



My branch is your branch: Talar morphology correlates with relative substrate size in platyrrhines at Tiputini Biodiversity Station, Ecuador

Doug M. Boyer^{a, *}, Gabriel S. Yapuncich^a, Noah T. Dunham^b, Allison McNamara^c, Liza J. Shapiro^c, Tobin L. Hieronymus^b, Jesse W. Young^b

^a Department of Evolutionary Anthropology, Duke University, Box 90383, Durham, NC, USA

^b Department of Anatomy and Neurobiology, Northeast Ohio Medical University, Rootstown, OH, USA

^c Department of Anthropology, University of Texas at Austin, Austin, TX, USA

ARTICLE INFO

Article history:

Received 6 February 2019

Accepted 24 May 2019

Available online 17 June 2019

Keywords:

Allometry

Fibular facet angle

Medial talotibial facet

Positional behavior

Adaptation

Functional morphology

ABSTRACT

Given that most species of primates are predominantly arboreal, maintaining the ability to move among branches of varying sizes has presumably been a common selective force in primate evolution. However, empirical evaluations of the relationships between morphological variation and characteristics of substrate geometry, such as substrate diameter relative to an animal's body mass, have been limited by the lack of quantified substrate usage in the wild. Here we use recently published quantitative data to assess the relationships between relative substrate size and talar morphology in nine New World monkey species at the Tiputini Biodiversity Station, Ecuador. Within this sample, both fibular facet angle (the angle between the fibular facet and the trochlear rims) and body-mass-standardized area of the medial tibial facet decrease as average and maximum relative substrate size increases. Correlations between medial tibial facet area and relative substrate size are driven by the inclusion of callitrichids in this sample. Nevertheless, these findings strengthen the hypothesis that variation in fibular facet orientation and medial tibial facet area are functionally correlated with habitual degrees of pedal inversion. They also strengthen the notion that evolutionarily changing body mass could impact habitat geometry experienced by a lineage and thereby substantially impact major trends in primate morphological evolution. This study highlights the importance of empirical data on substrate use in living primates for inferring functional and evolutionary implications of morphological variation.

© 2019 Elsevier Ltd. All rights reserved.

1. Introduction

Primate postcranial morphologies and their variation are usually interpreted as adaptations to the mechanical rigors of positional behaviors necessitated by arboreal habitats (e.g., Jones, 1916; Ashton and Oxnard, 1964; Napier and Walker, 1967; Rein et al., 2011). However, the difficulties of establishing relationships between morphology and behavior are also well recognized (e.g., Bock and von Wahlert, 1965; Lauder, 1995). For many primates species, one major limitation in our ability to understand form-function relationships is thought to be the lack of detailed information on positional behavior and habitat architecture (Kinzey, 1967; Ripley, 1967). In their review of primate positional behavior studies, Dagosto and Gebo (1998) identified 'Ripley's challenge' as

the pursuit of all information required for "an exhaustive study of total locomotor pattern" (Ripley, 1967:149), including data on behavioral repertoires, frequency of behaviors, environmental context, kinematics, and energetic costs.

Since the formulation of Ripley's challenge, several detailed studies have expanded the literature on primate positional behavior (reviewed in Bezanson, 2017). Among these contributions, a recent study by Dunham et al. (2018) represents an important advance in meeting this challenge. Specifically, Dunham et al. (2018) developed methods to quantify gait kinematics and substrate properties in free-ranging primate populations at a level of detail previously limited to laboratory settings. They tested and applied these methods at the Tiputini Biodiversity Station (TBS), Ecuador, collecting data on nine sympatric platyrrhine species. Data of the type collected by Dunham et al. (2018) are tremendously valuable for evaluating hypotheses relating morphological features to primate positional behavior. In this paper, we use empirical data from Dunham et al. (2018) to evaluate multiple hypotheses linking

* Corresponding author.

E-mail address: dmb65@duke.edu (D.M. Boyer).

