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Does pace angulation correlate with limb posture?

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ABSTRACT

Femoral abduction angle, pelvic rotation angle and motion speed of eight species of modern crocodiles and lizards were measured to determine the factors affecting pace angulation and to assess whether limb posture can be estimated from trackways. Film sequences of dorsal views of free walking reptiles were filmed with a digital video camera recorder, then positions of the ankle, knee and hip joints were digitized and x–y coordinates were obtained for each of the half frames. Pace angulation and abduction angle of the supporting femur were calculated from the coordinates, together with motion speed and pelvic rotation. Multiple stepwise regression analysis showed that the femoral abduction angle was the most influential factor, explaining 47% of the variation in pace angulation value. The parameter estimate for the femoral abduction angle (-0.71) indicates that an animal with a more erect limb posture (i.e., lower femur abduction angle) makes a trackway with a higher pace angulation. Pelvic rotation also contributed significantly to the model, whereas motion speed did not. By inverse prediction, a trackway with an average pace angulation value of 108° or less is unlikely to have been produced by an animal with a fully erect gait. A major implication of our study is that limb posture of extinct tetrapods can be reconstructed from fossilized trackways. Fossil trackways are an important source of information about posture. Analyses of fossilized trackways can complement information obtained from body fossils or, in case where body fossils are rare or lacking, fossilized trackways may be the primary source of information about posture, locomotion and behavior.

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1. Introduction

Limb posture in tetrapods ranges from sprawling to erect. In erect tetrapods, limbs are held under the body and move in a parasagittal plane parallel to the midline of the body. In sprawling tetrapods, limbs are highly abducted and swing largely in a horizontal plane (Blob, 2000). It is known that differences in the degree of limb abduction will affect trackways. Pace angulation, which is defined as the angle formed by three sequential fore or hind footprints (e.g., right–left–right: Fig. 1), was proposed as an indicator of the trackmaker's limb posture (Peabody, 1948, 1959) and has been widely used in ichnological studies (e.g., Berman and Henrici, 2003; Marsicano and Barredo, 2004). The assumption is that an erect animal produces a trackway with a high pace angulation, whereas a sprawler produces a trackway with a low pace angulation. This assumption seems reasonable, because the laterally projecting limbs of sprawlers will widen the trackways and, consequently, will decrease the pace angulation value (Fig. 1).

In the present study, femoral abduction angle, which is defined as the smallest angle between the sagittal plane and the femoral longitudinal axis, is used as a quantitative measure of limb posture (Fig. 2) and its influence on the pace angulation value is assessed. The practice of recognizing two (erect and sprawling) or three (erect, semi-erect and sprawling) qualitative categories of posture has been criticized for masking details and diversities of tetrapod limb posture, which is continuous rather than intermittent (Gatesy, 1991). The femoral abduction angle was proposed as a substitute for these qualitative posture categories (Gatesy, 1991). So far, however, this angle has only been measured in a few mammalian (Jenkins and Camazine, 1977) and one crocodilian species (Gatesy, 1991; Reilly and Elias, 1998). According to these studies, femoral abduction angles are 25° to 35° in raccoons, 5° to 15° in foxes, about 0° in cats (Jenkins and Camazine, 1977), 31° to 63° in sprawling alligators (Reilly and Elias, 1998) and 31° to 66° (Reilly and Elias, 1998) or 20° to 50° (Gatesy, 1991) in alligators walking in a semi-erect posture.

