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Role of Lateral Body Bending in Crocodylian Track Making

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Locomotion in the alligatorids *Caiman* and *Alligator* show ontogenetic changes in gait width, manus orientation, and the amount of lateral body movement. In addition, the trackway of an adult *Caiman* is narrower than predicted for a semierect position of the limbs based on stance. The narrowness of the *Caiman* trackway is due to lateral movement of the body during locomotion. This movement allows placement of the feet closer to the trackway midline than would occur if no lateral bending occurred. Lateral movement is widespread among limbed tetrapods, yet little consideration has been given to its effects in trackmaking. Inferring stance from fossil trackways must take into account lateral body movement, otherwise the resultant hypothesis will be flawed.

Keywords Crocodylian, locomotion, lateral body movement, trackways

INTRODUCTION

Fossil footprints and trackways have been a source of important stratigraphic, morphological, functional, evolutionary, and behavioral data for the vertebrate paleontologist. The interpretation of these tracks has been aided by the study of tracks made by living animals beginning more than 150 years ago when Hitchcock (1848) impressed the feet of dead reptiles and birds into clay to look at the resultant print in order to assess the makers of the tracks he was studying from what is today called the Newark Supergroup. Later studies utilized living animals, both captive (Schaeffer, 1941; Padian and Olsen, 1984a; Farlow, 1989) and wild (Reineck and Howard, 1978). Such studies provided important clues about the identity of the print maker, its behavior, the kinematics of its foot, and the effects of different substrate conditions. Padian and Olsen (1984a, b) also have noted that footprints can reveal the maker's stance and gait, but as I show below, such inferences must be used with caution when applied to quadrupedal trackways.

Among extant archosaurs, the crocodylians utilize a variety of gaits during locomotion (Schaeffer, 1942; Cott, 1961; Parrish,

1987): belly slide (low walk), high walk, and gallop (Webb and Gans, 1982). Of these, the high walk involves a semi-erect stance (semi-improved stance of Charig, 1972) in which the limbs assume a static adduction angle of about 55–70° (Reilly and Elias, 1998; Gatsey, 1991). This semi-erect stance has long been considered transitional in the sprawling-to-erect stance of archosaur evolution (e.g., Bakker, 1971; Charig, 1972; Parrish, 1986), although Reilly and Elias (1998) recently have challenged this. They note that extant crocodylians rely upon the distal limb elements to increase locomotion speed rather than the proximal element as used by other terrestrial vertebrates. This difference is due to crocodylians having acquired their semi-erect stance secondarily and is not simply a reversion back to the plesiomorphic state (Parrish, 1987). Whether this transition from erect to semi-erect stance in the evolution of crocodylians can be recognized in fossil trackways has yet to be explored. There is, in fact, reasonable doubt that such a transition can be recognized based on trackways of a modern crocodylian.

MATERIALS AND METHODS

An adult *Caiman sclerops* was obtained from the Monell Chemical Senses Center in Philadelphia, Pennsylvania, USA. It had a snout-vent length (SVL) of 70 cm and an overall length of 148 cm. The *Caiman* was placed in a small room having only a single exit. A shallow, wood trough measuring 35 cm wide, 75 cm long, and 4 cm deep was placed at the exit. The trough had walls 30 cm tall on each side of the trough to restrict movement to its long axis. Mud was spread along the bottom of the trough and smoothed flat to a uniform thickness of about 2.5 cm. The *Caiman* was photographed as it exited the room towards the camera; coaxing was not needed. This front view is in contrast to most photographic studies which only capture profile and top views (e.g., Reilly and Elias, 1998, fig. 3). Several runs through the mud were made, and each trackway was photographed before being smoothed.

