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Complete List of Authors:	Chapelle, Kimberley; University of the Witwatersrand, Evolutionary Studies Institute; University of the Witwatersrand, School of Geosciences Benson, Roger; University of Oxford, Department of Earth Sciences Stiegler, Josef; George Washington University, Department of Biological Sciences Otero, Alejandro; Museo de la Plata, División Paleontología de Vertebrados Zhao, Qi; University of Bristol Choiniere, Jonah; University of the Witwatersrand, Evolutionary Studies Institute
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A quantitative method for inferring locomotory shifts in amniotes during ontogeny, its application to dinosaurs, and its bearing on the evolution of posture.

BY KIMBERLEY E. J. CHAPELLE[1, 2*]; ROGER B. J. BENSON[1, 3]; JOSEF STIEGLER[4]; ALEJANDRO OTERO[5]; QI ZHAO[6] AND JONAH N. CHOINIERE[1]

[1]Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; e-mails: kimi.chapelle@gmail.com

[2]School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa

[3]Department of Earth Sciences, University of Oxford, Oxford, UK

[4]The George Washington University, Washington, Unites States of America

[5]Museo de La Plata, La Plata, Argentina

[6]University of Bristol, Bristol, United Kingdom

*Corresponding authors

ABSTRACT

Evolutionary transitions between quadrupedal and bipedal postures are pivotal to the diversification of amniotes on land, including in our own lineage (Hominini). Heterochrony is suggested as a macroevolutionary mechanism for postural transitions, but understanding postural evolution in deep time is hindered by a lack of methods for inferring posture in extinct species. Dinosaurs are an excellent natural laboratory for understanding postural transitions, because their lineage contains at least four instances of quadrupedality evolving from bipedality, and because heterochronic processes have been put forward as an explanatory model for these transitions. We extend a quantitative method for reliably inferring posture in tetrapods to the study of ontogenetic postural transitions, using measurements of proportional limb robusticity. We apply this method to ontogenetic series of living and extinct amniotes, with a focus on dinosaurs. Our method correctly predicts the general pattern of ontogenetic conservation of quadrupedal and bipedal postures in many living amniote species and infers the same pattern in some dinosaurs. Furthermore, it correctly predicts the ontogenetic postural shift from quadrupedal crawling to bipedal walking in humans. We also infer a transition from early ontogenetic quadrupedality to late-ontogenetic bipedality in the transitional sauropodomorph dinosaur *Mussaurus patagonicus* and possibly in the early branching ceratopsian *Psittacosaurus lujiatunensis*. The phylogenetic positions of these ontogenetic shifts suggest that heterochrony may indeed play a role in the macroevolution of posture, at least in dinosaurs. Our method has substantial potential for testing evolutionary transitions between locomotor modes, especially in elucidating the role of evolutionary mechanisms such as heterochrony.

Key words: ontogeny, locomotion, amniotes, dinosaurs, posture.

INTRODUCTION

Changes in posture, from quadrupedal to bipedal or vice-versa, occurred rarely in tetrapod evolution. However, these changes characterize several successful living and extinct amniote lineages. Despite a wealth of studies on the anatomical changes associated with these shifts, and some studies exploring their pattern, little is known about how these changes in locomotion come to independently evolve several times, or whether they share an underlying mechanism such as heterochrony.

Most living amniotes are habitual quadrupeds (Maidment *et al.* 2014), but several extant groups represent independent locomotory transitions to bipedalism from quadrupedal ancestors. For example, in mammals these include several different groups of small rodents that use ricochetal locomotion such as dipodines (Eilam and Shefer 1997), *Neomys* (Stein 1990) and *Pedetes* (Peinke and Bernard 2005), as well as bipedally hopping Macropodiformes (including both small-bodied taxa, e.g. *Potorous*, and larger species of the genus Macropus) (Buchmann and Guiler 1974), and humans. The latter are the most intensively studied example, where despite 100 years of research on the origins of bipedality in Hominoidea, it remains controversial how, when, and why, our closest ancestors became obligate bipeds (Gebo 1992, 1996; Crompton *et al.* 2008; Kozma *et al.* 2018) .

Similar to modern mammals, dinosaurs also underwent multiple independent postural transitions, albeit with reversed polarity. The ancestral condition for Dinosauria is bipedal posture, but quadrupedality evolved as a derived condition multiple times across two major lineages (at least once in Sauropodomorpha and at least three times in Ornithischia) (Sereno 1997; Maidment and Barrett 2012; Maidment *et al.* 2014; Barrett and Maidment 2017; McPhee *et al.* 2018). The origins of locomotory shifts in dinosaurs appear to coincide with lineage diversification, e.g., in Sauropodomorpha where the evolution of quadrupedality is considered a key adaptation that facilitated the enormous body sizes of later-branching members (Sander *et al.* 2011; Sander 2013) . Because of their time-extensive record, well-understood phylogeny, and history of in-depth anatomical research, dinosaurs represent an excellent study system in which to understand macroevolutionary locomotory shifts.

Patterns of postural evolution in dinosaurs have been characterized (Sereno 1997; Sander *et al.* 2011; Maidment *et al.* 2014; McPhee *et al.* 2018), but process-based hypotheses explaining these patterns have been lacking. In dinosaurs, at least, paedomorphosis has been proposed as a mechanism by which postural shifts might occur (Bonaparte and Vince 1979), allowing a hypothesised juvenile phase of quadrupedality in ancestor species (with bipedal adults) to be retained in adults of descendent species (with quadrupedal adults). However, observed ontogenetic postural shifts are rare among extant amniotes. This makes it difficult to test a heterochronic model for postural evolution difficult using data from extant species only. Indeed, we know of only one extant species that has protracted quadrupedal and bipedal phases during its ontogeny, *Homo sapiens*.

In contrast, postural ontogenetic shifts have been hypothesized in several dinosaur species, and may have been widespread. These include shifts from bipedalism to quadrupedalism (such as in the ornithopods *Maiasaura peeblesorum* (Dilkes 2001) and *Iguanodon bernissartensis* (Norman 1980)), and from quadrupedalism to bipedalism in the basal ceratopsian *Psittacosaurus lujiatunensis* (Zhao *et al.* 2013), the ornithopod *Dryosaurus lettowvorbecki* (Heinrich *et al.* 1993), as well as the sauropodomorphs *Massospondylus carinatus* (Reisz *et al.* 2005) and *Mussaurus patagonicus* (Otero *et al*. 2019). Dinosaur species with ontogenetic changes in posture might therefore be instructive in understanding how shifts occur in other lineages and they represent an opportunity for testing process-based models.

The relationship between phylogeny and ontogeny has been highly debated since the publication of the Biogenetic Law in 1866 (Haeckel 1866; Gould 1977; Nelson 1978).

Nevertheless, studying ontogenetic series has been shown to be a useful way of exploring transitions between distinctive phenotypic states in lineages (Heers *et al.* 2014). However, the study of posture in the ontogenetic series of dinosaurs presents a threefold problem that must be overcome if they are to be used to test this question. First, determining the postures (bipedal|quadrupedal) of extinct species is difficult, and few methods have been demonstrated to be reliable (Carrano 1998; Maidment *et al.* 2014; but see McPhee *et al.* 2018). Second, available methods often rely on relatively complete skeletons, meaning few individuals can be studied, and so limiting the ability to characterise posture across ontogenetic series within dinosaur species. Third, most studies of posture to-date have focused on single dinosaur species, and lack a broad comparative framework. Studies of dinosaur posture have used several different methods (Tarsitano 1983; Alexander 1985; Carrano 1998; Carrano and Biewener 1999; Bonnan and Senter 2007; Mallison 2010a, b; Grossi *et al.* 2014; Maidment *et al.* 2014; Barrett and Maidment 2017; Otero *et al.* 2017). These studies generally agree where phenotypic signal is clear (e.g., bipedal theropods with reduced arms or gigantic sauropods with columnar, quadrupedal postures), but give varying answers about taxa with less decisive characteristics. Because these studies are often not validated on extant taxa with known postures (but see Sereno and Shichin 1988; Carrano and Biewener 1999), it has been difficult to resolve the uncertainties about extinct taxa.

Among the disparate techniques used so far to infer postural shifts, only limb bone length allometry is broadly applicable and non-invasive (Norman 1980; Heinrich *et al.* 1993; Dilkes 2001; Reisz *et al.* 2005; Zhao *et al.* 2013). However, a recent method for assessing amniote posture showed that such measurements had essentially zero predictive power for determining posture in amniotes (McPhee *et al.* 2018). That study described a single, consistent quantitative method for assessing posture in adult individuals, using measurements of forelimb and hindlimb robusticity (we use ‘robustness’ and ‘robusticity’ to refer to the minimum circumference around the humeral and femoral shafts) (McPhee *et al.* 2018). Based on validation in extant species, this method can be used to confidently infer posture in extinct species. Futhermore, it is non-destructive, and can be used on poorly preserved or incomplete specimens that minimally preserve just the humeral and femoral shafts.

Here we modify McPhee *et al*’s (2018) method for postural determination for use on ontogenetic series. We validate this approach using growth series of extant amniotes, and use it to assess postural changes during ontogeny in extinct dinosaurs. Our results have bearing on the role of heterochrony during the evolution of dinosaurian posture, and by extension, the macroevolutionary processes behind postural shifts in amniotes.

METHODS

We compiled a database of limb measurements (minimum circumferences of the humeral and femoral diaphyses and total bone lengths) across ontogenetic series of living and extinct amniote species from published literature (Campione and Evans 2012; Kilbourne and Makovicky 2012; McPhee *et al.* 2018) and by measuring specimens using digital calipers and tailor's tapes (see S1 Table). For fossils embedded in matrix, we either estimated circumferences using diameters, or took measurements from reconstructed CT scans (S1 Table).

We included non-volant, terrestrial amniote taxa with a range of locomotory habits (e.g., bipeds, quadrupeds, fossorial species, and taxa with both known and hypothesized ontogenetic postural transitions). Powered flight and aquatic locomotion impart special demands on limb bone cortices (Habib and Ruff 2008) and taxa with these behaviours were therefore omitted. The final dataset (hereafter "ontogenetic dataset") included ontogenetic series of 29 mammal species, one squamate, two crocodylians, four birds, and six non-avian dinosaurs. For extant taxa, we assessed each species' posture (i.e., bipedal|quadrupedal) by focusing on the predominant mode of locomotion during travel, rather than the use of other postures during slow-speed and sporadic behaviours. For example, large-bodied macropodiforms use their tails to execute "pentapedal hopping" while grazing, but are obligate bipeds during travel (Dawson and Taylor 1973). Furthermore, approximately 50 species of lizards have at least some bipedal capabilities, predominantly for escape behaviours (Aerts *et al.* 2003). However, escape behaviours are generally sporadic, forming a small part of the animal's repertoire. In context of the definition of posture (bipedality|quadrupedality during travel) used here, our statistical analyses can be seen as tests of the hypothesis that posture during travel plays an important role in structuring the relative robustness of the humerus compared to that of the femur.

To predict the postures of each specimen in the ontogenetic series, we calibrated a discriminant function analysis (DFA; Manly 2016) using a training dataset comprising 303 adult amniote taxa with known posture. Of these, 31 are bipeds and 272 are quadrupeds.

The training dataset was compiled by combining the data of McPhee et al. (2018) [in turn extended from Campione & Evans (2012)], and the largest available specimens (and thus likely ontogenetically mature individuals) of living taxa from our ontogenetic dataset. We used the ratio of Log_{10}(humeral shaft circumference) (HC) to Log_{10}(femoral shaft circumference) (FC) as predictor variables of posture. The analysis was conducted using R Studio Version 1.1.453 (Team 2016) and its package MASS (Ripley *et al.* 2013), with visualizations done in its package ggplot2 (Wickham *et al.* 2013). Because of unequal sample sizes between bipeds and quadrupeds, we randomly subsampled our training dataset to 20 bipedal and 20 quadrupedal taxa, then generated postural class predictions (i.e., bipedal or quadrupedal) for each specimen in the ontogenetic series. We repeated this process 10 000 times to generate mean posterior probabilities of being bipedal [$pp_{bipedal}$] for each specimen in the ontogenetic dataset. In assigning posture to specimens, we chose arbitrary cutoffs in order to only predict posture where a reasonable level of confidence is present: specimens with $pp_{bipedal} \leq 0.333$ were predicted as being quadrupeds; specimens with $0.333 \leq pp_{bipedal} \leq 0.666$ were predicted as being equivocal; and specimens with $pp_{bipedal} \geq 0.666$ were predicted as being bipeds. We report simple descriptive $Log_{10}HC/Log_{10}FC$ ratios for selected taxa (S3), and distributions of posterior postural predictions for all dinosaurian taxa included (S4 Figs).

The same analyses were conducted using humeral and femoral lengths (HL and FL), which have been widely used to infer posture in previous works (Norman 1980; Heinrich *et al.* 1993; Dilkes 2001; Reisz *et al.* 2005).

RESULTS

Comparisons of humeral and femoral shaft circumference are effective in assessing posture in individual amniotes. A split between bipeds and quadrupeds is clearly observed when Log_{10}(humeral circumference) is plotted against Log_{10}(femoral circumference) (Fig 1A). This pattern is mostly validated by our discriminant function analysis (Fig 2 and S3 Table). Data from ontogenetic series of obligate quadrupeds plot within the region of quadrupedal adults (Fig 1A), and this is also true for most bipeds (except for some specimens in three of the ontogenetic series: *Macropus giganteus*, *Macropus rufus*, and *Smutsia temminckii*) (Fig 1A). Our DFA predicts that humans make a transition from early quadrupedality, to a mix between quadrupedal and equivocal, to a late-ontogenetic mix between bipedal and equivocal during ontogeny (Fig 1A) ($0.084 \leq pp_{bipedal} \leq 0.296$ for specimens with a FC≤37mm except for one equivocal specimen with $pp_{bipedal}=0.414$; $0.307 \leq pp_{bipedal} \leq 0.523$ for specimens with a 38≤FC≤59mm; and $0.445 \leq pp_{bipedal} \leq 0.773$ for specimens with FC>59mm except for one adult with $pp_{bipedal}=0.277$ and therefore predicted as being quadrupedal). Even for equivocal specimens, all adult *Homo sapiens* specimens with FC>59 mm have a $Log_{10}HC/Log_{10}FC \leq 0.949$ (except for the one outlier specimen with FC=77mm and $Log_{10}HC/Log_{10}FC=0.968$). Other closely related adult hominids are quadrupeds, and have proportionally more robust humeri with $Log_{10}HC/Log_{10}FC=1$ for *Gorilla gorilla*, $Log_{10}HC/Log_{10}FC=0.987$ for *Pan troglodytes* and $Log_{10}HC/Log_{10}FC=1.02$ for *Pongo pygmaeus* (see supplement of McPhee *et al.* 2018).

The ontogenetic series of some taxa are predicted as being either partially equivocal and partially correctly identified (one of 36 species or 2.8% of taxa studied), or partially equivocal and partially misclassified (four of 36 species or 11% of taxa studied). The nine-banded armadillo, *Dasypus novemcinctus* and the tree-kangaroo, *Dendrolagus lumholtzi* fall in a region of graph space intermediate between known quadrupeds and bipeds, but natural history observations show that they are predominantly quadrupedal (Taber 1945; Heise-Pavlov 2017). As also found by McPhee et al. (2018), the posture of the tree kangaroo *Dendrolagus lumholtzi*, is inferred as being a mix between bipedal and equivocal by the DFA ($0.350 \leq pp_{bipedal} \leq 0.834$), and the same is true of *Dasypus novemcinctus* which is inferred as being a mix between bipedal, quadrupedal and equivocal by the DFA ($0.235 \leq pp_{bipedal} \leq 0.811$) (Fig 2). Most individuals of *Macropus giganteus* and *Macropus rufus* are correctly inferred to be bipeds by our DFA (Fig 2, S3 Table), and natural history observations show they are bipedal throughout development (Windsor and Dagg 1971; McGowan *et al.* 2008). However, the largest individuals are inferred to be quadrupeds or equivocal. Although observed as being habitual bipeds (Steyn *et al.* 2018). All four ground pangolin specimens (*Smutsia temminckii*) are predicted by the DFA as being quadrupedal or equivocal ($0.167 \leq pp_{bipedal} \leq 0.561$) (Fig 2).

Dinosaurs show a variety of patterns. In sauropodomorphs, *Rapetosaurus* is predicted as being quadrupedal or marginally equivocal throughout its ontogeny ($0.218 \leq pp_{bipedal} \leq 0.393$); *Massospondylus carinatus* is predicted as being bipedal throughout ontogeny ($0.734 \leq pp_{bipedal} \leq 0.946$) except for the embryonic data point, which is equivocally classified

($pp_{bipedal}$=0.415); and *Mussaurus* shifts from quadrupedal to bipedal during its ontogeny ($0.014 \leq pp_{bipedal} \leq 0.969$) (Fig 1B and 2). Within ornithischians, *Maiasaura* is predicted as bipedal throughout ontogeny ($0.896 \leq pp_{bipedal} \leq 0.985$), whereas the 22 individuals of *Psittacosaurus lujiatunensis* are alternately classified as bipedal, equivocal, or quadrupedal with no discernible ontogenetic pattern ($0.033 \leq pp_{bipedal} \leq 0.863$) (Fig 1C and 2). The hatchling specimen of *Psittacosaurus lujiatunensis* is predicted as being quadrupedal ($pp_{bipedal}$=0.033). The theropod *Limusuaurus* is bipedal throughout ontogeny ($0.989 \leq pp_{bipedal} \leq 0.999$) (Fig 1D and 2).

The use of log-transformed humeral and femoral lengths as predictor variables does not distinguish bipedal amniotes from quadrupedal amniotes (S5 Fig and S6 Table). In the DFA results using humeral and femoral lengths, 39% of the amniote's ontogenetic trajectories are misidentified. Nine of the 22 strictly quadrupedal taxa are misclassified as being almost strictly bipedal throughout ontogeny, or as shifting from quadrupedalism to bipedalism (Fig 3 and S7 Table). These include *Antilocapra americana* (the four smallest specimens are equivocal with $0.447 \leq pp_{bipedal} \leq 0.647$ and the rest of the series is bipedal with $0.688 \leq pp_{bipedal} \leq 0.807$), *Bison bison* (two equivocal specimens with $0.653 \leq pp_{bipedal} \leq 0.656$ and the rest of the series bipedal with $0.665 \leq pp_{bipedal} \leq 0.884$)*, Connochaetes taurinus* (five specimens equivocal with $0.574 \leq pp_{bipedal} \leq 0.593$ and the rest of the series is bipedal with $0.749 \leq pp_{bipedal} \leq 0.835$)*, Dendrolagus lumholtzi* (all bipedal with $0.668 \leq pp_{bipedal} \leq 0.731$)*, Hippopotamus amphibious* (two smallest specimens are equivocal with $0.430 \leq pp_{bipedal} \leq 0.647$ and the rest of the series is bipedal with $0.842 \leq pp_{bipedal} \leq 0.915$), *Myrmecophaga tridactyla* (five of the smallest specimens equivocal with $0.349 \leq pp_{bipedal} \leq 0.597$ and the rest of the series is bipedal with $0.728 \leq pp_{bipedal} \leq 0.827$), *Odocoileus virginianus* (13 smallest specimens quadrupedal or equivocal with $0.184 \leq pp_{bipedal} \leq 0.630$ and the rest of the series is bipedal with $0.733 \leq pp_{bipedal} \leq 0.850$), *Okapia johnstoni* (nine smallest specimens are quadrupedal or equivocal with $0.086 \leq pp_{bipedal} \leq 0.632$ and the rest of the series is bipedal with $0.717 \leq pp_{bipedal} \leq 0.804$ and *Ursus americanus* (seven smallest specimens are quadrupedal or equivocal with $0.037 \leq pp_{bipedal} \leq 0.635$ and the rest of the series is bipedal with $0.699 \leq pp_{bipedal} \leq 0.836$) although natural observations of these taxa show that they are strictly quadrupedal or ambiguous in the case of the tree kangaroos (Geist *et al.* 2004; Kingdon 2015). The ontogenetic shift from quadrupedal crawling to bipedal walking in *Homo sapiens* is correctly identified (smallest eight specimens quadrupedal with $0.223 \leq pp_{bipedal} \leq 0.326$, middle 18 specimens equivocal with $0.358 \leq pp_{bipedal} \leq 0.658$ and 34 largest specimens with $0.687 \leq pp_{bipedal} \leq 0.938$). In bipedal mammals, *Macropus rufus* is predicted as undergoing a shift from quadrupedal to bipedal although in reality it is observed as being strictly bipedal throughout ontogeny ($0.042 \leq pp_{bipedal} \leq 0.910$). In ratites, *Rhea americana* and *Struthio camelus* are predicted as being strictly quadrupedal or equivocal although they are known bipeds ($0.087 \leq pp_{bipedal} \leq 0.384$ and $0.383 \leq pp_{bipedal} \leq 0.484$ respectively). Among dinosaurs, *Massospondylus carinatus* is predicted as being strictly bipedal ($0.907 \leq pp_{bipedal} \leq 0.969$), *Mussaurus* and *Rapetosaurus* appear to undergo a shift from quadrupedal to bipedal ($0.045 \leq pp_{bipedal} \leq 0.976$ and $0.066 \leq pp_{bipedal} \leq 0.718$ respectively) and *Psittacosaurus lujiatunensis* appears to be mostly equivocal and quadrupedal with a few bipedal specimens (15 specimens with $0.012 \leq pp_{bipedal} \leq 0.553$ and five specimens with $0.662 \leq pp_{bipedal} \leq 0.760$).

DISCUSSION

Postural predictions in extant ontogenetic series using limb robusiticty

Humeral and femoral minimum circumferences have been shown to reliably predict posture in living amniotes (McPhee *et al.* 2018). Here we show that they are also useful in predicting posture across developmental series (in 86% of cases, mainly mammals). Quadrupedal amniotes have proportionally robust humeri compared to bipedal taxa due to hypothesized differences in limb loading (McPhee *et al.* 2018). We show that this is true throughout ontogeny for 21 animals that are known to be quadrupedal at early ontogenetic stages and remain so throughout their development (e.g., *Procyon lotor*, *Ursus americanus* and *Hippopotamus amphibious*) (Fig 1 and 2, S3 Table). The ratio of humeral shaft circumference to femoral shaft circumference is also conserved through ontogeny in 10 bipedal taxa with proportionally gracile humeri (such as *Jaculus jaculus, Macropus agilis* and *Struthio camelus*) (Fig 1 and 2, S3 Table). In our sole example where ontogenetic postural shifts are known to occur (humans), this transition is correctly identified by application of our method.

