Supplementary Material

Evolutionary history of quadrupedal walking gaits shows Mammalian release from locomotor constraint.

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S1 Methods

S1.1 Calculation of Duty Factor and Phase

"Hildebrand Plots" are used to visualize footfall patterns by using two quantitative variables to describe quadrupedal locomotion. Traditionally, Hildebrand Plots are first broken up into walking and running based on duty factor (i.e. the percentage of time each foot is on the ground in a steady gait). The second variable of consideration is phase, or the time it takes for a given hindfoot to follow the forefoot on the same side of the body. Limb phases can be divided along an axis into lateral (i.e., a given hindfoot is followed by the ipsilateral forefoot) and diagonal (i.e., a given hindfoot is followed by the contralateral forefoot) sequence gaits. Within each designated sequence, there is another breakdown into a lateral (i.e., fore- and hindfoot on the same side of the body contact ground at roughly the same time) or diagonal (i.e., the diagonally opposing forefoot and hindfoot contact at similar times) couplets [25, 26, 27].

The Hildebrand plot representing phase and duty factor for our data can be found in Main Text Figure 1. We only collected animal gait information if there was a duty factor of above 50%, indicating a walking gait. Footfall data were collected from 244 quadrupedal terrestrial species throughout Gnathostomata. If values were not recorded in the literature (see S2), they were gathered from freely available internet videos. Videos were used if the full gait sequence could be accounted for (duration of time from when a given hindfoot touches the substrate to the next time it contacts), and if footfalls or limb loading could clearly be observed.

Although the equation below uses the right side of the body as an example, it can be used for the left side of the body as well. In practice, we took data from whichever side of the body was clearly visible in the video. A YouTube converter (y2mate.guru) was used to download each video and VirtualDub V.1.9.11 (http://www.virtualdub.org/) was used to observe footfall timings frame by frame in order to calculate duty factor and phase. The frame number for each action was taken in order to calculate the equations below. If several gait cycles were observed for a given species, the average phase and duty factor was used. Only walking strides (duty factors > 50) were used for subsequent analyses.

We calculated phase (time for the forefoot to follow the hindfoot on the same side of the body divided by total stride duration) as,

\[
\text{Phase} = \frac{\text{RFD} + \text{RHD}_1}{\text{RHD}_2 + \text{RHD}_1}\tag{1}
\]

where \( \text{RHD}_1 \) = first time the right hindfoot touches ground, \( \text{RHD}_2 \) = second time the right hindfoot touches ground, and \( \text{RFD} \) = right forefoot touches ground [27]. We calculated duty factor (time on the ground divided by total stride length) as,

\[
\text{Duty Factor} = \frac{\text{RHU} + \text{RHD}_1}{\text{RHD}_2 + \text{RHD}_1}.	ag{2}
\]

where all abbreviations follow that of equation 1 and \( \text{RHU} \) = right hindfoot up.

S1.2 Limitations

We recognize several limitations exist within this study regarding our data collection techniques. First is the use of freely available internet videos for data collection. We are not the first group to use this approach [53] and consider this practice to be a resourceful way to gather informative data on gait parameters. Calculating duty factor and phase only requires the timing of footfalls by identifying actions from individual frames, and therefore does not depend on certain video procedures such as specific frame rates or views. While there may
be justified concerns about the physical condition of the animals in the online videos, we only used videos in which the animal appeared healthy and did not deviate from a continuous gait (i.e., not limping, etc.). A supplementary file is provided with the downloaded videos used for data collection if the link provided in the citation (Table S1) is no longer working.

Another important consideration when evaluating our data is speed, which is known to affect several biomechanical gait variables (e.g. [6, 9, 10, 17]). While experimental designs should make every effort to either standardize locomotor speed across trials in initial data collection or account for the confounding influence of speed through appropriate statistical testing, we were unable to account for this in our study. However, in the context of this study we only collected data that included walking gaits (i.e., duty factor > 50%), which assured physiologically similar gaits across subjects [24]. Although our sample is large, and to our knowledge represents one of the most taxonomically diverse samples of tetrapod gaits to date (244 species of Tetrapoda with the inclusion of a few select non-tetrapod Gnathostomes that demonstrate symmetrical quadrupedal walking gaits), we recognize that this sample does not represent all species. Related to this, many species are capable of quite a bit of intraspecific variation (e.g., [31]) that was not accounted for in our initial sampling. These limitations should be considered when interpreting the results of our manuscript, and we hope that future studies will test our conclusions while taking these potentially confounding issues into account.

In this study, we used the total length of the hindlimb as our proxy for limb length. Arguably, a more appropriate proxy would have been effective limb length, which takes into account differences in crouch versus extended limb postures during locomotor behaviors [25]. However, effective limb length is rarely reported in the literature and this would have severely reduced our phylogenetic diversity. Similarly, we used total limb length as a proportion of the cubed root of body mass to reflect relative limb length. While such a ratio is valid, overall body mass includes both the mass of the limbs themselves and the head. A more appropriate measure would have been just to use linear trunk length (i.e., shoulder to hip length) as the denominator. However, as with effective limb length, this measurement is not available for most species. Reconstructing trunk length from isolated vertebrae is marked with its own challenges. Isolating our sample to only species where a trunk length was available would limited the phylogenetic scope of our sample.

S1.3 Phylogenetic ANCOVA

We used phylogenetic regressions to assess the scaling of phase with body mass, limb length, relative limb length, and duty factor (see Methods). These last two factors, in particular, have been proposed as important determinants of limb phase; relative limb length as a predictor of LSLC gaits [25, 26, 27] and duty factor as a positive correlate of phase due to mechanical work constraints [53]. Our evolutionary regressions (Main Text Fig. 3) found no support for these hypotheses but it is notable that the long-limbed primates are conspicuous outliers in these plots (Main Text Figs 3C,D) and [53] noted that limb phase in Primates appeared to follow a distinct scaling relationship with duty factor, relative to other tetrapods. Thus, it is possible that the lack of predicted relationships in these analyses results from the influence of these distinctive taxa.