In addition to femoral abduction angle, other factors may also affect pace angulation value, such as motion speed or pelvic rotation. As an animal moves faster, the stride length increases, and consequently the pace angulation increases (Fig. 1). Smith (1993) attributed the high pace angulation value of an upper Permian trackway to a large pelvic rotation, which would have increased the stride length. Thus the influences of motion speed and pelvic rotation must be evaluated to see whether they mask the effect of femoral abduction angle. However, the effect of femoral abduction angle,

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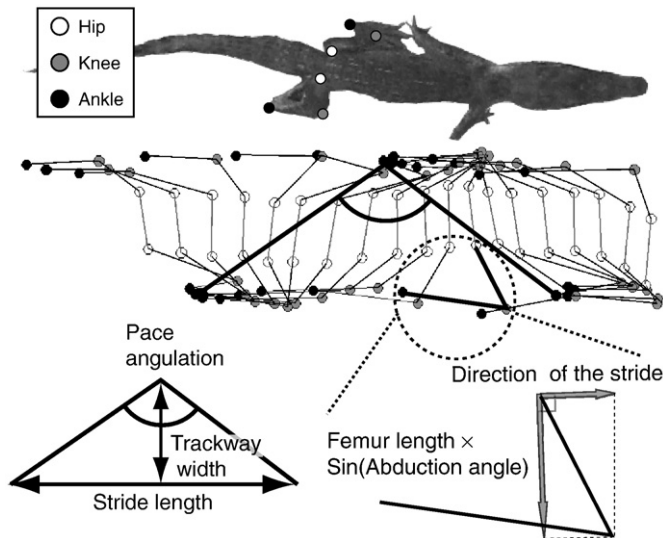E-mail address: tai.kubo@gov.ab.ca (T. Kubo).

Fig. 1. Stick figure plots in the dorsal view of hind limb positions of a juvenile *Crocodylus porosus* used in this study and the geometrical relationships of stride length, trackway width and pace angulation value. The stick figures were made by connecting ankle joints, knee joints and hip joints digitized from frames (12 Hz) in the film sequence. Schematic diagram (thick, solid lines) of pace angulation value is overlaid onto the stick figure plots. A single stick figure of the right limb within dotted circle is enlarged in lower right to show the relationship between the femoral abduction angle, the stride direction and the femur length.

Table 1
Body weight, femur length, number of trials and total number of strides from all trials measured and recorded for three species of crocodiles and five species of lizards.

Taxon	Body weight (g)	Femur length (cm)	Number of trials	Number of strides
Paleosuchus trigonatus	210	3.5	1	6
Crocodylus porosus	2100	7.9	2	4
Crocodylus porosus	1100	5.6	1	5
Tomistoma schlegelii	1100	5.4	1	3
Varanus exanthematicus	474	3.5	5	6
Shinisaurus crocodilurus	111	2.1	4	16
Shinisaurus crocodilurus	113	2.1	2	6
Pogona vitticeps	268	3.9	2	8
Pogona vitticeps	296	3.6	2	7
Tiliqua scincoides	478	2.1	2	7
Tiliqua scincoides	457	2.2	2	8
Tiliqua scincoides	435	2.5	2	9
Eublepharis macularius	29	1.4	5	34
Eublepharis macularius	54	1.7	2	11
Eublepharis macularius	80	1.9	2	12
Total			35	142

the pace angulation value as an indicator of limb posture in extinct trackmakers.

2. Materials and methods

2.1. Studied animals and recording procedures

Pace angulation values, femoral abduction angles, pelvic rotation angle and motion speed were obtained from three species of juvenile crocodilians (four individuals) and five species of lizards (11 individuals), all reared in the Ueno Zoo, Tokyo, Japan (Table 1, Fig. 3). Adult crocodilians were not used because they could not be safely handled. Film sequences (30 Hz) of dorsal views of each individual were filmed using a digital video camera recorder (FVM300, Canon, Japan). The video camera was set up on a tripod and each individual reptile was allowed to walk freely. This procedure was repeated until each individual had walked straight across the view range of the video camera. The number of recorded trials varied among species and/or individuals, because some of them were reluctant to walk (Table 1). Length of femora (the distance between knee and hip joints) and width between two hip joints of lizards were measured directly for each of the 11 lizard individuals with calipers. For the four crocodilians, the same measurements were taken from photographs in dorsal view of individuals resting on the floor alongside a ruler.

motion speed and pelvic rotation on pace angulation has never been assessed previously through experiments using extant animals. This study is the first attempt to remedy this situation.

