skin

and occupies the ventral and ventro-lateral aspect of the trunk between the pelvic girdle and the pectoralis muscle. The muscle fibers are oriented parallel to the long axis of the trunk. This muscle originates from a thick tendon that attaches to the ischia and inserts onto costal cartilages and the posterior aspect of the pectoralis fascia. The most lateral portion of the RA is slightly thicker than the ventral portion and attaches solely to the pectoralis fascia. The thinner, more medial portion of the RA attaches to both the costal cartilages and the pectoralis fascia.

The external oblique (EO) muscle also lies just beneath the skin and occupies the lateral aspect of the trunk. In *Iguana iguana*, the EO is composed of both a superficial and a deep layer. The single layer of EO present in *Varanus salvator* is considered to be the superficial layer (Gasc, 1981). Both layers originate from the pubis posteriorly and the lateral edge of the RA more anteriorly. The muscle fibers run anteriorly and dorsally and insert either onto the transverse septum *via* a broad aponeurosis or onto the ribs by distinct tendons.

#### *Lateral trunk bending*

Values of the bending–footfall delay were negative except at the slowest speeds, indicating that maximum concave curvature of the trunk occurs before ipsilateral rear foot strike (Fig. 4). The significant regression between speed and bending–footfall delay indicates that, as speed increases, an increasing percentage of the locomotor cycle elapses between the time of maximum concave curvature and ipsilateral rear foot strike (Fig. 4). Values of the bending–footfall delay range from 0% at the slowest speeds to –40% at the highest speeds.

#### *Muscle activity*

All animals used in the EMG analyses had electrodes implanted in the middle EMG site (Fig. 1); therefore, the following discussion of the pattern of muscle activity is based on data from that site. Sufficient data from all three sites were not available for a statistical analysis, but examination of the available data indicated no regular pattern of differences between sites within a muscle in EMG onset or offset times, nor in relative EMG duration. EMG onset and offset times for the profundus and superficialis portions of the EO of *Iguana iguana* were essentially identical. All five axial muscles exhibited a pattern of alternating left- and right-side activity with one period

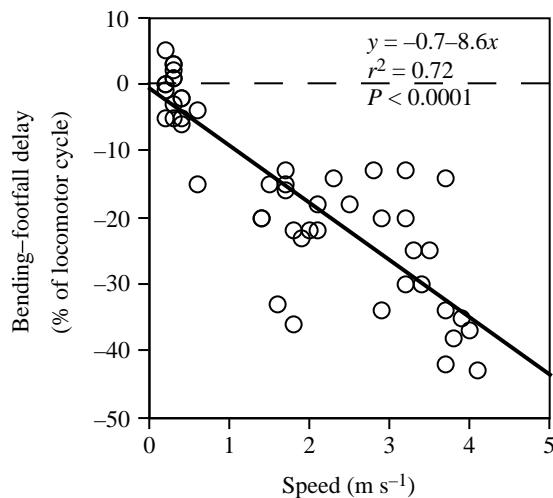


Fig. 4. Bending-footfall delay of *Iguana iguana*, calculated using data from the middle trunk angle (subtended by points 2, 3 and 4 of Fig. 1), as a function of speed. The bending-footfall delay represents the percentage of the locomotor cycle that elapses between maximum concavity of the trunk and ipsilateral rear foot strike. Each point represents a mean value for one locomotor trial, which encompasses 2–3 consecutive locomotor cycles. The temporal relationship between lateral trunk bending and foot support varies linearly with speed. As speed increases, a progressively larger percentage of the locomotor cycle separates the time of maximum concavity and the time of ipsilateral rear foot strike. These data are from three individuals, 49 trials and 100 locomotor cycles.

of activity per muscle per locomotor cycle (Figs 5, 6). The relative durations of muscle activity were constant across the range of speeds for which data are available (Tables 1, 2).