To investigate this possibility, we performed phylogenetically informed Analyses of Covariance (pANCOVA) using the gls.ancova function from the EvoMap package [49] for R. This method employs a generalized least squares framework to assess whether models with separate intercepts, slopes, or intercepts and slopes for two or more group level effects provide a better fit to the data than a single slope - single intercept model [50]. We compared the fit of models allowing for different combinations of slopes and intercepts for Primates and non-primate mammals for arcsine phase as a function of relative limb length and of arcsine duty factor.

For relative limb length, we recovered non-significant relationships with phase for non-primate mammals (arcsine phase = 0.5524221 + 0.0797901 x log(relative limb length); t=0.746929, p = 0.4566) and Primates (arcsine phase = 0.8780632 - 0.0082062 x log(relative limb length); t=-0.0379004, p = 0.9700) when analyzed separately (Fig. S4). Unsurprisingly, this result yields no support for differences in slope using pANCOVA (Table S4). The larger intercept found for Primates, compared with non-primate mammals, suggests that
primates may simply occupy a stable but higher phase regime than other mammals, irrespective of relative limb length. Support for a two-intercept model is weak, but not unsubstantial ($F=3.35$, $p = 0.0692$), and better sampling may lend support to this model.

For arcsine duty factor (Fig. S4), we recover non-significant relationships with phase for non-primate mammals ($\text{arcsin phase} = 0.6102991 + 0.0320012 \times \text{arcsine duty factor}; t=0.249758, p = 0.8032$) and Primates ($\text{arcsin phase} = 1.2493816 - 0.4347258 \times \log(\text{relative limb length}); t=-1.557660, p = 0.1295$), though the primate scaling relationship is more pronounced than that of non-primates and is clearly more negative. Phylogenetic ANCOVA does not provide support for a distinct slope model alone, but support ($t=3.7, p = 0.056$) is recovered for variable intercepts, with Primates again exhibiting a higher ancestral phase, relative to duty factor, compared with non-primate mammals. Some degree of support for distinct slopes and intercepts is also present (Table S4). Taken as a whole, these results provide no further support for Hildebrand’s hypothesis that relative limb length drives the use of LSLC gaits or Usherwood and Self-Davies’ hypothesis that mechanical work demands constrain the relationship between duty factor and phase to be positive. They do corroborate the idea that Primates are distinctive, relative to other mammals, in their use of symmetric walking gaits.
S2 Supplementary Figures
Figure S1: 95% credible set of rate shifts from BAMM analysis of phase. For each panel, f is the frequency of that shift configuration in the posterior sample. A shift in mammals (yellow clade) is recovered in all most credible configurations. A single additional shift within Lepidosauria is recovered in about 70% of the credible set but the precise location of this shift cannot be determined.
Figure S2: The configuration with the highest posterior probability recovers a single shift in the branch leading to mammals (red branches).
Figure S3: Mean rates of phase evolution, averaged over all possible shift configurations. Branch labels indicate marginal probabilities of a shift occurring along that edge. The large label corresponds to the mammalian shift. Smaller labels correspond to uncertain shift positions in acrodont squamates, which result in the fastest model-averaged rates of all.
S3 Supplementary Tables

Table S1: Table with species information and references for duty factor and phase. The reported numbers for each gait parameter are the averaged value if several strides were taken. Habitat categories were determined using gait sources and Animal Diversity Web ([https://animaldiversity.org/](https://animaldiversity.org/)). Q = aquatic, A = arboreal, T = terrestrial. FMNH = Field Museum of Natural History, Chicago IL; NMNH = Smithsonian National Museum of Natural History, Washington D.C.; UWBM = University of Washington Burke Museum, Seattle WA. Data on stride number was not reported in [38].

