**ESTIMATING SPEEDS OF DINOSAURS FROM TRACKWAYS: A RE-EVALUATION OF ASSUMPTIONS**

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**ABSTRACT**

For 30 years, using equations determined by Alexander (1976), paleontologists have estimated speeds of dinosaurs from their trackways; the fundamental assumption, based on limited observations, was that dinosaur hip height is approximately four times foot length. Thulborn (1990) subsequently determined that the leg length to foot length ratio ranges from 4.5-6.0, according to type and size of dinosaur. Given that the focus of many published footprint studies is to estimate dinosaur speed from Alexander’s equations, it is critical that the hip height of the track maker can be ascertained from the footprint measurement. If there is high variability in the ratio of hip height:foot length within a group of dinosaurs, speed estimates are going to be extremely unreliable.

This study examined the relationship between foot length and leg length in a variety of dinosaurs. Measurements of 24 dinosaur specimens included ornithischians (bipedal and quadrupedal), theropods, dinosauriforms, birds, and sauropods. Leg length was defined as femur + tibia + metatarsal III; foot length was defined as that part of the foot preserved in footprints (digit III phalanges ± claw + metatarsal III – metatarsal IV). Leg and foot lengths were compared and it was found that in bipedal ornithischians the foot to leg length ratio is ~5.4-5.9, and in theropods, 2.8-4.2. Contrary to previous studies, we found that (1) there is no correlation between dinosaur size and foot to leg length ratio, (2) the foot to leg length ratio is greater than previously estimated, and (3) the foot to leg length ratio is highly variable for each group of dinosaurs. We conclude that estimating dinosaur speed from trackways should not be undertaken lightly, and the results be interpreted with caution.

**INTRODUCTION**

In 1976, Alexander proposed that dinosaur speeds could be estimated from their trackways, using an equation based upon the principals of fluid dynamics:

\[ u = 0.25 g^{0.5} \lambda^{1.67} h^{-1.17} \]

where \( \lambda \) is stride length (length between successive prints of same foot), \( h \) is hip height, \( g \) is acceleration due to gravity, and \( u \) is velocity. While \( \lambda \) can be measured directly from a trackway, \( h \) must be estimated. Using published data and estimated measurements from photographs, Alexander (1976) determined that for many bipedal dinosaurs including both theropods and ornithopods, the footprint length (FL) would be 0.23\( h \) to 0.28\( h \), assuming that the rear of the footprint was the metatarsophalangeal articulation. For the sauropod *Apatosaurus*, Alexander (1976) estimated that footprint length was 0.25\( h \). Alexander (1976) therefore stated, for simplicity, that hip height \( h \) was four times the footprint length (which was assumed to always be only the digital portion of the foot). Within a short time, several studies appeared which provided dinosaurian speed estimates from trackways (e.g., Russell and Béland 1976, Tucker and Burchette 1977, Coombs 1978, Thulborn and Wade 1979, Farlow 1981, Thulborn 1981).
Figure 1. Hip height above the ground depends on the angle of flexion at the knee, ankle, and metatarsophalangeal joints (left), which must be estimated; Thulborn (1990) eliminated this uncertainty by approximating hip height to be the sum of the femur, tibia and mt III lengths (right). (Image modified from Thulborn 1990.)

<table>
<thead>
<tr>
<th>Group</th>
<th>Morphometric</th>
<th>Allometric</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small theropods</td>
<td>$h \approx 4.5FL$</td>
<td>$h \approx 3.06FL^{1.14}$</td>
</tr>
<tr>
<td>Large theropods</td>
<td>$h \approx 4.9FL$</td>
<td>$h \approx 8.6FL^{0.85}$</td>
</tr>
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<td>Small ornithopods</td>
<td>$h \approx 4.8FL$</td>
<td>$h \approx 3.97FL^{1.08}$</td>
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<tr>
<td>Large ornithopods</td>
<td>$h \approx 5.9FL$</td>
<td>$h \approx 5.06FL^{1.07}$</td>
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<tr>
<td>Small bipedal dinosaurs</td>
<td>$h \approx 4.6FL$</td>
<td></td>
</tr>
<tr>
<td>Large bipedal dinosaurs</td>
<td>$h \approx 5.7FL$</td>
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</tr>
<tr>
<td>Theropods (in general)</td>
<td></td>
<td>$h \approx 3.14FL^{1.14}$</td>
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<tr>
<td>Ornithopods (in general)</td>
<td></td>
<td>$h \approx 3.76FL^{1.16}$</td>
</tr>
</tbody>
</table>