The goals of the present study are to 1) evaluate the influences of three factors (femoral abduction angle, motion speed and pelvic rotation) on the pace angulation values, and 2) assess the potential of
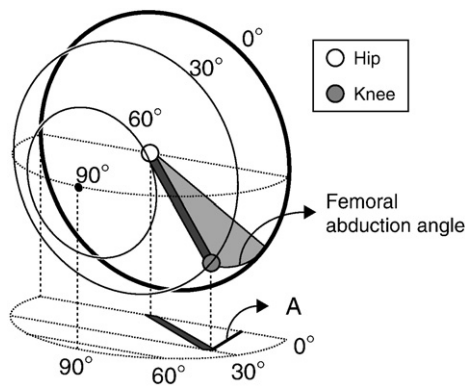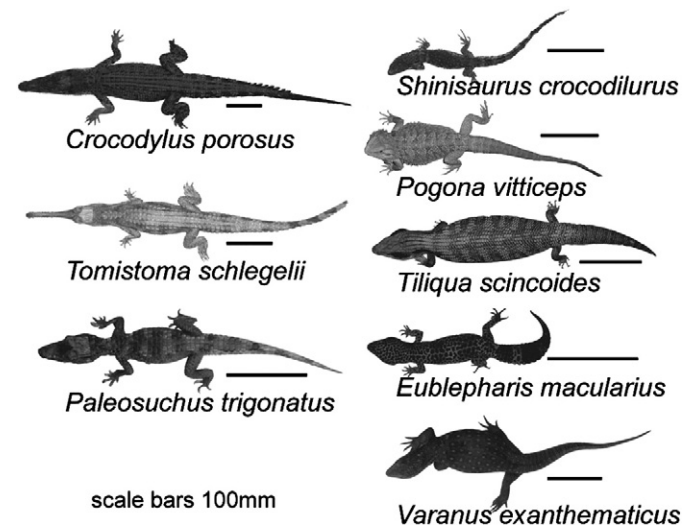

Fig. 2. Diagrams illustrating femoral abduction angle and how it is measured in this study. Upper diagram of half a hemisphere in oblique view (laterodorsal and slightly anterior or posterior) depict movement of femur around the hip joint. Base (thick line) of the hemisphere labeled 0° represents a parasagittal plane at an abduction angle of 0°. Lateral from the base are two smaller circles (thin line) and a point (Solid dot) that represent abduction angles at 30°, 60° and 90°. The hip joints or proximal end of femur (open circle) is fixed in the center of the 0° parasagittal plane and the knee joint or distal end of the femur (gray circle) may lie at any point between 0° and 90°. The longitudinal axis of femur is represented by the narrow, dark rectangle extending between the hip and knee joints. The femoral abduction angle is the smallest angle between the parasagittal plane and the longitudinal axis of the femur. For example, if the knee joint is located anywhere on the 30° circle, the femoral abduction angle is 30°. Lower diagram (semi-circle) depicts projected dorsal view; this is equivalent to viewing a flattened image of the upper diagram from the dorsal perspective, which is how specimens were filmed in this study. Femur length (the distance between hip and knee joints in the upper diagram) and distant at right angle from 0° parasagittal plane to knee joint in lower diagram (thinner black line labeled A) were measured from specimen and video images respectively. The value *A* is divided by femur length then arcsine transformed to calculate femoral abduction angle.

Fig. 3. Dorsal views of studied reptile species (three crocodilians on the left and five lizards on the right) reared in the Ueno Zoo, Tokyo, Japan.