| Class           | Order       | Species                      | Strides | Duty Factor | Phase | Ref      | Habitat |
|-----------------|-------------|------------------------------|---------|-------------|-------|---------|---------|
| Actinopterygii  | Cypriniformes| Cryptotora thamicola         | 6       | 65.45       | 51.18 | [11]    | Q       |
| Actinopterygii  | Lophiiformes| Antennarius striatus         | 5       | 67.65       | 46.04 | [71]    | Q       |
| Lissamphibia    | Anura       | Kassina maculata             | 1       | 78          | 44    | [53]    | T       |
| Lissamphibia    | Anura       | Agalychnis calidryas         | 3       | 82.27       | 34.26 | [61]    | A       |
| Lissamphibia    | Anura       | Breviiceps mossambicus       | 5       | 67.87       | 39.09 | [139]   | T       |
| Lissamphibia    | Anura       | Lepidobatrachus laevis       | 4       | 65.02       | 39.04 | [125]   | Q       |
| Lissamphibia    | Anura       | Pelobates syriacus           | 4       | 79.99       | 32.39 | [106]   | T       |
| Lissamphibia    | Anura       | Phyllomedusa hypochondrialis| 6       | 70.03       | 39.18 | [110]   | A       |
| Lissamphibia    | Anura       | Rana catesbeiana             | 4       | 71.77       | 39.79 | [89]    | T       |
| Lissamphibia    | Anura       | Rhinella marina              | 7       | 75.30       | 39.05 | [104]   | T       |
| Lissamphibia    | Urodela     | Ambystoma tigrinum           | 1       | 80          | 40    | [53]    | T       |
| Lissamphibia    | Urodela     | Andrias japonicus            | 1       | 74          | 40    | [53]    | Q       |
| Lissamphibia    | Urodela     | Ambystoma maculatum          | 8       | 72.14       | 44.34 | [83]    | T       |
| Lissamphibia    | Urodela     | Ambystoma mexicanum          | 2       | 53.82       | 44.86 | [88]    | Q       |
| Lissamphibia    | Urodela     | Ambystoma texanum            | 10      | 67.68       | 44.50 | [179]   | T       |
| Lissamphibia    | Urodela     | Cryptobranchus alleganiensis| 4       | 59.39       | 50.30 | [120]   | Q       |
| Lissamphibia    | Urodela     | Dicamptodon tenebrosus       | 5       | 72.08       | 36.42 | [68]    | T       |
| Lissamphibia    | Urodela     | Hynobius kimurae             | 2       | 71.09       | 49.49 | [117]   | T       |
| Lissamphibia    | Urodela     | Necturus maculosus           | 3       | 71.88       | 41.67 | [105]   | Q       |
| Lissamphibia    | Urodela     | Plethodon vehiculum          | 6       | 71.46       | 45.36 | [150]   | T       |
| Lissamphibia    | Urodela     | Psuedotriton ruber            | 5       | 75.77       | 49.59 | [77]    | Q       |
| Lissamphibia    | Urodela     | Rhyacochitlon variegatus      | 4       | 77.13       | 43.83 | [75]    | Q       |
| Lissamphibia    | Urodela     | Salamandra infrnimaculata    | 4       | 76.46       | 36.91 | [60]    | T       |
| Lissamphibia    | Urodela     | Taricha torosa               | 7       | 65.59       | 38.16 | [96]    | T       |
| Archelosaurus   | Crocodylia  | Alligator mississippiensis   | 3       | 87          | 42    | [83]    | T       |
| Archelosaurus   | Crocodylia  | Caiman crocodilus            | 2       | 78          | 43    | [83]    | T       |
| Archelosaurus   | Crocodylia  | Crocodylus palustris         | 1       | 78          | 49    | [83]    | T       |
| Class                  | Order              | Species                  | Strides | Duty Factor | Phase | Ref | Habitat |
|-----------------------|--------------------|--------------------------|---------|-------------|-------|-----|---------|
| Archelosauria         | Crocodilia         | Gavialis gangeticus      | 1       | 52.24       | 41.79 | 116 | T       |
| Archelosauria         | Opisthocomiformes  | Opisthocomus hoazin      | 4       | 92.96       | 39.06 | 116 | T       |
| Archelosauria         | Testudines         | Centrochelys sulcata     | 2       | 82          | 42    | 53  | T       |
| Archelosauria         | Testudines         | Apalone spinifera        | 2       | 70.71       | 39.05 | 53  | T       |
| Archelosauria         | Testudines         | Carettochelys insculpta  | 2       | 58.41       | 50.47 | 83  | T       |
| Archelosauria         | Testudines         | Chelodina piscata       | 1       | 84.88       | 51.16 | 83  | T       |
| Archelosauria         | Testudines         | Chelydra serpentina     | 2       | 62.91       | 55.49 | 53  | T       |
| Archelosauria         | Testudines         | Chersina angulata       | 4       | 67.22       | 39.93 | 53  | T       |
| Archelosauria         | Testudines         | Chrysemys picta        | 3       | 73.43       | 29.35 | 53  | T       |
| Archelosauria         | Testudines         | Cuora amboinensis       | 2       | 74.57       | 41.57 | 53  | T       |
| Archelosauria         | Testudines         | Deirochelys reticularia | 3       | 73.58       | 43.29 | 53  | T       |
| Archelosauria         | Testudines         | Podocnemis expansa      | 2       | 73.05       | 45.21 | 53  | T       |
| Archelosauria         | Testudines         | Terrapene carolina      | 2       | 59.63       | 43.38 | 53  | T       |
| Archelosauria         | Testudines         | Testudo horsfieldii     | 41      | 83.88       | 38.64 | 53  | T       |
| Chondrichthyes        | Orectolobiformes   | Hemiscyllium ocellatum  | 6       | 71.49       | 47.37 | 53  | Q       |
| Dipnoi                | Lepidosireniformes | Protopterus annectens   | 3       | 66.76       | 43.84 | 53  | Q       |
| Lepidosauria          | Squamata           | Acantodactylus boskianus| -       | 53          | 57    | 53  | T       |
| Lepidosauria          | Squamata           | Ameiva ameiva           | -       | 53          | 38    | 53  | T       |
| Lepidosauria          | Squamata           | Eumeces schneideri      | -       | 73          | 50    | 53  | T       |
| Lepidosauria          | Squamata           | Lepidodoma flaminiculatum| 1     | 80.53       | 55.45 | 53  | T       |
| Lepidosauria          | Squamata           | Oplurus cuvieri         | 20      | 52.04       | 52.18 | 53  | T       |
| Lepidosauria          | Squamata           | Sceloporus malachiticus | 20      | 52.93       | 52.13 | 53  | T       |
| Lepidosauria          | Squamata           | Smaug warreni           | 2       | 53.45       | 50.34 | 53  | T       |
| Lepidosauria          | Squamata           | Trachelotyphus peteri   | -       | 72          | 43    | 53  | T       |
| Lepidosauria          | Squamata           | Tropidurus torquatus    | 1       | 50.12       | 44.24 | 53  | T       |
| Lepidosauria          | Squamata           | Tupinambis teguixin     | -       | 56          | 34    | 53  | T       |
| Lepidosauria          | Squamata           | Varanus exanthematicus  | -       | 69          | 40    | 53  | T       |
| Lepidosauria          | Squamata           | Amblablychnys cristatus | 1       | 85          | 41    | 53  | T       |
| Lepidosauria          | Squamata           | Conolophus pallidus     | 1       | 84          | 47    | 53  | T       |
| Lepidosauria          | Squamata           | Eublepharis macularius  | 2       | 79          | 43    | 53  | T       |
| Lepidosauria          | Squamata           | Iguana iguana           | 2       | 75          | 44    | 53  | T       |
| Lepidosauria          | Squamata           | Pogona vitticeps        | 1       | 78          | 48    | 53  | T       |
| Lepidosauria          | Squamata           | Anolis carolinensis     | 4       | 77.74       | 40.03 | 53  | A       |
| Lepidosauria          | Squamata           | Anolis equestris        | 2       | 60.19       | 43.70 | 53  | A       |
| Lepidosauria          | Squamata           | Anolis proboscis        | 2       | 64.31       | 36.67 | 53  | A       |
| Lepidosauria          | Squamata           | Aspidoscelis ornata     | 3       | 58.89       | 52.22 | 53  | T       |
| Lepidosauria          | Squamata           | Basiliscus plumifrons  | 1       | 50          | 33.33 | 53  | T       |
| Lepidosauria          | Squamata           | Chamaeleo calyptratus   | 8       | 65.55       | 44.07 | 53  | A       |
| Lepidosauria          | Squamata           | Chamaeleo namaquensis   | 6       | 75.03       | 40.94 | 53  | T       |
| Lepidosauria          | Squamata           | Chamaeleo zealandicus   | 6       | 65.35       | 59.22 | 53  | T       |
| Lepidosauria          | Squamata           | Ecleopos zuerwaldi      | 1       | 66.67       | 33.33 | 53  | T       |
| Lepidosauria          | Squamata           | Furcifer pardalis      | 8       | 70.06       | 35.15 | 53  | A       |
| Lepidosauria          | Squamata           | Grkko gecko            | 2       | 57.08       | 28.99 | 53  | A       |
| Lepidosauria          | Squamata           | Heloderma suspectum    | 6       | 71.11       | 46.69 | 53  | T       |
| Lepidosauria          | Squamata           | Lanthanotus borneensis  | 3       | 60.22       | 48.04 | 53  | T       |
| Lepidosauria          | Squamata           | Matobosaurus validus    | 2       | 69.83       | 52.72 | 53  | T       |
| Lepidosauria          | Squamata           | Moloch horridus        | 4       | 90.03       | 36.07 | 53  | T       |
| Lepidosauria          | Squamata           | Phrynosoma platyrhinos | 1       | 60.01       | 58.33 | 53  | T       |
| Lepidosauria          | Squamata           | Podarcis siculus       | 7       | 61.15       | 43.41 | 53  | T       |
| Lepidosauria          | Squamata           | Shinisaurus crocodilurus| 1      | 76.19       | 57.14 | 53  | T       |
| Lepidosauria          | Squamata           | Tiliqua scincoides      | 6       | 68.69       | 46.92 | 53  | T       |
| Lepidosauria          | Squamata           | Timon lepidus          | 3       | 69.72       | 42.5  | 53  | T       |
| Lepidosauria          | Squamata           | Trioceros jacksonii     | 4       | 61.35       | 42.08 | 53  | A       |
| Lepidosauria          | Squamata           | Xenosaurus platyrhinos | 1       | 85          | 60    | 53  | T       |
| Lepidosauria          | Squamata           | Stellagama stellio     | 3       | 51.49       | 50.11 | 53  | T       |
| Mammalia              | Afrotheria         | Dendrohyrax arbores     | 1       | 57.55       | 22.22 | 53  | A       |
| Mammalia              | Afrotheria         | Orycteropus afer        | 3       | 69.78       | 49.46 | 53  | T       |
| Mammalia              | Afrotheria         | Elephas maximus         | 1       | 73          | 19    | 53  | T       |
| Mammalia              | Afrotheria         | Loxodonta africana     | 4       | 74          | 17    | 53  | T       |
| Mammalia              | Artiodactyla       | Cephalophus natalensis | 2       | 60          | 22.5  | 53  | T       |