#### *Iguana iguana epaxial muscles*

The relative EMG onset and offset of the IC and LD muscles of *Iguana iguana* were invariant over the range of speeds recorded (Table 1; Figs 5, 7A). This indicates that activity of these muscles occurs in a regular way relative to rear foot support, regardless of speed. Muscle activity began in the early stage of ipsilateral rear foot support, continued throughout the remainder of the support phase, and ceased at approximately the time of contralateral rear foot strike (Table 1; Fig. 5). Both muscles were active for approximately 40% of the locomotor cycle (Table 1).

The EMG onset- and offset-bending delays of the IC and LD muscles were variable over the range of speeds recorded and exhibited a significant regression against speed (Table 1; Fig. 7A). Values for the onset-bending delay were usually negative, indicating that EMG onset typically preceded maximum ipsilateral convexity (Fig. 7A). Maximum values recorded for onset-bending delay were -90 and -80 ms for the IC and LD, respectively. Similarly, values for offset-bending delay were usually negative, indicating that EMG offset typically preceded maximum ipsilateral concavity (Fig. 7A). Maximum values recorded for offset-bending delay were -135 and -100 ms for the IC and LD, respectively.

Table 1. Results of least-squares regressions of calculated parameters (which describe the temporal relationship between electromyographic and kinematic events) against speed for the epaxial muscles of three *Iguana iguana*

Variable	F	P	r <sup>2</sup>	Mean (s.d.) or y-intercept, slope	Supports
<b>Iliocostalis (1.4–4.1 m s<sup>-1</sup>)</b>					
Relative EMG onset (28)	<0.01	0.98	<0.01	12 (6)	Stabilization
Relative EMG offset (28)	0.01	0.94	<0.01	52 (6)	Stabilization
Onset-bending delay (25)	24.15	<0.01	0.51	-89, 21	Stabilization
Offset-bending delay (25)	7.43	0.01	0.24	-118, 22	Stabilization
Relative EMG duration (28)	0.11	0.75	<0.01	40 (8)	-
<b>Longissimus dorsi (1.4–4.1 m s<sup>-1</sup>)</b>					
Relative EMG onset (28)	0.02	0.89	<0.01	15 (7)	Stabilization
Relative EMG offset (28)	2.73	0.11	0.10	57 (6)	Stabilization
Onset-bending delay (25)	16.92	<0.01	0.42	-82, 21	Stabilization
Offset-bending delay (25)	8.69	<0.01	0.27	-104, 18	Stabilization
Relative EMG duration (28)	1.62	0.21	0.06	42 (8)	-
<b>Transversospinalis (0.2–4.1 m s<sup>-1</sup>)</b>					
Relative EMG onset (38)	66.73	<0.01	0.65	49, -10	Bending
Relative EMG offset (38)	70.23	<0.01	0.66	85, -9.0	Bending
Onset-bending delay (35)	4.57	0.04	0.12	25, -10	Stabilization
Offset-bending delay (35)	14.3	<0.01	0.30	-99, 18	Stabilization
Relative EMG duration (38)	0.41	0.53	0.01	38 (8)	-

Numbers in parentheses beside each muscle name indicate the range of speeds recorded for that muscle.

Numbers in parentheses after each calculated parameter indicate the total number of locomotor trials used for regression analysis.

The far right column indicates which of the two functional hypotheses is supported by the regression analysis.

See text for description of parameters.