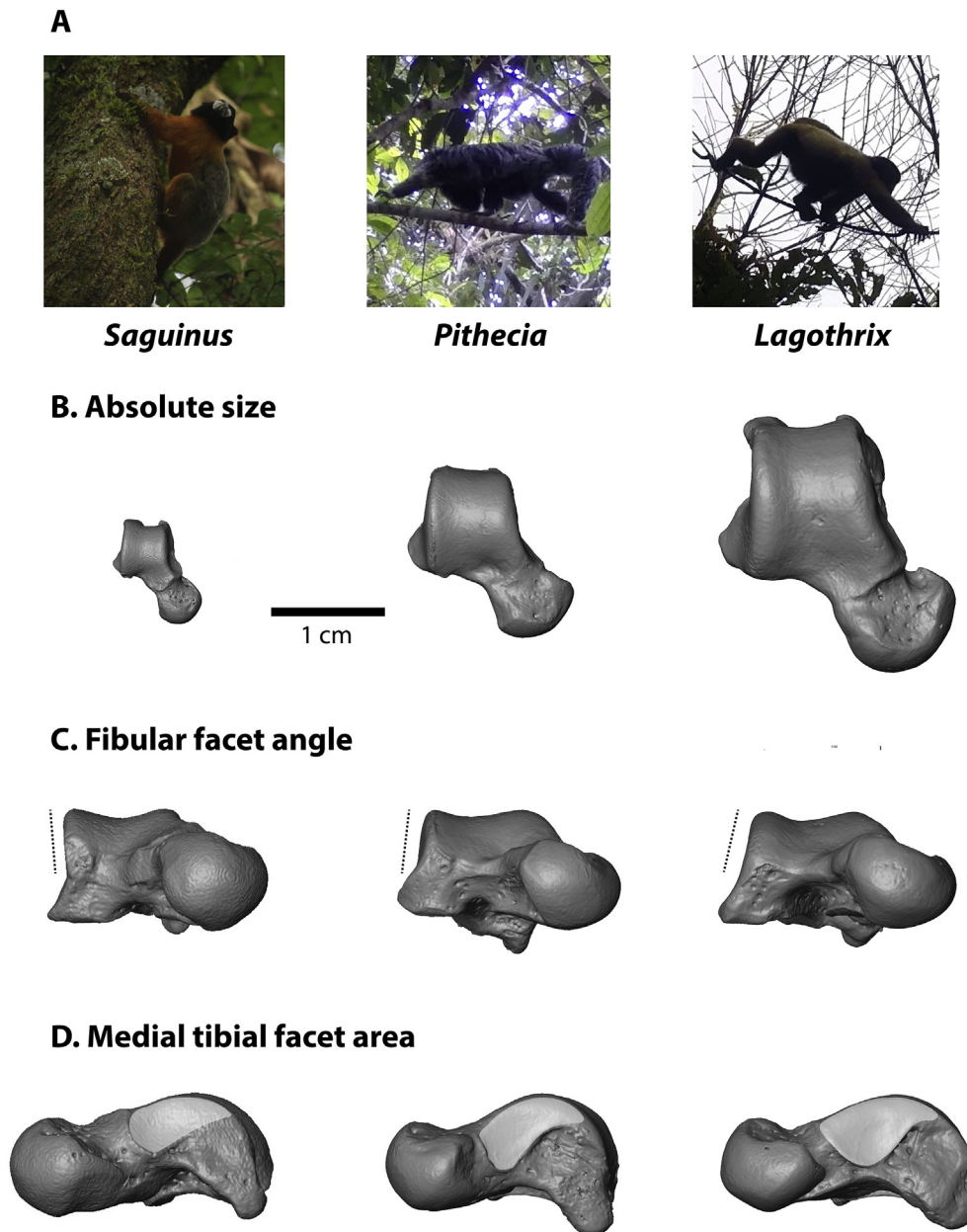


Figure 1. Three panel figure showing photos of differently sized monkeys from Tiputini with a 3D model of the talus below showing variation. Direct links in MorphoSource to all 3D models measured for the morphology data of this study can be found in [SOM Table S1](#).

variation in talar morphology with relative substrate size (Fig. 1; Boyer and Seiffert, 2013; Boyer et al., 2015; Yapuncich et al., 2017).