1 Unpublished data
| Class     | Order        | Species                  | Strides | Duty Factor | Phase | Ref  | Habitat |
|-----------|--------------|--------------------------|---------|-------------|-------|------|---------|
| Mammalia  | Artiodactyla | Okapia johnstoni         | 4       | 60.65       | 16.91 | T    |         |
| Mammalia  | Artiodactyla | Viconoga pacos           | 41      | 55.81       | 12.93 | T    |         |
| Mammalia  | Artiodactyla | Hippopotamus amphibius   | 4       | 76          | 45    | T    |         |
| Mammalia  | Artiodactyla | Oryx gazella             | 2       | 66.66       | 14.81 | T    |         |
| Mammalia  | Artiodactyla | Pecari tajacu            | 2       | 65.17       | 23.79 | T    |         |
| Mammalia  | Artiodactyla | Cephalophus silvicoltor  | 2       | 67.2        | 23.12 | T    |         |
| Mammalia  | Artiodactyla | Tragelaphus strepsiceros | 3       | 62.68       | 32.03 | T    |         |
| Mammalia  | Artiodactyla | Giraffa camelopardalis   | 5       | 68          | 14    | T    |         |
| Mammalia  | Artiodactyla | Camelus dromedarius      | 2       | 75.02       | 22.79 | T    |         |
| Mammalia  | Artiodactyla | Ammotragus levis         | 1       | 71          | 26    | T    |         |
| Mammalia  | Artiodactyla | Camelus bactrianus       | 1       | 72          | 21    | T    |         |
| Mammalia  | Artiodactyla | Sus scrofa               | 2       | 70.80       | 25.75 | T    |         |
| Mammalia  | Artiodactyla | Moschidae meminna       | 2       | 68.18       | 20.76 | T    |         |
| Mammalia  | Artiodactyla | Aepyceros melampus      | 1       | 68          | 19    | T    |         |
| Mammalia  | Artiodactyla | Bison bison              | 1       | 71          | 16    | T    |         |
| Mammalia  | Artiodactyla | Bos taurus               | 5       | 69          | 29    | T    |         |
| Mammalia  | Artiodactyla | Capra aegagrus           | 1       | 72          | 23    | T    |         |
| Mammalia  | Artiodactyla | Camelus dromedarius      | 2       | 72.68       | 32.03 | T    |         |
| Mammalia  | Artiodactyla | Camelus bactrianus       | 1       | 72          | 21    | T    |         |
| Mammalia  | Artiodactyla | Sus scrofa               | 2       | 70.80       | 25.75 | T    |         |
| Mammalia  | Artiodactyla | Moschidae meminna       | 2       | 68.18       | 20.76 | T    |         |
| Mammalia  | Artiodactyla | Aepyceros melampus      | 1       | 68          | 19    | T    |         |
| Mammalia  | Artiodactyla | Bison bison              | 1       | 71          | 16    | T    |         |
| Mammalia  | Artiodactyla | Bos taurus               | 5       | 69          | 29    | T    |         |
| Mammalia  | Artiodactyla | Capra aegagrus           | 1       | 72          | 23    | T    |         |
| Mammalia  | Artiodactyla | Camelus bactrianus       | 1       | 72          | 21    | T    |         |
| Mammalia  | Artiodactyla | Sus scrofa               | 2       | 70.80       | 25.75 | T    |         |
| Mammalia  | Artiodactyla | Moschidae meminna       | 2       | 68.18       | 20.76 | T    |         |
| Mammalia  | Artiodactyla | Aepyceros melampus      | 1       | 68          | 19    | T    |         |
| Class                  | Order            | Species                      | Strides | Duty Factor | Phase | Ref | Habitat |
|-----------------------|------------------|------------------------------|---------|-------------|-------|-----|---------|
| Mammalia              | Dasyuromorphia   | Sarcophilus harrisii         | 4       | 62.32       | 20.12 |     | T       |
| Mammalia              | Dasyuromorphia   | Dasyurus maculatus           | 16      | 64.27       | 41.40 |     | T       |
| Mammalia              | Didelphimorphia  | Philander opossum            | 18      | 62.84       | 54.05 |     | T       |
| Mammalia              | Didelphimorphia  | Caluromys philander          | 85      | 67.03       | 58    |     | A       |
| Mammalia              | Didelphimorphia  | Monodelphis domestica        | 15      | 68.60       | 46.31 |     | T       |
| Mammalia              | Didelphimorphia  | Didelphis virginiana         | 2       | 76.54       | 34.86 |     | T       |
| Mammalia              | Diprotodontia    | Dasyurus breviceps           | 160     | 61.5        | 45    |     | A       |
| Mammalia              | Diprotodontia    | Phascolarctos cinerreus      | 4       | 69.70       | 45.51 |     | T       |
| Mammalia              | Diprotodontia    | Vombatus ursinus             | 2       | 67.33       | 22.42 |     | T       |
| Mammalia              | Diprotodontia    | Vombatus ursinus             | 13      | 63.66       | 33.33 |     | T       |
| Mammalia              | Eulipotyphla     | Talpa europaea               | 1       | 62.96       | 33.33 |     | T       |
| Mammalia              | Eulipotyphla     | Erinaceus europaeus          | 1       | 62.96       | 33.33 |     | T       |
| Mammalia              | Monotremata      | Zaglossus bruijni            | 3       | 67.16       | 24.28 |     | T       |
| Mammalia              | Monotremata      | Ornithorhynchus anatinus     | 10      | 58.60       | 44.36 |     | T       |
| Mammalia              | Monotremata      | Tachyglossus weberi          | 1       | 65.77       | 28.92 |     | T       |
| Mammalia              | Monotremata      | Tachyglossus weberi          | 28      | 67.24       | 24    |     | T       |
| Mammalia              | Peramelemorpha   | Equus asinus                 | 1       | 73          | 25    |     | T       |
| Mammalia              | Perissodactyla   | Ceratotherium simum          | 2       | 68          | 21    |     | T       |
| Mammalia              | Perissodactyla   | Tapirus bairdii              | 2       | 65.01       | 21.97 |     | T       |
| Mammalia              | Perissodactyla   | Tapirus terrestris           | 1       | 70          | 26    |     | T       |
| Mammalia              | Perissodactyla   | Tapirus indicus              | 1       | 61          | 26    |     | T       |
| Mammalia              | Perissodactyla   | Equis burchellii             | 28      | 67          | 24    |     | T       |
| Mammalia              | Perissodactyla   | Equis caballus               | 2       | 67          | 24    |     | T       |
| Mammalia              | Pilosa           | Myrmecophaga triactyla       | 1       | 70          | 27    |     | T       |
| Mammalia              | Pilosa           | Cyclopes didactylus          | 2       | 87.63       | 64.59 |     | A       |
| Mammalia              | Pilosa           | Bradytarsus variegatus       | 1       | 78.57       | 52.04 |     | A       |
| Mammalia              | Pilosa           | Choloepus didactylus         | 37      | 72.63       | 49.43 |     | A       |
| Mammalia              | Primates         | Ateles paniscus              | 46      | 60.60       | 63.99 |     | A       |
| Mammalia              | Primates         | Nycticebus pygmaeus          | 22      | 53.52       | 55.67 |     | A       |
| Mammalia              | Primates         | Mandrillus sphinx            | 2       | 64.00       | 56.09 |     | T       |
| Mammalia              | Primates         | Ateles geoffroyi             | 24      | 60.68       | 71.88 |     | A       |
| Mammalia              | Primates         | Lemur catta                  | 89      | 64.50       | 65.25 |     | T       |
| Mammalia              | Primates         | Aotus nancyma               | 34      | 59.59       | 58.38 |     | A       |
| Mammalia              | Primates         | Leontopithecus rosalia       | 2       | 65.77       | 58.27 |     | A       |
| Mammalia              | Primates         | Papio ursinus               | 2       | 64.76       | 56.90 |     | T       |
| Mammalia              | Primates         | Loris tardigradus            | 33      | 51.89       | 55.85 |     | A       |
| Mammalia              | Primates         | Gorilla gorilla             | 2       | 61.55       | 43.43 |     | T       |
| Mammalia              | Primates         | Pan troglodytes              | 2       | 62.78       | 48.06 |     | T       |
| Mammalia              | Primates         | Pygathrix nemaeus            | 7       | 63.21       | 64.94 |     | A       |
| Mammalia              | Primates         | Cebus capucinus             | 39      | 55.98       | 62.84 |     | A       |
| Mammalia              | Primates         | Rhinopithecus roxellana      | 193     | 69.44       | 62.15 |     | A       |
| Mammalia              | Primates         | Macaca fascicularis          | 60      | 60.21       | 63.08 |     | T       |
| Mammalia              | Primates         | Ateles fuscipes             | 22      | 59.80       | 71.24 |     | A       |
| Mammalia              | Primates         | Alouatta seniculus          | 27      | 68.33       | 56.90 |     | A       |
| Mammalia              | Primates         | Saimiri sciureus            | 98      | 54.26       | 58.77 |     | A       |
| Mammalia              | Primates         | Pithecia pithecia           | 28      | 65.78       | 28.92 |     | A       |
| Mammalia              | Primates         | Chiropotes satanas          | 31      | 66.84       | 44.79 |     | A       |
| Mammalia              | Primates         | Sapajus apella             | 29      | 65.60       | 49.54 |     | A       |
| Mammalia              | Primates         | Macaca mulatta              | 22      | 62.76       | 63.03 |     | T       |
| Mammalia              | Primates         | Trachypithecus hainihensis   | 12      | 60.93       | 61.45 |     | A       |
| Mammalia              | Primates         | Cheirogaleus medius         | 32      | 54.58       | 55.44 |     | A       |
| Mammalia              | Primates         | Duabentonia madagascariensis| 50      | 57.36       | 65.79 |     | A       |
| Mammalia              | Primates         | Hapalemur griseus            | 20      | 61.92       | 64.62 |     | A       |
| Mammalia              | Primates         | Pygathrix cinerea           | 15      | 66.19       | 64.50 |     | A       |
| Mammalia              | Primates         | Varecia variegata           | 57      | 57.20       | 64.54 |     | A       |
| Mammalia              | Primates         | Eulemur mongoz              | 29      | 53.53       | 62.44 |     | A       |
| Mammalia              | Primates         | Propithecus coquereli       | 49      | 63.27       | 62.89 |     | T       |
| Mammalia              | Primates         | Trachypithecus delacouri    | 6       | 60.89       | 59.73 |     | A       |
| Mammalia              | Primates         | Trachypithecus phayrei      | 11      | 63.83       | 61.25 |     | A       |
| Mammalia              | Primates         | Trachypithecus poliophaeus  | 10      | 60.99       | 64.10 |     | A       |