Table 1. Equations for hip height for various dinosaurian groups as determined by Thulborn (1989, 1990). Morphometric equations assume constant ratios between the various hind leg bones; allometric ratios consider that dinosaurs of different sizes will not have the same hip height:foot length ratio. For the morphometric equations, $FL$ is the footprint length (i.e., length of digit III); for the allometric equations, $FL$ was substituted for metatarsal III length. ‘Small’ dinosaurs are defined as those with footprint lengths < 25 cm; conversely, ‘large’ dinosaurs are those with footprint lengths > 25 cm.
Thulborn (1990) discussed the possible meanings of ‘hip height’ (height of the hip above the ground [Alexander 1976], height of the hip joint above the ground in a dinosaur skeleton [Thulborn and Wade 1984], height of the hindlimb from top of the femur to sole of the foot [Thulborn 1982]), and stated that, except in very large dinosaurs, a practical measure of hip height could be considered the sum of the lengths of the femur, tibia, and third metatarsal (Figure 1). Thulborn (1990) provided revised estimates of the foot length to hip height ratio, recognizing that different groups of dinosaurs had slightly different ratios (Table 1). In addition, Thulborn (1990) noted that this ratio would also vary over an individual dinosaur’s life due to allometric growth patterns; thus, this ratio would overestimate hip height for juveniles and underestimate it for adults. Because it is not possible to identify the trackmaker species for any given footprint – at best, we might identify the trackmaker to family level (see Rainforth 2005 for discussion) – we are unable, for a given footprint, to ascertain whether it is a juvenile or small individual of a large species, or a full-grown adult of a smaller species.

Thulborn (1990) also noted that the length of metatarsal III correlates to the sum of the lengths of the femur, tibia, and metatarsal III (i.e., the approximate hip height). He provided a series of allometric equations for bipedal dinosaurs (Table 1), with the assumption that metatarsal III is approximately equal in length to the phalangeal portion of digit III, which (in turn) is assumed to be footprint length.

Recently, Henderson (2003) constructed computer models to test the hip height prediction equations of Alexander (1976) and Thulborn (both morphometric and allometric equations [summarized in Thulborn 1990]) for three theropods (Tyrannosaurus rex, Allosaurus fragilis, and Coelophysis bauri) and three ornithopods (Edmontosaurus regalis, Iguanodon bernissartensis, and Hypsilophodon foxii). Henderson (2003) recognized that hip height would vary during the step cycle, and with different limb flexion angles. The models generated simulated trackways, from which footprint length could be measured and methods for determining hip height from footprint length could be tested. Henderson (2003) concluded that for all of these dinosaurs except Coelophysis (the only ‘small theropod’ sensu Thulborn 1990), Alexander’s method for estimating hip height (i.e., \( h = 4 FL \)) provided the most reliable results (for Coelophysis, Henderson concluded that Thulborn’s morphometric equations provided the best estimates of hip height).

**THIS STUDY**

Alexander’s (1976) equation for estimating dinosaur speeds from trackways has received much use since it was first introduced, and (as shown above) many refinements have been suggested. However, there seem to be some fundamental assumptions that have not been examined in a manner that considers both the skeletal structure and footprint morphology. Some questions that should be addressed include:

1. Does it make a difference whether we use actual hip height in Alexander’s (1976) speed equation, or will summing the lengths of the femur, tibia and metatarsal III provide an adequate proxy for hip height? (The height of the hip depends on the angle of flexion in the knee, ankle, and metatarsophalangeal joints, as well as the amount of flesh separating the foot from the ground; these must all be estimated. In contrast, the lengths of the femur, tibia, and metatarsal III can be measured directly from skeletons.)

2. FL, footprint length, is measured directly from the footprint. However, what bones does this length correspond to? It is not simply the length of the digit III phalanges (including ungual), because mt III is the longest metatarsal; the proximal pad in footprints of bipedal dinosaurs is formed by the metatarsophalangeal pad on digit IV. All equations to date use either morphometric ratios (e.g. Thulborn 1990) or allometric ratios with the assumption that metatarsal III is the same length as the phalangeal portion of digit III, which in turn is
the footprint length. What, then, is the relationship between the measured footprint length and the length of mt III?

3. In light of Henderson’s (2003) models, is there a simple relationship between hip height and foot length (e.g., \( h = 4FL \))? Do we need to resort to allometric equations for any groups of bipedal dinosaurs?

It appears, from casual observation of either mounted dinosaur skeletons or illustrations of dinosaurs, that the \( h:FL \) ratio is highly variable, both within and between dinosaurian groups. If this is in fact the case, then assuming \( h = 4FL \) (Alexander 1976, Henderson 2003) is going to result in highly inaccurate estimates of dinosaurian speeds from trackway data.