As emphasized by Jenkins (1974), substrate size is a relative concept, meaningful only with respect to the size of the animal. Across a common environment, the larger primate species may tend to use relatively smaller substrates than the smaller primates.¹ While earlier studies of sympatric primates found that bigger primates actually selectively use larger branches (e.g., Fleagle and Mittermeier, 1980), results from Dunham et al. (2018)

indicate that primate species of different sizes generally use similarly sized substrates. Specifically, they recovered an inverse relationship between relative substrate diameter and body mass in platyrrhine species at the TBS. Mean and maximum absolute substrate diameters were not significantly correlated with body mass, further emphasizing that it is the relative size of substrates that pose biomechanical challenges for primates at TBS.

A relationship between relative substrate size and body mass has been a crucial assumption for multiple studies of talar morphological variation in primates. For example, Dagosto (1988) proposed that derived characteristics of the strepsirrhine ankle (including a sloping fibular facet, a relatively large medial tibial facet [MTF], and a laterally positioned groove for the tendon of flexor fibularis) evolved as a result of basal increases in body size within the strepsirrhine lineage. Essentially, Dagosto (1988)

¹ In theory, a set of sympatric species with a range of body sizes could be restricted to specific substrate sizes (i.e., a substrate size 'niche'), so that there is no variation in relative substrate size. However, to our knowledge, there is no evidence for this type of partitioning among sympatric primate species. It is likely that selection pressures for traveling and foraging across a wide range of substrate sizes force primates of different sizes to navigate a range of relative substrate sizes.

proposed that strepsirrhine talar morphology reflects selective pressures for pedal grasping of relatively smaller substrates.

Building on [Dagosto \(1988\)](#) and other qualitative work ([Dagosto, 1985; Gebo, 1986a, b, 1987a, b, 1988, 1993; Dagosto, 1990, 1993](#)), Boyer and colleagues conducted quantitative surveys of several talar features ([Boyer and Seiffert, 2013; Boyer et al., 2015; Yapuncich et al., 2017](#)) and made multiple predictions relying on the assumption that larger primates utilize relatively smaller substrates. To date, in vivo kinematic support for this assumption has been very limited to non-existent. [Yapuncich et al. \(2017:6\)](#) cited [Toussaint et al. \(2015\)](#) when stating “larger-bodied euarchontans may more frequently encounter relatively small substrates that require more highly abducted and inverted foot postures”. While [Toussaint et al. \(2015\)](#) documented an apparent preference for relatively large substrates in the smallest living primate *Microcebus*, these findings do not necessarily imply the inverse condition (more frequent use of relatively smaller substrates among large bodied primates). Moreover, [Toussaint et al.'s \(2015\)](#) study was conducted in a laboratory setting, and it is not clear whether *Microcebus* would behave similarly in its natural environment. In fact, earlier studies of wild primates present evidence that larger species use absolutely larger branches (e.g., [Fleagle and Mittermier, 1980; McGraw, 1996](#)), thereby implying that relative substrate size does not vary profoundly with body size. Therefore, the results from [Dunham et al. \(2018\)](#) are intriguing for their support of the conceit that larger free-ranging primate species use relatively smaller substrates and because they permit the direct assessment of the relationships between talar morphology and relative substrate size.