2 Unpublished data
3 Unpublished data
| Class | Order  | Species               | Strides | Factor | Phase | Ref | Habitat |
|-------|--------|-----------------------|---------|--------|-------|-----|----------|
| Mammalia | Rodentia | Micromys minutus      | 66      | 66.63  | 34.05 | 31  | T        |
| Mammalia | Rodentia | Castor canadensis     | 3       | 74.16  | 36.68 | 172 | T        |
| Mammalia | Rodentia | Mus musculus          | 1       | 86     | 40    | 55  | T        |
| Mammalia | Rodentia | Sciurus niger         | 7       | 67.06  | 26.26 | M.C.G. A |
| Mammalia | Rodentia | Hydrochoerus hydrochaeris | 2      | 69.21  | 28.16 | 106 | T        |
| Mammalia | Rodentia | Thallomys paedulcus   | 14      | 71.88  | 31.89 | 32  | T        |
| Mammalia | Rodentia | Rattus norvegicus     | 1       | 62     | 36    | 36  | T        |
| Mammalia | Rodentia | Muscardinus avellanarius | 10  | 64.25  | 36.74 | 36  | T        |
| Mammalia | Rodentia | Myodes glareolus      | 54      | 68.35  | 25.86 | 50  | T        |
| Mammalia | Rodentia | Sciurus griseus       | 6       | 66.29  | 35.33 | 114 | A        |
| Mammalia | Rodentia | Erethizon dorsatum    | 2       | 75     | 29    | 53  | T        |
| Mammalia | Scandentia | Tupaia tana         | 2       | 64.62  | 38.08 | 173 | A        |