**MATERIALS**

Feet and legs were measured in 44 specimens, including dinosauriforms, bipedal and quadrupedal ornithischians, sauropods, theropods, and birds. However, due to incomplete material, only 24 of these specimens are used in the present analysis. All specimens used in this study consisted of bones from a single individual; while composite and/or reconstructed dinosaurs abound in museum displays, they were excluded here.

Several Late Triassic and Early Jurassic dinosaur specimens are included in the present study, including *Coelophysis* (YPM 5705), *Dilophosaurus* (UCMP 37302), and *Scelidosaurus* (BMNH R1111) – small theropod, large theropod, and quadrupedal ornithischian respectively.

(Institutional abbreviations: BMNH, Natural History Museum (London); UCMP, University of California Museum of Paleontology (Berkeley); YPM, Peabody Museum, Yale University.)

**METHODS**

Because we are ultimately interested in footprint data, to reduce error we should only be measuring the undersides of feet (i.e., dorsal surfaces of phalanges). However, one can not always do so, for instance if a specimen is mounted, or still partially encased in rock. Therefore, many of the measurements of phalangeal and digit lengths were of top (ventral) surfaces. For each instance where both dorsal and ventral surfaces of phalanges were measured, we compared the measurements to ascertain if dorsal and ventral data could be used interchangeably. For individual phalanges, differences in dorsal and ventral measurements ranged from negligible (<5% difference, probably simply measurement error) to high (>20% difference). There does not seem to be any systematic trends in these differences: one can not generalize for a clade, for instance. Therefore, when one is interested in measurements of individual phalanges, for comparison with footprints, only dorsal measurements should be used. This is a significant finding: in those few osteological descriptions which include phalangeal measurements (most of the time, one is lucky if the digits are measured!), it is not stated which surface is being measured; using published osteological measurements could therefore lead to significant problems when working with footprints!

We also compared dorsal and ventral measurements for complete digits (phalangeal portions). In most cases, differences were negligible (<5% difference) and likely due to measurement error. In a very few instances, differences were much higher (15-23% differences).

For consistency, even though in this study we were only interested in lengths of digits (rather than individual phalanges), we only included in the analysis those dinosaurs with ventral surface measurements; while dorsal measurements would have been preferable (as being directly relatable to footprints), the nature of the materials was such that we had few dorsal measurements.
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Because Alexander’s (1976) speed equation requires us to estimate a skeletal dimension (hip height) from trackway data, we need to ensure that we know how our footprint measurements relate to feet. All previous studies have assumed that footprint length corresponds to the length of the phalangeal portion of digit III. However, the footprints of bipedal dinosaurs generally do not possess a pad for the metatarsophalangeal joint on digit III, so we do not know the length of the proximal phalange on that digit. In addition, the rear of the footprint is generally the pad made by the metatarsophalangeal joint of digit IV, and because metatarsal IV is always shorter than digit III, the footprint length is therefore going to be greater than simply the sum of the phalanges of digit III (Figure 2). Assuming that the phalangeal pad is made by a joint (i.e., the arthral condition) (Baird 1957), one can directly measure lengths of some pedal elements from footprints (Olsen et al. 1998), thus permitting direct comparisons of osteological data with data derived from footprints. The size and position of the claw in a single footprint species can be highly variable, and the length of the ungual bone cannot be directly measured from footprints, because the length of the keratin sheath covering the claws is usually unknown (Rainforth 2003); therefore, in this study, we conducted our analyses twice, with claws either included or excluded.

In this study, we define foot length ($F$) as follows:

$$F = \text{digit III phalanges} + \text{metatarsal III} - \text{metatarsal IV}$$

Foot length including the claw on digit III permits comparison with previously published skeletal measurements and equations (e.g. Alexander 1976, Thulborn 1990); foot length excluding the claw on digit III provides a better comparison with footprints (Rainforth 2003). Leg length is defined here as the sum of the lengths of the femur and tibia. We exclude mt III (contra Thulborn 1989, 1990) because the contribution of the tarsus to leg length is often unknown: tarsal elements are small and disarticulate upon death, so many specimens are preserved without these bones.

RESULTS

We graphed various combinations of skeletal measurements and ratios in order to determine if there was a single ratio of leg length:foot length (using our definitions of leg and foot length), following Alexander (1976) and Henderson (2003), or a range of ratios, following Thulborn (1989, 1990). We would not necessarily expect to find exactly the same ratios as Alexander (1976) or Thulborn (1989, 1990), because our definitions of leg length and foot length are not quite the same as either Alexander’s or Thulborn’s definitions. Figure 2 plots the ratio of leg length to foot length for our specimens; the ‘multiplier’ of our y-axis is the factor by which $FL$ is multiplied to obtain $h$.