Some bipedal animals have robust humeri, including the ground pangolin *Smutsia temminckii*, which is a burrower (Steyn *et al.* 2018), and large kangaroos (*Macropus giganteus* and *Macropus rufus*). *S. temminickii* was classified as a biped in our dataset, and indeed makes relatively little use of the forelimb during locomotion. However, we also observed that the forelimb contacts the ground every 3–5 steps of the hindlimbs. Its posture during travel is therefore arguably best classified as being equivocal. Large kangaroos have strong sexual dimorphism with stereotypical male behaviours and concomitant sexual selection involving the forelimb (Jarman 1983; Warburton *et al.* 2013). The largest specimens of *Macropus rufus* and *Macropus giganteus* in our sample are males, and are predicted as being equivocal or quadrupedal, whereas smaller specimens are predicted as being bipedal. Male kangaroos are known to reach twice the body mass of females (making it difficult to look at ontogeny in a mixed-sex sample) and to use their forearms in combat with other males (Jarman 1983; Warburton *et al.* 2013). If only female kangaroos were used, we hypothesize that the humerus to femoral robustness ratio would be conserved during ontogeny and would plot with other bipedal taxa. Positive allometry of forelimb robustness is also present in ratites (*Rhea Americana* and *Struthio camelus*) (S2 Table), which use forelimb feather arrays during sexual display, although large individuals of our ratite species are nevertheless correctly inferred as bipeds. These results indicate that the proportional robusticity can be overprinted by certain lineage-specific behaviours, but this only rarely leads to misclassifications with our method. Proportionally robust humeri were found in all quadrupeds regardless of whether their habitual forelimb posture was erect (e.g. in mammals) or sprawling (e.g. in non-dinosaurian reptiles).

Some extant taxa are predicted as having a mix of locomotory postures during ontogeny and have circumference ratios intermediate between those of most bipeds and most quadrupeds. These include the armadillo *Dasypus novemcinctus* (a quadrupedal species in which the majority of the specimens were classified as being equivocal), and the tree-kangaroo *Dendrolagus lumholtzi* (a quadrupedal species that our method predicts variably to be bipedal, equivocal or quadrupedal). The predominant locomotory habits of armadillos are not observed to vary during development (Taber 1945; Geist *et al.* 2004), however tree-kangaroos appear to have an ambiguous predominant locomotory posture, alternating between quadrupedalism and bipedalism both arboreally and terrestrially (Heise-Pavlov 2017).

Detailed behavioural studies of these living, equivocal or misclassified taxa have great potential to enlighten the reasons for these seemingly erroneous inferences. For example, *Dasypus* engages in some bipedal alert behaviours (McDonough and Loughry 2013) and uses the hindlimbs and tail for support when initiating digging with its forelimbs (Clerici *et al.* 2018), but is exclusively quadrupedal during locomotion (Costa *et al.* 2019). However, some species of armadillo employ plantigrade hindlimb postures and unguligrade forelimb postures during locomotion, suggesting a greater role for the hindlimbs in weight-bearing in at least some cingulates (Vizcaíno and Milne 2002). The closely related, extinct glyptodonts have also been interpreted as having posteriorly positioned centers of mass and possibly bipedal behaviours when using their armoured tails for defense (Vizcaino *et al.* 2011). The apparent tendency for armored terrestrial mammals to possess posteriorly positioned centers of mass (including the bipedal ground pangolin) may indicate a role for elongate and/or armored tails and axial rigidity in transmitting the majority of the animal's mass through the hindlimbs, and may explain the prevalence of forelimb-assisted fossorial behaviours in these animals.

Tree kangaroos spend a large majority of their time as arboreal quadrupeds. However, observations of various *Dendrolagus* species in the wild show that they do frequently engage in bipedal saltation when locomoting terrestrially, exhibit bipedal alert postures when feeding perched on tree limbs, and primarily use the hindlimbs for power when climbing vertically (Procter-Gray and Ganslosser 1986). *D. lumholtzi* and *D. inustus* are early-diverging species of tree kangaroos among extant taxa (Eldridge *et al.* 2018) and engage in some bipedal locomotor behaviours not reported in other *Dendrolagus* species (Procter-Gray and Ganslosser 1986)*. D. dorianus* is phylogenetically nested among more arboreally adapted tree kangaroos, uses a quadrupedal walk during terrestrial locomotion, and was accurately predicted as a quadruped in this study.

Postural predictions in extant ontogenetic series using limb length measurements

Long bone length ratios are very poor indicators of posture in amniotes. Although the use of relative lengths correctly identifies the postural shift seen in humans, it also results in the erroneous identification of an ontogenetic locomotor transition in many species where it is in fact absent (39% false positive rate for locomotory shifts). For example, *Felis silvestris*, *Connochaetes taurinus* and *Crocodilus niloticus* all have a negative allometric relationship between $Log_{10}HL$ and $Log_{10}FL$ during growth (slope ≤1, S6 Table), but these animals are quadrupedal throughout their ontogeny. This falsifies previous hypotheses that a negative allometric relationship between humerus length and femoral length during ontogeny is a reliable indicator of a shift toward bipedalism (Reisz *et al.* 2005). This extremely high false positive rate causes us to reject this approach.

Postural predictions in ontogenetic series of extinct dinosaurs using limb robusiticty

Dinosaurs exhibited a variety of ontogenetic patterns, even within major groups. Taxa deeply nested within presumed bipedal groups are predicted as remaining bipedal throughout their ontogeny by our method. These include the only non-avian theropod in the study, *Limusaurus inextricabilis*, the early branching sauropodomorph *Massospondylus carinatus*, and the iguanodontian *Maiasaura peeblesorum*. The derived sauropod *Rapetosaurus krausei*, which is deeply nested in a quadrupedal group, was predicted to be quadrupedal throughought ontogeny by our method. This result corroborates previous studies that suggesteed that members of Sauropoda are obligate quadrupeds throughout their development based on near isometry of limb proportions during ontogeny (Rogers *et al.* 2016).

Previous inferences of ontogenetic shifts from quadrupedalism to bipedalism in non-avian dinosaur taxa were used to hypothesize a more widespread pattern of ontogenetic postural change in Dinosauria (Reisz *et al.* 2005; Zhao *et al.* 2013), however our results contradict some of the conclusions on which this hypothesis was based. In particular, we reject the hypothesis that *Massospondylus carinatus* had an early quadrupedal phase in its ontogeny (Reisz *et al.* 2005), which was previously supported by observations of allometric scaling of the relative limb lengths (shown here to have high error rates). Instead, *Massospondylus carinatus* has limb bone shaft circumference ratios that remain consistent throughout ontogeny (S3 Table) and is predicted as being bipedal from hatchling to adult stage, suggesting that it was strictly bipedal throughout its development. This is consistent with previous observations of functional morphology (Bonnan and Senter 2007) and with observations of the endosseous labyrinth (Neenan *et al.* 2018). We also reject the hypothesis that *Maiasaura* was bipedal as a juvenile and became quadrupedal as an adult (Dilkes 2001), which was previously suggested based on biomechanical and morphometric analyses. More ontogenetic series of non-avian dinosaur taxa that can be confidently inferred to contain postural shifts are necessary to construct general hypotheses about the prevalence of this phenomenon within Dinosauria.muss

Two taxa are inferred to have undergone ontogenetic postural shifts: *Mussaurus patagonicus* within transitional Sauropodomorpha; and the early ceratopsian *Psittacosaurus lujiatunensis* within Ornithischia (Bonnan and Yates 2007; Otero and Pol 2013; Barrett and Maidment 2017). An ontogenetic postural transition from early-ontogenetic quadrupedality to late-ontogenetic bipedality is confidently inferred in *Mussaurus* (Fig 2). *Mussaurus* had been hypothesized as being erect and at least facultatively bipedal as an adult (Otero *et al.* 2017), and a recent study has hypothesized a shift from quadrupedalism to bipedalism during ontogeny based on change in the body plan and its center of mass (Otero *et al.* 2019).

Psittacosaurus lujiatunensis has a mix of quadrupedal, equivocal and bipedal posture predictions throughout its ontogeny. However, the hatchling is confidently inferred as quadrupedal and the largest two specimens as bipedal, supporting the hypothesis of a lengthy ontogenetic transition from quadrupedality to bipedality. This is consistent with previous research that hypothesized an ontogenetic postural shift from quadrupedalism to bipedalism based on limb length allometry as well as osteohistology (vascularisation showing that the hindlimb grew rapidly during the during the middle part of development) (Zhao et al. 2013).

Postural predictions in embryos

Caution should be taken when including fossil embryos in locomotory studies if the developmental stage is not identifiable. The sole dinosaur embryo in our study, an in-ovo individual of *Massospondylus carninatus*, is predicted as being equivocal ($pp_{bipedal}$=0.415). All larger individuals of *Massospondylus carinatus*, including the smallest juvenile (which has appropriate size to be a recent hatchling), are predicted as being bipedal. Previous inferences on the ontogenetic locomotory shifts of this taxon were based on samples that included this embryo (Reisz *et al.* 2005), under the assumption that it was near hatching. However, the equivocal prediction of the embryo could be due to it being earlier in development than previously hypothesized and could therefore be explained by one of two hypotheses: 1) in the absence of limb loading, embryonic limbs might respond to simple growth promotion signals during development, thus having more equivalent limb robusticities; 2) In the absence of loading, embryos could develop towards what their functional demands as young individuals are likely to be (i.e. as hatchlings, the embryos would be quadrupedal and then shift to bipedalism later in development). In order to confirm which of these two explanations is correct, it would be necessary to include embryonic specimens in the ontogenetic sample of each extant amniote used in this study.

The implications of ontogenetic locomotory shifts

Although studying ontogenetic series has been shown to be useful for looking at macroevolutionary patterns in lineages (Heers *et al.* 2014), there is little consensus on the relationship of these hypothesized ontogenetic patterns to dinosaur macroevolution. The ontogenetic shift from quadrupedality to bipedality in the early ceratopsian *Psittacosaurus lujiatunensis* was suggested to reflect plesiomorphic retention of the ancestral condition of quadrupedal basal archosaurs at early ontogenetic stages (Zhao *et al.* 2013). A hypothesized shift from quadrupedalism to bipedalism during the ontogeny of the early branching sauropodomorph *Massospondylus carinatus* prompted the hypothesis that quadrupedalism in later-branching sauropods could have evolved through paedomorphosis (Reisz *et al.* 2005). This would imply a pattern whereby the early ontogenetic stages of progressively more derived sauropodomorphs have a quadrupedal posture which is retained at progressively later ontogenetic stages in more crownward taxa. Although not formally tested, it has been shown that the pattern of evolution of quadrupedality in sauropodomorphs is complex, with at least two, and possibly three, independent origins (at least among ontogenetically mature individuals) (McPhee *et al.* 2018). We found the *Massospondylus carinatus* embryo to be equivocal and the next specimen after the embryo in the *Massospondylus carinatus* growth series is approximately hatchling size and predicted as being bipedal. This counters previous hypotheses that basal members of the three major dinosaur clades had quadrupedal hatchlings and therefore that the quadrupedal to bipedal ontogenetic shifts correspond to a recapitulation of the postural shift seen from basal quadrupedal archosaurs to bipedal avemetatarsalians (Zhao *et al.* 2013).

The two taxa with probable locomotory ontogenetic shifts occupy parts of the dinosaur tree where evolutionary transitions of posture are likely to have occurred based on optimizations of adult stances (Fig 4). *Mussaurus* is more closely related to the obligately quadrupedal sauropods, and is nested within a clade that shows high incidence of quadrupedal adults (McPhee *et al.* 2018). We have the highest confidence in inferring a postural shift in *Mussaurus* among the dinosaurs in our study, and the macroevolutionary significance of this is different depending on phylogenetic hypotheses. If *Mussaurus* is phylogenetically placed among quadrupedal sauropodomorphs, then it represents a recent evolutionary origin of bipedalism from quadrupedal ancestors. If so, then its ontogenetic trajectory is potentially recapitulatory, because the hypothesized ancestral state for posture in sauropodomorphs is bipedalism throughout ontogeny, as supported by our observations in the earlier-branching *Massospondylus* and from other recent studies (Otero *et al.* 2017; McPhee *et al.* 2018). If *Mussaurus* is instead optimized as ancestrally bipedal, then it implies that the quadrupedality that characterises all sauropods might have appeared first among juveniles of ancestral species with bipedal adults. *Psittacosaurus lujiatunensis*, being an intermediate ceratopsian, represents one of three independent transitions from bipedality to quadrupedality in Ornithischia (Maidment *et al.* 2014). While earlier-branching ceratopsians are likely bipeds (e.g., *Yinglong downsi*; Han *et al.* 2018) and derived members like ceratopsids are certain obligate quadrupeds.

Most extinct and extant amniote species conserve their posture throughout their ontogeny. Even though our sample is limited, the scarcity of “transitional” locomotory values might reflect that macroeveolutionary transitions in posture are fleeting events that involve rapid changes in the ontogenetic sequence and thus are unlikely to have been preserved in the fossil record. This rapidity of change in posture was also suggested by McPhee et al (2018) based on optimization of a smaller sample of adult postures of sauropodomorph dinosaurs, but our analysis supports a more general application of this hypothesis.

CONCLUSION

Proportional humeral and femoral robusticity is more reliable than the ratio of humeral to femoral length for predicting habitual amniote posture across ontogenetic trajectories. Most living and extinct amniote species examined conserve their posture across ontogeny, and where a shift does occur in *Homo sapiens*, our method correctly identifies it. We falsify previous hypotheses that such shifts were widespread in dinosaurs, at least among the dinosaurs we measured. Instead we hypothesize only two such shifts occurred, in the sauropodomorph *Mussaurus patagonicus*, and potentially in the ornithischian *Psittacosaurus lujiatunensis*. These two hypothesized shifts occur in lineages that are temporally and phylogenetically proximate to hypothesized macroevolutionary postural changes. The lack of widespread 'transitional' postural values more distal to these inferred changes suggests that postural shifts are evolutionarily rapid and leave only ephemeral signals in the fossil record and in ontogenetic sequences. Complex locomotor repertoires, forelimb assisted digging, and adaptations for axial stiffness may confound inferences of habitual locomotor posture using limb robusticity.

<u>Institutional abbreviations:</u>

AMNH - American Museum of Natural History, New York, USA
DMNH: Delaware Museum of Natural History, Wilmington, USA
ESI – Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa
FMNH - Field Museum of Natural History, Chicago, USA
IVPP - Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
MPM: Museo "Padre Molina", Río Gallegos, Argentina
MLP: Museo de La Plata, La Plata, Argentina
NHMUK: National History Museum, London, England
OUMNH: Oxford University Museum of Natural History, Oxford, England
PVL: Instituto "Miguel Lillo", Tucumán, Argentina
QG - Zimbabwe Natural History Museum, Bulawayo, Zimbabwe

RDC - Raymond Dart Collection, Deptartment of Anatomical Sciences, University of the Witwatersrand, Johannesburg, South Africa

ROM: Royal Ontario Museum, Ontario, Canada

SAM - South African Museum (Iziko Museums of Cape Town), Cape Town

Smithsonian Institution, Washington, DC.

USNM - National Museum of Natural History (formerly United States National Museum),

WLSM: Wits Life Sciences Museum, Johannesburg, South Africa

YPM: Yale Peabody Museum, New Haven, United States of America

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SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article:

S1 Table: Measurement sources

S2 Table: Log_{10}HC vs Log_{10}FC regression coefficients

S3 Table: DFA results using femoral and humeral circumferences

S4 Figs: Histograms displaying the distribution of the posterior probabilities of being bipedal over the 10 000 replicates in dinosaurs (using Log_{10}HC and Log_{10}FC).

S5 Figure: Log_{10}HL vs Log_{10}FL. Line and point colours reflect observed posture during habitual locomotion (travel), Homo sapiens in grey. Point shapes reflect posture predicted by the DFA. Silhouettes for small, medium and large size class bipeds|quadrupeds and dinosaurs.

S6 Table: Log_{10}HL vs $_{\mathrm{Log}10}$FL regression coefficients

S7 Table: DFA results using femoral and humeral lengths

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FIGURE CAPTIONS

Figure 1: Humeral to femoral circumference ratios during ontogeny. Line and point colors reflect observed posture during habitual locomotion (travel), *Homo sapiens* in grey. Point shapes reflect posture predicted by the DFA. Silhouettes for small, medium and large size class bipeds|quadrupeds and dinosaurs. A) Extant amniotes. B) Ontogenetic series of sauropodomorph dinosaurs in red overlying extant amniotes. C) Ontogenetic series of ornithischian dinosaurs in red. D) Ontogenetic series of theropod dinosaur *Limusaurus* in red.

Figure 2: Mean posterior probabilities obtained from the DFA analysis using minimum humeral and femoral circumferences. Log10(Femoral Circumference) used as proxy for body mass. Silhouettes indicate different size class examples.

Figure 3: Mean posterior probabilities obtained from the DFA analysis using humeral and femoral maximum lengths. Log10(Femoral Length) used as proxy for body mass. Silhouettes indicate different size class examples.

Figure 4: Simplified phylogenetic tree of Dinosauria showing independent appearances of quadrupedalism (blue stars). Orange lines represent bipedal lineages; blue lines represent quadrupedal lineages. Silhouettes represent taxa included in our analyses.

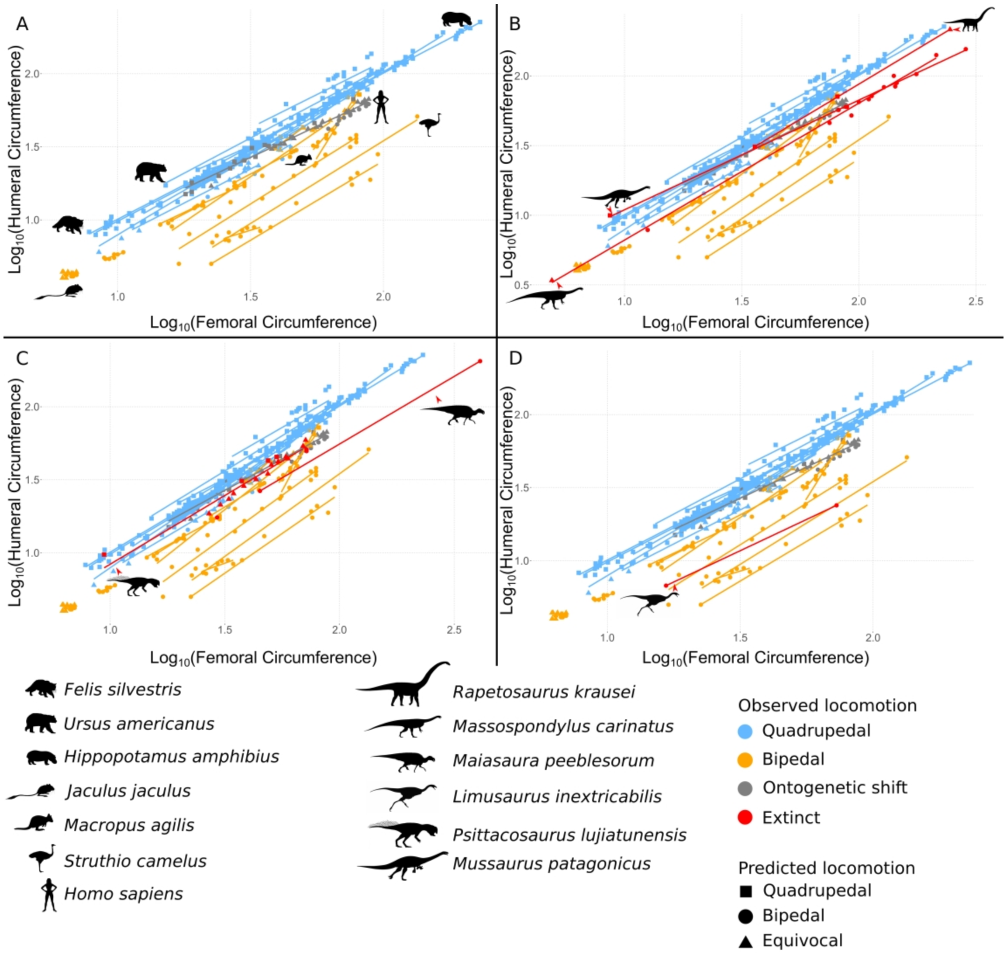


Figure 1: Humeral to femoral circumference ratios during ontogeny. Line and point colors reflect observed posture during habitual locomotion (travel), Homo sapiens in grey. Point shapes reflect posture predicted by the DFA. Silhouettes for small, medium and large size class bipeds|quadrupeds and dinosaurs. A) Extant amniotes. B) Ontogenetic series of sauropodomorph dinosaurs in red overlying extant amniotes. C) Ontogenetic series of ornithischian dinosaurs in red. D) Ontogenetic series of theropod dinosaur Limusaurus in red.