RESULTS

Although not reported before, the forelimbs of the *Caiman* are able to assume a sprawled stance when the animal is

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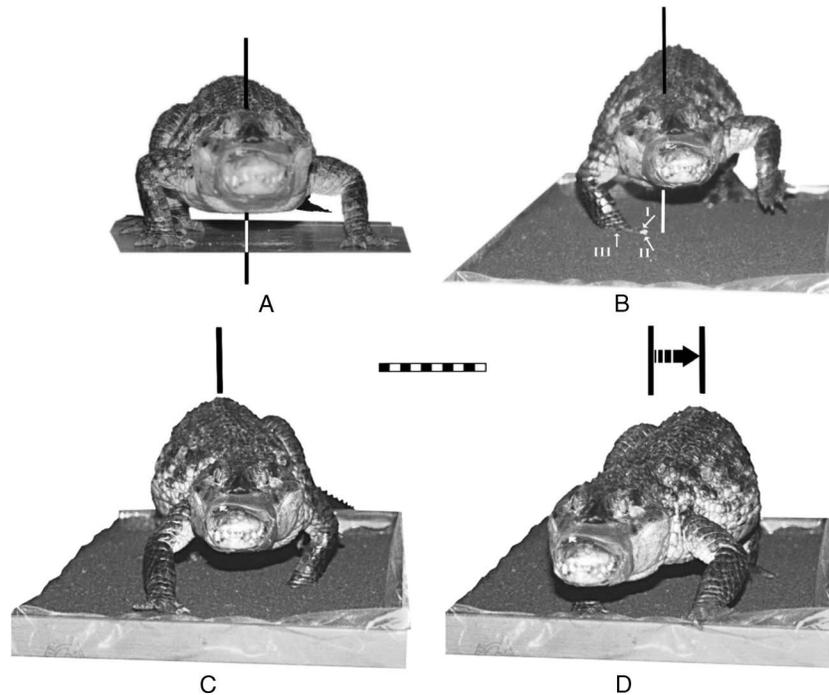


FIG. 1. Anterior or cranial view of an adult *Caiman* during stance and locomotion. Heavy vertical line or reference axis between the pectoral girdles shows the position of the midline. When stationary (A), the forelimbs can assume a sprawled position with the upper arm horizontal and the lower arm at right angles. In this stance, center of the manus is about 13 cm lateral from the reference axis. Contrast this with the semi-erect stance (B), where the upper arm moves through an anterior-posterior arc that is about 60° below horizontal. The lower arm, however, remains approximately vertical. In this semi-erect stance, the supporting manus is about 6.5 cm from the midline. Lateral movement of the body is visible in this sequence (C, D), with the total distance (dashed arrow) of about 5 cm, or 7% SVL. Scale in cm.

stationary. However this position is only maintained for a short time before it lowers itself to its belly. In this stance, the upper arm is horizontal and the lower arm perpendicular (Fig. 1A) resembling the sprawling stance of lizards.

The *Caiman* always exited the room in a high walk. Although speed data are not available, the speed was leisurely, not a run or rapid walk. During the high walk, the humerus assumed a semi-erect position approximately 60° below horizontal (Fig. 1B, right leg) and the femur about 65° . During locomotion, the vertebral column moved laterally, pivoting near the pectoral and pelvic girdles in a manner similar to that illustrated by Shaeffer (1942) and Reilly and Elias (1998). This side-to-side motion of the dorsal column does not move posteriorly in a sine-wave as seen in fish swimming (traveling wave of Ritter, 1992), but rather all points of the column reach their maximum lateral displacement at approximately the same time, producing what Ritter (1992) refers to as a standing wave. From the photographs (Fig. 1C–D), the caiman's body moved approximately 2.5 cm laterally on each side of the midline, or about 3.5% of the SVL.

The high walk trackway produced (Fig. 2A, B) is narrow, with the center of the manus print about 6.5 cm from the midline. The manus print shows slight negative (i.e., outward) rotation so that the impression of digit II is subparallel with the midline; a neutral position would be if the digit III was parallel with the midline. The manus print is also slightly medial to the pes print,

a feature that might be mistaken to imply a more erect forelimb stance had only the trackway been known.