Here, in an effort to strengthen the relationship between skeletal morphology and postural behavior, we test for correlations between quantified talar features (fibular facet angle, relative MTF size, and flexor hallucis longus groove position) and relative substrate size in the genera at TBS. The predictions of this study are motivated by results of [Boyer and Seiffert \(2013\), Boyer et al. \(2015\), and Yapuncich et al. \(2017\)](#). Specifically, [Boyer and Seiffert \(2013\)](#) recovered significant correlations between body mass and fibular facet angle among strepsirrhines and platyrrhines. [Boyer et al. \(2015\)](#) recovered a significant positive correlation between body mass and relative MTF area in strepsirrhines (but not platyrrhines). Both studies proposed that these correlations were driven by the use of more inverted foot postures in larger bodied species in order to accommodate grasping relatively smaller substrates. We therefore predict that fibular facet angle and relative MTF area will increase as relative substrate size decreases across genera. [Yapuncich et al. \(2017\)](#) recovered significant correlations between body mass and flexor hallucis longus groove position among strepsirrhines and anthropoids, and argued this correlation reflects a tendency of smaller species to use more abducted foot postures on relatively larger vertical supports. We therefore predict that the flexor hallucis longus groove will become more laterally positioned as relative substrate size increases across genera. Although significant correlations with body size were not observed within platyrrhines for certain talar features (relative MTF area and flexor hallucis longus groove position), recovering significant correlations in the kinematic data from TBS would nonetheless provide support that these features are related to postures thought to correlate with relative substrate size (degrees of pedal inversion and/or abduction).

While we think that exploring correlations between substrate size and talar morphology is a valid approach for testing form-function hypotheses, there is a substantial risk of type II error (accepting a false null hypothesis) in this study due to the many assumptions required. Additional factors could interact to produce negative results even if it is true that talar morphological variables of this study are influenced by selection for different, substrate-size

correlated tendencies in pedal inversion. There are three kinds of assumptions: 1) intrageneric and intraspecific differences in behavior are minimal and/or have not had a strong impact on postcranial morphology; 2) different tendencies in positional behavior and/or grasping mode among focal species are less important drivers of tarsal variation than relative support size; and 3) behavioral tendencies observed at TBS are representative of the conditions under which each species/genus evolved.

The first assumption is required because this study uses genus-level groups of morphology. Generic averages were used because species level matches between the morphological and kinematic datasets were not always possible. For the morphological variables examined in this study, ranges for different species of the same genus generally overlap ([Boyer and Seiffert, 2013; Boyer et al., 2015; Yapuncich et al., 2017](#)), but it is possible that increased sampling could reveal important differences in mean values. This assumption also implies that variation among individuals due to postnatal effects tend to be inconsequential for the features of interest.

Regarding the second assumption, pronounced diversity in positional behavior among species in this sample could be an important confounding variable. Among the examined species, *Ateles* and *Lagothrix* tend to emphasize suspensory postures; *Saimiri*, *Alouatta* and *Callicebus* are arboreal quadrupeds; *Cebus*—also a quadruped—may use terrestrial substrates more frequently; *Pithecia* is a more specialized leaper than the others; and *Callithrix* and *Saguinus* frequently use vertical supports (e.g., [Fleagle and Mittermier, 1980; Youlatos, 1999; Cant et al., 2003; Barrett et al., 2018; Dunham et al., 2018](#)). Even for species in the same locomotor category, qualitatively different anatomical traits may substantially alter the stress environment experienced by their joints. In particular, *Cebus* and the atelids in this sample have prehensile tails that they use during locomotion (albeit with different frequencies), while the callitrichids have functional claws instead of nails. It seems plausible that taxonomic differences in positional behavior could impose stresses that override selective effects of variation in foot inversion tendencies as mediated by relative support size during the bouts of pronograde locomotion observed by [Dunham et al. \(2018\)](#). Unfortunately applying statistical tests of the effect of ‘locomotor category’ is not possible due to the small number of species relative to the number of categories.

2. Methods

We examined six talar morphological variables ([Fig. 2](#)): fibular facet angle (Ffa), medial tibial facet area standardized to body mass (MTF0), medial tibial facet area standardized to ectal facet area (MTF1), medial tibial facet shape (MTF2), medial tibial facet coverage of the medial surface of the trochlea (MTF3), and flexor hallucis longus groove position (FHLG-P). For each morphological variable, we computed generic averages for the nine genera observed at TBS ([Table 1](#)).