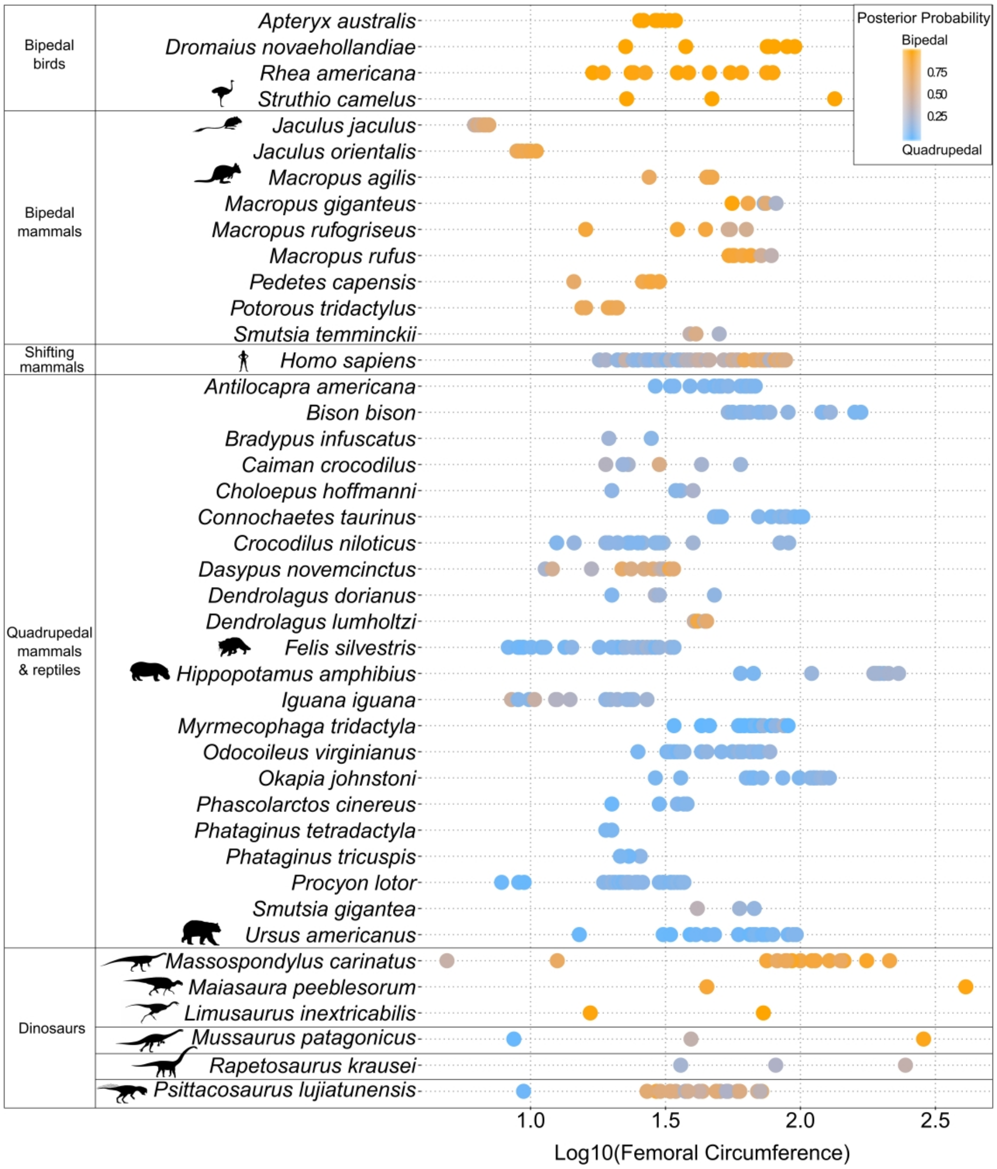


Figure 2: Mean posterior probabilities obtained from the DFA analysis using minimum humeral and femoral circumferences. Log_{10}(Femoral Circumference) used as proxy for body mass. Silhouettes indicate different size class examples.

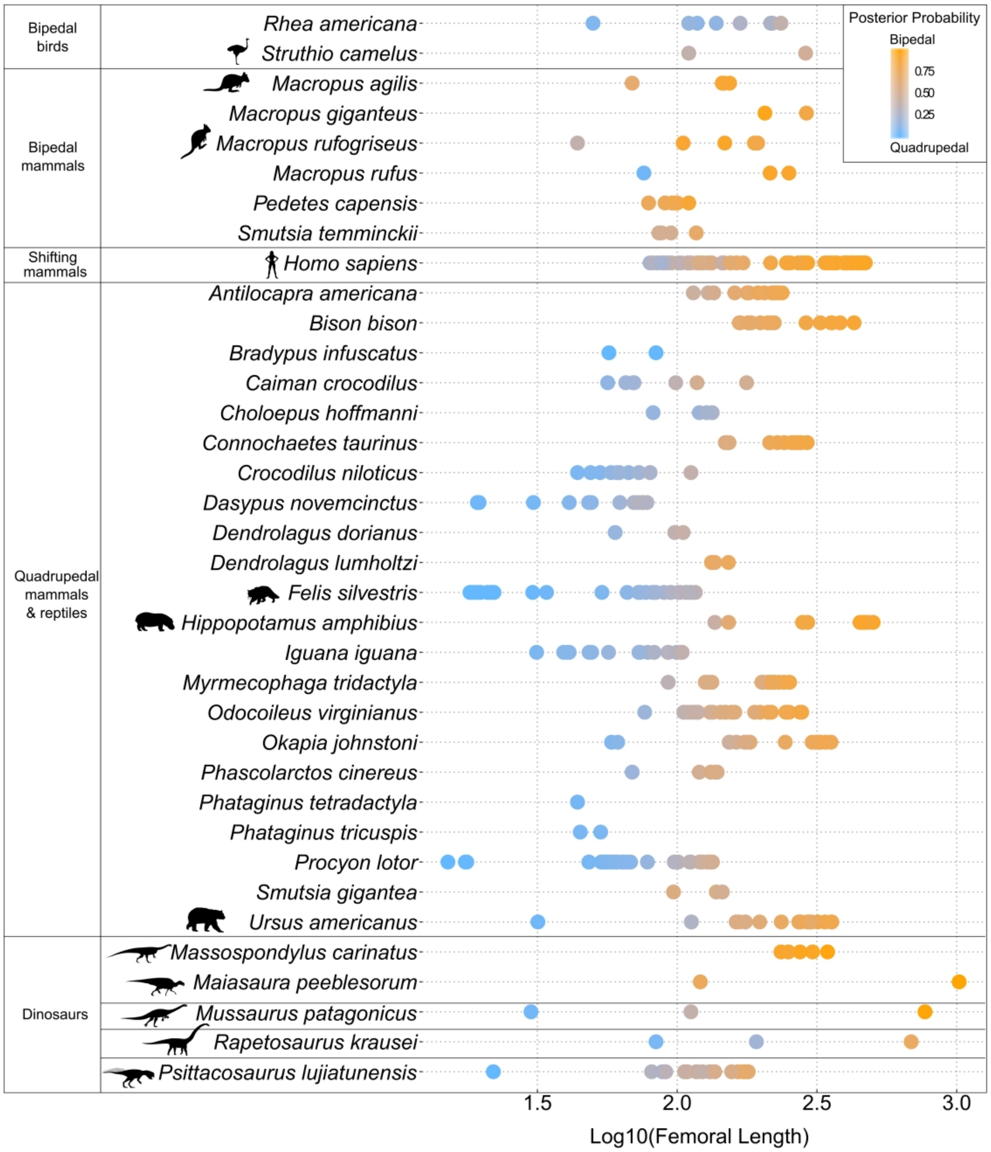


Figure 3: Mean posterior probabilities obtained from the DFA analysis using humeral and femoral maximum lengths. Log_{10}(Femoral Length) used as proxy for body mass. Silhouettes indicate different size class examples.

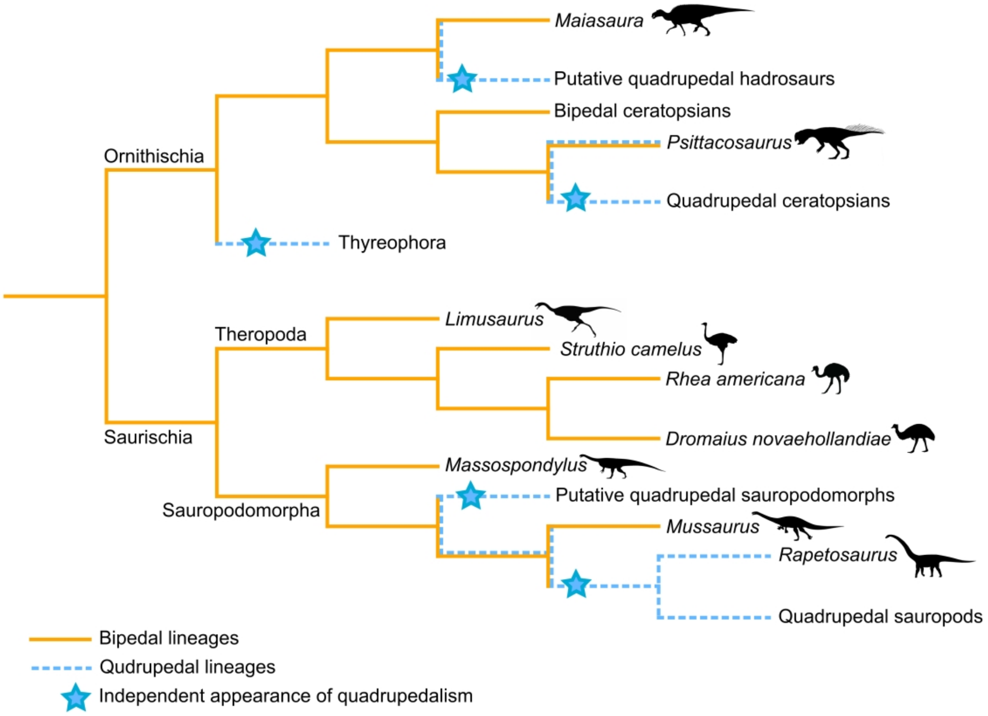


Figure 4: Simplified phylogenetic tree of Dinosauria showing independent appearances of quadrupedalism (blue stars). Orange lines represent bipedal lineages; blue lines represent quadrupedal lineages. Silhouettes represent taxa included in our analyses.

S1 Table: Measurement sources

Species name	Data source	Specimen source
Antilocapra americana	From Kilbourne and Makovicky, 2012	FMN; AMNH
Apteryx australis	Collected by authors	Smithsonian
Bison bison	From Kilbourne and Makovicky, 2012	FMN; AMNH
Bradypus infuscatus	Collected by authors	NHMUK
Caiman crocodilus	From Kilbourne and Makovicky, 2012	FMNH
Choloepus hoffmanni	Collected by authors	NHMUK
Connochaetes taurinus	From Kilbourne and Makovicky, 2012	FMNH
Crocodilus niloticus	Collected by authors	BPI; WLSM
Dasypus novemcinctus	From Kilbourne and Makovicky, 2012	AMNH
Dendrolagus dorianus	Collected by authors	NHMUK
Dendrolagus lumholtzi	Collected by authors	AMNH
Dromaius novaehollandiae	Collected by authors	Smithsonian
Felis silvestris	From Kilbourne and Makovicky, 2012	FMNH
Hippopotamus amphibius	From Kilbourne and Makovicky, 2012	FMN; AMNH
Homo sapiens	Collected by authors	RDC
Iguana iguana	From Kilbourne and Makovicky, 2012	AMNH, FMNH
Jaculus jaculus	Collected by authors	Smithsonian
Jaculus orientalis	Collected by authors	Smithsonian
Limusaurus inextricabilis	Collected by authors	IVPP
Macropus agilis	Collected by authors	NHMUK
Macropus giganteus	Collected by authors	Smithsonian
Macropus rufogriseus	Collected by authors	NHMUK, OUMNH

Macropus rufus	Collected by authors	NHMUK, Smithsonian, AZ
Maiasaura peeblesorum	Collected by authors	ROM, YPM
Massospondylus carinatus	Collected by authors	ESI; SAM; QG; NMQR
Mussaurus patagonicus	Collected by authors	MLP ; PVL; MPM
Myrmecophaga tridactyla	From Kilbourne and Makovicky, 2012	FMN; AMNH
Odocoileus virginianus	From Kilbourne and Makovicky, 2012	FMN; AMNH
Okapia johnstoni	From Kilbourne and Makovicky, 2012	FMN; AMNH
Pedetes capensis	Collected by authors	OUMNH, WLSM
Phascolarctos cinereus	Collected by authors	NHMUK,
Phataginus tetradactyla	Collected by authors	NHMUK
Phataginus tricuspis	Collected by authors	NHMUK, AMNH
Potorous tridactylus	Collected by authors	Smithsonian
Procyon lotor	From Kilbourne and Makovicky, 2012	FMNH
Psittacosaurus lujiatunensis	Collected by authors	IVPP; DMNH
Rapetosaurus krausei	From Curry Rogers et al 2016	UA, FMNHPR
Rhea americana	Collected by authors	NHMUK, Smithsonian
Smutsia gigantea	Collected by authors	NHMUK, AMNH
Smutsia temminckii	Collected by authors	NHMUK, AZ, WLSM
Struthio camelus	Collected by authors	WLSM, Smithsonian
Ursus americanus	From Kilbourne and Makovicky, 2012	FMN; AMNH

KILBOURNE, B. M. and MAKOVICKY, P. J. 2012. Data from: Postnatal long bone growth in terrestrial placental mammals: allometry, life history, and organismal traits. *Journal of Morphology*, **273**, 1111-1126.

S2 Table: $Log_{10}HC$ vs $Log_{10}FC$ regression coefficients

Species	Intercept	Slope	R2
Antilocapra americana	-0.0315147483934176	1.023004704385	0.992343063327147
Apteryx australis	0.091737659866493	0.558081471016583	0.561862378415113
Bison bison	-0.218708934828641	1.11577470311927	0.990621012322565
Bradypus infuscatus	-0.403968583355646	1.25690622060034	1
Caiman crocodilus	-0.152761018888796	1.05439430423571	0.958299633204194
Choloepus hoffmanni	-0.0110986955458769	0.977933055556748	0.977918755184107
Connochaetes taurinus	-0.211339159220261	1.12447957533395	0.989173177355812
Crocodilus niloticus	-0.093634286890316	1.03590950616042	0.994542790192789
Dasypus novemcinctus	-0.0507224631330361	0.93227941554909	0.963485694514523
Dendrolagus dorianus	-0.0498581127569553	1.00080932786108	0.967799129141032
Dendrolagus lumholtzi	-0.216078535536475	1.0483822436871	0.196863627234146
Dromaius novaehollandiae	-0.769822284692955	1.08683912836212	0.969353102591445
Felis silvestris	0.0520000676645122	0.938543142837183	0.987015283484453
Hippopotamus amphibius	0.0974012761839798	0.953454023340376	0.99512186590065
Homo sapiens	0.143483021658157	0.8556585123184	0.980216913662177
Iguana iguana	-0.194996498155777	1.09229219869285	0.975669616144188
Jaculus jaculus	0.586309670537908	0.0492243960834728	0.00405636021229633
Jaculus orientalis	0.147521029947944	0.614237097407921	0.754006504490583
Limusaurus inextricabilis	-0.216895312940664	0.856746391593576	1
Macropus agilis	-0.127989600748151	0.961184427435489	0.999775197151271
Macropus giganteus	-3.67083383761496	2.91210326333658	0.924507363008487
Macropus rufogriseus	-0.572165619101066	1.24494221504549	0.980575124098413
Macropus rufus	-2.03692049983941	2.02618330996259	0.945465383569936
Maiasaura peeblesorum	-0.107534024350245	0.925942602894092	1
Manis gigantea	-0.631036285193624	1.33237728786009	0.999969430104514
Massospondylus carinatus	-0.159695998836752	0.981845172638382	0.995184070711216
Mussaurus patagonicus	0.252705550482805	0.786718621133581	0.999483193589313
Myrmecophaga tridactyla	0.268500689291092	0.908198655707597	0.654828849610357
Odocoileus virginianus	0.052596333930176	0.965344987985909	0.985363763425958
Okapia johnstoni	-0.0102230777709838	1.0108874797365	0.995227905719649
Pedetes capensis	-0.0238448456090812	0.859664089095399	0.976823666114562
Phascolarctos cinereus	0.287299121727718	0.81244763054788	0.994485840645836
Phataginus tetradactyla	0.952492900812307	0.246082456339994	0.0320930728635834
Phataginus tricuspis	0.533765466151342	0.60463967931012	0.420957467331853
Potorous tridactylus	-0.168620662340784	0.967571631213046	0.975821536912527
Procyon lotor	0.0667531595861718	0.93726228962830 8	0.982675941170817

Psittacosaurus lujiatunensis	-0.0199559095199344	0.941358020737635	0.938486561320121
Rapetosaurus krausei	-0.0778603874010931	1.00934173123031	0.999966595972079
Rhea americana	-0.600701345541552	1.13965396003529	0.96937374570869
Smutsia temminckii	-0.614486544273011	1.32368157261532	0.742287089169333
Struthio camelus	-0.722311221396286	1.13157839996391	0.987855610964991
Ursus americanus	0.112963854216806	0.964720562433517	0.987326439613617

S3 Table: DFA results using femoral and humeral circumferences

Species	SP#	$\mathrm{Log}_{10}\mathrm{HC}/\mathrm{Log}_{10}\mathrm{FC}$	Class prediction	Mean posterior probability bipedal
Massospondylus carinatus	QG21A	0.910720	Bipedal	0.854548
Massospondylus carinatus	BP/1/5347a	0.772370	Equivocal	0.415405
Massospondylus carinatus	BP/1/4934	0.922248	Bipedal	0.858949
Massospondylus carinatus	BP/1/5241	0.901924	Bipedal	0.905944
Massospondylus carinatus	BP/1/4266	0.886775	Bipedal	0.884181
Massospondylus carinatus	SAMPK 388	0.917474	Bipedal	0.733864
Massospondylus carinatus	BP/1/4860	0.892798	Bipedal	0.932021
Massospondylus carinatus	BP/1/4998	0.930571	Bipedal	0.742257
Massospondylus carinatus	BP/1/5193	0.906457	Bipedal	0.840384
Massospondylus carinatus	BP/1/5397	0.896382	Bipedal	0.937792
Massospondylus carinatus	BP/1/4751	0.871739	Bipedal	0.946186
Massospondylus carinatus	SAMPK 391	0.912158	Bipedal	0.787323
Massospondylus carinatus	SAMPK 413	0.814266	Bipedal	0.734155
Massospondylus carinatus	SAMPK 1314	0.914460	Bipedal	0.770011
Massospondylus carinatus	SAMPK 1304	0.897267	Bipedal	0.893846
Massospondylus carinatus	NMQR3055	0.902883	Bipedal	0.875120
Psittacosaurus lujiatunensis	IVPP V14341	0.846905	Bipedal	0.863387
Psittacosaurus lujiatunensis	IVPP V16902.2	1.014620	Quadrupedal	0.032961
Psittacosaurus lujiatunensis	IVPP V14341.5	0.885676	Equivocal	0.648984
Psittacosaurus lujiatunensis	IVPP V14342	0.913602	Equivocal	0.525992
Psittacosaurus lujiatunensis	IVPP V14748	0.917182	Equivocal	0.567455
Psittacosaurus lujiatunensis	IVPP V14749	0.932223	Equivocal	0.432040
Psittacosaurus lujiatunensis	IVPP V12617	0.937416	Equivocal	0.454815
Psittacosaurus lujiatunensis	ND2584	0.919051	Bipedal	0.691230
Psittacosaurus lujiatunensis	D2599	0.948077	Quadrupedal	0.285028
Psittacosaurus lujiatunensis	D2594	0.940676	Equivocal	0.408875
Psittacosaurus lujiatunensis	D2593	0.964436	Quadrupedal	0.229178
Psittacosaurus lujiatunensis	D2591	0.939885	Equivocal	0.497208
Psittacosaurus lujiatunensis	D2590	0.919796	Equivocal	0.508129
Psittacosaurus lujiatunensis	D2587	0.938211	Equivocal	0.468067
Psittacosaurus lujiatunensis	D2585	0.966086	Quadrupedal	0.219392
Psittacosaurus lujiatunensis	D2584	0.912772	Equivocal	0.638099
Psittacosaurus lujiatunensis	D2583	0.901154	Equivocal	0.606834
Psittacosaurus lujiatunensis	D2582	0.896755	Equivocal	0.611174
Psittacosaurus lujiatunensis	D2581	0.959701	Quadrupedal	0.272894
Psittacosaurus lujiatunensis	D1202	0.913547	Bipedal	0.732814
Psittacosaurus lujiatunensis	BoxSpecimenD	0.926250	Equivocal	0.581578
Psittacosaurus lujiatunensis	BoxSpecimenB	0.956216	Equivocal	0.355419
Mussaurus patagonicus	MPM1813	0.935379	Equivocal	0.388111
Mussaurus patagonicus	MLP 68-II-27-1	0.892356	Bipedal	0.968631
Mussaurus patagonicus	PVL4068	1.065613	Quadrupedal	0.014076

Limusaurus inextricabilis	V15301	0.679139	Bipedal	0.988940
Limusaurus inextricabilis	V15923	0.740299	Bipedal	0.998810
Homo sapiens	3980	0.936921	Quadrupedal	0.208271
Homo sapiens	614	0.981638	Quadrupedal	0.083534
Homo sapiens	2813a	0.930853	Quadrupedal	0.245595
Homo sapiens	661	0.949368	Quadrupedal	0.181162
Homo sapiens	2813b	0.958367	Quadrupedal	0.148868
Homo sapiens	662	0.960975	Quadrupedal	0.145110
Homo sapiens	3190	0.970101	Quadrupedal	0.119791
Homo sapiens	808	0.909973	Equivocal	0.414254
Homo sapiens	807	0.972621	Quadrupedal	0.117734
Homo sapiens	3020	0.942631	Quadrupedal	0.231841
Homo sapiens	664	0.957983	Quadrupedal	0.164966
Homo sapiens	713	0.974096	Quadrupedal	0.116665
Homo sapiens	809	0.950070	Quadrupedal	0.211998
Homo sapiens	535	0.951350	Quadrupedal	0.208786
Homo sapiens	810	0.971242	Quadrupedal	0.132620
Homo sapiens	3191	0.967571	Quadrupedal	0.149983
Homo sapiens	3018	0.984228	Quadrupedal	0.099754
Homo sapiens	1572	0.973835	Quadrupedal	0.130207
Homo sapiens	472	0.957926	Quadrupedal	0.193318
Homo sapiens	3021	0.952217	Quadrupedal	0.220942
Homo sapiens	608	0.959770	Quadrupedal	0.189311
Homo sapiens	476	0.990839	Quadrupedal	0.089228
Homo sapiens	1235	0.942608	Quadrupedal	0.294333
Homo sapiens	806	0.983450	Quadrupedal	0.113402
Homo sapiens	2846	0.973351	Quadrupedal	0.148825
Homo sapiens	712	0.959794	Quadrupedal	0.213753
Homo sapiens	3148	0.939559	Equivocal	0.347633
Homo sapiens	3017	0.941703	Equivocal	0.337940
Homo sapiens	1327	0.946002	Quadrupedal	0.307195
Homo sapiens	1469	0.941548	Equivocal	0.350871
Homo sapiens	854	0.935478	Equivocal	0.404770
Homo sapiens	3019	0.932525	Equivocal	0.432288
Homo sapiens	3015	0.948578	Quadrupedal	0.319314
Homo sapiens	1320	0.935977	Equivocal	0.424746
Homo sapiens	722	0.945948	Equivocal	0.372152
Homo sapiens	1244	0.955409	Quadrupedal	0.309764
Homo sapiens	1439	0.934378	Equivocal	0.491662
Homo sapiens	972	0.931965	Equivocal	0.522987
Homo sapiens	161	0.944234	Equivocal	0.416981
Homo sapiens	769	0.905633	Bipedal	0.753431
Homo sapiens	439	0.905337	Bipedal	0.772732
Homo sapiens	1630	0.931821	Equivocal	0.566978
Homo sapiens	507	0.917453	Bipedal	0.690266
Homo sapiens	2243	0.917738	Bipedal	0.698609