DISCUSSION

Most studies of archosaurian locomotion have focused on the hind limbs probably because it is the main source of propulsion (e.g., Brinkman, 1980; Parrish, 1986, 1987). Even studies of dinosaurian locomotion have concentrated mostly on the hindlimb (e.g., Gatsey, 1991; Carrano, 2000). In contrast, the forelimb of quadrupeds has received less attention, except for discussions on stance (e.g., Bakker, 1971, 1972; Reilly and Elias, 1998; Christian et al., 1999), especially of ceratopsians (Johnson and Ostrom, 1995; Lockley and Hunt, 1995; Dodson and Farlow, 1997). Two exceptions, however, are the discussion of ceratopsian forelimb locomotion by Paul and Christiansen (2000) and Thompson and Holmes (2007). Footprints ascribed to ceratopsians have been used to interpret their forelimb stance (Fig. 3; Paul, 1991; Lockley and Hunt, 1995; Dodson and Farlow, 1997; Garstka and Burnham, 1997; Paul and Christiansen 2000). But this use of trackways to infer stance must be used with caution because the trackways reflect animals in motion, not in stasis.

During locomotion, tetrapods utilize lateral motions of the body to maximize support of the body by the weight-bearing

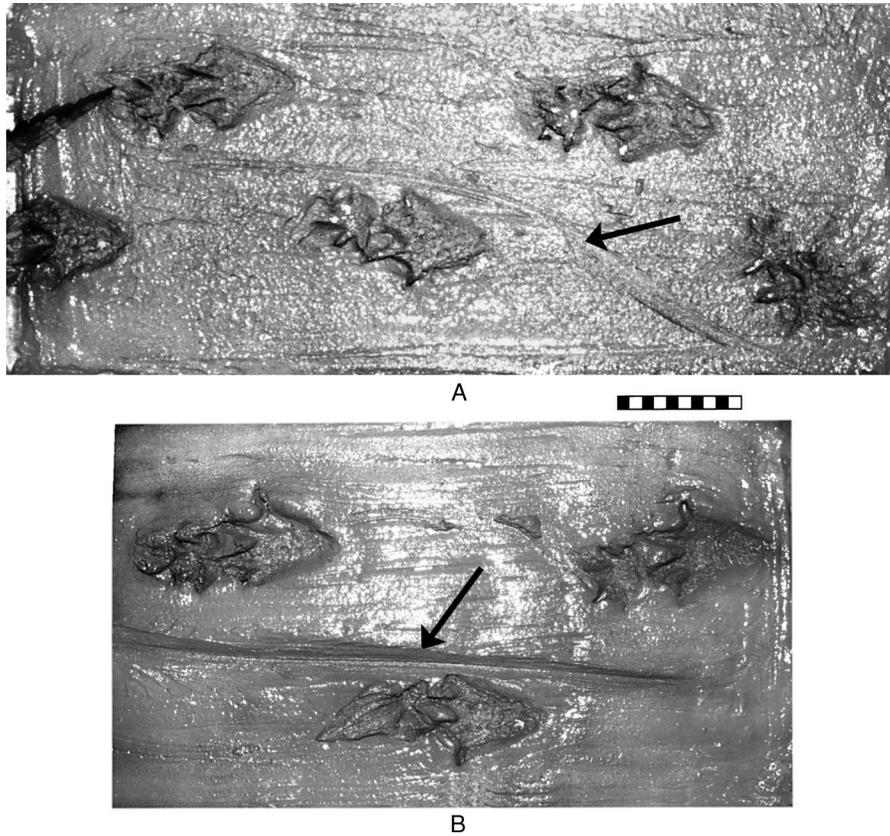


FIG. 2. Two trackways made by the same 130 cm *Caiman* across mud (see text) (A, B). The midpoint of the manus prints are about 13 cm apart, or about 6.5 cm on each side of the trackway midline. Arrows indicate tail drag marks. Note that the manus tracks are slightly medial to the midline of the pes tracks.