2.2. Data acquisition protocol

From each digital frame, a series of half-frames (60 Hz) was obtained by extracting odd-row and even-row frames (Pike and Alexander, 2002). Midpoints of the proximal edge of left and right femora, anteriormost points of left and right knees and posteriormost points of left and right feet were digitized in two dimensions for each half frame and the x–y coordinates of each point were obtained. The obtained points were identified as, respectively, hip joints, knee joints and ankle joints. Because joint markers were not allowed to be physically attached on the animals, the digitized joint points may have fluctuated to some extent (Pike and Alexander, 2002). For digitization we used the software Motion-viewer Free (Physicalsoft, http://www.physicalsoft.jp/). Pace angulation values were calculated from the x–y coordinate positions of ankles in three subsequent foot placements (Fig. 1). The smallest angle between the femoral axis and the sagittal plane was defined as the femoral abduction angle (Fig. 2). In this study, the sagittal plane is defined as a plane perpendicular to the ground and parallel to the direction of stride; the latter orientation was purposefully selected because stride direction can be determined from both extant and fossil trackways. For the calculation of the femoral abduction angle, a projective femur length, which is defined as two dimensional length of femur from the dorsal view, was calculated from x–y coordinates of each half frame. Width between left and right hip joints was used for calibration. The projective femur length was resolved into two components that are perpendicular and parallel to the stride direction (Fig. 1). Then the component perpendicular to the stride direction was divided by the actual femur length measured from each individual. This value was arcsine transformed to compute an abduction angle (Figs. 1, 2). In cases where the value exceeded 1, an abduction angle was recorded as 90°.

The angle between the stride direction and the line that connects the hip joints was calculated for each half frame. The maximum and minimum angles were selected for each stance phase. The difference between maximum and minimum angles was divided by two to calculate the pelvic rotation angle. Motion speed was calculated for each trial. The distance between midpoints of left and right hip joints in the first and last half-frames used in the analysis was measured, then divided by the duration between the first and the last half-frames to calculate absolute speed. The weight of studied animals ranged from 29 g to 2.1 kg. In order to remove a body size effect, the Froude number, which is an index of size-controlled speed, was calculated from the absolute speed and femoral length (Alexander, 1976; Aerts et al., 2000).

2.3. Data analysis

A walking gait can be divided into swing and stance phases (Reilly and Elias, 1998). During swing phase the foot is off the ground and during stance phase the foot is in contact with the ground. Stance phase contains all three phases recognized by Thulborn and Wade (1989), namely touch-down phase, weight-bearing phase and kick-off phase. Every stance phase produces only one pace angulation during walking, whereas femoral abduction angles were obtained from each half frame. Averages of the femoral abduction angles were calculated for each stance phase to correlate with pace angulation value. Because the preceding stance phase affects the subsequent stance phase, the measurements taken during the same trial are not statistically independent of each other. To compensate that averages of the femoral abduction angle, pelvic rotation angle and pace angulation were calculated for each trial and then used in the regression analysis. When applying the results of this study to a fossilized trackway, an average value of a trial is equivalent to an average value of a trackway.

In the present study, species and individuals were not distinguished for following reasons. First, limb abduction angles can differ significantly depending on locomotory posture within individuals of the same species, especially in crocodilians (Reilly and Elias, 1998), and our analysis includes both sprawling and semi-erect locomotory postures for the crocodilian *Crocodylus porosus*. Second, it is difficult and often impossible to reliably identify a species of trackmaker from a trackway (Farlow and Pianka, 2000). Thus analyses of fossilized trackways must be based not on species but on a trackway, which as noted above is considered equivalent to a trial in this study.

To evaluate the factors influencing the pace angulation value, we used multiple stepwise regression with the abduction angle of the supporting femur, motion speed (either absolute or relative) and pelvic rotation as predictors of pace angulation value. None of the predictor variables were correlated (Spearman's rank order correlations, all $P>0.05$). Forward selection was used to accept additional variables in the model. Variables were accepted when the associated P-value was <0.05. Because the major aim of this study was to test whether pace angulation can be an index of the femoral abduction angle, inverse prediction was applied to estimate femoral abduction angles from given pace angulation values with other prediction variables fixed to its average. Femoral abduction angles at the pace angulation value of 60°, 90° and 120° were estimated together with their 95% prediction intervals. All statistical analyses were performed using JMP 6.3.0 (SAS Institute Inc., Cary, USA).