Homo sapiens	3671	0.935509	Equivocal	0.549550
Homo sapiens	176	0.929734	Equivocal	0.604387
Homo sapiens	3014	0.933160	Equivocal	0.576624
Homo sapiens	1875	0.915172	Bipedal	0.730850
Homo sapiens	2178	0.919584	Bipedal	0.697297
Homo sapiens	101	0.926688	Equivocal	0.644790
Homo sapiens	266	0.967974	Quadrupedal	0.276766
Homo sapiens	100	0.949078	Equivocal	0.445368
Homo sapiens	151	0.920036	Bipedal	0.711698
Homo sapiens	97	0.937607	Equivocal	0.563901
Homo sapiens	3	0.932582	Equivocal	0.616610
Homo sapiens	3784	0.943053	Equivocal	0.517511
Homo sapiens	13	0.919179	Bipedal	0.731578
Homo sapiens	9	0.933668	Equivocal	0.609489
Homo sapiens	1	0.926541	Bipedal	0.672689
Homo sapiens	14	0.921783	Bipedal	0.716689
Homo sapiens	8	0.939106	Equivocal	0.563941
Felis silvestris	FMNH 104913	0.977735	Quadrupedal	0.057947
Felis silvestris	FMNH 60067	0.991293	Quadrupedal	0.048142
Felis silvestris	FMNH 104922	1.009432	Quadrupedal	0.035611
Felis silvestris	FMNH 101853	0.993035	Quadrupedal	0.047108
Felis silvestris	FMNH 104921	0.994230	Quadrupedal	0.046579
Felis silvestris	FMNH 60016	1.018115	Quadrupedal	0.031048
Felis silvestris	FMNH 104920	0.985997	Quadrupedal	0.055403
Felis silvestris	FMNH 60041	0.955401	Quadrupedal	0.100387
Felis silvestris	FMNH 60466	1.001127	Quadrupedal	0.043916
Felis silvestris	FMNH 104919	0.976758	Quadrupedal	0.069385
Felis silvestris	FMNH 104909	0.993621	Quadrupedal	0.054675
Felis silvestris	FMNH 60040	0.956183	Quadrupedal	0.118451
Felis silvestris	FMNH 60137	0.999230	Quadrupedal	0.055317
Felis silvestris	FMNH 60442	0.980225	Quadrupedal	0.083596
Felis silvestris	FMNH 18009	0.982878	Quadrupedal	0.083602
Felis silvestris	FMNH 60081	0.982878	Quadrupedal	0.083602
Felis silvestris	FMNH 60443	0.967127	Quadrupedal	0.122542
Felis silvestris	FMNH 104929	0.983974	Quadrupedal	0.083775
Felis silvestris	FMNH 101878	0.983974	Quadrupedal	0.083775
Felis silvestris	FMNH 60080	1.000000	Quadrupedal	0.059357
Felis silvestris	FMNH 60504	1.014381	Quadrupedal	0.042563
Felis silvestris	FMNH 60417	0.962170	Quadrupedal	0.143457
Felis silvestris	FMNH 60017	0.972621	Quadrupedal	0.117734
Felis silvestris	FMNH 104916	0.957983	Quadrupedal	0.164966
Felis silvestris	FMNH 104914	1.000000	Quadrupedal	0.062886
Felis silvestris	FMNH 60271	0.960286	Quadrupedal	0.161046
Felis silvestris	FMNH 60280	0.962370	Quadrupedal	0.157664
Felis silvestris	FMNH 60353	0.975433	Quadrupedal	0.115796
Felis silvestris	FMNH 58006	0.964263	Quadrupedal	0.154736

Felis silvestris	FMNH 60039	0.951350	Quadrupedal	0.208786
Felis silvestris	FMNH 60141	0.965990	Quadrupedal	0.152194
Felis silvestris	FMNH 60336	1.000000	Quadrupedal	0.067383
Felis silvestris	FMNH 152104	0.969023	Quadrupedal	0.148056
Felis silvestris	FMNH 60570	0.963045	Quadrupedal	0.182575
Felis silvestris	FMNH 60089	0.982808	Quadrupedal	0.113349
Odocoileus virginianus	FMNH 165366	1.000000	Quadrupedal	0.062886
Odocoileus virginianus	AMNH 181986	1.025857	Quadrupedal	0.036437
Odocoileus virginianus	FMNH 153837	1.008879	Quadrupedal	0.056260
Odocoileus virginianus	FMNH 167204	1.004386	Quadrupedal	0.063568
Odocoileus virginianus	AMNH 181987	0.991199	Quadrupedal	0.089884
Odocoileus virginianus	FMNH 167207	0.991199	Quadrupedal	0.089884
Odocoileus virginianus	FMNH 154737	1.000000	Quadrupedal	0.072721
Odocoileus virginianus	FMNH 154736	1.015630	Quadrupedal	0.048993
Odocoileus virginianus	FMNH 60664	0.984050	Quadrupedal	0.113506
Odocoileus virginianus	FMNH 153836	0.984611	Quadrupedal	0.113655
Odocoileus virginianus	FMNH 154735	1.000000	Quadrupedal	0.081689
Odocoileus virginianus	AMNH 130296	0.981876	Quadrupedal	0.137169
Odocoileus virginianus	AMNH 130204	1.000000	Quadrupedal	0.089095
Odocoileus virginianus	AMNH 121477	0.995524	Quadrupedal	0.106297
Odocoileus virginianus	FMNH 60772	1.000000	Quadrupedal	0.093494
Odocoileus virginianus	FMNH 46955	0.987202	Quadrupedal	0.138738
Odocoileus virginianus	AMNH 245629	0.983149	Quadrupedal	0.157107
Odocoileus virginianus	FMNH 18844	0.995979	Quadrupedal	0.109859
Odocoileus virginianus	AMNH 130203	1.000000	Quadrupedal	0.101025
Odocoileus virginianus	FMNH 15574	0.992792	Quadrupedal	0.126870
Odocoileus virginianus	FMNH 54014	1.006631	Quadrupedal	0.086130
Odocoileus virginianus	AMNH 125590	1.003281	Quadrupedal	0.095911
Odocoileus virginianus	ROM_59338	0.984544	Quadrupedal	0.174503
Ursus americanus	FMNH 57142	1.046224	Quadrupedal	0.019711
Ursus americanus	FMNH 154705	1.043545	Quadrupedal	0.023094
Ursus americanus	FMNH 51805	1.047777	Quadrupedal	0.020992
Ursus americanus	AMNH 18130	1.056677	Quadrupedal	0.017115
Ursus americanus	FMNH 165353	1.025068	Quadrupedal	0.040388
Ursus americanus	AMNH 3762	1.027678	Quadrupedal	0.038827
Ursus americanus	FMNH 141990	1.020676	Quadrupedal	0.048337
Ursus americanus	AMNH 77787	1.034818	Quadrupedal	0.034699
Ursus americanus	AMNH 131828	1.052717	Quadrupedal	0.021062
Ursus americanus	FMNH 154193	1.029976	Quadrupedal	0.041875
Ursus americanus	AMNH 5044	1.006870	Quadrupedal	0.084303
Ursus americanus	FMNH 57282	1.013546	Quadrupedal	0.069023
Ursus americanus	FMNH 18864	1.027541	Quadrupedal	0.046321
Ursus americanus	AMNH 3761	1.038198	Quadrupedal	0.033659
Ursus americanus	AMNH 90333	1.031699	Quadrupedal	0.041438
Ursus americanus	FMNH 44725	1.016753	Quadrupedal	0.067026
Ursus americanus	AMNH 45149	1.034257	Quadrupedal	0.040953

Ursus americanus	FMNH 57290	1.025626	Quadrupedal	0.053779
Ursus americanus	AMNH 5032	1.006915	Quadrupedal	0.098842
Ursus americanus	ROM_71435	1.011055	Quadrupedal	0.087919
Bison bison	FMNH 137424	0.980707	Quadrupedal	0.157970
Bison bison	FMNH 104902	0.995524	Quadrupedal	0.106297
Bison bison	AMNH 244376	1.004037	Quadrupedal	0.086146
Bison bison	FMNH 60182	0.995979	Quadrupedal	0.109859
Bison bison	FMNH 104897	1.000000	Quadrupedal	0.098567
Bison bison	AMNH 213140	0.992513	Quadrupedal	0.125783
Bison bison	AMNH 35631	1.000000	Quadrupedal	0.105014
Bison bison	FMNH 134415	1.003171	Quadrupedal	0.097600
Bison bison	AMNH 16869	0.990851	Quadrupedal	0.145084
Bison bison	AMNH 98955	0.995006	Quadrupedal	0.139507
Bison bison	AMNH 19177	0.992919	Quadrupedal	0.173286
Bison bison	FMNH 44708	1.014960	Quadrupedal	0.086400
Bison bison	AMNH 98957	1.021201	Quadrupedal	0.072523
Bison bison	FMNH 18850	0.996785	Quadrupedal	0.159586
Bison bison	FMNH 18849	1.024473	Quadrupedal	0.071324
Bison bison	AHR1985	1.026148	Quadrupedal	0.068930
Procyon lotor	FMNH 156868	1.027843	Quadrupedal	0.025660
Procyon lotor	FMNH 156869	1.025878	Quadrupedal	0.027035
Procyon lotor	FMNH 156870	1.045502	Quadrupedal	0.019521
Procyon lotor	FMNH 167196	0.970366	Quadrupedal	0.105778
Procyon lotor	FMNH 167195	0.991115	Quadrupedal	0.068738
Procyon lotor	FMNH 154706	0.971873	Quadrupedal	0.105730
Procyon lotor	FMNH 154719	0.956923	Quadrupedal	0.149393
Procyon lotor	FMNH 154712	0.974630	Quadrupedal	0.102264
Procyon lotor	FMNH 154708	1.000615	Quadrupedal	0.057646
Procyon lotor	FMNH 154716	0.987679	Quadrupedal	0.078057
Procyon lotor	FMNH 154713	0.981740	Quadrupedal	0.089593
Procyon lotor	FMNH 178212	1.000000	Quadrupedal	0.059357
Procyon lotor	FMNH 167194	0.957194	Quadrupedal	0.161438
Procyon lotor	FMNH 154715	0.974672	Quadrupedal	0.108572
Procyon lotor	FMNH 178210	0.985823	Quadrupedal	0.084369
Procyon lotor	FMNH 178211	0.985823	Quadrupedal	0.084369
Procyon lotor	FMNH 154718	0.967403	Quadrupedal	0.129987
Procyon lotor	FMNH 154714	0.975332	Quadrupedal	0.111661
Procyon lotor	ROM_88247	0.980464	Quadrupedal	0.118755
Procyon lotor	FMNH 154711	0.968822	Quadrupedal	0.131316
Procyon lotor	FMNH 178213	0.974096	Quadrupedal	0.116665
Procyon lotor	FMNH 167059	0.974096	Quadrupedal	0.116665
Procyon lotor	FMNH 65845	0.975433	Quadrupedal	0.115796
Procyon lotor	FMNH 135302	0.990032	Quadrupedal	0.087962
Procyon lotor	FMNH 167058	0.990451	Quadrupedal	0.088586
Procyon lotor	FMNH 167060	1.000000	Quadrupedal	0.069553
Procyon lotor	FMNH 167061	0.990451	Quadrupedal	0.088586

Procyon lotor	FMNH 175312	1.000000	Quadrupedal	0.071676
Procyon lotor	FMNH 104987	1.000000	Quadrupedal	0.071676
Procyon lotor	FMNH 154709	0.991534	Quadrupedal	0.090552
Procyon lotor	FMNH 104968	0.983450	Quadrupedal	0.113402
Procyon lotor	FMNH 167197	0.992139	Quadrupedal	0.091918
Procyon lotor	FMNH 167062	0.984611	Quadrupedal	0.113655
Okapia johnstoni	AMNH 51240	1.000000	Quadrupedal	0.067383
Okapia johnstoni	AMNH 51240	1.000000	Quadrupedal	0.074780
Okapia johnstoni	FMNH 99430	1.003801	Quadrupedal	0.088893
Okapia johnstoni	FMNH 60185	1.010809	Quadrupedal	0.073352
Okapia johnstoni	AMNH 51237	1.003589	Quadrupedal	0.091576
Okapia johnstoni	AMNH 188792	0.992792	Quadrupedal	0.126870
Okapia johnstoni	AMNH 51238	1.006995	Quadrupedal	0.083379
Okapia johnstoni	FMNH 121226	1.020398	Quadrupedal	0.055825
Okapia johnstoni	FMNH 153734	1.006407	Quadrupedal	0.087929
Okapia johnstoni	AMNH 51224	1.010206	Quadrupedal	0.085398
Okapia johnstoni	AMNH 51220	1.016911	Quadrupedal	0.073915
Okapia johnstoni	FMNH 58839	1.003876	Quadrupedal	0.117141
Okapia johnstoni	FMNH 108987	1.012019	Quadrupedal	0.091396
Okapia johnstoni	AMNH 51222	1.003751	Quadrupedal	0.119229
Okapia johnstoni	FMNH 26066	1.007437	Quadrupedal	0.106059
Okapia johnstoni	FMNH 152135	1.003711	Quadrupedal	0.119917
Okapia johnstoni	AMNH 51196	1.007206	Quadrupedal	0.108250
Okapia johnstoni	FMNH 165349	0.998234	Quadrupedal	0.146308
Okapia johnstoni	FMNH 134544	0.996559	Quadrupedal	0.156162
Okapia johnstoni	ZMUC_M_4221	1.004775	Quadrupedal	0.123400
Connochaetes taurinus	FMNH 60388	1.005191	Quadrupedal	0.075436
Connochaetes taurinus	FMNH 60385	1.000000	Quadrupedal	0.086373
Connochaetes taurinus	FMNH 66971	0.994836	Quadrupedal	0.101967
Connochaetes taurinus	FMNH 60558	1.004939	Quadrupedal	0.077465
Connochaetes taurinus	FMNH 59003	1.004939	Quadrupedal	0.077465
Connochaetes taurinus	FMNH 127911	1.006631	Quadrupedal	0.086130
Connochaetes taurinus	FMNH 57592	1.003339	Quadrupedal	0.095057
Connochaetes taurinus	FMNH 127907	1.014261	Quadrupedal	0.071946
Connochaetes taurinus	FMNH 127908	1.002671	Quadrupedal	0.106479
Connochaetes taurinus	FMNH 127909	1.024039	Quadrupedal	0.056004
Connochaetes taurinus	FMNH 29522	1.000000	Quadrupedal	0.119078
Connochaetes taurinus	FMNH 127912	1.015612	Quadrupedal	0.075573
Connochaetes taurinus	FMNH 127905	1.017755	Quadrupedal	0.070619
Connochaetes taurinus	AHR1985	1.030349	Quadrupedal	0.048305
Connochaetes taurinus	FMNH 127910	1.027809	Quadrupedal	0.052833
Antilocapra americana	FMNH 60149	1.000000	Quadrupedal	0.067383
Antilocapra americana	AMNH 122380	1.008538	Quadrupedal	0.057507
Antilocapra americana	AMNH 122381	1.000000	Quadrupedal	0.072721
Antilocapra americana	AMNH 16592	1.000000	Quadrupedal	0.077795
Antilocapra americana	AMNH 80242	1.000000	Quadrupedal	0.082642

Antilocapra americana	AMNH 130128	1.010545	Quadrupedal	0.064267
Antilocapra americana	FMNH 47167	1.015660	Quadrupedal	0.055660
Antilocapra americana	FMNH 44279	0.994836	Quadrupedal	0.101967
Antilocapra americana	AMNH 237995	1.004939	Quadrupedal	0.077465
Antilocapra americana	FMNH 57216	1.009117	Quadrupedal	0.070653
Antilocapra americana	FMNH 60471	0.995314	Quadrupedal	0.104859
Antilocapra americana	FMNH 60605	1.004037	Quadrupedal	0.086146
Antilocapra americana	FMNH 51438	1.000000	Quadrupedal	0.098567
Antilocapra americana	FMNH 57217	1.003801	Quadrupedal	0.088893
Antilocapra americana	FMNH 74239	1.014858	Quadrupedal	0.064117
Antilocapra americana	FMNH 57215	1.003657	Quadrupedal	0.090689
Antilocapra americana	AMNH 75243	1.003589	Quadrupedal	0.091576
Antilocapra americana	AMNH 142361	1.010232	Quadrupedal	0.076236
Hippopotamus amphibius	AMNH 130267	1.008009	Quadrupedal	0.076700
Hippopotamus amphibius	FMNH 60538	1.013791	Quadrupedal	0.068055
Hippopotamus amphibius	AMNH 180372	0.992120	Quadrupedal	0.169603
Hippopotamus amphibius	FMNH 127869	0.985124	Quadrupedal	0.273662
Hippopotamus amphibius	FMNH 60190	0.992754	Quadrupedal	0.218188
Hippopotamus amphibius	AMNH 15898	0.999001	Quadrupedal	0.180702
Hippopotamus amphibius	AMNH 113816	1.001935	Quadrupedal	0.166069
Hippopotamus amphibius	FMNH 22367	0.998069	Quadrupedal	0.188899
Hippopotamus amphibius	FMNH 127870	1.004553	Quadrupedal	0.155781
Hippopotamus amphibius	AMNH 99367	0.993732	Quadrupedal	0.224001
Hippopotamus amphibius	ROM_94513	0.993826	Quadrupedal	0.211340
Hippopotamus amphibius	FMNH 127871	0.995979	Quadrupedal	0.217263
Dasypus novemcinctus	AMNH 13372	0.907893	Quadrupedal	0.235396
Dasypus novemcinctus	AMNH 13373	0.856274	Equivocal	0.509452
Dasypus novemcinctus	AMNH 133261	0.916205	Quadrupedal	0.291880
Dasypus novemcinctus	AMNH 133369	0.864287	Bipedal	0.704500
Dasypus novemcinctus	AMNH 133259	0.887674	Equivocal	0.587488
Dasypus novemcinctus	AMNH 133260	0.895438	Equivocal	0.572698
Dasypus novemcinctus	AMNH 205707	0.890835	Equivocal	0.631990
Dasypus novemcinctus	AMNH 133270	0.914811	Equivocal	0.473085
Dasypus novemcinctus	AMNH 133381	0.909979	Equivocal	0.519992
Dasypus novemcinctus	AMNH 133268	0.930658	Equivocal	0.362156
Dasypus novemcinctus	AMNH 133266	0.867106	Bipedal	0.811107
Dasypus novemcinctus	AMNH 133269	0.895701	Equivocal	0.655515
Myrmecophaga tridactyla	AMNH 167320	1.053089	Quadrupedal	0.018420
Myrmecophaga tridactyla	AMNH 48072	1.097292	Quadrupedal	0.005905
Myrmecophaga tridactyla	AMNH 98514	1.060544	Quadrupedal	0.015790
Myrmecophaga tridactyla	NHMUK1965.8.17.2	1.034818	Quadrupedal	0.034699
Myrmecophaga tridactyla	AMNH 35710	1.057735	Quadrupedal	0.017873
Myrmecophaga tridactyla	AMNH 77902	1.092976	Quadrupedal	0.006520
Myrmecophaga tridactyla	AMNH 100136	1.085812	Quadrupedal	0.008010
Myrmecophaga tridactyla	FMNH 49342	1.089433	Quadrupedal	0.007220
Myrmecophaga tridactyla	AMNH 130242	1.090441	Quadrupedal	0.007015

Myrmecophaga tridactyla	NHMUK3.7.7.176	1.023221	Quadrupedal	0.051600
Myrmecophaga tridactyla	AMNH 100143	1.070770	Quadrupedal	0.012543
Myrmecophaga tridactyla	FMNH 49338	1.084992	Quadrupedal	0.008241
Myrmecophaga tridactyla	FMNH 98159	0.986866	Quadrupedal	0.158243
Myrmecophaga tridactyla	FMNH 28309	1.074695	Quadrupedal	0.011300
Myrmecophaga tridactyla	NHMUK1965.8.17.9	1.010969	Quadrupedal	0.081038
Myrmecophaga tridactyla	NHMUK1964.6.2.1	0.997173	Quadrupedal	0.123477
Myrmecophaga tridactyla	AMNH 70041	1.089932	Quadrupedal	0.007204
Myrmecophaga tridactyla	FMNH 60688	0.975548	Quadrupedal	0.241810
Myrmecophaga tridactyla	FMNH 159987	1.093375	Quadrupedal	0.006501
Macropus giganteus	SMT49995	0.987808	Quadrupedal	0.154416
Macropus giganteus	SMT221170	0.794322	Bipedal	0.989652
Macropus giganteus	SMT240989	0.894678	Bipedal	0.824029
Macropus giganteus	SMT597841	0.926204	Equivocal	0.640751
Macropus giganteus	SMT151726	0.972651	Quadrupedal	0.251735
Dendrolagus dorianus	NHMUK1978,2193	0.982878	Quadrupedal	0.083602
Dendrolagus dorianus	NHMUK78,2194	0.943800	Quadrupedal	0.260724
Dendrolagus dorianus	NHMUK78,2065	0.957926	Quadrupedal	0.193318
Dendrolagus lumholtzi	AMNH35623	0.920999	Equivocal	0.514375
Dendrolagus lumholtzi	AMNH65260	0.934158	Equivocal	0.407295
Dendrolagus lumholtzi	AMNH65265	0.874287	Bipedal	0.833785
Dendrolagus lumholtzi	AMNH35642	0.944065	Equivocal	0.349663
Dendrolagus lumholtzi	AMNH65261	0.904214	Bipedal	0.679846
Dendrolagus dorianus	NMS 2006.38	0.983329	Quadrupedal	0.137026
Iguana iguana	FMNH 2694	0.837245	Equivocal	0.447651
Iguana iguana	FMNH 211937	0.946395	Quadrupedal	0.101908
Iguana iguana	AMNH 88423	0.945974	Quadrupedal	0.109955
Iguana iguana	AMNH 82125	0.859673	Equivocal	0.426237
Iguana iguana	AMNH 74623	0.898094	Quadrupedal	0.299737
Iguana iguana	AMNH 81871	0.900894	Quadrupedal	0.290235
Iguana iguana	FMNH 222373	0.908618	Quadrupedal	0.283134
Iguana iguana	FMNH 207655	0.962225	Quadrupedal	0.127701
Iguana iguana	AMNH 84101	0.955052	Quadrupedal	0.153253
Iguana iguana	FMNH 211878	0.930594	Quadrupedal	0.267847
Iguana iguana	FMNH 22041	0.949368	Quadrupedal	0.181162
Iguana iguana	AMNH 74736	0.921477	Equivocal	0.348952
Iguana iguana	AMNH 74628	0.957983	Quadrupedal	0.164966
Iguana iguana	FMNH 31024	0.957983	Quadrupedal	0.164966
Iguana iguana	ROM_R5821	0.962744	Quadrupedal	0.142682
Iguana iguana	FMNH 22085	0.951350	Quadrupedal	0.208786
Struthio camelus	APES407	0.802767	Bipedal	0.997321
Struthio camelus	APES1521	0.666195	Bipedal	0.999546
Struthio camelus	553658	0.623217	Bipedal	0.998631
Pedetes capensis	OUMNH-uncat_M27156	0.833972	Bipedal	0.704665
Pedetes capensis	OUMNH13552	0.850984	Bipedal	0.821270