foot. This has the added benefit of also extending the stride of the forelimb (Ritter, 1992). This lateral movement of the tetrapod body is not a retention of the plesiomorphic condition seen in the lateral undulations of fishes as stated by Paul and Christiansen (2000, p. 454). Electromyography of the axial muscles has shown that both epaxial and hypaxial muscles are used in lateral undulations during swimming in both fishes and amphibians (Bennett et al., 2001). However, epaxial muscles (iliocostalis, longissimus dorsi, and transversospinalis) are used to support the vertebral column in lizards and mammals, and hypaxial muscles (rectes abdominis and external oblique) are used to produce lateral bending in these animals (Carrier, 1990; Ritter, 1995, 1996). In addition, hypaxial muscles in mammals stabilize the trunk against sagittal shearing forces (Fife et al., 2001). Ritter (1995, 1996) considers the use of hypaxial muscles rather than the epaxials in lateral movement the derived condition.

The presence of ossified tendons along the dorsal neural spines in ceratopsians lead Paul and Christiansen (2000) to assume these prevented lateral motion. However, ossified tendons are anisotropic, being stiff, strong, and tough under tension (parallel to the length of the tendon) but compliant in transverse direction (Currey, 1999). The ossified tendons of ceratopsians (and most ornithischian dinosaurs) are typically

laterally flattened, which would facilitate bending in that direction. Positionally, the ossified tendons are apparently associated with the transversospinalis of the epaxial group (Organ, 2006) where they probably functioned with the epaxial muscles to counter sagittal bounce of the back and tail during locomotion in a manner analogous to that reported by Ritter et al. (2001) for dogs.

Most studies of crocodylian locomotion have utilized juveniles (e.g., Schaeffer, 1942; Reilly and Elias, 1998), whereas an adult was used for this study. There does seem to be some difference between the locomotion of the juveniles and the adult, although this interpretation must be viewed with caution because the adult is of *Caiman sclerops*, whereas the juveniles are *Alligator mississippiensis*. Nevertheless, the comparison is plausible because both alligatorids have similar terrestrial gaits (Meers, personal communication).

The smallest specimen, illustrated by Schaeffer (1942, fig. 17), is clearly a very young individual, perhaps only a few months old based on the shape of the head. The head is more immature than a young 17.4 cm SVL preserved specimen (*Caiman sclerops*) I have (estimated age 9–12 months old). The differences in locomotion are evident based on the foot position relative to the midline of the back (compare manus impression

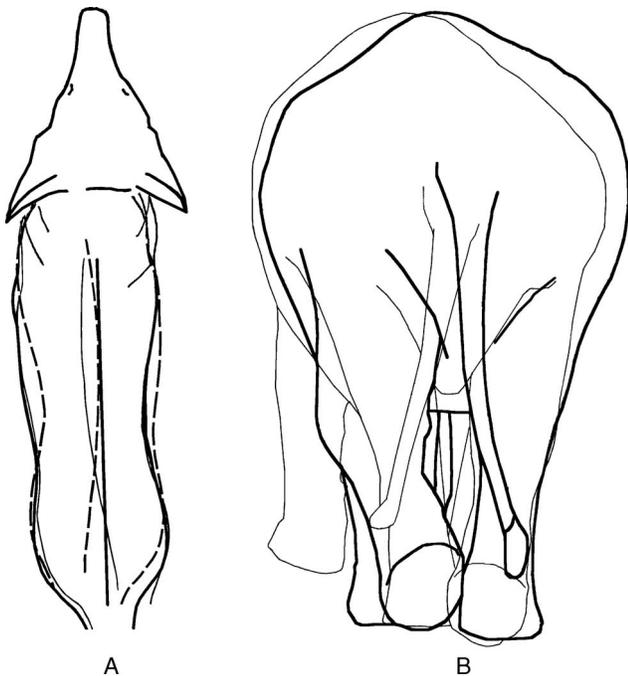


FIG. 3. Lateral motion of the body as seen in higher quadrupedal vertebrates serves to keep the center of mass nearer the weight-bearing legs as also occurs in the *Caiman* (FIG. 1): (A) *Canis familiaris* (drawn from video); (B), *Elephas maximus* (drawn from Muybridge, 1957, pl. 111, frames 1 and 12).