Measurement and computational protocols are presented in detail in previous publications ([Boyer and Seiffert, 2013; Boyer et al., 2015; Yapuncich et al., 2017](#)). Values were collated from the supplementary data of [Boyer et al. \(2015: Table S3\)](#) for MTF0 and of [Boyer et al. \(2017: Table S4\)](#) for the others. See also [Supplementary Online Material \(SOM\) Tables S1–S2](#) of the current study for data used to make [Table 1](#). Data in [SOM Table S1](#) also includes data plotted in [Fig. 4](#). Finally, [SOM Table S1](#) of the current study includes DOI links (pointing to [MorphoSource.org](#)) to 3D models of all tali measured by previous authors and used in this study.

In brief, here are the protocols used by previous studies to measure and compute morphological variables utilized here. In all cases, these previous studies performed measurements on 3D models instead of physical specimens. Measurements were

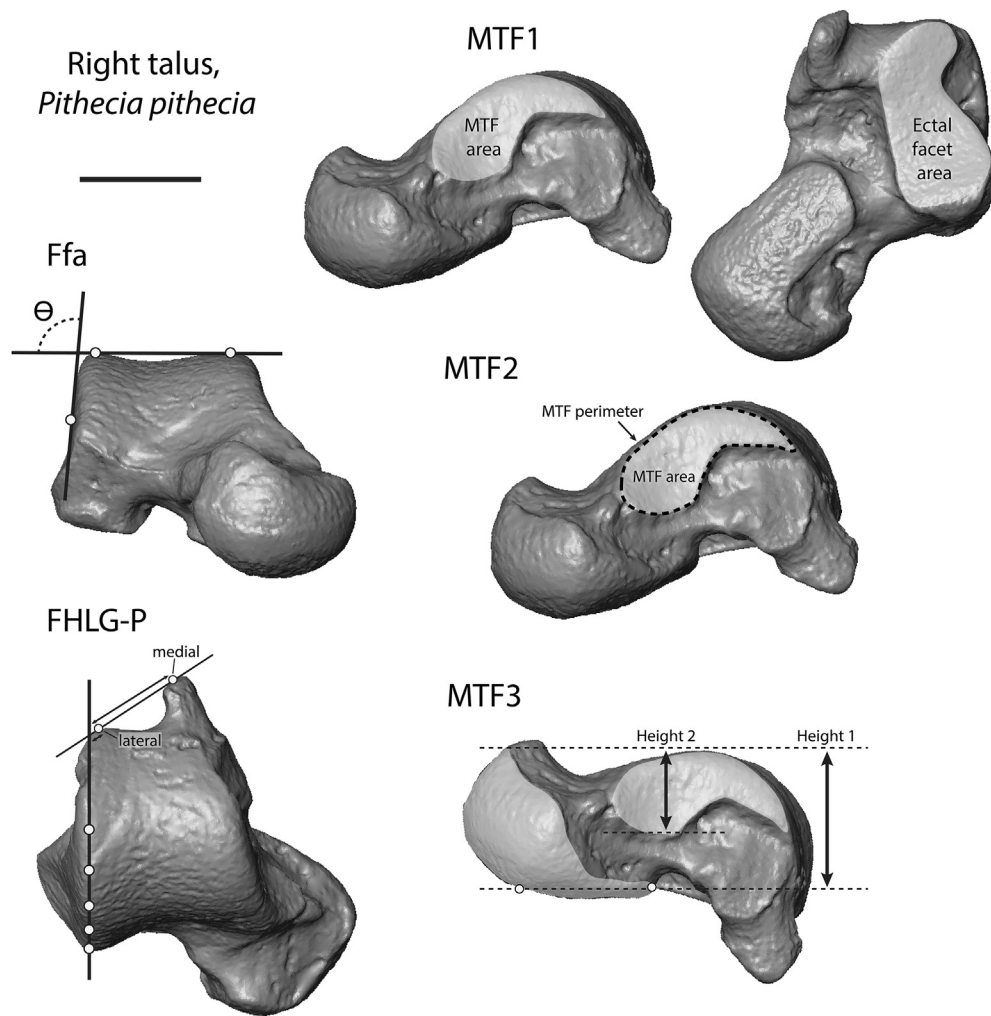


Figure 2. Illustration of talar measurements examined in this study using *Pithecia* (AMNH M 149149). Scale bar = 5 mm.

Table 1
Dataset used in all analyses. Morphological variables are defined in methods and taken from Boyer et al. (2015, 2017). MeanD, minD, and maxD summarize substrate diameter data from Dunham et al. (2018).

Taxon	Mass ^a	n (talus) ^b	Ffa ^a	MTF0	MTF1	MTF2	MTF3	FHLG1	FHLG2	meanD ^a	minD	maxD	n (D) ^c
<i>Alouatta</i>	5.95	3	98.00	−1.14	−0.39	1.60	0.29	−0.73	0.77	5.61	1.40	15.10	206
<i>Ateles</i>	8.10	3–6	100.33	−1.06	−0.35	1.57	0.22	−0.81	1.21	8.79	1.50	19.40	97
<i>Callicebus</i>	1.05	5	96.48	−0.99	−0.15	1.66	0.33	−0.76	1.13	2.76	0.40	11.90	203
<i>Cebuella</i>	0.12	5	80.90	−1.26	−0.18	1.73	0.26	−0.73	0.12	12.45	0.40	55.60	98
<i>Cebus</i>	2.75	3–5	90.52	−1.02	−0.13	1.74	0.27	−0.73	1.30	6.01	2.80	9.60	15