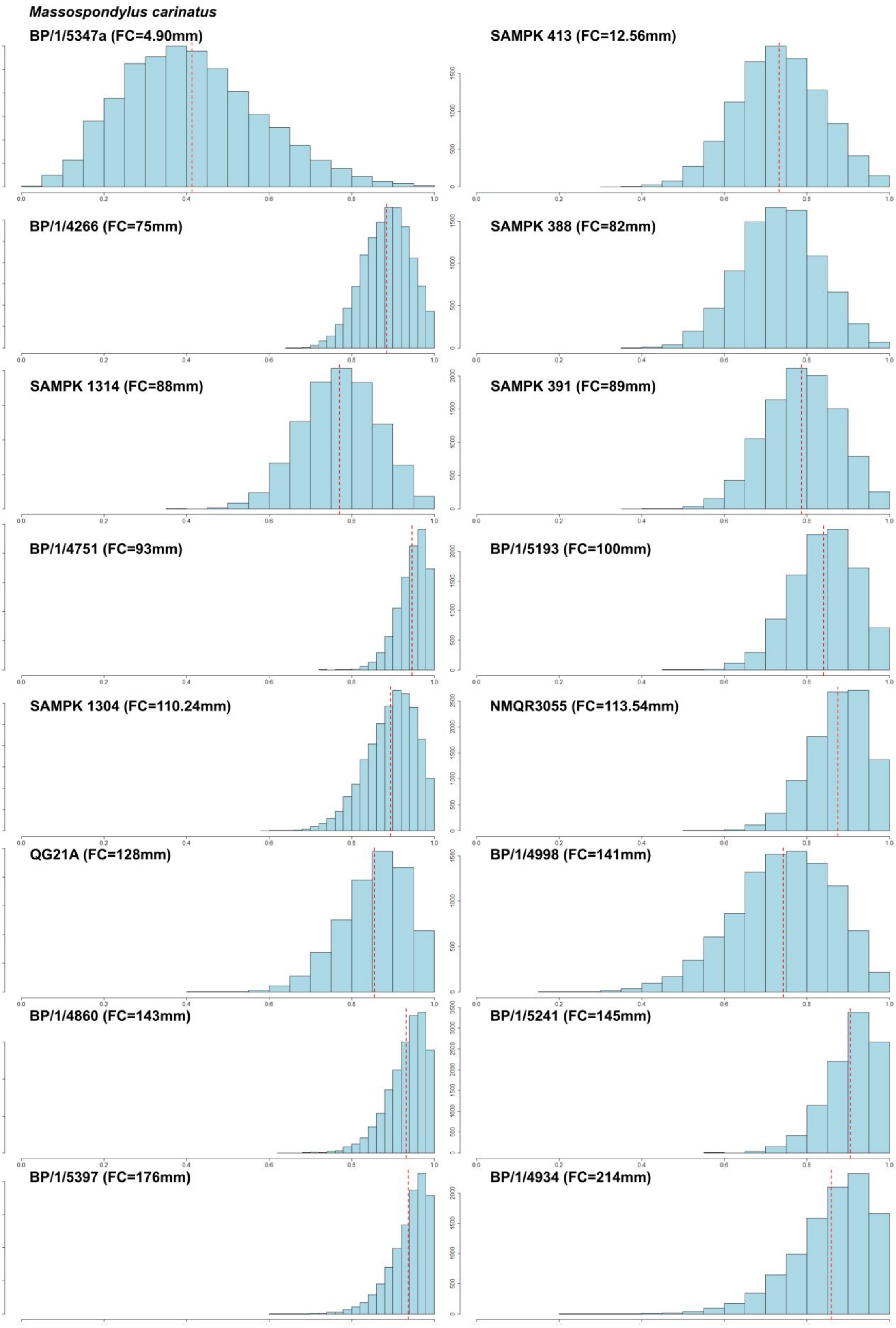
Pedetes capensis	OUMNH13557	0.854875	Bipedal	0.819849
Pedetes capensis	OUMNH13548	0.850252	Bipedal	0.842078
Pedetes capensis	OUMNH13551	0.850252	Bipedal	0.842078
Pedetes capensis	OUMNH13550	0.841293	Bipedal	0.872003
Pedetes capensis	OUMNH13554	0.841527	Bipedal	0.884487
Pedetes capensis	OUMNH13549	0.833005	Bipedal	0.906344
Pedetes capensis	OUMNH13553	0.833005	Bipedal	0.906344
Pedetes capensis	OUMNH13555	0.833005	Bipedal	0.906344
Pedetes capensis	WLSM154	0.849810	Bipedal	0.858808
Rapetosaurus krausei	UA998	0.970015	Quadrupedal	0.269981
Rapetosaurus krausei	FMNHPR2209	0.976256	Equivocal	0.392775
Rapetosaurus krausei	HatchlingEst	0.958272	Quadrupedal	0.217690
Macropus rufus	SMIT399293	0.868781	Bipedal	0.899506
Macropus rufus	SMIT588788	0.858659	Bipedal	0.928967
Macropus rufus	SMIT534280	0.872962	Bipedal	0.892676
Macropus rufus	NHMUK62-12-26-3	0.871717	Bipedal	0.905893
Macropus rufus	AZ1222	0.884869	Bipedal	0.860449
Macropus rufus	SMIT597991	0.877244	Bipedal	0.898407
Macropus rufus	ROM_31178	0.941724	Equivocal	0.487611
Macropus rufus	SMIT145752	0.956379	Equivocal	0.373012
Macropus agilis	NHMUK1966.1.7.1	0.872121	Bipedal	0.737352
Macropus agilis	NHMUK1970,2191	0.884580	Bipedal	0.802279
Macropus agilis	NHMUK1970,2191	0.884580	Bipedal	0.802279
Macropus agilis	NHMUK70,368	0.883966	Bipedal	0.810298
Macropus agilis	NHMUK1970,219	0.883394	Bipedal	0.817776
Macropus rufogriseus	NHMUK258D	0.792481	Bipedal	0.880757
Macropus rufogriseus	NHMUK51.4.24.1	0.842599	Bipedal	0.906987
Macropus rufogriseus	NHMUK49.6.20.4	0.868356	Bipedal	0.869860
Macropus rufogriseus	NHMUK58.5.26.10	0.930957	Equivocal	0.512387
Macropus rufogriseus	NHMUK1965.12.2.2	0.932707	Equivocal	0.501773
Macropus rufogriseus	OUMNH8066	0.934365	Equivocal	0.523391
Phascolarctos cinereus	NHMUK253.c	1.031815	Quadrupedal	0.027890
Phascolarctos cinereus	NHMUK253e --- 64.5.7.3	1.009641	Quadrupedal	0.053709
Phascolarctos cinereus	NHMUK230	1.009641	Quadrupedal	0.053709
Phascolarctos cinereus	NHMUK75,1828	0.991847	Quadrupedal	0.091230
Phascolarctos cinereus	NHMUK231	1.000000	Quadrupedal	0.075795
Phascolarctos cinereus	NHMUK229	0.992669	Quadrupedal	0.093315
Rhea americana	NHMUKS/1952.1.12	0.568061	Bipedal	0.998822
Rhea americana	614473	0.711367	Bipedal	0.984184
Rhea americana	555661	0.649783	Bipedal	0.997849
Rhea americana	614472	0.738912	Bipedal	0.984918
Rhea americana	614471	0.786433	Bipedal	0.962695
Rhea americana	NHMUK1899.11.10.5	0.742278	Bipedal	0.993292
Rhea americana	NHMUKS/2013.13.1	0.767905	Bipedal	0.989433
Rhea americana	NHMUK1899.11.10.6	0.782453	Bipedal	0.989192

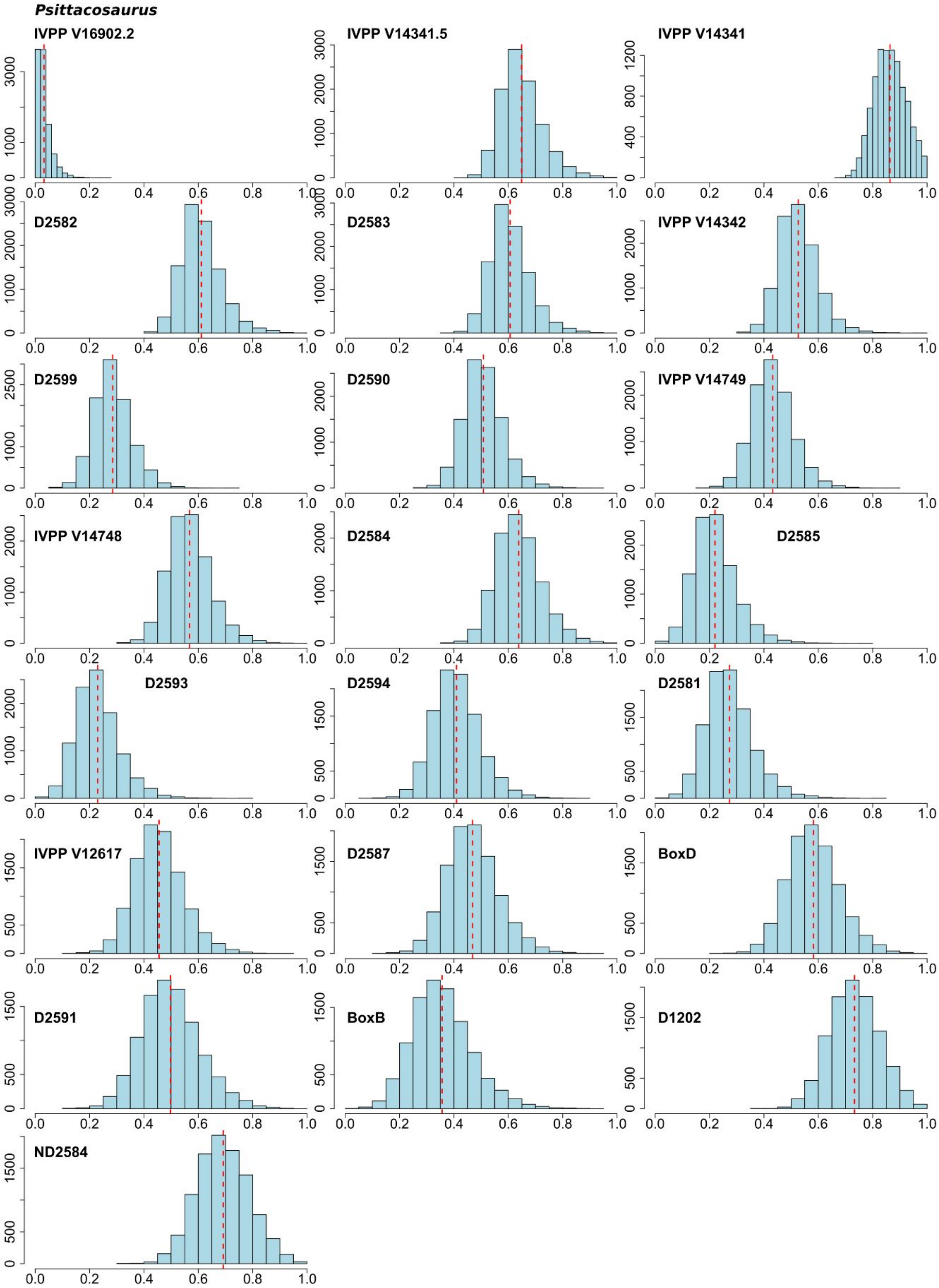
Rhea americana	NHMUK1915.3.31.1	0.787806	Bipedal	0.991217
Rhea americana	635757	0.811337	Bipedal	0.985173
Rhea americana	NHMUKS/1952.1.4	0.799073	Bipedal	0.993198
Rhea americana	NHMUK1846.11.18.21	0.830001	Bipedal	0.981656
Rhea americana	NHMUKS/1972.1.155	0.807049	Bipedal	0.992027
Rhea americana	NHMUKS/2018.12.1	0.832505	Bipedal	0.981734
Rhea americana	NHMUK1907.2.5.1	0.820131	Bipedal	0.987818
Jaculus jaculus	308387	0.759801	Equivocal	0.596289
Jaculus jaculus	308402	0.812039	Equivocal	0.401953
Jaculus jaculus	308407	0.808479	Equivocal	0.419170
Jaculus jaculus	267337	0.773090	Equivocal	0.566415
Jaculus jaculus	308405	0.746806	Equivocal	0.659378
Jaculus jaculus	308403	0.791539	Equivocal	0.504845
Jaculus jaculus	308410	0.741802	Bipedal	0.700968
Jaculus jaculus	308406	0.766842	Equivocal	0.615603
Jaculus jaculus	322827	0.766842	Equivocal	0.615603
Jaculus jaculus	308396	0.736069	Bipedal	0.726430
Jaculus jaculus	308390	0.760915	Equivocal	0.645190
Jaculus jaculus	267371	0.737488	Bipedal	0.737034
Jaculus jaculus	308389	0.737488	Bipedal	0.737034
Jaculus jaculus	322826	0.761394	Equivocal	0.659495
Jaculus orientalis	308383	0.779830	Bipedal	0.715887
Jaculus orientalis	475919	0.767513	Bipedal	0.762637
Jaculus orientalis	475921	0.756228	Bipedal	0.809266
Jaculus orientalis	475916	0.750288	Bipedal	0.839648
Jaculus orientalis	256516	0.773662	Bipedal	0.774813
Jaculus orientalis	308384	0.763428	Bipedal	0.816777
Jaculus orientalis	475893	0.762005	Bipedal	0.837477
Potorous tridactylus	522021	0.821388	Bipedal	0.784030
Potorous tridactylus	311769	0.830482	Bipedal	0.758501
Potorous tridactylus	399273	0.838003	Bipedal	0.791164
Potorous tridactylus	xxxx	0.840669	Bipedal	0.783320
Potorous tridactylus	538107	0.843109	Bipedal	0.779284
Potorous tridactylus	582008	0.834854	Bipedal	0.822234
Potorous tridactylus	124641	0.837444	Bipedal	0.813940
Potorous tridactylus	237718	0.829598	Bipedal	0.844194
Potorous tridactylus	395524	0.848737	Bipedal	0.769829
Dromaius novaehollandiae	614474	0.516920	Bipedal	0.999838
Dromaius novaehollandiae	614475	0.602715	Bipedal	0.999817
Dromaius novaehollandiae	346696	0.683773	Bipedal	0.999785
Dromaius novaehollandiae	500380	0.659381	Bipedal	0.999894
Dromaius novaehollandiae	343393	0.694082	Bipedal	0.999750
Dromaius novaehollandiae	500379	0.653292	Bipedal	0.999941
Dromaius novaehollandiae	500849	0.732005	Bipedal	0.999488
Apteryx australis	18277	0.614537	Bipedal	0.999198
Apteryx australis	18278	0.604478	Bipedal	0.999415

Apteryx australis	19875	0.644302	Bipedal	0.998601
Apteryx australis	289727	0.606190	Bipedal	0.999558
Apteryx australis	638636	0.632969	Bipedal	0.999229
Apteryx australis	614807	0.635101	Bipedal	0.999288
Apteryx australis	19025	0.627398	Bipedal	0.999501
Apteryx australis	500629	0.601526	Bipedal	0.999765
Choloepus hoffmanni	NHMUK1966.7.8.3	0.964830	Quadrupedal	0.124870
Choloepus hoffmanni	NHMUK75,182	0.975719	Quadrupedal	0.140714
Choloepus hoffmanni	ROM_89635	0.985299	Quadrupedal	0.107228
Choloepus hoffmanni	NHMUK90,521	0.955944	Quadrupedal	0.247654
Bradypus infuscatus	NHMUK1966.7.8.5	0.943761	Quadrupedal	0.192869
Bradypus infuscatus	NHMUK1966.7.8.4	0.977760	Quadrupedal	0.114540
Smutsia gigantea	NHMUK1934.7.4.1	0.942521	Equivocal	0.346359
Smutsia gigantea	NHMUK1965.5.12.1	0.976262	Quadrupedal	0.189340
Smutsia gigantea	AMNH53854	0.987672	Quadrupedal	0.147729
Smutsia temminckii	NHMUK93.7.9.18	0.935126	Equivocal	0.388109
Smutsia temminckii	NHMUK76,135	0.961446	Quadrupedal	0.250876
Smutsia temminckii	AZ534	0.972357	Quadrupedal	0.166599
Smutsia temminckii	WLSM794	0.915883	Equivocal	0.561318
Phataginus tetradactyla	NHMUK1939,2647	0.990943	Quadrupedal	0.068020
Phataginus tetradactyla	NHMUK63.2.13.23	0.964830	Quadrupedal	0.124870
Phataginus tetradactyla	NHMUK75,1832	0.991549	Quadrupedal	0.068825
Phataginus tricuspis	NHMUK1999,117	0.974780	Quadrupedal	0.116208
Phataginus tricuspis	AMNH53918	1.018039	Quadrupedal	0.039769
Phataginus tricuspis	NHMUK10.6.11.4	0.992330	Quadrupedal	0.070073
Maiasaura peeblesorum	ROM 44770	0.884786	Bipedal	0.984849
Maiasaura peeblesorum	YPM22401	0.860897	Bipedal	0.895661
Caiman crocodilus	FMNH 9150	0.978748	Quadrupedal	0.177674
Caiman crocodilus	FMNH 229976	0.919717	Quadrupedal	0.303935
Caiman crocodilus	FMNH 98961	0.984950	Quadrupedal	0.084036
Caiman crocodilus	FMNH 13062	0.902051	Equivocal	0.569149
Caiman crocodilus	FMNH 217066	0.939067	Quadrupedal	0.242025
Caiman crocodilus	FMNH 217159	0.952572	Quadrupedal	0.174873
Caiman crocodilus	ROM_R6872	0.962191	Quadrupedal	0.222919
Crocodilus niloticus	WLSM16	0.952086	Quadrupedal	0.158705
Crocodilus niloticus	WLSM1561	0.958367	Quadrupedal	0.148868
Crocodilus niloticus	WLSM	0.955426	Quadrupedal	0.169531
Crocodilus niloticus	WLSM	0.949923	Quadrupedal	0.227232
Crocodilus niloticus	WLSM1564	0.962370	Quadrupedal	0.157664
Crocodilus niloticus	WLSM	0.973835	Quadrupedal	0.130207
Crocodilus niloticus	WLSM9	0.956739	Quadrupedal	0.167160
Crocodilus niloticus	WLSM1565	0.985823	Quadrupedal	0.084369
Crocodilus niloticus	WLSM6	0.983974	Quadrupedal	0.083775
Crocodilus niloticus	WLSM	0.963802	Quadrupedal	0.203994
Crocodilus niloticus	WLSM16	0.978779	Quadrupedal	0.114111
Crocodilus niloticus	WLSM8	0.967127	Quadrupedal	0.122542

Crocodilus niloticus	WLSM1565	0.987318	Quadrupedal	0.085207
Crocodilus niloticus	WLSM1562	0.965113	Quadrupedal	0.166422
Crocodilus niloticus	WLSM	0.963570	Quadrupedal	0.126216
Crocodilus niloticus	WLSM1564	0.979715	Quadrupedal	0.113790
Crocodilus niloticus	BPcrocArt	0.991792	Quadrupedal	0.148029
Crocodilus niloticus	BP/4/1105	0.992518	Quadrupedal	0.150862
Crocodilus niloticus	BP/4/1126	0.966987	Quadrupedal	0.088289
Crocodilus niloticus	BP/4/1127	0.959165	Quadrupedal	0.113235
Crocodilus niloticus	BP/4/1128	0.944498	Quadrupedal	0.151113

S4 Figs: Histograms displaying the distribution of the posterior probabilities of being bipedal over the 10 000 replicates in dinosaurs