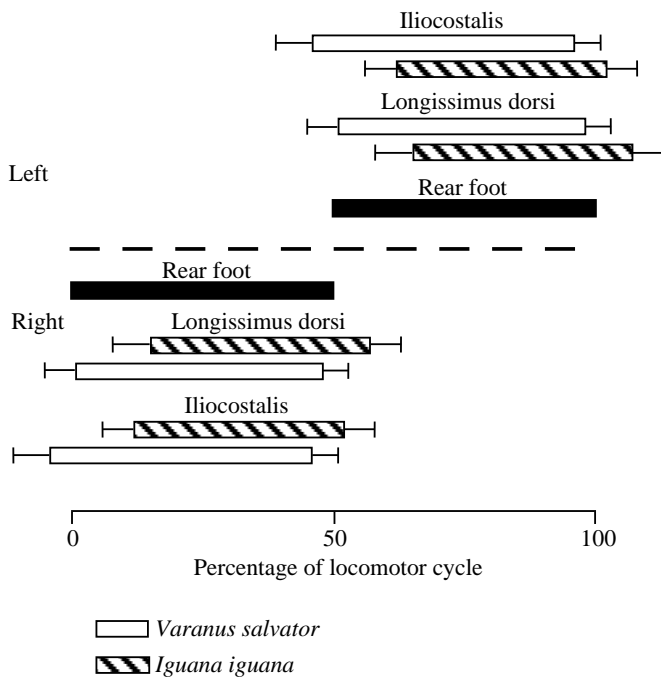


Fig. 5. Summary diagram of EMG activity of the two most lateral epaxial muscles (iliocostalis and longissimus dorsi) relative to rear foot support from *Iguana iguana* (hatched bars) and *Varanus salvator* (open bars, data from Ritter, 1995). Relative times of EMG onset and offset did not vary with speed over the range recorded ( $1.4\text{--}4.1\text{ m s}^{-1}$  for *Iguana iguana*,  $0.5\text{--}3.5\text{ m s}^{-1}$  for *Varanus salvator*). Conversely, the times of EMG onset and offset relative to the times of maximum trunk bending varied with speed (Table 1; Fig. 7A), and therefore the times of maximum bending cannot be accurately placed on this figure. The central dashed line separates the left and right sides of the animal, dark bars representing periods of rear foot support are lateral to the central dashed line, and the EMG data are lateral to these. EMG data are from the middle site of electrode implantation (see Fig. 1). The thin horizontal bars at the end of each EMG bar represent 1 s.d. of the relative EMG onset and offset times and are calculated using pooled data from three animals. See text for calculations of relative times of EMG onset and offset.

Although all three animals did locomote at speeds below  $1.4\text{ m s}^{-1}$ , activity from the LD and IC muscles was highly variable in terms of its presence or absence, its temporal relationship to kinematic events and its intensity and duration at these lower speeds.

Data from the IC and LD muscles of *Iguana iguana* indicate a variable relationship, and therefore a lack of coupling, between muscle activity and lateral bending of the trunk. Conversely, an invariant relationship, indicating the presence of coupling, was found between muscle activity and foot support. These results support a functional hypothesis that these two epaxial muscles stabilize the trunk during locomotion and do not participate in lateral bending of the trunk (Table 1).

Data from the TS support this muscle's role in both lateral bending and trunk stabilization. Relative EMG onset and offset exhibit a significant regression against speed (Table 1),