of adult in Fig. 1B with juvenile in figure 17H of Schaeffer, 1942). In the adult, the anatomical right manus (on the left side

of the figure) is partially beneath the right side of the body to bear the greater mass as the left forefoot is brought forward. Digits I and II are beneath the body and would not be visible in dorsal view; digit III may be partially visible. This is in contrast to the juvenile *Alligator* in which digit I is barely visible in dorsal view, and digits II and III are clearly visible. An identical situation is seen in the other juvenile *Alligator* illustrated by Reilly and Elias (1998, fig. 3, frame 800). Ontogenetic changes in locomotion have been reported for various lizards (Garland, 1985; Marsh, 1988; Irschick and Jayne, 2000); therefore, similar results are not surprising for crocodylians.

This change in foot position in these alligatorids probably correlates with increased body mass with age and the need to keep the center of mass nearer to the weight-bearing limb in the larger individual. As Alexander (1985) noted, locomotory behavior is affected by body mass; therefore, we might predict trackways of juveniles to be proportionally wider relative to stride length than in the adult (see Farlow and Britton, 2000, for other ontogenetic changes expected in the *Alligator* that would affect trackway appearance). This narrowing of the trackway with increased body size occurs with an increase in amplitude of the lateral movements of the body during locomotion (compare Schaeffer, 1942, fig. 17; Reilly and Elias, 1998, fig. 3; and Fig. 1D).

The narrowing of the gait relative to body size suggests some minor but significant changes in the pectoral girdle, either within the joint anatomy, within the muscles, or both. These changes might be difficult to recognize because they may fall within the range of variation noted by Meers (2003) in his dissections of

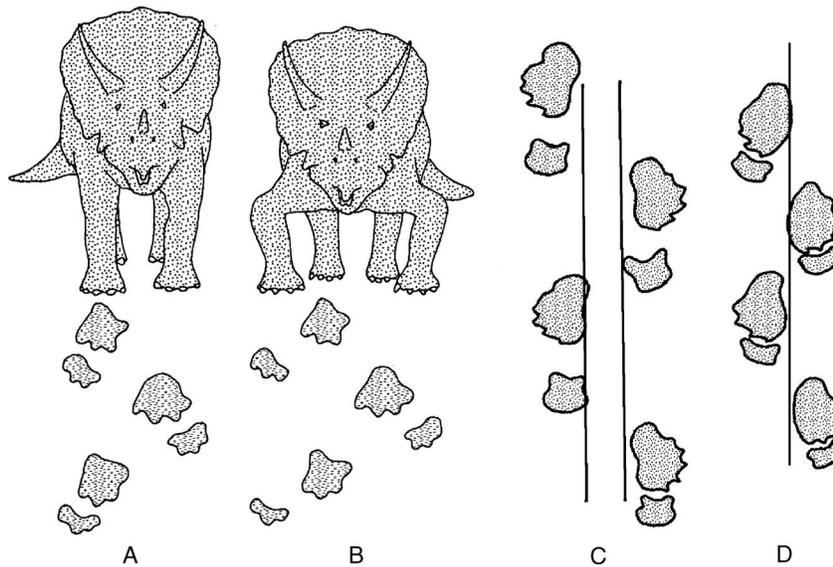


FIG. 4. Trackways record animals in motion, not stationary. Therefore, assumption of an erect stationary stance for *Triceratops* (A) from a *Ceratopsipes* trackway, assumes no lateral motion of the body, which would bring the center of gravity closer to the weight bearing limb (compare *Caiman* trackway of Fig. 2A, B, with anterior view of *Caiman* walking in Fig. 1B–D). Furthermore, in light of the *Caiman* locomotion, the prediction that a semi-erect stance in *Triceratops* would produce wider manus tracks than pes tracks (B) is incorrect (modified from Lockley and Hunt, 1995). It is also erroneous to assume no influence of lateral motion in sauropod locomotion and the resulting trackways. It is possible that wide gauge tracks (C) were made by a taxon that had less lateral motion than the maker of the narrow gauge tracks (D). See also Fig. 5. (Modified from Wilson and Carrano, 1999).