4 Unpublished data
Table S2: Body mass (g) and absolute hindlimb length (mm) (sum of femur, tibia, and metatarsal III) data for mammalian species.

| Order          | Species                              | Body Mass | Ref | Limb Length |
|----------------|--------------------------------------|-----------|-----|-------------|
| Afrotheria     | Dendrohyrax arboreus                 | 2981.11   | 25  | 147.37 FMNH 163768 |
| Afrotheria     | Elephas maximus                      | 3269794.34| 25  | 1902.45 FMNH 49894 |
| Afrotheria     | Loxodonta africana                  | 3824539.93| 25  | 1860 FMNH 52255 |
| Afrotheria     | Orycteropus afer                     | 56175.2   | 25  | 399.58 FMNH 33477 |
| Artiodactyla   | Aepyceros melampus                  | 52591.69  | 25  | 723 6 |
| Artiodactyla   | Alcelaphus busefalaphus              | 160937.86 | 25  | 805 6 |
| Artiodactyla   | Antilopahapagallus lervia           | 94202.22  | 25  | 628.97 FMNH 52423 |
| Artiodactyla   | Antilocapra americana               | 47450.01  | 25  | 733 6 |
| Artiodactyla   | Bison bison                          | 624577.07 | 25  | 992 6 |
| Artiodactyla   | Bos taurus                           | 618642.42 | 25  | 958 6 |
| Artiodactyla   | Bubalus bubalis                      | 929500.97 | 25  | 815 6 |
| Artiodactyla   | Camelus bactrianus                  | 554515.91 | 25  | 1291 FMNH 60013 |
| Artiodactyla   | Camelus dromedarius                 | 492714.47 | 25  | 1418 FMNH 52325 |
| Artiodactyla   | Capra aegagrus                      | 47386.47  | 25  | 546 6 |
| Artiodactyla   | Cephalophas natinski                | 12724.51  | 25  | 328.93 FMNH 10184 |
| Artiodactyla   | Cephalophas silvicullor             | 62006.6   | 25  | 615 FMNH 174410 |
| Artiodactyla   | Cervus elaphus                      | 166562.5  | 25  | 859.0135 FMNH 8 |
| Artiodactyla   | Connochaetes taurinus               | 198619.68 | 25  | 920 6 |
| Artiodactyla   | Cervus elaphus                      | 964654.73 | 25  | 1448.5 FMNH 34424 |
| Artiodactyla   | Capra aegagrus                      | 75901.25  | 25  | 560 6 |
| Artiodactyla   | Okapia johnstoni                    | 230001.14 | 25  | 900 FMNH 104923 |
| Artiodactyla   | Oreotragus oreotragus               | 13486.55  | 25  | 409 6 |
| Artiodactyla   | Oxyn gazella                        | 188404.45 | 25  | 823 FMNH 127968 |
| Artiodactyla   | Ovis aries                          | 39097.89  | 25  | 537 6 |
| Artiodactyla   | Ovis canadensis                     | 74644.87  | 25  | 739 6 |
| Artiodactyla   | Pecari tajacau                      | 21133.69  | 25  | 350.54 FMNH 134434 |
| Artiodactyla   | Saiga tatarica                      | 37734.01  | 25  | 577 6 |
| Artiodactyla   | Sus scrofa                          | 84471.54  | 25  | 534.89 FMNH 97884 |
| Artiodactyla   | Tragelaphus strepsiceros            | 206056.41 | 25  | 981 FMNH 18815 |
| Artiodactyla   | Viva pacos                          | 44400.00  | 25  | 685 FMNH 121665 |
| Carnivora      | Acinonyx jubatus                    | 49270.00  | 25  | 616.87 6 |
| Carnivora      | Aiurpoda melanoleuca               | 117999.99 | 25  | 552.3 6 |
| Carnivora      | Aiurul fulgens                      | 5170.08   | 25  | 236.4 6 |
| Carnivora      | Panthera leo                        | 175890.00 | 25  | 741.72 6 |
| Carnivora      | Panthera onca                      | 8335.00   | 25  | 549.75 6 |
| Carnivora      | Panthera tigris                    | 142000.00 | 25  | 744.94 6 |
| Carnivora      | Paradoxurus hermaphroditus          | 3200.00   | 25  | 227.38 FMNH 140476 |
| Carnivora      | Potos flavus                        | 2441.81   | 25  | 234.89 7 |
| Carnivora      | Procyon lotor                       | 6179.00   | 25  | 320 7 |
| Carnivora      | Ursus americanus                    | 110500.00 | 25  | 639.7348 5 |
| Carnivora      | Ursus arctos                        | 196287.5  | 25  | 709.5778 5 |
| Carnivora      | Ursus maritimus                    | 371703.81 | 25  | 785.2356 5 |
| Carnivora      | Vulpes vulpes                      | 4750.00   | 25  | 318.38 2 |
| Carnivora      | Zalophus wollebacki                 | 158090.00 | 25  | 415 FMNH 226759 |
| Chiropetra     | Desmodus rotundus                  | 23.1      | 25  | 47.471 5 |
| Chiropetra     | Mystacina tuberculata              | 13.9      | 25  | 41.573 5 |
| Chiropetra     | Pteropus vampyrus                  | 1027.54   | 25  | 199.05 14 |
| Cingulata      | Dasypus novemcinctus               | 3580.00   | 25  | 161.78 31 |
| Cingulata      | Monodelphius domestica             | 40641.89  | 25  | 346.5 FMNH 72913 |
| Dasyuromorphia | Dasyurus maculatus                 | 3284.15   | 25  | 181.877 FMNH 57803 |
| Dasyuromorphia | Myrmecobius fasciatus              | 511.44    | 25  | 112.04 FMNH 19982 |
| Dasyuromorphia | Sarcophilus harrisii               | 8202.25   | 25  | 214.237 FMNH 46006 |
| Didelphimorphia| Caluromys philander                | 246.47    | 25  | 105.05 2 |
| Didelphimorphia| Didelphis virginiana               | 2290.00   | 25  | 154.79 31 |
| Didelphimorphia| Monodelphius dasyurus              | 70.00     | 25  | 56.19 31 |
| Didelphimorphia| Philander opossum                  | 425.81    | 25  | 125.05 2 |
| Diprotodontia  | Acrobatis pygmaeus                 | 13.84     | 25  | 36.888 UWBM 68896 |