3. Results

Thirty-five trials containing 142 stance phases were analyzed (Table 1). Multiple stepwise regression showed that the abduction angle of the supporting femur was the most influential factor and explained 47% of the variation in the pace angulation value ($R^2 = 0.47$, $P<0.001$). Pelvic rotation also contributed to the model significantly ($P=0.02$), whereas motion speed did not (for the absolute speed, $P=0.26$; for the Froude number, $P=0.42$). To graphically illustrate these results, the pace angulation value was regressed against the femoral abduction angle (Fig. 4A), and the residuals from the regression line were plotted against the pelvic rotation (Fig. 4B). The model including the femoral abduction angle and the pelvic rotation explained 56% of the variation in the pace angulation value ($R^2 = 0.56$, $F_{2,32} = 20.42$, $P<0.001$). The negative value of the parameter estimate for the femoral abduction angle (-0.71) indicates that an animal with more erect limb posture (i.e., lower femur abduction angle) makes a trackway with a higher pace angulation. The parameter estimate for the pelvic rotation was 0.35, which indicates that greater pelvic rotation increases the pace angulation value.

In order to obtain a prediction equation of the femoral abduction angle by the pace angulation value, rearrangement of the fitted model was conducted. The prediction equation is expressed as follows:

$$\text{Supporting femur abduction angle} = -1.42 \times \text{Pace angulation} + 0.50 \times \text{Pelvic rotation} + 169.61 \tag{1}$$

where all variables are given in degrees. When the pelvic rotation was fixed to its average (27.3°), the estimated abduction angles of the supporting femur at the pace angulation values of 60°, 90° and 120° were 98.1° (95% prediction interval; 71.3°–138.4°), 55.6° (29.9°–84.1°) and 13.0° (-20.0°–38.3°), respectively. The pace angulation value of 108° (or less) did not include 0° as a possible angle of femoral abduction, within the 95% prediction interval (95% prediction interval of femoral abduction angle; 1.1°–55.6°).

4. Discussion and conclusions

Multiple stepwise regression indicates the significant influence of the femoral abduction angle on the pace angulation value. As assumed by Peabody (1959), tetrapods with relatively adducted femora produce trackways with a higher pace angulation, whereas tetrapods
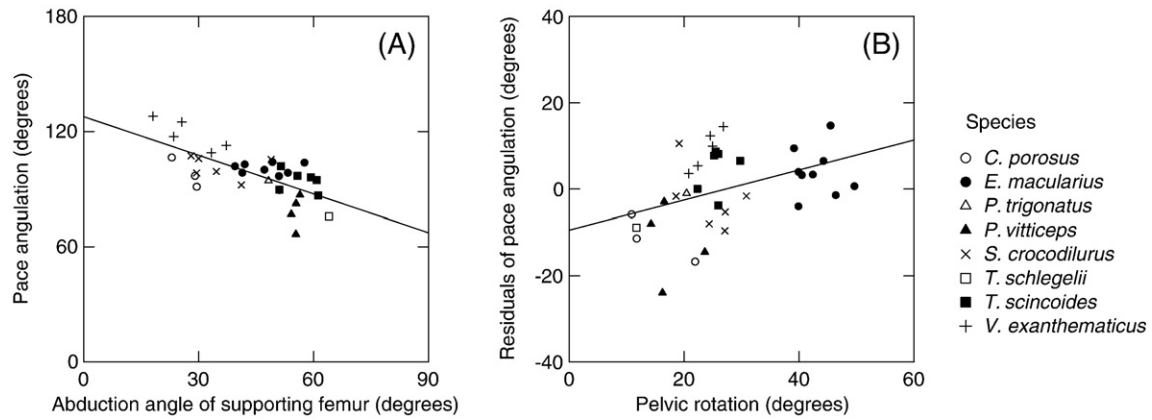
Fig. 4. Results of regression analyses. (A) Least squares regression of pace angulation on average abduction angle of supporting femur for three species of crocodiles and five species of lizards. Each point represents a trial. The line represents a regression line based on an average of all trials (*n* = 35). (B) Residuals of the pace angulation value from the regression line (Fig. 4A) plotted against the pelvic rotation angle. Open symbols represent data taken from crocodilians and other symbols represent data taken from lizards.