FIG. 5. Influence of lateral motion during locomotion is apparent in the overlay of the adult *Caiman* trackway (heavy lines; traced from Fig. 2A) on (A) the sauropod trackway *Brontopodus* (light lines; modified from Farlow, 1987) and (B) the alleged ceratopsian trackway *Ceratopsipes* (light lines; modified from Lockley and Hunt, 1995). All are to the same pes length. Note that the tracks coincide fairly well, yet the *Caiman* is known to walk semi-erect and to have significant lateral body movement (see Fig. 1).

crocodilian forelimbs. Regardless, the weight-bearing manus is brought closer to the midline in the larger individual than in the smaller. In the adult *Caiman* used in this study, during a step the manus is placed down about 6.5 cm from the midline, then the mass of the body is shifted forward and toward that side to bear the body's weight. Only then is the opposite forelimb raised for the next step (see Schaeffer, 1942, and Reilly and Elias, 1998, for a more detailed discussion of the step cycle). Accompanying this change in gait width is a change in the orientation of the manus as the amount of adduction and lateral movement of the body changes. Using digit III as the morphological midline axis of the manus, its angle relative to the midline axis of the body ranges from about 26–33° in Schaeffer's specimen, 12–25° in the Reilly and Elias specimen, and 8–14° in the large adult of this study.

Lateral body movement in crocodiles and vertebrates in general is possible because the vertebral column is a flexible structure with varying amounts and directions of movement among various sections (neck, back, tail) (Slijper, 1946). This flexibility is usually not taken into account in studies of locomotion, especially those based on trackways. Lockley and Hunt (1995) attempted to reconstruct stance in *Triceratops* based on the probable ceratopsian trackway they named *Ceratopsipes* (Fig. 4). Because the manus prints were in line with the pes tracks, they concluded that the forelimb stance indicated an erect posture (Fig. 4A) rather than a semi-erect stance (Fig. 4B). In a similar vein, Wilson and Carrano (1999) viewed the difference between wide gauge sauropod tracks (*Brontopodus*; Fig. 4C) and narrow gauge (*Parabrontopodus*; Fig. 4D) only in terms of limb bone posture and orientation. In both ceratopsian and sauropod trackways, no consideration was given to lateral movement of the body and the influence this has on trackway width. That lateral motion does influence track making is apparent from overlaying the adult *Caiman* trackway with those of *Ceratopsipes* and *Brontopodus* drawn to the same pes length (Fig. 5). There is remarkable similarity in trackway width, with the notable exception that the *Ceratopsipes* manus prints are farther from the midline than in the *Caiman* and *Brontopodus* trackways. It is therefore possible that the wide-gauge *Brontopodus* trackway indicate a taxon with less

lateral movement than in the taxon responsible for the narrow-gauge trackways; further work is needed to test this hypothesis. Regardless, the conclusion is inescapable: trackway analysis must include the whole animal, not just the limbs.

CONCLUSIONS

All limbed terrestrial vertebrates, including those with erect posture, utilize some degree of lateral motion during locomotion to keep the center of mass over the weight-bearing limb and to increase the stride of the forelimbs (Fig. 3). In the *Alligator* figured by Reilly and Elias (1998, fig 3), lateral motion increases the step of the forelimb about 13–15% than if there was no lateral movement. Lateral movement, therefore, is an important consideration in inferring stance and limb posture from trackways.

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