5 Used Capra hircus
6 Used Cephalophas monticola
| Order                | Species                          | Body Mass | Ref | Limb Length | Ref |
|----------------------|----------------------------------|-----------|-----|-------------|-----|
| Diprotodontia        | Dendrolagus goodfellowi          | 7948.78   | 29  | 308.61      | FMNH 98158 |
| Diprotodontia        | Lasiorhinus krueii               | 31849.99  | 29  | 275.66      | FMNH 49085 |
| Diprotodontia        | Petaurus breviceps               | 120.76    | 29  | 77.81       | FMNH 129430 |
| Diprotodontia        | Phascolarctos cinereus          | 6527.84   | 29  | 267.58      | FMNH 19803 |
| Diprotodontia        | Pseudocheirus peregrinus         | 895.22    | 29  | 133.4       | FMNH 134502 |
| Diprotodontia        | Trichosurus vulpecula            | 13208.8   | 39  | 213.82      | |
| Diprotodontia        | Vombatus ursinus                 | 26000     | 29  | 275.66      | FMNH 49085 |
| Eulipotyphla         | Erinaceus europaeus              | 777.95    | 29  | 101.65      | |
| Eulipotyphla         | Taipia europaea                  | 87.53     | 29  | 46.28       | |
| Monotremata          | Ornithorhynchus anatinus         | 48142.73  | 39  | 158.79      | |
| Monotremata          | Tachyglossus aculeatus           | 3700      | 51  | 127.74      | |
| Monotremata          | Zaglossus bruijni                | 8951.71   | 29  | 212.55      | |
| Peramelemorphia      | Isoodon macrourus                | 1505.77   | 29  | 192.98      | NMNH 238438 |
| Perissodactyla       | Ceratotherium simum              | 2285393.43| 29  | 1057        | |
| Perissodactyla       | Equus asinus                     | 164998.49 | 29  | 748.1695    | |
| Perissodactyla       | Equus burchelli                  | 279160.65 | 29  | 881         | |
| Perissodactyla       | Equus caballus                   | 403598.53 | 29  | 1063        | |
| Perissodactyla       | Tapirus bairdii                  | 293781.59 | 29  | 665.65      | FMNH 34665 |
| Perissodactyla       | Tapirus indicus                  | 312209.19 | 29  | 359.22      | |
| Pilosa               | Bradypus variegatus              | 4136.36   | 29  | 217.35      | FMNH 69589 |
| Pilosa               | Choledpus didactylus             | 6646.5    | 29  | 356.99      | FMNH 95448 |
| Pilosa               | Cyclopes didactylus              | 263.95    | 29  | 91.86       | FMNH 61853 |
| Pilosa               | Myrmecophaga tridactyla          | 295318.3  | 29  | 486.29      | FMNH 28309 |
| Primates             | Alouatta seniculus               | 6398.31   | 29  | 359.22      | |
| Primates             | Aotus nancymaeae                 | 791.03    | 29  | 215.28      | FMNH 127397 |
| Primates             | Atelos fusciceps                 | 9067.94   | 29  | 384.64      | FMNH 68810 |
| Primates             | Atelos geoffroyi                 | 7582.4    | 29  | 432.53      | FMNH 121526 |
| Primates             | Atelos paniscus                  | 8697.25   | 29  | 432.53      | FMNH 121546 |
| Primates             | Cebus capucinus                  | 3005.99   | 29  | 291.03      | |
| Primates             | Cheirogaleus medius              | 196.76    | 29  | 89.27       | |
| Primates             | Chiroptes satanas                | 2967.27   | 29  | 291.38      | |
| Primates             | Daubentonia madagascariensis     | 2731.37   | 29  | 362.12      | |
| Primates             | Eulemur mongoz                   | 1771.13   | 29  | 313.78      | |
| Primates             | Gorilla gorilla                  | 112588.99 | 29  | 713.32      | FMNH 18402 |
| Primates             | Hapalemu griseus                 | 916       | 29  | 214.86      | |
| Primates             | Lemur catta                      | 2626.48   | 29  | 294.15      | FMNH 127368 |
| Primates             | Leontopithecus rosalia           | 592.52    | 29  | 172.08      | FMNH 134505 |
| Primates             | Loris tardigradus                | 249.22    | 29  | 132.74      | FMNH 180671 |
| Primates             | Macaca fascicularis              | 4569.32   | 29  | 313.28      | FMNH 61026 |
| Primates             | Macaca mulatta                   | 6455.19   | 29  | 311.22      | FMNH 99668 |
| Primates             | Mandrillus sphinx                | 16685.06  | 29  | 564.95      | FMNH 121292 |
| Primates             | Nycticebus pygmaeus              | 342.32    | 29  | 144.04      | FMNH 108856 |
| Primates             | Pan troglodytes                  | 45000     | 29  | 613.14      | |
| Primates             | Papio ursinus                    | 17722.44  | 29  | 407.61      | FMNH 159985 |
| Primates             | Pithecus pithecus                | 1667.19   | 29  | 285.07      | FMNH 95509 |
| Primates             | Propithecus coquereli            | 4189.27   | 29  | 482.8       | |
| Primates             | Pygathrix cinerea                | 10990     | 29  | 476.37      | |
| Primates             | Pygathrix nemaeus                | 9411.1    | 29  | 441.83      | FMNH 214917 |
| Primates             | Rhinopithecus roxellana          | 13456.8   | 29  | 399.82      | FMNH 31143 |
| Primates             | Saimiri sciureus                 | 749.47    | 29  | 199.81      | FMNH 93519 |
| Primates             | Sapajus apella                  | 2758.38   | 29  | 290.62      | FMNH 98046 |
| Primates             | Trachypithecus delacouri         | 8200      | 29  | 452.21      | |
| Primates             | Trachypithecus hatinhensis       | 8700      | 29  | 487.94      | |
| Primates             | Trachypithecus payrerl           | 7681.72   | 29  | 496.73      | |
| Primates             | Trachypithecus poliocephalus     | 9000      | 29  | 466.64      | |
| Primates             | Varecia variegata                | 3849.99   | 29  | 323.41      | |
| Rodentia             | Apodemus agrarius                | 21.11     | 29  | 59.96       | FMNH 179117 |
| Rodentia             | Apodemus flavicolis              | 31.6      | 29  | 59.96       | FMNH 179117 |
| Rodentia             | Castor canadensis                | 18124.41  | 29  | 201.94      | FMNH 134455 |
| Rodentia             | Eretihzon dorsatum               | 7419.46   | 29  | 206         | M.C.G. |
| Rodentia             | Hydrochoerus hydrochaeris        | 48144.91  | 29  | 473.96      | FMNH 51536 |