with relatively abducted femora produce a trackway with a lower pace angulation. This can be explained geometrically. Pace angulation is the apex angle of a triangle, with the base being stride length and the height being trackway width. Usually this triangle produced by a walking animal resembles an isosceles triangle (Fig. 1), thus pace angulation angle can be expressed as follows;

$$\text{Pace angulation} \approx 2 \times arctan\left(\frac{stride\ length\ /\ 2}{trackway\ width}\right) \qquad (2)$$

Because a laterally projected femur during stance phase (i.e., with a higher abduction angle) increases the trackway width and decreases the stride length, the pace angulation will be lower than in a tetrapod with a more adducted femur.

The regression analysis also shows that the pelvic rotation angle significantly contributes to variations in the pace angulation value, after controlling for the femoral abduction angle (Fig. 4B). The magnitude of pelvic rotation generally is large in sprawling animals and small or even negligible in erect animals (Reilly and Elias, 1998). Thus, the pace angulation values of sprawlers may be larger than what might be expected only from their femoral abduction angles. Among the reptiles studied here, *Eublepharis macularius* had the largest average pelvic rotation (43.0°), whereas other reptiles had values that clustered between 25.8° to 11.7° which suggest this change to emphasize the "patchy distribution" of these values. Compared to this patchy distribution, the average abduction angle is more evenly distributed between the largest (64.0° in *Tomistoma*

schlegelii) and smallest (27.2° in *Crocodylus porosus*) individuals (Fig. 4). Ranges of variation in these two variables are almost equivalent or, if the exceptionally large angle for *E. macularius* is excluded, smaller in the pelvic rotation. In the fitted regression, the absolute values of the parameter estimate for the femoral abduction angle (−0.71) was larger than that for pelvic rotation (0.35). This establishes that the femoral abduction angle has a greater affect on pace angulation value than does pelvic rotation, and that high pace angulation values of fossil trackways are unlikely to be explained only by pelvic rotation.

Contrary to our expectations, speed was not a significant component in the multiple linear regression model. We then plotted the pace angulation value against absolute speed and relative speed (Froude number) to assess trends among those variables (Fig. 5). There was no significant correlation found between speed and the pace angulation value for both the absolute speed and the relative speed ($r^2 = 0.08$ and 0.004, $p = 0.80$ and 0.70, $n = 35$, Fig. 5). When regressions were fitted for each species, a significant positive correlation between speed and pace angulation was found only in *Pogona vitticeps* (slope = 67.3, $r^2 = 0.97$, $p = 0.02$, $n = 4$). In that species, pace angulation values increased as individuals moved faster, as expected. As only walking gaits were analyzed in this study, relatively small variations in speed may mask the effect of motion speed. However, in comparisons above the species level, speed did not significantly influence pace angulation.

Hind limb pace angulation values are determined by movement and relative length of five body segments, namely the pelvic region, the right and left femora and the right and left crura. Movement of the
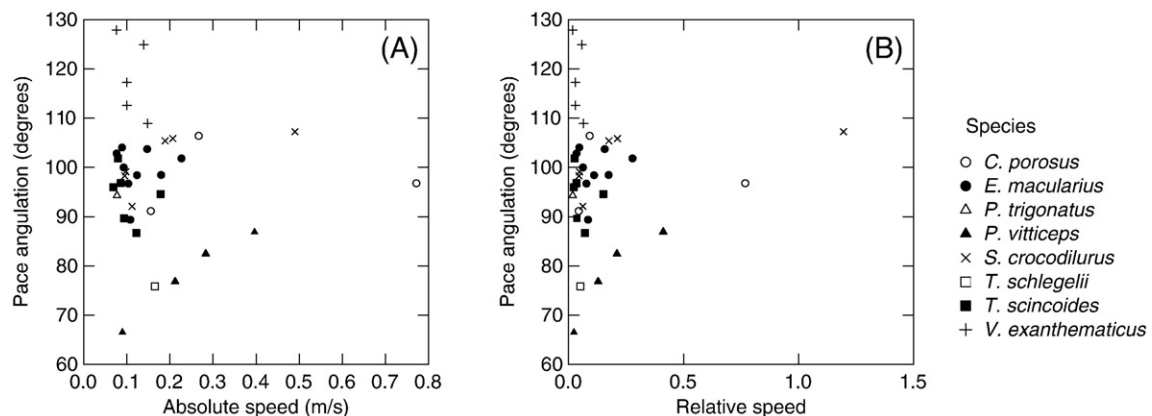