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IVPP V14341
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800
1200
D2582
0
1000
2000
3000
D2583
0
1000
2000
3000
IVPP V14342
0
1000
2000
D2599
0
1000
2500
D2590
0
1000
2000
IVPP V14749
0
1000
2000
IVPP V14748
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2000
D2584
0
1000
2000
D2585
0
1000
2000
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D2594
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1500
D2581
0
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1500
IVPP V12617
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D2587
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500
1500
BoxD
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500
1500
D2591
0
500
1500
BoxB
0
500
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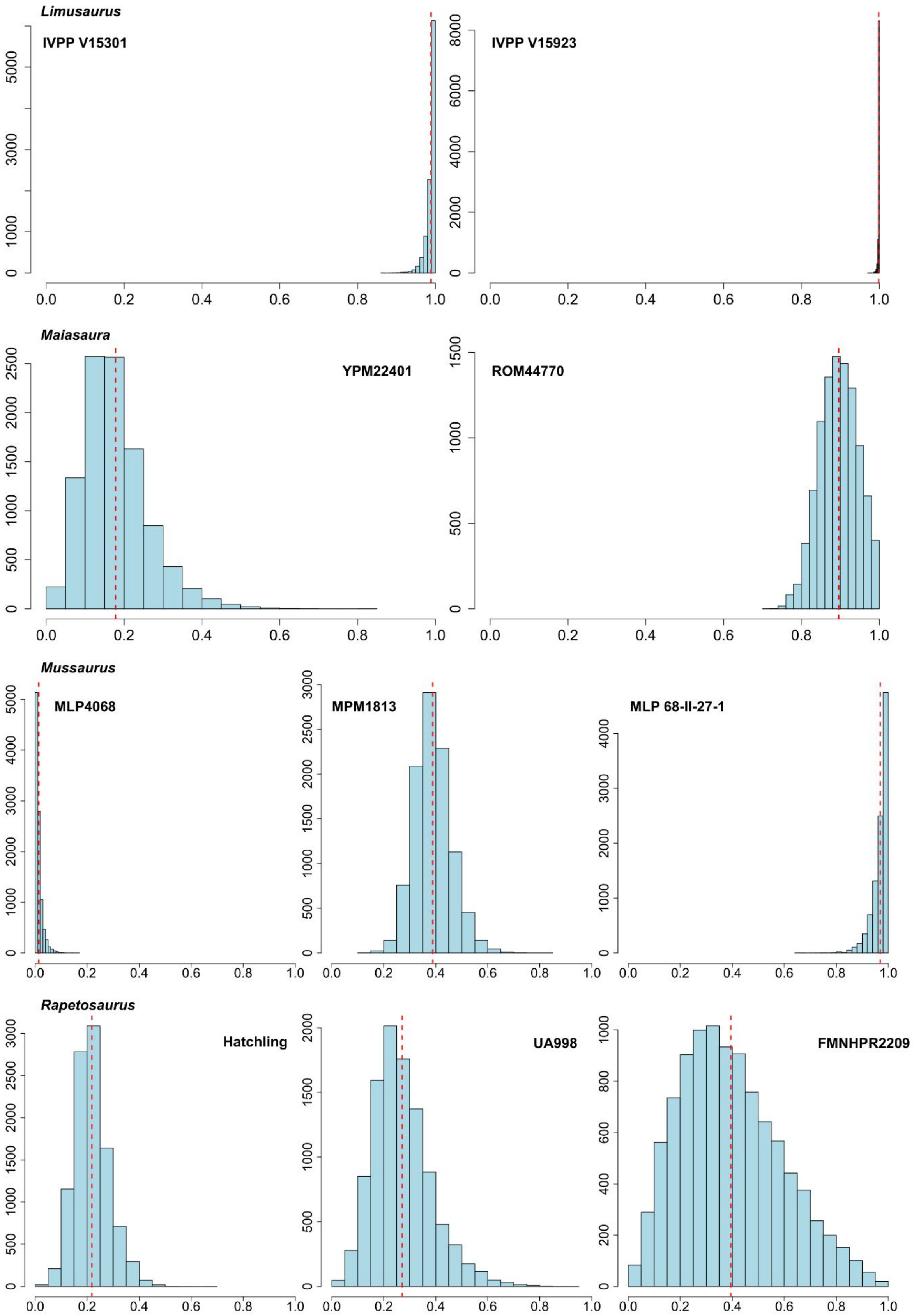
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6000
8000
0.0
0.2
0.4
0.6
0.8
1.0
Maiasaura
YPM22401
0
500
1000
1500
2000
2500
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0.4
0.6
0.8
1.0
ROM44770
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0.6
0.8
1.0
Mussaurus
MLP4068
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MLP 68-II-27-1
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0.2
0.4
0.6
0.8
1.0
Rapetosaurus
Hatchling
0
500
1000
1500
2000
2500
3000
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0.4
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UA998
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500
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0.2
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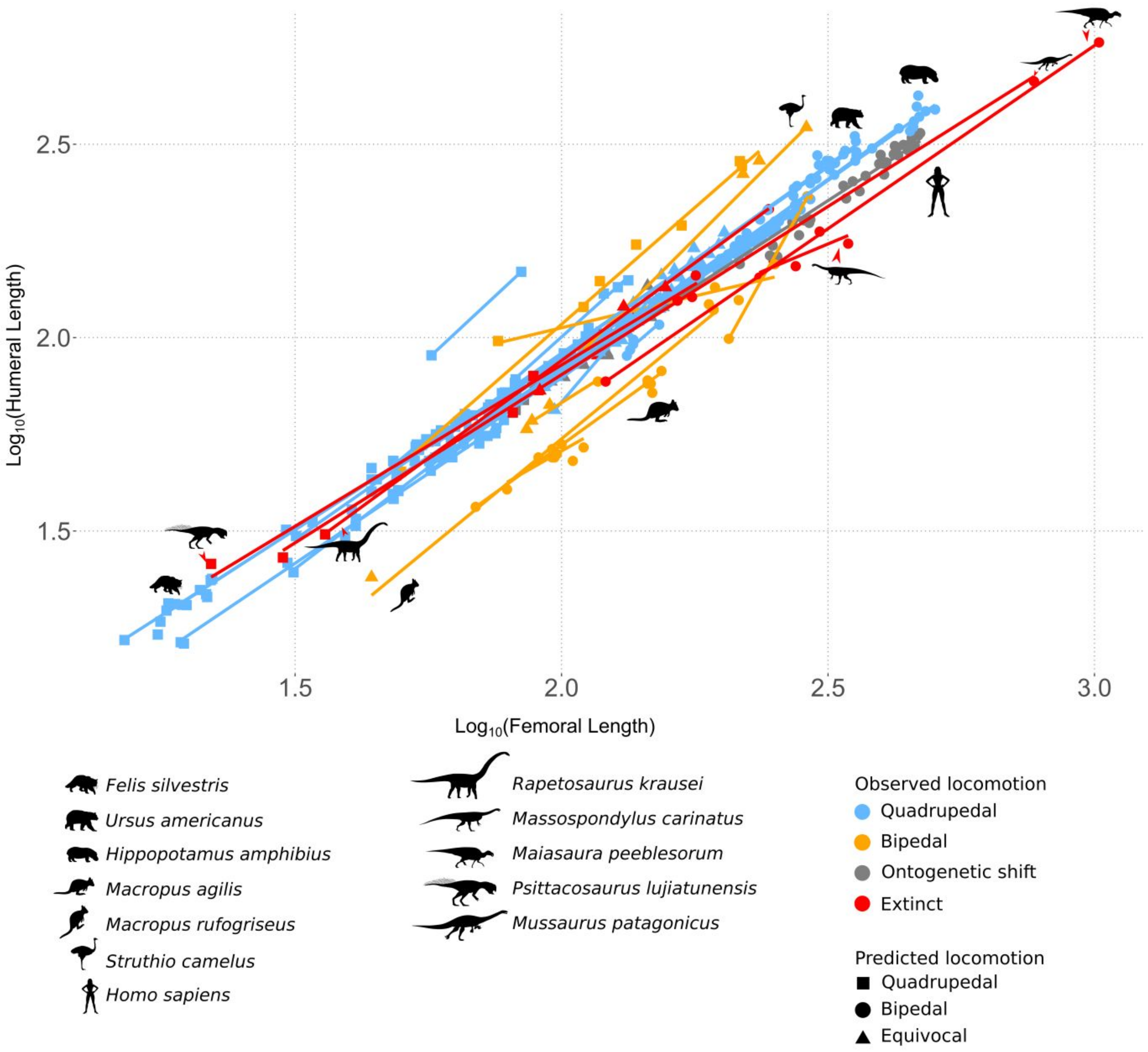
0.6
0.8
1.0
FMNHPR2209
0
200
400
600
800
1000
0.0
0.2
0.4
0.6
0.8
1.0

S5 Figure: Log$_{10}$HL vs Log$_{10}$FL. Line and point colors reflect observed posture during habitual locomotion (travel), *Homo sapiens* in grey. Point shapes reflect posture predicted by the DFA. Silhouettes for small, medium and large size class bipeds|quadrupeds and dinosaurs.



S6 Table: Log$_{10}$HL vs Log$_{10}$FL Regression coefficients

Species	Intercept	Slope	R2
Antilocapra americana	0.111494354353197	0.907256182954018	0.991675990064902
Bison bison	-0.107174497951855	1.0068034696709	0.997217483040947
Bradypus infuscatus	-0.298089517709827	1.28274063488797	1
Caiman crocodilus	-0.267713930534299	1.09629351924689	0.981112103996344
Choloepus hoffmanni	-0.477162959075718	1.23946760876446	0.993302757272631
Connochaetes taurinus	0.0704278584345603	0.928528427505978	0.998570879214641
Crocodilus niloticus	0.102210305783171	0.908258009758844	0.973150796880929
Dasypus novemcinctus	0.0238551694864586	0.928435384998453	0.997754936192971
Dendrolagus dorianus	-0.0530964694120962	0.980306742455681	0.999912224574647
Dendrolagus lumholtzi	-0.545965687694747	1.1830116094334	0.890171127856289
Felis silvestris	0.166743603513834	0.891082419111918	0.998626285461688
Hippopotamus amphibius	-0.0272201127470807	0.973401764194324	0.981811054325471
Homo sapiens	0.125352115478304	0.891583778570905	0.99209419219178
Iguana iguana	-0.168912177506608	1.04757206394726	0.992858720649792
Macropus agilis	-0.269059656460134	0.995807579825297	0.998476591889043
Macropus giganteus	-3.74428307899818	2.48122808299156	1
Macropus rufogriseus	-0.531535340554682	1.13495350936974	0.95406893360658
Macropus rufus	1.36894138876196	0.328257948850368	0.872086366068124
Maiasaura peeblesorum	-0.0863359248629825	0.947205928249689	1
Massospondylus carinatus	0.800993361454938	0.576504394326066	0.662870773870469
Mussaurus patagonicus	0.165020939191043	0.86962891287123	0.99812817814178
Myrmecophaga tridactyla	-0.0623942131254636	0.978972435906276	0.993181483341613
Odocoileus virginianus	0.134646853462688	0.898015190605337	0.99485437912229
Okapia johnstoni	-0.0024721932504763	0.979533897587339	0.99512044916423
Pedetes capensis	0.128864689499805	0.788908282117635	0.792367312691582
Phascolarctos cinereus	0.0418738402578511	0.934903131635039	0.992192176156652
Phataginus tricuspis	0,2765	1,1553	1
Procyon lotor	0.178213823953546	0.883290805617193	0.995987214264318
Psittacosaurus lujiatunensis	0.260560450319923	0.834367161832707	0.97398987311191
Rapetosaurus krausei	0.00933647829238066	0.956226765303743	0.999803438827318
Rhea americana	-0.378694511115992	1.20659229249038	0.993093500766706
Smutsia gigantea	-1.38329203244603	1.60840518993591	0.998884743728708
Smutsia temminckii	0.0891254425102752	0.87128289124208	0.961153520555603
Struthio camelus	-0.842511690518457	1.37699848711593	1
Ursus americanus	0.0333449366530436	0.963198158391326	0.996042000001984

S7 Table: DFA results using femoral and humeral lengths

Species	SP#	$Log_{10}HL/Log_{10}FL$	Class prediction	Mean posterior probability bipedal
Massospondylus carinatus	QG21A	0.915412	Bipedal	0.929183
Massospondylus carinatus	SAMPK 388	0.909015	Bipedal	0.906602
Massospondylus carinatus	BP/1/4998	0.883845	Bipedal	0.968585
Massospondylus carinatus	BP/1/5193	0.895610	Bipedal	0.943513
Massospondylus carinatus	SAMPK 391	0.916894	Bipedal	0.901743
Psittacosaurus lujiatunensis	IVPP V16902.2	1.054045	Quadrupedal	0.012120
Psittacosaurus lujiatunensis	IVPP V14342	0.946395	Quadrupedal	0.294642
Psittacosaurus lujiatunensis	IVPP V14748	0.960113	Equivocal	0.397427
Psittacosaurus lujiatunensis	IVPP V14749	0.944907	Equivocal	0.528289
Psittacosaurus lujiatunensis	IVPP V12617	0.955801	Bipedal	0.673724
Psittacosaurus lujiatunensis	ND2584	0.937667	Bipedal	0.759723
Psittacosaurus lujiatunensis	D2599	0.976263	Quadrupedal	0.216622
Psittacosaurus lujiatunensis	D2594	0.962132	Equivocal	0.464140
Psittacosaurus lujiatunensis	D2593	0.968345	Equivocal	0.404682
Psittacosaurus lujiatunensis	D2591	0.962112	Bipedal	0.662390
Psittacosaurus lujiatunensis	D2590	0.953514	Equivocal	0.420317
Psittacosaurus lujiatunensis	D2587	0.944976	Bipedal	0.705365
Psittacosaurus lujiatunensis	D2585	0.954052	Equivocal	0.545747
Psittacosaurus lujiatunensis	D2584	0.954360	Equivocal	0.430098
Psittacosaurus lujiatunensis	D2583	0.952651	Quadrupedal	0.327412
Psittacosaurus lujiatunensis	D2582	0.951056	Equivocal	0.338364
Psittacosaurus lujiatunensis	D2581	0.982912	Equivocal	0.383142
Psittacosaurus lujiatunensis	D1202	0.970485	Equivocal	0.553006

Psittacosaurus lujiatunensis	BoxSpecimenD	0.958917	Equivocal	0.540505
Psittacosaurus lujiatunensis	BoxSpecimenB	0.959547	Bipedal	0.672327
Mussaurus patagonicus	MPM1813	0.965111	Equivocal	0.389557
Mussaurus patagonicus	MLP 68-II-27-1	0.922490	Bipedal	0.976474
Mussaurus patagonicus	PVL4068	0.969023	Quadrupedal	0.044673
Rapetosaurus krausei	UA998	0.970015	Quadrupedal	0.203817
Rapetosaurus krausei	FMNHPR2209	0.976256	Bipedal	0.718257
Rapetosaurus krausei	HatchlingEst	0.958272	Quadrupedal	0.065614
Homo sapiens	614	0.961871	Quadrupedal	0.275887
Homo sapiens	2813a	0.962426	Quadrupedal	0.279120
Homo sapiens	661	0.962912	Quadrupedal	0.223254
Homo sapiens	2813b	0.947278	Quadrupedal	0.297301
Homo sapiens	662	0.953058	Quadrupedal	0.290787
Homo sapiens	3190	0.956601	Quadrupedal	0.320672
Homo sapiens	808	0.952771	Equivocal	0.358455
Homo sapiens	807	0.954819	Quadrupedal	0.326210
Homo sapiens	3020	0.946768	Equivocal	0.425400
Homo sapiens	664	0.949481	Equivocal	0.458884
Homo sapiens	713	0.936676	Equivocal	0.597103
Homo sapiens	809	0.971622	Quadrupedal	0.231123
Homo sapiens	535	0.945148	Equivocal	0.488739
Homo sapiens	810	0.965032	Equivocal	0.343257
Homo sapiens	3191	0.962869	Equivocal	0.401759
Homo sapiens	3018	0.953289	Equivocal	0.516942
Homo sapiens	1572	0.949821	Equivocal	0.513979
Homo sapiens	472	0.957308	Equivocal	0.421226
Homo sapiens	3021	0.950941	Equivocal	0.497482
Homo sapiens	608	0.947290	Equivocal	0.641896
Homo sapiens	476	0.961525	Equivocal	0.494440
Homo sapiens	1235	0.953600	Equivocal	0.555920
Homo sapiens	806	0.949195	Equivocal	0.575420
Homo sapiens	2846	0.987124	Equivocal	0.417756
Homo sapiens	712	0.947890	Bipedal	0.687015
Homo sapiens	3148	0.925240	Bipedal	0.882537
Homo sapiens	3017	0.940921	Equivocal	0.572367
Homo sapiens	1327	0.949254	Equivocal	0.657806
Homo sapiens	1469	0.951500	Bipedal	0.693591
Homo sapiens	854	0.938263	Bipedal	0.820656
Homo sapiens	3019	0.918781	Bipedal	0.900656
Homo sapiens	3015	0.926077	Bipedal	0.900981

Homo sapiens	1320	0.933998	Bipedal	0.864716
Homo sapiens	722	0.938225	Bipedal	0.879555
Homo sapiens	1244	0.931847	Bipedal	0.896422
Homo sapiens	1439	0.934526	Bipedal	0.891877
Homo sapiens	972	0.931259	Bipedal	0.918288
Homo sapiens	161	0.944876	Bipedal	0.854122
Homo sapiens	769	0.940775	Bipedal	0.912372
Homo sapiens	439	0.946135	Bipedal	0.889562
Homo sapiens	1630	0.929313	Bipedal	0.927467
Homo sapiens	507	0.929490	Bipedal	0.937082
Homo sapiens	2243	0.944016	Bipedal	0.899540
Homo sapiens	3671	0.943542	Bipedal	0.914459
Homo sapiens	176	0.943188	Bipedal	0.921754
Homo sapiens	3014	0.940500	Bipedal	0.922429
Homo sapiens	1875	0.940189	Bipedal	0.922144
Homo sapiens	2178	0.942479	Bipedal	0.929262
Homo sapiens	101	0.940115	Bipedal	0.923268
Homo sapiens	266	0.939139	Bipedal	0.929577
Homo sapiens	100	0.937363	Bipedal	0.935815
Homo sapiens	151	0.951503	Bipedal	0.900951
Homo sapiens	97	0.945802	Bipedal	0.921949
Homo sapiens	3	0.950570	Bipedal	0.910056
Homo sapiens	3784	0.947363	Bipedal	0.923098
Homo sapiens	13	0.937723	Bipedal	0.937723
Homo sapiens	9	0.944977	Bipedal	0.929280
Homo sapiens	1	0.946089	Bipedal	0.928459
Homo sapiens	14	0.947499	Bipedal	0.916344
Homo sapiens	8	0.940414	Bipedal	0.932723
Felis silvestris	FMNH 104913	1.028635	Quadrupedal	0.013754
Felis silvestris	FMNH 60067	0.995609	Quadrupedal	0.022277
Felis silvestris	FMNH 104922	1.009183	Quadrupedal	0.017599
Felis silvestris	FMNH 101853	1.040087	Quadrupedal	0.011959
Felis silvestris	FMNH 104921	1.016796	Quadrupedal	0.015951
Felis silvestris	FMNH 60016	1.002562	Quadrupedal	0.020580
Felis silvestris	FMNH 104920	1.019630	Quadrupedal	0.016709
Felis silvestris	FMNH 60041	1.028291	Quadrupedal	0.013349
Felis silvestris	FMNH 60466	1.023655	Quadrupedal	0.016867
Felis silvestris	FMNH 104919	1.023315	Quadrupedal	0.016816
Felis silvestris	FMNH 104909	0.993611	Quadrupedal	0.038862
Felis silvestris	FMNH 60040	1.013543	Quadrupedal	0.026488
Felis silvestris	FMNH 60137	0.987574	Quadrupedal	0.078909
Felis silvestris	FMNH 60442	0.983107	Quadrupedal	0.116804
Felis silvestris	FMNH 18009	0.978766	Quadrupedal	0.148968
Felis silvestris	FMNH 60081	0.979105	Quadrupedal	0.148089
Felis silvestris	FMNH 60443	0.973818	Quadrupedal	0.197056
Felis silvestris	FMNH 104929	0.977047	Quadrupedal	0.150512

Felis silvestris	FMNH 101878	0.971421	Quadrupedal	0.240309
Felis silvestris	FMNH 60080	0.983175	Quadrupedal	0.151251
Felis silvestris	FMNH 60504	0.984683	Quadrupedal	0.162807
Felis silvestris	FMNH 60417	0.975518	Quadrupedal	0.189337
Felis silvestris	FMNH 60017	0.976387	Quadrupedal	0.195747
Felis silvestris	FMNH 104916	0.973611	Equivocal	0.344013
Felis silvestris	FMNH 104914	0.975169	Quadrupedal	0.248620
Felis silvestris	FMNH 60271	0.973342	Quadrupedal	0.289935
Felis silvestris	FMNH 60280	0.969255	Quadrupedal	0.276368
Felis silvestris	FMNH 60353	0.977659	Quadrupedal	0.269558
Felis silvestris	FMNH 58006	0.969831	Quadrupedal	0.313068
Felis silvestris	FMNH 60039	0.969485	Equivocal	0.363846
Felis silvestris	FMNH 60141	0.976303	Quadrupedal	0.307062
Felis silvestris	FMNH 60336	0.973208	Equivocal	0.367406
Felis silvestris	FMNH 152104	0.974403	Quadrupedal	0.319772
Felis silvestris	FMNH 60570	0.977232	Quadrupedal	0.325622
Felis silvestris	FMNH 60089	0.979355	Quadrupedal	0.310761
Odocoileus virginianus	FMNH 165366	0.970004	Quadrupedal	0.184121
Odocoileus virginianus	AMNH 181986	0.961324	Equivocal	0.415598
Odocoileus virginianus	FMNH 153837	0.955617	Equivocal	0.537034
Odocoileus virginianus	FMNH 167204	0.964119	Equivocal	0.359176
Odocoileus virginianus	AMNH 181987	0.963099	Equivocal	0.385630
Odocoileus virginianus	FMNH 167207	0.961899	Equivocal	0.430404
Odocoileus virginianus	FMNH 154737	0.966956	Equivocal	0.414308
Odocoileus virginianus	FMNH 154736	0.963458	Equivocal	0.506704
Odocoileus virginianus	FMNH 60664	0.958786	Equivocal	0.567617
Odocoileus virginianus	FMNH 153836	0.959538	Equivocal	0.585399
Odocoileus virginianus	FMNH 154735	0.959822	Equivocal	0.608882
Odocoileus virginianus	AMNH 130296	0.962141	Equivocal	0.610794
Odocoileus virginianus	AMNH 130204	0.954963	Bipedal	0.733292
Odocoileus virginianus	AMNH 121477	0.950728	Bipedal	0.780737
Odocoileus virginianus	FMNH 60772	0.973268	Equivocal	0.630631
Odocoileus virginianus	FMNH 46955	0.951606	Bipedal	0.771756