Even though our sample size is small, several important results can be seen on these plots:

1. no single multiplier applies for all dinosaurs (contra Alexander 1976, Henderson 2003); the total range for bipedal dinosaurs (when claw is included in measurements) is 2.8 to 5.9. If one is unable to identify a footprint beyond ‘bipetal dinosaur’ (i.e., unable to ascertain if it is a theropod or ornithischian print), speed estimates could be incorrect by a factor of 2.
2. within dinosaurian groups, there is a wide range of variation in multipliers; this variation is greater than reported by Thulborn (1990) (note that Thulborn categorized ‘small’ dinosaurs as those with foot lengths $<$25 cm; on Figure 2, dinosaurs with $FL<$25 cm are those with leg lengths $<$1 m);
3. the variation in multipliers within dinosaurian groups is independent of overall size of the individual dinosaurs (e.g., the multiplier for theropods [using foot length including claw] ranges from 2.8-4.2, regardless of animal size: both small and large animals have ratios at each end of the spectrum)
Figure 2. Ratios of leg length to foot length for various dinosaurian specimens, plotted as leg length vs. multiplier (where multiplier = h/FL). Foot length as defined here includes only that portion of the foot that is commonly preserved in footprints, in order to allow direct comparison with footprint data. Because there can be variability in claw length (due to keratin sheath on claw) and claw position in footprints, we determined the leg:foot ratios both with and without unguals (left and right graphs respectively). Several specimens were missing the ungual; the left graph allows direct comparison with previous studies, whereas the right graph, with more specimens represented, better allows variability to be examined. The one sauropod specimen was omitted from these plots; its multiplier is 10.4 (with claw) or 25.2 (without claw). Ornithischian-B: bipedal ornithischians; Ornithischian-Q: quadrupedal ornithischians.

To compare directly with Thulborn’s morphometric ratio results (Table 1), we can summarize the multipliers we obtained (for foot length including claws); at this time, we have not determined allometric equations for comparison with Thulborn’s (1990) equations.

- Small theropods: 2.9-4.2
- Large theropods: 2.8-4.2
- Small ornithopods: no data
- Large ornithopods: 5.4-5.9
- Small bipedal dinosaurs in general: 2.9-4.2
- Large bipedal dinosaurs in general: 2.8-5.9
- Birds: 2.9-3.8

We also examined Thulborn’s (1990) assumption that the length of mtIII can be used in place of footprint length; this assumption was critical to Thulborn’s allometric equations. Figure 3 shows that the expected footprint length for a particular dinosaur (our ‘foot length’, defined above) is shorter than the length of mtIII; and within each group of dinosaurs, the relationship is variable (e.g., in small theropods,
footprint length is 57-77% of mtIII length; in large theropods, footprint length is 57-111% of mtIII; in large bipedal ornithischians it is 73-83%, and in the sauropod, 50%). Thus, it does not seem reasonable to use footprint length as a proxy for mtIII length, and therefore, the allometric equations provided by Thulborn (1990) are imprecise.

Figure 3. Relationship between length of mt III and foot length (as defined herein, i.e., that portion of the foot that makes a footprint).

PRELIMINARY CONCLUSIONS

With the caveat that our sample size is small, we can draw the following conclusions:
- there is no simple relationship between ‘hip height’ and ‘foot length’ (contra Alexander 1976, Henderson 2003) when one uses measurements that limit the number of assumptions about these metrics;
- mtIII length is not a good predictor of footprint length (and vice versa)

These findings have major implications for estimates of dinosaur speeds from trackway data; because there is no reliable way to estimate hip height from footprint length, either using morphometric or allometric equations, speed estimates can be off by a factor of 2 or more.
FUTURE WORK

Ongoing and future work will further address the three questions posed above (‘This Study’). One line of study will be to examine the variability in $h:FL$ ratio within individual species, in particular focusing on the ratios for different size (age) individuals; simple observation on individuals indicate allometric growth patterns. The degree of variability will then enable judgments to be made concerning these ratios for different size classes of footprints; for a footprint of a particular size, we can not ascertain if it was made by a large individual of a small species, or a small representative of a large species. We will also examine whether the range of ratios for a particular group of dinosaurs remains constant through time, or if it varies over time (as the clade evolves). If there is a change over time, then even though we will not know which species (or genus) within a clade made a particular footprint, the age of the footprint will enable us to narrow down the $h:FL$ ratio and thus get a better estimate of dinosaur speed.

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