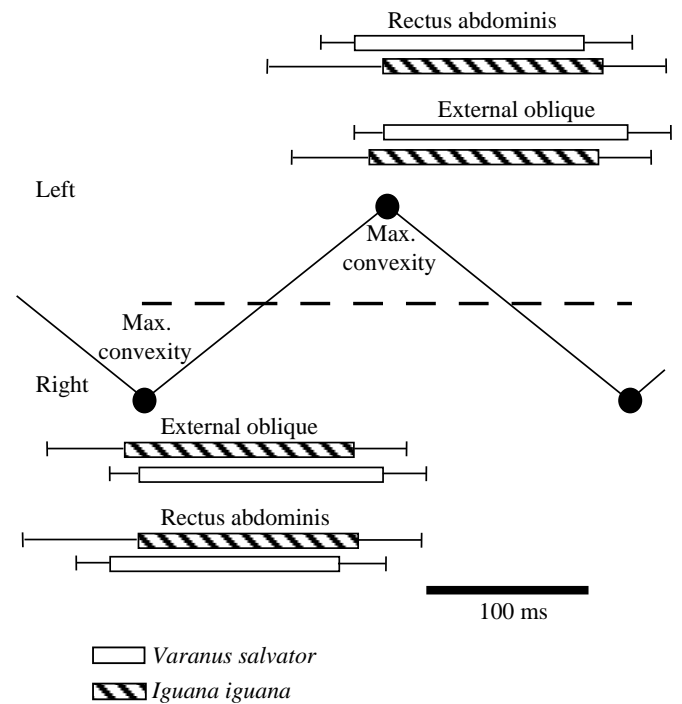


Fig. 6. Summary diagram of EMG activity of two of the hypaxial muscles (external oblique and rectus abdominis) relative to lateral trunk bending for *Iguana iguana* (hatched bars) and *Varanus salvator* (open bars). The central dashed line separates the left and right sides of the animal, filled circles lateral to the central dashed line represent the times of maximum convexity of that side of the trunk. Maximum convexity of one side of the trunk corresponds to maximum concavity of the opposite side. Although the absolute durations of both the locomotor cycles and the muscle activity periods will vary with speed (i.e. longer at lower speeds, shorter at higher speeds), there is a statistically invariant time lag between maximum convexity of the trunk and ipsilateral muscle onset, and also between maximum concavity of the trunk and ipsilateral muscle offset, over the range of speeds recorded in this study ( $0.2\text{--}4.1\text{ m s}^{-1}$  for *Iguana iguana*,  $0.2\text{--}3.2\text{ m s}^{-1}$  for *Varanus salvator*). Conversely, the times of muscle onset and offset relative to rear foot support varied with speed (Table 2; Fig. 7B) and, therefore, the periods of rear foot support cannot be accurately placed on this figure. The data shown here are scaled to a locomotor cycle of 300 ms in duration, which corresponds to a speed of approximately  $2\text{ m s}^{-1}$  in both lizard species.

supporting a hypothesis of lateral bending. In addition, the onset- and offset-bending delays also show a significant regression against speed, supporting a hypothesis of stabilization of the trunk. Only the relative duration of EMG activity was unaffected by speed, with a mean value of 38% (Table 1).

*Iguana iguana and Varanus salvator hypaxial muscles*

In both species, the relative EMG onset and offset of the EO and RA muscles exhibited a significant regression against speed, indicating a lack of coupling between EMG activity and rear foot support (Table 2; Fig. 7B). In both species, the pattern of variation with speed in relative EMG onset and offset is similar to the pattern seen in Fig. 7B for the EO

Table 2. Results of least-squares regressions of calculated parameters (which describe the temporal relationship between electromyographic and kinematic events) against speed for two of the hypaxial muscles of three *Iguana iguana* and three *Varanus salvator*

Variable	<i>F</i>	<i>P</i>	<i>r</i> <sup>2</sup>	Mean (s.d.) or y-intercept, slope	Supports
<i>Iguana iguana</i>					
External oblique (0.2–4.1 m s <sup>-1</sup> )					
Relative EMG onset (29)	126.90	<0.01	0.83	50, -11	Bending
Relative EMG offset (29)	72.40	<0.01	0.73	99, -11	Bending
Onset–bending delay (25)	0.10	0.76	<0.01	-12 (47)	Bending
Offset–bending delay (25)	0.05	0.82	<0.01	-21 (35)	Bending
Relative EMG duration (29)	0.35	0.56	0.01	50 (6)	–
Rectus abdominis (0.2–4.0 m s <sup>-1</sup> )					
Relative EMG onset (25)	56.0	<0.01	0.71	51, -11	Bending
Relative EMG offset (25)	39.71	<0.01	0.63	102, -13	Bending
Onset–bending delay (23)	0.25	0.62	0.01	-2 (72)	Bending
Offset–bending delay (23)	0.18	0.67	0.01	-19 (39)	Bending
Relative EMG duration (25)	2.18	0.16	0.09	48 (8)	–
<i>Varanus salvator</i>					
External oblique (0.2–3.2 m s <sup>-1</sup> )					
Relative EMG onset (37)	98.64	<0.01	0.74	48, -13	Bending
Relative EMG offset (37)	24.60	<0.01	0.41	96, -10	Bending
Onset–bending delay (35)	3.98	0.06	0.11	-2 (18)	Bending
Offset–bending delay (35)	<0.01	0.99	<0.01	-2 (27)	Bending
Relative EMG duration (37)	2.04	0.16	0.06	54 (11)	–
Rectus abdominis (0.2–3.1 m s <sup>-1</sup> )					
Relative EMG onset (27)	54.44	<0.01	0.69	46, -15	Bending
Relative EMG offset (27)	42.71	<0.01	0.63	89, -13	Bending
Onset–bending delay (27)	2.62	0.12	0.10	-22 (23)	Bending
Offset–bending delay (27)	0.02	0.90	<0.01	-31 (29)	Bending
Relative EMG duration (27)	1.21	0.28	0.05	47 (7)	–

Numbers in parentheses beside each muscle name indicate the range of speeds recorded for that muscle.