Odocoileus virginianus	AMNH 245629	0.953671	Bipedal	0.761200
Odocoileus virginianus	FMNH 18844	0.953355	Bipedal	0.807181
Odocoileus virginianus	AMNH 130203	0.951969	Bipedal	0.809772
Odocoileus virginianus	FMNH 15574	0.958380	Bipedal	0.795550
Odocoileus virginianus	FMNH 54014	0.956198	Bipedal	0.827321
Odocoileus virginianus	AMNH 125590	0.947568	Bipedal	0.849997
Odocoileus virginianus	ROM_59338	0.954551	Bipedal	0.833465
Ursus americanus	FMNH 57142	0.990180	Quadrupedal	0.037108
Ursus americanus	FMNH 154705	0.973428	Equivocal	0.347652
Ursus americanus	FMNH 51805	0.987701	Quadrupedal	0.277154
Ursus americanus	AMNH 18130	0.975898	Equivocal	0.542828
Ursus americanus	FMNH 165353	0.970086	Equivocal	0.587248
Ursus americanus	AMNH 3762	0.976115	Equivocal	0.634577
Ursus americanus	FMNH 141990	0.977365	Equivocal	0.573421
Ursus americanus	AMNH 77787	0.971841	Bipedal	0.724012
Ursus americanus	AMNH 131828	0.972663	Bipedal	0.786357
Ursus americanus	FMNH 154193	0.973059	Bipedal	0.791853
Ursus americanus	AMNH 5044	0.971794	Bipedal	0.769527
Ursus americanus	FMNH 57282	0.979660	Bipedal	0.743267
Ursus americanus	FMNH 18864	0.979201	Bipedal	0.740822
Ursus americanus	AMNH 3761	0.976673	Bipedal	0.771816
Ursus americanus	AMNH 90333	0.976759	Bipedal	0.772962
Ursus americanus	FMNH 44725	0.972991	Bipedal	0.805864
Ursus americanus	AMNH 45149	0.971455	Bipedal	0.836031
Ursus americanus	FMNH 57290	0.978221	Bipedal	0.802709
Ursus americanus	AMNH 5032	0.982428	Bipedal	0.800859
Ursus americanus	ROM_71435	0.996486	Bipedal	0.698644
Bison bison	FMNH 137424	0.958019	Equivocal	0.652980
Bison bison	FMNH 104902	0.954746	Bipedal	0.665269
Bison bison	AMNH 244376	0.958861	Bipedal	0.718095
Bison bison	FMNH 60182	0.954629	Bipedal	0.702022
Bison bison	FMNH 104897	0.965583	Equivocal	0.655958
Bison bison	AMNH 213140	0.956280	Bipedal	0.689784
Bison bison	AMNH 35631	0.964646	Bipedal	0.724308
Bison bison	FMNH 134415	0.967000	Bipedal	0.724587
Bison bison	AMNH 16869	0.961930	Bipedal	0.727690
Bison bison	AMNH 98955	0.961154	Bipedal	0.821487
Bison bison	AMNH 19177	0.963834	Bipedal	0.838998
Bison bison	FMNH 44708	0.967749	Bipedal	0.846760
Bison bison	AMNH 98957	0.963823	Bipedal	0.868857

Bison bison	FMNH 18850	0.963272	Bipedal	0.857789
Bison bison	FMNH 18849	0.965078	Bipedal	0.883507
Procyon lotor	FMNH 156868	1.032353	Quadrupedal	0.010970
Procyon lotor	FMNH 156869	1.014663	Quadrupedal	0.014907
Procyon lotor	FMNH 156870	0.991903	Quadrupedal	0.018432
Procyon lotor	FMNH 167196	0.998554	Quadrupedal	0.057604
Procyon lotor	FMNH 167195	0.997267	Quadrupedal	0.058790
Procyon lotor	FMNH 154706	0.990931	Quadrupedal	0.076968
Procyon lotor	FMNH 154719	0.981377	Quadrupedal	0.125675
Procyon lotor	FMNH 154712	0.987288	Quadrupedal	0.079661
Procyon lotor	FMNH 154708	0.982907	Quadrupedal	0.108450
Procyon lotor	FMNH 154716	0.994905	Quadrupedal	0.074562
Procyon lotor	FMNH 154713	0.991904	Quadrupedal	0.083033
Procyon lotor	FMNH 178212	0.987125	Quadrupedal	0.103920
Procyon lotor	FMNH 167194	0.986147	Quadrupedal	0.097418
Procyon lotor	FMNH 154715	0.988540	Quadrupedal	0.084400
Procyon lotor	FMNH 178210	0.991245	Quadrupedal	0.101816
Procyon lotor	FMNH 178211	0.992463	Quadrupedal	0.085080
Procyon lotor	FMNH 154718	0.997449	Quadrupedal	0.067590
Procyon lotor	FMNH 154714	0.988852	Quadrupedal	0.082713
Procyon lotor	ROM_88247	0.970104	Equivocal	0.463054
Procyon lotor	FMNH 154711	0.981327	Quadrupedal	0.159439
Procyon lotor	FMNH 178213	0.986971	Quadrupedal	0.094869
Procyon lotor	FMNH 167059	0.958419	Equivocal	0.361662
Procyon lotor	FMNH 65845	0.964604	Quadrupedal	0.314689
Procyon lotor	FMNH 135302	0.967908	Quadrupedal	0.296727
Procyon lotor	FMNH 167058	0.963721	Equivocal	0.448266
Procyon lotor	FMNH 167060	0.961528	Equivocal	0.452758
Procyon lotor	FMNH 167061	0.970276	Equivocal	0.355699
Procyon lotor	FMNH 175312	0.971081	Equivocal	0.357463
Procyon lotor	FMNH 104987	0.968704	Equivocal	0.450289
Procyon lotor	FMNH 154709	0.960163	Equivocal	0.522859
Procyon lotor	FMNH 104968	0.962570	Equivocal	0.460118
Procyon lotor	FMNH 167197	0.967525	Equivocal	0.456165
Procyon lotor	FMNH 167062	0.963211	Equivocal	0.496334
Okapia johnstoni	AMNH 51240	0.989605	Quadrupedal	0.086283
Okapia johnstoni	AMNH 51240	0.978886	Quadrupedal	0.109917
Okapia johnstoni	FMNH 99430	0.969616	Equivocal	0.631790
Okapia johnstoni	FMNH 60185	0.972011	Equivocal	0.603298
Okapia johnstoni	AMNH 51237	0.975510	Equivocal	0.579809
Okapia johnstoni	AMNH 188792	0.959581	Equivocal	0.600906
Okapia johnstoni	AMNH 51238	0.988169	Equivocal	0.444573
Okapia johnstoni	FMNH 121226	0.983590	Equivocal	0.500737
Okapia johnstoni	FMNH 153734	0.976456	Equivocal	0.575581
Okapia johnstoni	AMNH 51224	0.976189	Bipedal	0.716494
Okapia johnstoni	AMNH 51220	0.976846	Bipedal	0.796359

Okapia johnstoni	FMNH 58839	0.974191	Bipedal	0.801397
Okapia johnstoni	FMNH 108987	0.977463	Bipedal	0.790976
Okapia johnstoni	AMNH 51222	0.975400	Bipedal	0.803661
Okapia johnstoni	FMNH 26066	0.981540	Bipedal	0.775962
Okapia johnstoni	FMNH 152135	0.983965	Bipedal	0.763355
Okapia johnstoni	AMNH 51196	0.976395	Bipedal	0.796193
Okapia johnstoni	FMNH 165349	0.980749	Bipedal	0.795666
Okapia johnstoni	FMNH 134544	0.985247	Bipedal	0.748834
Okapia johnstoni	ZMUC_M_4221	0.988593	Bipedal	0.777813
Connochaetes taurinus	FMNH 60388	0.961911	Equivocal	0.583647
Connochaetes taurinus	FMNH 60385	0.961491	Equivocal	0.574005
Connochaetes taurinus	FMNH 66971	0.959534	Equivocal	0.591341
Connochaetes taurinus	FMNH 60558	0.962277	Equivocal	0.576782
Connochaetes taurinus	FMNH 59003	0.960878	Equivocal	0.593463
Connochaetes taurinus	FMNH 127911	0.957857	Bipedal	0.749043
Connochaetes taurinus	FMNH 57592	0.956935	Bipedal	0.773274
Connochaetes taurinus	FMNH 127907	0.956038	Bipedal	0.792603
Connochaetes taurinus	FMNH 127908	0.955344	Bipedal	0.810376
Connochaetes taurinus	FMNH 127909	0.957949	Bipedal	0.807642
Connochaetes taurinus	FMNH 29522	0.955960	Bipedal	0.818106
Connochaetes taurinus	FMNH 127912	0.960989	Bipedal	0.809518
Connochaetes taurinus	FMNH 127905	0.959746	Bipedal	0.816932
Connochaetes taurinus	FMNH 127910	0.957439	Bipedal	0.834801
Antilocapra americana	FMNH 60149	0.956729	Equivocal	0.447410
Antilocapra americana	AMNH 122380	0.967626	Equivocal	0.460466
Antilocapra americana	AMNH 122381	0.960947	Equivocal	0.524563
Antilocapra americana	AMNH 16592	0.954819	Equivocal	0.647490
Antilocapra americana	AMNH 80242	0.953059	Bipedal	0.700396
Antilocapra americana	AMNH 130128	0.956003	Bipedal	0.687384

Antilocapra americana	FMNH 47167	0.959818	Bipedal	0.675840
Antilocapra americana	FMNH 44279	0.951039	Bipedal	0.760758
Antilocapra americana	AMNH 237995	0.952116	Bipedal	0.738939
Antilocapra americana	FMNH 57216	0.957214	Bipedal	0.762349
Antilocapra americana	FMNH 60471	0.957981	Bipedal	0.733883
Antilocapra americana	FMNH 60605	0.954339	Bipedal	0.777669
Antilocapra americana	FMNH 51438	0.958250	Bipedal	0.753592
Antilocapra americana	FMNH 57217	0.955734	Bipedal	0.778190
Antilocapra americana	FMNH 74239	0.951635	Bipedal	0.794306
Antilocapra americana	FMNH 57215	0.950410	Bipedal	0.807058
Antilocapra americana	AMNH 75243	0.958525	Bipedal	0.756520
Antilocapra americana	AMNH 142361	0.956819	Bipedal	0.772528
Hippopotamus amphibius	AMNH 130267	0.978695	Equivocal	0.430380
Hippopotamus amphibius	FMNH 60538	0.949948	Equivocal	0.647355
Hippopotamus amphibius	AMNH 180372	0.951945	Bipedal	0.842446
Hippopotamus amphibius	FMNH 127869	0.955815	Bipedal	0.840413
Hippopotamus amphibius	FMNH 60190	0.962546	Bipedal	0.900322
Hippopotamus amphibius	AMNH 15898	0.961645	Bipedal	0.899317
Hippopotamus amphibius	AMNH 113816	0.958818	Bipedal	0.914778
Hippopotamus amphibius	FMNH 22367	0.974038	Bipedal	0.874102
Hippopotamus amphibius	FMNH 127870	0.954748	Bipedal	0.910178
Hippopotamus amphibius	AMNH 99367	0.963604	Bipedal	0.901564
Hippopotamus amphibius	ROM_94513	0.983707	Bipedal	0.850344
Hippopotamus amphibius	FMNH 127871	0.956661	Bipedal	0.908305
Dasypus novemcinctus	AMNH 13372	0.943093	Quadrupedal	0.033678

Dasypus novemcinctus	AMNH 13373	0.936199	Quadrupedal	0.036783
Dasypus novemcinctus	AMNH 133261	0.954286	Quadrupedal	0.054826
Dasypus novemcinctus	AMNH 133369	0.948744	Quadrupedal	0.090442
Dasypus novemcinctus	AMNH 133259	0.948090	Quadrupedal	0.117198
Dasypus novemcinctus	AMNH 133260	0.948266	Quadrupedal	0.121232
Dasypus novemcinctus	AMNH 205707	0.941774	Quadrupedal	0.197405
Dasypus novemcinctus	AMNH 133270	0.938069	Quadrupedal	0.273561
Dasypus novemcinctus	AMNH 133381	0.935329	Quadrupedal	0.266918
Dasypus novemcinctus	AMNH 133268	0.940861	Quadrupedal	0.281230
Dasypus novemcinctus	AMNH 133266	0.934319	Quadrupedal	0.307053
Dasypus novemcinctus	AMNH 133269	0.944604	Quadrupedal	0.282238
Myrmecophaga tridactyla	AMNH 167320	0.951351	Equivocal	0.349089
Myrmecophaga tridactyla	AMNH 48072	0.943257	Equivocal	0.597494
Myrmecophaga tridactyla	AMNH 98514	0.947142	Equivocal	0.590861
Myrmecophaga tridactyla	NHMUK1965.8.17.2	0.945915	Equivocal	0.566637
Myrmecophaga tridactyla	AMNH 35710	0.949202	Bipedal	0.763798
Myrmecophaga tridactyla	AMNH 77902	0.954848	Bipedal	0.771626
Myrmecophaga tridactyla	AMNH 100136	0.954590	Bipedal	0.775299
Myrmecophaga tridactyla	FMNH 49342	0.945725	Bipedal	0.805673
Myrmecophaga tridactyla	AMNH 130242	0.957559	Bipedal	0.727913
Myrmecophaga tridactyla	NHMUK3.7.7.176	0.952111	Bipedal	0.793809
Myrmecophaga tridactyla	AMNH 100143	0.951352	Bipedal	0.777534
Myrmecophaga tridactyla	FMNH 49338	0.948074	Bipedal	0.786785
Myrmecophaga tridactyla	FMNH 98159	0.954454	Bipedal	0.756772
Myrmecophaga tridactyla	FMNH 28309	0.953517	Bipedal	0.800195

Myrmecophaga tridactyla	NHMUK1965.8.17.9	0.985465	Equivocal	0.596945
Myrmecophaga tridactyla	NHMUK1964.6.2.1	0.957061	Bipedal	0.758103
Myrmecophaga tridactyla	AMNH 70041	0.949202	Bipedal	0.826356
Myrmecophaga tridactyla	FMNH 60688	0.959748	Bipedal	0.752621
Myrmecophaga tridactyla	FMNH 159987	0.950684	Bipedal	0.820034
Macropus giganteus	SMT49995	0.960644	Bipedal	0.823891
Macropus giganteus	SMT221170	0.863035	Bipedal	0.950855
Dendrolagus dorianus	NHMUK1978,2193	0.950536	Quadrupedal	0.162375
Dendrolagus dorianus	NHMUK78,2194	0.952994	Equivocal	0.373034
Dendrolagus dorianus	NHMUK78,2065	0.954596	Equivocal	0.407188
Dendrolagus lumholtzi	AMNH35623	0.934318	Bipedal	0.667818
Dendrolagus lumholtzi	AMNH65260	0.929107	Bipedal	0.691430
Dendrolagus lumholtzi	AMNH65265	0.920253	Bipedal	0.717445
Dendrolagus lumholtzi	AMNH35642	0.931366	Bipedal	0.730800
Dendrolagus lumholtzi	AMNH65261	0.924725	Bipedal	0.704683
Iguana iguana	FMNH 2694	0.930518	Quadrupedal	0.075871
Iguana iguana	FMNH 211937	0.968224	Quadrupedal	0.068007
Iguana iguana	AMNH 88423	0.937772	Quadrupedal	0.104427
Iguana iguana	AMNH 82125	0.931809	Quadrupedal	0.105054
Iguana iguana	AMNH 74623	0.939535	Quadrupedal	0.132661
Iguana iguana	AMNH 81871	0.946435	Quadrupedal	0.124778
Iguana iguana	FMNH 222373	0.943736	Quadrupedal	0.163334
Iguana iguana	FMNH 207655	0.960455	Quadrupedal	0.199444
Iguana iguana	AMNH 84101	0.959804	Quadrupedal	0.226055
Iguana iguana	FMNH 211878	0.970919	Quadrupedal	0.166763
Iguana iguana	FMNH 22041	0.960543	Quadrupedal	0.304938
Iguana iguana	AMNH 74736	0.958260	Quadrupedal	0.313399
Iguana iguana	AMNH 74628	0.959207	Equivocal	0.369120
Iguana iguana	FMNH 31024	0.969452	Quadrupedal	0.299059
Iguana iguana	ROM_R5821	0.958322	Quadrupedal	0.255015
Iguana iguana	FMNH 22085	0.958824	Equivocal	0.379574
Struthio camelus	APES407	1.034429	Equivocal	0.484099
Struthio camelus	APES1521	0.964284	Equivocal	0.383199
Pedetes capensis	OUMNH13552	0.847087	Bipedal	0.755425

Pedetes capensis	OUMNH13557	0.853228	Bipedal	0.827988
Pedetes capensis	OUMNH13548	0.852656	Bipedal	0.822191
Pedetes capensis	OUMNH13551	0.853228	Bipedal	0.827988
Pedetes capensis	OUMNH13550	0.863822	Bipedal	0.761905
Pedetes capensis	OUMNH13554	0.862138	Bipedal	0.809715
Pedetes capensis	OUMNH13549	0.850725	Bipedal	0.831221
Pedetes capensis	OUMNH13553	0.852656	Bipedal	0.822191
Pedetes capensis	OUMNH13555	0.863559	Bipedal	0.789003
Pedetes capensis	WLSM154	0.840604	Bipedal	0.889929
Macropus rufus	NHMUK62-12-26-3	1.058705	Quadrupedal	0.042125
Macropus rufus	AZ1222	0.899021	Bipedal	0.910486
Macropus rufus	ROM_31178	0.912346	Bipedal	0.910362
Macropus agilis	NHMUK1966.1.7.1	0.849604	Bipedal	0.665975
Macropus agilis	NHMUK1970,2191	0.870196	Bipedal	0.893847
Macropus agilis	NHMUK1970,2191	0.874878	Bipedal	0.896881
Macropus agilis	NHMUK70,368	0.867807	Bipedal	0.900779
Macropus agilis	NHMUK1970,219	0.874123	Bipedal	0.886316
Macropus rufogriseus	NHMUK258D	0.839824	Equivocal	0.384161
Macropus rufogriseus	NHMUK51.4.24.1	0.831808	Bipedal	0.895301
Macropus rufogriseus	NHMUK49.6.20.4	0.855810	Bipedal	0.920790
Macropus rufogriseus	NHMUK58.5.26.10	0.916492	Bipedal	0.849085
Macropus rufogriseus	NHMUK1965.12.2.2	0.906511	Bipedal	0.877626
Macropus rufogriseus	OUMNH8066	0.931171	Bipedal	0.813603
Phascolarctos cinereus	NHMUK253.c	0.958985	Quadrupedal	0.182106
Phascolarctos cinereus	NHMUK253e --- 64.5.7.3	0.951203	Equivocal	0.508838
Phascolarctos cinereus	NHMUK230	0.949195	Equivocal	0.575420
Phascolarctos cinereus	NHMUK75,1828	0.952580	Equivocal	0.585812
Phascolarctos cinereus	NHMUK231	0.961588	Equivocal	0.537048
Phascolarctos cinereus	NHMUK229	0.957225	Equivocal	0.552851
Rhea americana	NHMUKS/1952.1.12	0.973068	Quadrupedal	0.087197
Rhea americana	NHMUK1899.11.10.5	1.035835	Quadrupedal	0.126411
Rhea americana	NHMUKS/2013.13.1	1.018511	Quadrupedal	0.154060
Rhea americana	NHMUK1899.11.10.6	1.047045	Quadrupedal	0.135838
Rhea americana	NHMUK1915.3.31.1	1.029086	Quadrupedal	0.272344
Rhea americana	NHMUKS/1952.1.4	1.035379	Equivocal	0.359518
Rhea americana	NHMUK1846.11.18.21	1.046484	Quadrupedal	0.300322

Rhea americana	NHMUKS/1972.1.155	1.045153	Quadrupedal	0.306941
Rhea americana	NHMUKS/2018.12.1	1.052223	Quadrupedal	0.268950
Rhea americana	NHMUK1907.2.5.1	1.036614	Equivocal	0.384310
Choloepus hoffmanni	NHMUK1966.7.8.3	0.988651	Quadrupedal	0.153314
Choloepus hoffmanni	NHMUK75,182	1.016719	Quadrupedal	0.187453
Choloepus hoffmanni	ROM_89635	1.010738	Quadrupedal	0.253947
Choloepus hoffmanni	NHMUK90,521	1.011790	Quadrupedal	0.229606
Bradypus infuscatus	NHMUK1966.7.8.5	1.112974	Quadrupedal	0.013132
Bradypus infuscatus	NHMUK1966.7.8.4	1.127831	Quadrupedal	0.015035
Smutsia gigantea	NHMUK1934.7.4.1	0.912492	Equivocal	0.585176
Smutsia gigantea	NHMUK1965.5.12.1	0.959437	Equivocal	0.544830
Smutsia gigantea	AMNH53854	0.970640	Equivocal	0.510603
Smutsia temminckii	NHMUK93.7.9.18	0.918152	Equivocal	0.490268
Smutsia temminckii	NHMUK76,135	0.912148	Bipedal	0.693345
Smutsia temminckii	AZ534	0.923322	Equivocal	0.513875
Smutsia temminckii	WLSM794	0.911569	Equivocal	0.509996
Phataginus tetradactyla	NHMUK1939,2647	1.011747	Quadrupedal	0.042255
Phataginus tetradactyla	NHMUK63.2.13.23	0.993925	Quadrupedal	0.054073
Phataginus tricuspis	AMNH53918	0.995133	Quadrupedal	0.069501
Phataginus tricuspis	NHMUK10.6.11.4	0.988057	Quadrupedal	0.060508
Maiasaura peeblesorum	ROM 44770	0.918510	Bipedal	0.984599
Maiasaura peeblesorum	YPM22401	0.905754	Bipedal	0.736153
Caiman crocodilus	FMNH 9150	0.992494	Equivocal	0.494707
Caiman crocodilus	FMNH 229976	0.959820	Quadrupedal	0.127838
Caiman crocodilus	FMNH 98961	0.940370	Quadrupedal	0.248009
Caiman crocodilus	FMNH 13062	0.955339	Equivocal	0.365917
Caiman crocodilus	FMNH 217066	0.950075	Quadrupedal	0.190203
Caiman crocodilus	FMNH 217159	0.955577	Quadrupedal	0.194927

Caiman crocodilus	ROM_R6872	0.947679	Equivocal	0.516885
Crocodilus niloticus	WLSM16	0.974814	Quadrupedal	0.070375
Crocodilus niloticus	WLSM1561	0.975042	Quadrupedal	0.092652
Crocodilus niloticus	WLSM	0.982401	Quadrupedal	0.095543
Crocodilus niloticus	WLSM	0.965693	Quadrupedal	0.156062
Crocodilus niloticus	WLSM1564	0.966526	Quadrupedal	0.135176
Crocodilus niloticus	WLSM	0.969333	Quadrupedal	0.171089
Crocodilus niloticus	WLSM9	0.956445	Quadrupedal	0.153020
Crocodilus niloticus	WLSM1565	0.961997	Quadrupedal	0.144736
Crocodilus niloticus	WLSM6	0.958472	Quadrupedal	0.136466
Crocodilus niloticus	WLSM	0.965111	Equivocal	0.389557
Crocodilus niloticus	WLSM16	0.962912	Quadrupedal	0.223254
Crocodilus niloticus	WLSM8	0.972344	Quadrupedal	0.085441
Crocodilus niloticus	WLSM1565	0.947879	Quadrupedal	0.178634
Crocodilus niloticus	WLSM1562	0.958143	Quadrupedal	0.203886
Crocodilus niloticus	WLSM1564	0.956100	Quadrupedal	0.248455

We thank the editor and reviewers for their helpful feedback on our manuscript. We have addressed each comment in red below. We hope that this will satisfactory.