7Used Vombatus ursinus
8Zhe-Xi Luo personal collection
9Zhe-Xi Luo personal collection
10Used Ateles geoffroyi
11Used Apodemus mystacinus
12Used Apodemus mystacinus
13Unpublished data
| Order     | Species               | Mass  | Ref | Length | Ref       |
|-----------|-----------------------|-------|-----|--------|-----------|
| Rodentia  | Mesocricetus auratus  | 98.6  | [29] | 65.02  | [29] FMNH 122237 |
| Rodentia  | Micromys minutus      | 6.99  | [29] | 28.41  | [29] FMNH 129466 |
| Rodentia  | Mus musculus          | 19.3  | [29] | 31.2   | [29] FMNH 140454 |
| Rodentia  | Muscardinus avellanarius | 29.19 | [29] | 41.44  | [29] FMNH 157986 |
| Rodentia  | Myodes glareolus      | 20.73 | [29] | 38.86  | [29] FMNH 163360 |
| Rodentia  | Rattus norvegicus     | 282.89| [29] | 94.63  | [29] FMNH 178182 |
| Rodentia  | Sciurus griseus       | 703.85| [29] | 141.94 | [29] FMNH 186950 |
| Rodentia  | Sciurus niger         | 765.9 | [29] | 179.8  | [29] FMNH 211205 |
| Rodentia  | Thallomys paedulcus   | 77.7  | [29] | 49.64  | [29] FMNH 145465 |
| Scandentia| Tupaia tana           | 182.33| [29] | 108.85 | [29] FMNH 145465 |

14 Used Muscardinus graphiurus
15 Used Myodes gapperi
16 Used Sciurus carolinensis
17 Used Grammomys macmillani
Table S3: Estimated ancestral phase values for key nodes derived using a phylogeny with temporal branch lengths and rate–based branch lengths

| Clade      | Time–based mean (95% CIs) | Rate–based mean (95% CIs) |
|------------|----------------------------|----------------------------|
| Gnathostomes | 44.44 (17.72–73.04)       | 46.76 (41.24–52.32)       |
| Tetrapods  | 42.54 (24.19–62.03)       | 42.44 (37.14–47.83)       |
| Amniotes   | 42.28 (25.21–60.36)       | 42.36 (36.32–48.52)       |
| Mammals    | 37.99 (22.08–55.36)       | 40.68 (30.28–51.52)       |
| Theria     | 37.90 (23.45–53.54)       | 41.46 (28.87–54.65)       |
Table S4: Comparison of fits for variable slope, variable intercept, and variable slope plus intercept models to single slope intercept models for phase as a function of relative limb length and of duty factor.

| predictor | model               | df | SS    | F      | P     |
|-----------|---------------------|----|-------|--------|-------|
| relative  | Common model        | 2  | 9.6684|        |       |
| limb      | Variable Slopes     | 3  | 9.5055| 2.5876 | 0.1098|
| length    | Variable Intercept  | 3  | 9.4586| 3.3497 | 0.0692|
|           | Variable Slope + Intercept | 4 | 9.4522| 1.7154 | 0.1834|
| arcsine   | Common model        | 2  | 9.7178|        |       |
| duty      | Variable Slopes     | 3  | 9.6154| 1.6069 | 0.2069|
| factor    | Variable Intercept  | 3  | 9.4848| 3.7081 | 0.056 |
|           | Variable Slope + Intercept | 4 | 9.3603| 2.864  | 0.0602|
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