Numbers in parentheses after each calculated parameter indicate the total number of locomotor trials used for regression analysis.

The far right column indicates which of the two functional hypotheses is supported by the regression analysis.

See text for description of parameters.

muscle of *Varanus salvator*. Relative EMG onset was approximately 50% at the lowest speeds and in all cases decreased to approximately 0% at the highest speeds. Values of relative EMG offset were approximately 100% at the lowest speeds and decreased to approximately 50% at the highest speeds. Therefore, at the lowest speeds, both muscles are active contralateral to rear limb support, while at the highest speeds the muscles are active ipsilateral to rear limb support.

The onset- and offset-bending delays for both of these muscles in both species do not show a significant regression against speed, indicating coupling between muscle activity and lateral bending (Table 2). The mean onset- and offset-bending delays are negative, indicating that muscle onset precedes maximum ipsilateral convexity, and muscle offset precedes maximum ipsilateral concavity (Table 2).

In both species, the EO and RA muscles exhibited a regular

pattern of activity at all speeds, even at the lowest speeds recorded of 0.2 m s<sup>-1</sup>. All data from the EO and RA muscles of both species indicate an invariant relationship between muscle activity and lateral bending and a variable relationship between muscle activity and foot support. These results support a functional hypothesis that these two hypaxial muscles bend the trunk laterally during locomotion and are not involved in stabilization of the trunk (Table 2).

## Discussion

The general goal of this study was to further our understanding of the locomotor role of the axial muscles of lizards in particular as well as the evolution of the locomotor role of the axial muscles in vertebrates in general. The functional analyses performed were possible because of the variable relationship between limb and trunk movements, so