An important change which was made to the manuscript is the removal of the *Massospondylus* specimen BP/1/4779 as this specimen can no longer be referred to *Massospondylus*. An additional *Massospondylus* specimen of similar body size and presumed ontogenetic stage was added (SAMPK388) in order to maintain the same sample size. This did not affect any of the results of the manuscript, however certain DFA values had to be slightly adjusted throughout the manuscript. All supplementary files and figures were updated accordingly.

Referee: 1

Comments to the Author

•P3L20ff: Did Reisz et al. (2005) not also propose a paedomorphic process for the quadropedal gait of sauropods? As the authors actually falsify an ontogenetic shift in locomotion of Massospondylus, they might add this to the introduction.
The hypothesis of paedomorphosis is mentioned in the introduction and the reference to the work on *Massospondylus* by *Reisz* (2005) is mentioned in the Discussion as:
"A hypothesized shift from quadrupedalism to bipedalism during the ontogeny of the early branching sauropodomorph *Massospondylus carinatus* prompted the hypothesis that quadrupedalism in later-branching sauropods could have evolved through paedomorphosis (Reisz et al. 2005). "

•P3L24f: The correct citation is Bonaparte and Vince 1979 (→ Martin Vince). Please, correct the reference list.
This reference has been fixed.

•P5L44f: I guess the authors mean "the ratio of log10(humeral shaft circumference) and log10(femoral shaft circumference)".
"log10(humeral shaft circumference) and log10(femoral shaft circumference)" was changed to "ratio of log10(humeral shaft circumference) and log10(femoral shaft circumference)".

Results:
•I think it would be easier to read if the ratio results are presented in form of a table instead of stated in the text. Too much numbers between words.
The LogHC/LogFC information was removed from the text, except for *Homo sapiens* as the ratio is necessary in order to compare to closely related taxa such as *Pan troglodytes* and *Gorilla gorilla.* These ratios can now be found in the supplementary tables (S3 and S7).

Discussion:

•I would appreciate, if the authors could go a deeper into the early evolution of quadropedalism in sauropods, considering the different results for Massospondylus and Mussasaurus. The different developmental modes in these closely related taxa should get more attention in my view.

The evolution of quadrupedalism in sauropodomorphs is discussed in further detail under *The implications of ontogenetic locomotory shifts* section of the discussion.

•P10L21f: I guess the bipedal behaviour of glyptodonts refers to a resting or feeding posture, but not actual locomotion, i.e. bipedal walking/running. Please clarify.

Bipedalism in glyptodonts has been hypothesized to occur when using their armoured tail for defence, but not for locomotion. This was added in text.

Conclusion:

•It would be worth to state that limb circumferences produce more reliable results than the lengths.

This was added to the conclusion as “Proportional humeral and femoral robusticity is more reliable than the ratio of humeral to femoral length for predicting habitual amniote posture across ontogenetic trajectories.”

Referee: 2

Comments to the Author

Abstract (and to an extent, throughout): I feel use of the word “identify” when it comes to postural shifts in extinct animals is a little too definitive. The method (like most applied to extinct animals) is not bulletproof so a word that is more suggestive/less definitive would be more appropriate I think.

“Identify” was changed to “predict” throughout the text

Abstract: I don’t really understand, practically, what is meant by the “even in extant taxa” part of the final sentence. It’s even more confusing given the authors later state in the introduction: “Observed ontogenetic postural shifts are rare among extant amniotes, making testing a heterochronic model for postural evolution difficult using neontology only. Indeed, we know of only one extant species that has protracted quadrupedal and bipedal phases during its ontogeny, Homo sapiens.” Even if the authors can explain it – is “even in extant taxa” necessary? The sentence makes the general point well without it.

“Even in extant taxa” was deleted from the final sentence of the abstract

Introduction, final sentence of the first paragraph: This is very pedantic, but I wonder if the authors should re-consider the wording here and specifically their focus on mechanisms that drive postural transitions. ‘Mechanisms that drive evolution’ could be interpreted as meaning a number of different things at different levels (from global/environmental down to genetic). What the authors are definitely attempting to do in this paper is understand the means by the evolutionary change occurred. Maybe it would be more appropriate to re-word here to place the focus on the “how” (which is still poorly understood and worthy of study) rather than focusing on the “why” and in doing so hinting that this study will shed light directly on the “why” (which I’m not sure it does). Just a thought, as the authors appear to have made a more conscious effort to use “mechanism” in the “how” rather than “why” context subsequently in the introduction section.

“Mechanisms that drive evolution” was changed to “how these changes in locomotion come to independently evolve several times, or whether they share an underlying mechanism such as heterochrony.”

Introduction, pg4 lines 11-16: Haven’t there been attempts to use centre of mass position to differentiate bipedality/quadrupedalism in dinosaurs? Or at least studies that show notable shifts in centre of mass positions across such transitions? It seems logical to me that a biped has to be able to place it’s hind feet under it’s centre of mass for static stability, while there’s little point in a quadruped having it’s centre of mass in such a posterior position as the forelimbs would contribute little to propulsion.

The recent study by Otero *et al.* (2019) which looked at the postural shift in *Mussaurus* using center of mass was added in the second last paragraph in the *Postural predictions in extinct ontogenetic series of extinct dinosaurs using limb robusitcty* section of the Discussion. Centre of mass position has indeed been used to study posture however these studies require fairly complete specimens, which is the second restriction mentioned in the introduction:

“First, postural determination (bipedal|quadrupedal) of members of extinct species is difficult, and few methods have been demonstrated to be reliable (Carrano 1998; Maidment et al. 2014; but see McPhee et al. 2018). Second, these methods often rely on relatively complete specimens, limiting the integration of relatively rare fossil ontogenetic sequence data. Third, most developmental studies to-date have focused on single dinosaur species, and lack a broad comparative framework. Studies of dinosaur posture have relied on several different methods (Tarsitano 1983; Alexander 1985; Carrano 1998; Carrano and Biewener 1999; Bonnan and Senter 2007; Mallison 2010a, b; Grossi et al. 2014; Maidment et al. 2014; Barrett and Maidment 2017; Otero et al. 2017).

Introduction, pg 4 line 42: I think the year of publication should probably appear in brackets after McPhee et al.

The year (2018) was added in brackets after McPhee et al.

Introduction and method: General comment. Having read the introduction, and the valid point made within it regarding the fact that only limb bone allometry (one-bone) approaches can generate large data sets and be widely used for macroevolutionary studies, I was expecting an extraordinarily large sample size (i.e. N = >100/200) in the methods section. But here the ontogenetic analysis is based on an extant species N = 36. I don't mention this in an attempt to undermine the statistics presented herein. Rather, just to point out that this N species somewhat clashes with the sentiment the authors have chosen to deliver in the introduction regarding the benefits of one-bone methods versus other methods.

We understand the reviewer's concern, and we hope that we can qualify our statements here in two ways: 1) to build classification models using DFA, we did assemble a dataset from measurements and from the literature comprising hundreds of specimens; 2) we worked for two years to assemble the largest ontogenetic dataset that we could, and the n=36 sample size represents our best attempts to collate these measurements for quadrupeds and bipeds. This reflects the difficulty in obtaining measurement data on specimens. However, in some instances for specific taxa in this ontogenetic dataset we did manage to get large sample sizes (N=60 in humans). We hope that the reviewer can appreciate this.

Methods, page 5, lines 9-33: In this section the authors attempt to define 'bipedal' versus 'quadrupedal.' Defining these terms and/or objectively assigning certain species to one versus the other is a real nightmare. I don't really agree with some of the terminology used in this section, but there's nothing objective to say my preferred terminology is any better, so ill refrain from writing down it here. I think some people will disagree with the assignment of giant pangolins as bipeds and macropods as pentapedal walkers vs hoppers, but I don't think there's any way to please everyone here. And it probably doesn't impact greatly on the specific goals of the paper anyway.

We understand the reviewer's point of view but cannot respond to it at this time in a meaningful way.

Methods. Pg 5-6: Can the authors provide informal justification/explanation/rationale for the arbitrary cutoffs chosen?

These cutoff are arbitrary and allow for a prediction of posture only when a reasonable amount of confidence is present.

This was elaborated as:

"In assigning posture to specimens, we chose arbitrary cutoffs in order to only predict posture where a reasonable level of confidence is present"

Methods. General comment. I spent quite a bit of time thinking about the DFA and whether or not it contains an element of circularity. I think it would help a generalist reader, such as myself, to add a few lay sentences to explain how the DFA works conceptually. Also, does the larger DFA data set contain any of the 36 species that also appear in the ontogenetic data set? If it does, should it?

DFA is a widely used statistical method for classifying unknowns based on multidimensional datasets. Hundreds of comparative studies across biology use this method. We have included a reference to a statistical text in case a reader might be seeking more information on the underpinnings of the method (see Manly 2016).

The calibration dataset includes the largest individuals of species with known locomotory modes. Because DFA training sets rely on specimens with known classes, and because these individuals have locomotory assignments based on real-world observations, it is a necessity that they are included in the DFA analysis. We did not, however, include the younger individuals of extant animals with known locomotory modes in the calibration dataset. This allowed us to determine if our method could predict their postures.

Methods. General comment. I also spent a lot of time thinking about the fact that the actual ages (and potentially in some cases, even the approximate ontogenetic stage?) of the extant animals being used here are not known. This is a pretty fundamental flaw/limitation, and in theory (though probably not in practice) has the potential to undermine everything related to ontogenetic assessments, particularly given that presumably we don't know a lot else about the provenance and life history of the specimens (e.g. body mass; gender; wild vs zoo; stressed vs non-stressed environment etc.). I don't think there's anything the authors can do about it now, and it is likely any errors resulting from the inclusion of specimens that have "unusual" femoral and/or humeral circumference for their age probably get lost in the wash, but I think it's important that such fundamental limitations are acknowledged more explicitly. In fact, what Id really, really like to see is full disclosure (perhaps by adding additional columns to the supplementary tables) of what is/isn't known about certain things (e.g. age, gender, body mass, zoo vs wild) for each specimen. I don't think it matters at this stage (in terms of publish-ability) whether or not such a table is dominated by "unknown", but it would be nice to see a study like this one acknowledge such things rather than it being left unsaid.

We agree with the reviewer that age data would improve the resolution of the study. However, this information is very difficult to acquire with any museum specimen. The only solution would be to section bones in order to look at histological data, which is not feasible given the sample size and geographic spread. Instead, we use femoral and humeral circumferences as a proxy for ontogenetic stage. We also assume that femoral and humeral circumference variance due to zoo vs wild, gender, etc. are minimal compared to variance introduced by postural differences. We cannot control for those complicating variables.

Results: Why don't the squamate and two crocodylians appear on Fig 1? At least they don't appear to.

Squamates and crocodylians do appear on figure 1, however not all taxa were labelled with silhouettes in order to avoid cluttering the figure. Please refer to table 2 (S2) in order to see the regression coefficients for all taxa.

Results, pg 6 lines 53-58: Please add a reference to point the reader towards the “natural history observations” that you’re referring to. Please do this for all other instances where you refer to “natural history observations” (e.g. page 7, line 10-11). Alternatively, if you what you mean by “natural history observations” is the “the lay person’s commonly held perception” then I think you need to explain this more openly.
References for natural observations were added where necessary.

Results: It looks like you’re saying that your DFA analysis fails to 100% correctly predict posture in 5 of the 36 extant taxa (Dasypus, Dendrolagus, Macropus x 2, and Smutsia). Is that correct. I think it would be nice to make the opening sentence of this paragraph (end of page 6) a little more quantitative and thereby informative. Something like: “The ontogenetic series of 5 taxa (i.e. ~14% of the data set by species) are either equivocal or misclassified.” Assuming I’m correct that the method misfires, at least partially, for 5 species. You could begin the description of logged humeral and femoral lengths results/predictions in similar way. That way the reader can better judge your opinion as to what constituents a method that works (bone circumference) versus one that, in your opinion, doesn’t work (bone length). At the moment it’s difficult to judge the success rate for bone lengths. 9 mammals and 2 ratites incorrectly identified? If that’s correct then 11 species (31%) are misidentified?
Misidentification percentages were added where relevant (14% for circumferences and 39% for lengths).

Discussion, sub-heading “Postural predictions in extant ontogenetic series using limb robusitictyˮ and throughout manuscript. I don’t like the word “robusiticity.” Are you really measuring “robusiticity” by using logHC and LogFC? I would argue not. Why not just call a spade a spade and use circumference (or relative circumference) rather than trying to make it sound more fancy and biomechanically meaningful than it actual is. The more I read on from this point, the more I felt robusticity was being misused/wasn’t appriopriate.
We have added a sentence in the second last paragraph of the introduction to explain what is meant by robusticity:
“(we use ‘robustness’ and ‘robusticity’ to refer to the minimum circumference around the humeral and femoral shafts).”

Discussion, page 8, lines 56-58: Following on my from suggestion about being specific about the success rates of the predictions in the results section. Here you immediately state: “Humeral and femoral minimum circumferences can be used to reliably predict posture in living amniotes, both in adults and across developmental series.” What you appear to have shown (and Im happy to be corrected if my numbers are wrong) is that the method correctly predict posture in 5 of the 36 (~86%) extant species studied. Whether or not this is "reliable" is fairly subjective call and perhaps depends on the predictive context in which it is subsequently employed. It's also pretty bold to state that your N of 36, which is biased heavily towards mammals, is representative of all amniotes. I think it's better to state what is certain (i.e. that it has a very high success rate for the N = 36 herein) rather than making quite open statements that could be interpreted to mean that the method is faultless and can universally applied hereafter.

Sentence changed to: "Humeral and femoral minimum circumferences have been shown to reliably predict posture in living amniotes (McPhee et al. 2018). Here we show that they are also useful in predicting posture across developmental series (in 86% of cases, although mainly mammals)."

Discussion, pg 9, lines 13-18: "The robusticity ratio is also conserved through ontogeny in 10 bipedal taxa with proportionally gracile humeri (such as Jaculus jaculus, Macropus agilis and Struthio camelus) (Fig 1 and 2, S3 Table). This supports our observation that postural transitions during ontogeny are rare among extant species." The last bit is confusing. It appears that you are artificially creating a hypothesis and suggesting your data supports it. How can your data "support" or not support the fact that postural transitions are rare among extant species? It's like you're saying that if you had observed a variable ratio in your data then we should stop believing that ostriches are bipedal throughout their ontogenetic and open ourselves to the possibility that they might walk quadrupedally at some point because that would fit your data better. Posture is the fixed/known variable here not the plastic one. I think the sentence "This supports our observation that postural transitions during ontogeny are rare among extant species" just needs to be deleted because it's making a non-relevant/meaningful point.

This sentence was deleted.

Discussion, page 9, lines 22-25: "….and large kangaroos (Macropus giganteus and Macropus rufus), which have strong sexual dimorphism with stereotypical male behaviours and concomitant sexual selection involving the forelimb." Reference needed.

References were added: (Jarman 1983; Warburton et al. 2013)

Discussion, lines 35-37: "If only female kangaroos were used, it is expected that the humerus to femoral robustness ratio would be conserved during ontogeny and would plot with other bipedal taxa." Again, the wording that's been chosen is very definitive here and basically assumes the answer that best supports the predictive capability of the method. You've no quantitative basis for saying "it is expected" like it's a biological rule. Something like "we hypothesise" would be fairer/carries less implication.

"it is expected" was changed to "we hypothesize"

Discussion, page 9 lines 39-40: "Positive allometry of forelimb robustness is also present in

ratites (Rhea Americana and Struthio camelus) (S3 Table),…" Im confused by this statement, in two ways. Firstly, table S3 shows DFA results and it's not clear to me how to directly interpret these in the context of allometry. Second, what's on your x axis when considering allometry given you don't seem to have any body masses? Again, Im worrying a little about circularity (or just it not meaning very much) if it's femoral circumference.
We apologize for referencing the wrong table in the initial draft. Please refer to table S2 for regression coefficients of LogHC vs LogFC (LogFC is an excellent proxy for body mass (based on Campione and Evans 2012).

Discussion, line 35-51: You could (and possibly should) extend this discussion to non-human apes. There's lot of data not only on their percentage split between arboreal and terrestrial locomotion, but also the split between bipedal vs quadrupedal in both environments. I think it's strange you haven't discussed this in the context of your results.
The main aim of this paper was to assess ontogenetic shifts in amniotes. We did not have access to ontogenetic series of non-human apes. We also have not tested our method for nuanced behavioural suites such as arboreal locomotory modes. We agree with the reviewer that this is an interesting avenue for further research, and hope to pursue it in a subsequent paper.

Discussion, lines 36-38: "Fewer dinosaur taxa appear to undergo an ontogenetic shift from quadrupedalism to bipedalism than previously thought (Reisz et al. 2005; Zhao et al. 2013)." Again, the wording (for me) is too definitive and carries the direct implication that the method is 100% definitive. Rarely can we be so definitive with extinct animals. Please change to something less definitive, like "The method predicts that fewer dinosaur taxa….". A similar change in the next sentence would probably be beneficial too.
Changed to "The method predicts that fewer"

Conclusion, first sentence (lines 32-33). Again, how are you objectively judging "reliably"? If you choose to paint a simplistic picture like this then it carries the implication that the method is never wrong and can be applied universally without error/uncertainty. Please be specific and fully explanatory: it works most of the time in a small data set of extant species studied herein.

Conclusion, third sentence (lines 36-38). I think you should separate the extant result (humans) from the dinosaurs. That way you can say that the method correctly predicts the known shift in humans, and then make the totally separate point that it leads you hypothesise that shifts occurred in the two dinosaurs.

Conclusion, third sentence to the end: Sorry to keep nagging on this point, but again I feel things are being over-egged a little. Your dinosaur sample size is tiny, yet if someone were to read this passage without reading the remainder of the manuscript they would probably think you'd analysed 100 dinosaur species. I think small acknowledgment (just a few words) that the sample size is low would be appropriate here.

In order to address all three of the comments on the conclusion, the conclusion was substantially edited and is now:
"Proportional humeral and femoral robusticity is more reliable than the ratio of humeral to femoral length for predicting habitual amniote posture across ontogenetic trajectories. Most living and extinct amniote species examined conserve their posture across ontogeny, and where a shift does occur in Homo sapiens, our method correctly identifies it. We falsify previous hypotheses that such shifts were widespread in dinosaurs, at least among the dinosaurs we measured. Instead we hypothesize only two such shifts occurred, in the sauropodomorph Mussaurus patagonicus, and potentially in the ornithischian Psittacosaurus lujiatunensis. These two hypothesized shifts occur in lineages that are temporally and phylogenetically proximate to hypothesized macroevolutionary postural changes. The lack of widespread 'transitional' postural values more distal to these inferred changes suggests that postural shifts are evolutionarily rapid and leave only ephemeral signals in the fossil record and in ontogenetic sequences. Complex locomotor repertoires, forelimb assisted digging, and adaptations for axial stiffness may confound inferences of habitual locomotor posture using limb robusticity."

Referee: 3

Please note that all figures are full page width

Comments to the Author
Fig. 1:
o The resolution of this file is slightly under 600 dpi at full page width (it needs to be approx. 3024 pixels wide). Do you have a higher resolution original file that you could supply? Please do not scale up from this file as it will not improve the quality of the image.
We have re-exported the figure at higher resolution.

o Some of the text on this figure would be too small to be legible at full page width (e.g. the axis labels and numbers).
We have increased text size.

o Would it be possible to use shapes as well as colours to distinguish the different points on the plots?
We have added shapes in addition to colour

o Even with shapes though this figure will need colour to work. If you do not have funding available to pay the colour printing fee (£150 for one figure, plus £50 for each additional one) please state this clearly in your cover letter as the Palaeontological Association is willing to cover the cost of essential colour where alternative funding is not available (at the Editor-in-Chief's discretion).

o Have you used any PhyloPic silhouettes on this (or any other) figure? If so, please ensure that you have checked the licence associated with each image for any attribution requests (not all images have the same requirements).
Phylopic acknowledgements have been added

▯ Figs 2, 3:
o The resolution of these files is fine for full page reproduction.
o The taxon names are towards the lower size limit at full page width; would it be possible to increase the size of the text for the group names on the left and on the legend and horizontal axis label?
o I'm not sure that the end colours used in your range will be very clear in greyscale. Can these be adjusted to give a high contrast between the end members (rather than between the middle or the two ends).
We have increased text size. We attempted to change the colours, however this makes differentiating between the middle of the spectrum and the rest of the spectrum very difficult.

▯ Fig. 4:
o The resolution of this file is slightly below the ideal; do you have a higher resolution original?
We have re-extracted the figure at higher resolution.

o Would it be possible to use solid and dotted lines as well as different colours, and to add a visual legend rather than describing them in the caption (thus removing the need to refer to colour in the caption)?
We have made the blue lines dotted lines and have added a visual legend.