Fig. 5. Scatter plots of pace angulation against motion speed for three species of crocodiles and five species of lizards. Each point represents a trial. In both absolute speed (A) and relative speed adjusted by femur length (B), there are no significant correlations between the variables. Open symbols represent data taken from crocodilians and other symbols represent data taken from lizards.

crus and proportions of body segments may also explain variations in pace angulation that could not explained by the femoral abduction angle and the pelvic rotation angle.

For further investigation, it will be important to use a broader and more representative sample of species in order to better apply the findings of those investigations to interpreting fossil trackways. Because dorsal views of animals were analyzed in this study, the femur could not be easily observed when it moves close to the sagittal plane (i.e., moves beneath the body trunk). Tetrapods with relatively erect limbs, namely mammals and birds, could not be analyzed in this study; for that reason, we limited our study to tetrapods that were conventionally categorized as having semi-erect or sprawling postures. Thus, when reconstructing femoral abduction angle from pace angulation extrapolation of the prediction equation beyond the original range of data (average pace angulation of a trackway from 66° to 125°) should be avoided, and prediction intervals must also be considered.

Limb posture reconstructions using body fossils usually assign extinct animals to three qualitative postural categories: erect, semi-erect or sprawling (e.g., Charig, 1972; Kemp, 1982; Bonaparte, 1984; Parrish, 1987). Although prediction intervals derived from the present study are broad, limb posture reconstructions based on pace angulation values may be comparable to reconstructions based on body fossils. By inverse prediction we estimated femoral abduction angles of trackmakers with 60°, 90° and 120° of pace angulation that are 98.1° (95% prediction interval; 71.3° to 138.4°), 55.6° (29.9° to 84.1°) and 13.0° (−20.0° to 38.3°), respectively. Though the prediction intervals are overlapping to each other, it is obvious that a trackway with average pace angulation value of 120° or more could not be produced by trackmaker that is a true sprawler. We also estimated that at 108° for the pace angulation, the predicted range of the femoral abduction angle did not include 0°. This implies that a trackway with average pace angulation value of 108° or less is unlikely to be produced by an animal with fully erect limbs in which the femoral abduction angle is 0° (e.g., modern cats).

Because ichnofossils can be more abundant than relevant body fossils in some cases (Wilson, 2005), limb posture reconstructions from fossilized trackways can productively complement information from body fossils. Based on body fossil evidence, an erect gait evolved during the Permian and Triassic among therapsids and archosaurs (Charig, 1972; Kemp, 1982; Bonaparte, 1984; Parrish, 1987). High pace angulation trackways attributed to therapsids and archosaurs were reported from the Late Permian and Early Triassic (e.g., Smith, 1993; Demathieu and Demathieu, 2004). A recent analysis of Permian and Triassic fossilized trackways revealed that average pace angulation value of trackways increased primarily in the Early Triassic (Kubo and Benton, in press). The major finding of the present study, which is that pace angulation can be used to estimate limb posture, coupled with the fossil trackway evidence compiles by Kubo and Benton (in press) indicates that erect limb posture likely evolved during the Early Triassic. Because tetrapod body fossils are relatively scarce during the Early Triassic, information from trackways is critical for demonstrating that the shift towards more erect limb postures occurred during that interval. This example highlights how integrating studies of body fossils, ichnofossils and locomotion in extant organisms can improve our understanding of the locomotory evolution of tetrapods.

Acknowledgements

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