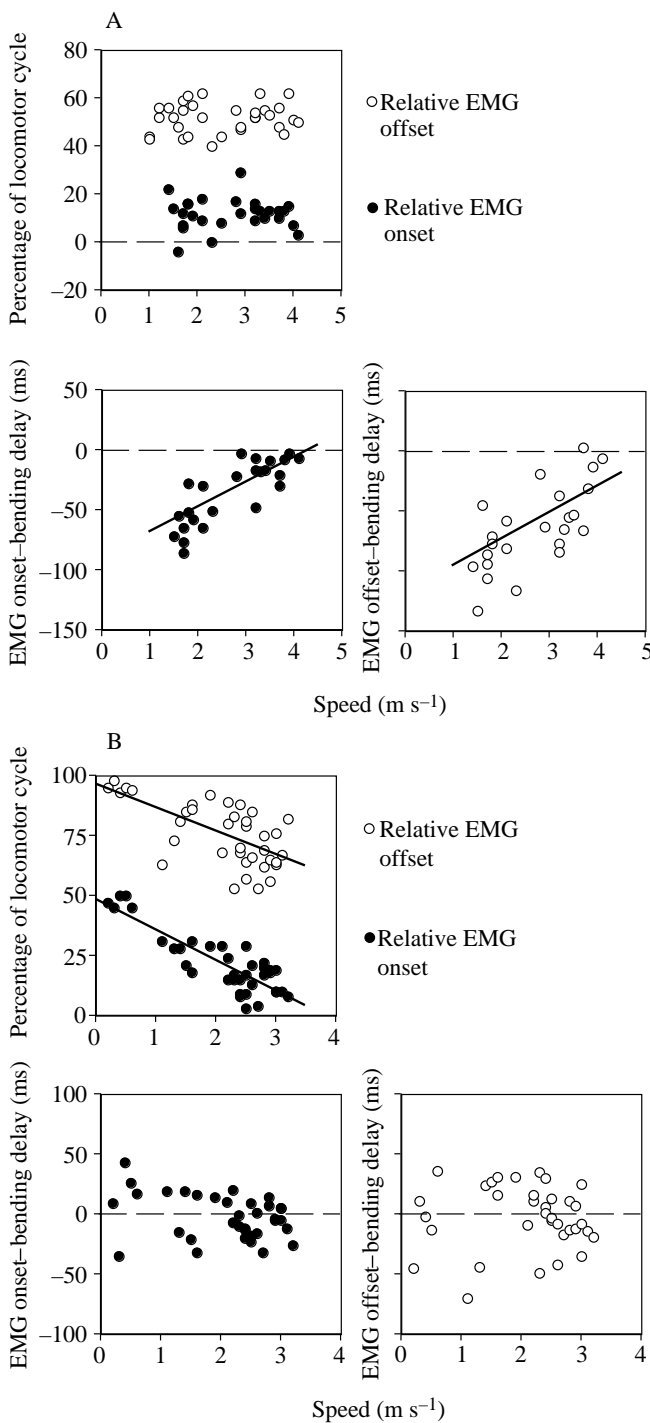


Fig. 7. Graphs of relative EMG onset and offset, onset-bending delay and offset-bending delay as a function of speed. (A) Data from the iliocostalis (IC) muscle of *Iguana iguana*, which support a functional hypothesis of stabilization of the trunk. Neither relative EMG onset nor EMG offset is significantly affected by speed, while both onset- and offset-bending delay are affected by speed. See Table 1 for mean values and regression parameters. (B) Data from the external oblique (EO) muscle of *Varanus salvator*, which support a functional hypothesis of lateral bending of the trunk. Here we see a pattern opposite that seen in the IC muscle of *Iguana iguana*. Both relative EMG onset and EMG offset are significantly affected by speed, while neither onset- nor offset-bending delay is significantly affected by speed. See Table 2 for mean values and regression parameters.

and speed is similar in the two species ( $-8.6$  in *Iguana iguana*,  $-8.3$  in *Varanus salvator*), although the y-intercepts are different ( $-0.7$  in *Iguana iguana*,  $-10.1$  in *Varanus salvator*). These data are relevant to at least one possible function of lateral bending during lizard locomotion, that of increasing stride length (e.g. Daan and Belterman, 1968). A maximal increase in stride length theoretically requires a bending-footfall delay of approximately zero, a value that is approached by *Varanus salvator* and attained by *Iguana iguana* only at low walking speeds. Therefore, it seems that, if lateral trunk bending does serve to increase stride length, this increase occurs mainly at low speeds. At higher speeds, the locomotor function of the trunk may be to provide propulsive force, to provide a stable base for limb support, or aspects of interlimb coordination may become an important determinant of trunk movements.

The kinematics of lateral trunk bending have been studied in relatively few lizard species (Daan and Belterman, 1968; Ritter, 1992), but two general conclusions are apparent. First, there is much variation in lateral bending, both within and among species. For example, both standing and traveling waves of bending have been described, and the amplitude of bending may be constant or variable along the length of the animals' trunk. Second, much of this variation appears to correlate with speed and with aspects of the morphology of the individual species. For example, some species switch from standing to traveling waves of bending as speed increases, and species with diminutive limbs tend to exhibit traveling waves even at their lowest speeds. Given the variation seen in lateral bending, it seems reasonable to expect that lateral bending may serve different functions in different lizard species. Further studies are needed to integrate the effects of body form and speed on the function of lateral bending during lizard locomotion.

*Axial muscle function*

My functional interpretation of the data presented here is that in both species the IC and LD muscles stabilize the trunk and the EO and RA muscles bend the trunk laterally during locomotion. These interpretations are based on the temporal relationship between kinematic and electromyographic events, and they are further supported by the anatomy of the muscles as well as by additional aspects of their EMG activity.

that relationship will be considered first. A discussion of the pattern of axial muscle activity in lizards as it relates to the function of these muscles follows. Finally, the broader implications of these data are discussed.

*Bending-footfall delay*

Both *Iguana iguana* and *Varanus salvator* exhibit a variable phase relationship between lateral bending of the trunk and rear foot strike (Fig. 4 and Ritter, 1995). The slope of the line that describes the relationship between the bending-footfall delay

In both species, the IC and LD muscles are active ipsilateral to rear foot support (Fig. 5) and exhibit an invariant relationship with rear foot strike (Table 1; Ritter, 1995). This pattern indicates that these muscles are involved in stabilization of the trunk during locomotion (Fig. 2; Table 1). Specifically, the IC and LD muscles may counteract the tendency for the unsupported side of the pectoral girdle to fall towards the ground (Ritter, 1995). The timing of muscle activity ipsilateral to rear foot support provides evidence for this interpretation because, when a rear foot is in the support phase, the ipsilateral front foot is in the swing phase. The TS of *Iguana iguana* exhibits a variable relationship to kinematic events (Table 1), and therefore a description of the mean activity of this muscle, as described for the IC and LD muscles, is not possible. It may be that the patch electrodes used to record from the TS actually recorded the activity of more than one element of this muscle. In other amniotes, the activity of the TS has been interpreted as adjusting the position of individual vertebrae relative to other vertebrae (e.g. Donisch and Basmajian, 1972), or more generally as helping to control the stiffness of the back (Carlson *et al.* 1979; English, 1980).

The majority of EO and RA muscle activity occurs as the ipsilateral trunk is moving from maximum convexity to maximum concavity (Fig. 6). Both muscles in both species show an initial period of activity before bending reverses direction, but it is of short duration (Table 2). Likewise, the muscles on one side cease activity slightly before maximum ipsilateral concavity (Fig. 6). The pattern of muscle activity relative to bending, and especially the invariant relationship between bending and muscle activity, supports the hypothesis that these two hypaxial muscles are involved in the production of lateral trunk bending. An earlier study of hypaxial muscle function during walking in *Iguana iguana* reported similar EMG activity of the EO and RA muscles, but suggested that these muscles function to counteract long-axis torsion of the trunk (Carrier, 1990), an interpretation that is appropriate for the walking speeds recorded in that study. As speed increases, however, the phase relationship between muscle activity and foot support changes until it is almost opposite that at the lowest speeds (e.g. Fig. 7B). If the EO and RA muscles were functioning to counter long-axis torsion of the trunk, an invariant relationship between muscle activity and footfalls would be expected. Instead, a variable relationship was found between muscle activity and footfalls, which does not support a stabilizing function for these muscles. However, it must be stressed that a lateral bending function is supported in only two of the hypaxial muscles (EO and RA). There are many other hypaxial muscles and any or all of them may function to stabilize the trunk as Carrier (1990) has suggested.

The functional conclusions reached in this study are supported by complementary aspects of the gross anatomy of lizard axial muscles. First, in order for an axial muscle to counter the vertically oriented ground reaction force (force of gravity), the muscle must be dorsal to the vertebral column, so that it has a net action of dorsi-flexion on the vertebral column. The epaxials are the only muscles dorsal to the vertebral

column. Therefore, if any muscle counteracts vertical forces, it must be a member of the epaxial muscle group. Second, while any axial muscle may contribute to lateral trunk bending so long as it produces a component of longitudinally oriented force, the effectiveness of a muscle in bending the trunk laterally will be greatest when the muscle is oriented parallel to and positioned furthest away from the bending axis of the trunk. The RA muscle has such a longitudinal orientation (Fig. 3). The EO, as its name suggests, has a more oblique orientation, but could still contribute substantially to lateral bending. The EO and RA muscles are the most lateral of the axial muscles, which gives them the best mechanical advantage of any axial muscle for the production of lateral bending.

Further evidence for these functional conclusions is provided by the absence of muscle activity in the IC and LD at slow walking speeds. Lateral trunk bending occurs at all speeds and exhibits its greatest amplitude at the lowest walking speeds in *Varanus salvator* (Ritter, 1995). However, in both the IC and LD muscles, no regular pattern of EMG activity is recorded below a minimum walking speed of approximately  $0.5 \text{ m s}^{-1}$  in *Varanus salvator* and  $1.4 \text{ m s}^{-1}$  in *Iguana iguana* (Table 1 and Ritter, 1995). The observation that the greatest lateral bending occurs in the absence of any EMG from the IC or LD argues against a lateral bending function for these muscles. In contrast, the EO and RA muscles of both species are active at even the slowest walking speeds recorded here ( $0.2 \text{ m s}^{-1}$ , Table 2), further supporting a function in lateral bending for these muscles. Peak vertical force decreases with decreasing speed and it is possible that, at some minimum speed, the trunks of lizards may not require active stabilization by axial muscles. Therefore, the lack of IC and LD activity at slow speeds does not contradict the hypothesis that these muscles function to stabilize the trunk during locomotion.

#### Broader implications

The results of this study support the hypothesis that a stabilizing role of the epaxial muscles is a general (basal) feature of lizards and also provide strong evidence that elements of the hypaxial musculature are the primary lateral bending muscles of lizards. This suggests refinements to the evolutionary scenario of axial muscle locomotor function outlined in the Introduction. One feature of that scenario is a retention of axial muscle function across the amphibian–reptile transition; in both salamanders (e.g., Liem, 1977) and lizards (e.g. Gasc, 1981), the epaxial muscles were believed to produce lateral bending of the trunk, while the hypaxial muscles were believed to provide stability to the trunk. However, the epaxial muscles of lizards do not retain the basal lateral bending function seen in fishes and amphibians. Instead, there appears to have been a major functional diversification of the epaxial muscles; a change from a lateral bending function in amphibians to a trunk stabilizing function in reptiles. Two correlative conditions consistent with this interpretation are: (1) the most significant anatomical diversification of the epaxial muscles occurs at the amphibian–reptile transition, from the myomeric dorsalis

trunci muscle of amphibians to the tripartite epaxial musculature of reptiles; and (2) a suite of physiological and ecological changes occurs with the advent of reptiles, as they are the first fully terrestrial tetrapods. In retrospect, given the changes in anatomy and ecology we see across the amphibian–reptile transition, it is not surprising to see this shift in the function of the epaxial muscles.

Although analysis of the EO and RA muscles of the two lizard species used in this study indicates that these muscles function in the production of lateral bending, it is unclear whether this represents the retention of a basal vertebrate function or a derived function of these muscles in lizards. Carrier (1993) came to the conclusion that the hypaxial muscles of a salamander (*Dicamptodon tenebrosus*) functioned to resist long-axis torsion of the trunk during terrestrial locomotion. This indicates that a lateral bending function of the EO and RA muscles of lizards is a derived feature. Carrier's (1993) interpretation of hypaxial muscle function in salamanders was based in part on the observation that, during terrestrial locomotion, the internal oblique and EO muscles of opposite sides of the body exhibited synchronous activity. However, EMG activity of the EO muscle was appropriately timed for the production of lateral bending. Activity of the RA was not recorded. Therefore, it is possible that the EO and RA muscles of salamanders are lateral bending muscles, in which case the lateral bending function of these muscles in lizards would represent the retention of an ancestral function. Muscle denervation experiments in progress will test the function of the hypaxial musculature during terrestrial locomotion in salamanders.

The major difference between the epaxial EMG patterns of *Iguana iguana* and *Varanus salvator* relates to burst duration; at all speeds, there is a greater duration of IC and LD muscle activity in *Varanus salvator*, which occurs because of the earlier onset of muscle activity relative to rear foot strike (Fig. 5). These differences in muscle activity may be associated with differences in musculoskeletal anatomy, locomotor habit or some other aspect(s) of the ecology of the two species. *Varanus salvator* has fewer sternal ribs than *Iguana iguana* (three versus six) as well as more robustly developed ribs in the posterior portion of the trunk (Hoffstetter and Gasc, 1969). Individual muscle fascicles of the IC of *Varanus salvator* span 4–5 vertebral segments, while the IC muscle of *Iguana iguana* retains a myomeric pattern, with each muscle subunit crossing a single vertebral segment. Varanid lizards are generally wide-ranging insectivorous or carnivorous foragers, while *Iguana iguana* is a strictly herbivorous, largely arboreal species. Further studies of axial muscle function will be required in order to determine the manner in which these anatomical and ecological differences interact.

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