<i>Lagothrix</i>	7.11	4	101.96	−1.17	−0.27	1.58	0.15	−0.76	0.41	7.55	1.20	23.90	204
<i>Pithecia</i>	2.36	2–3	96.90	−1.05	−0.24	1.68	0.30	−0.75	0.64	4.56	1.00	25.20	208
<i>Saguinus</i>	0.35	6	86.09	−1.14	−0.19	1.65	0.31	−0.75	0.38	4.83	0.60	45.20	89
<i>Saimiri</i>	0.72	4–5	93.64	−0.96	−0.14	1.72	0.21	−0.76	1.21	3.84	0.60	19.40	204

^a Units: mass in kg, FFA in degrees, D in cm.
^b n (talus) is the number of individuals included in each talar variable. It is a range because MTF0 comes from a slightly different dataset (Boyer et al., 2015:Table S3) than the other variables (Boyer et al., 2017:Table S4) and therefore some species are represented by a different number of individuals. However, in all cases the smaller sample is a subsample of the larger (rather than an independent sample).
^c n (D) is the number of independent observations of a species using a support that was measured and used to compute meanD, minD, and maxD.

performed in either Avizo 8.1 (Visualization Sciences, 2014) or Geomagic Studio v.2014 (3D Systems Inc., 2013). To compute Ffa, Boyer and Seiffert (2013) selected patches on the medial and lateral trochlear rims as well as on the fibular facet. To avoid the ‘lateral flare’ of the more plantar portion, the fibular facet selection was restricted to its dorsal portion. Separate planes were fit to the trochlear rim patches and the fibular facet patch in SPSS (IBM Corporation, 2010); the maximum angle of intersection between these two planes represents the fibular facet angle (Fig. 2). For MTF0, Boyer et al. (2015) selected the medial tibial facet (MTF) and computed its area. The relative area of the MTF was then expressed as a ratio of its square root to the cube root of species mean body mass. For MTF1, Boyer et al. (2015) expressed MTF area as a ratio of its square root to the square root of ectal

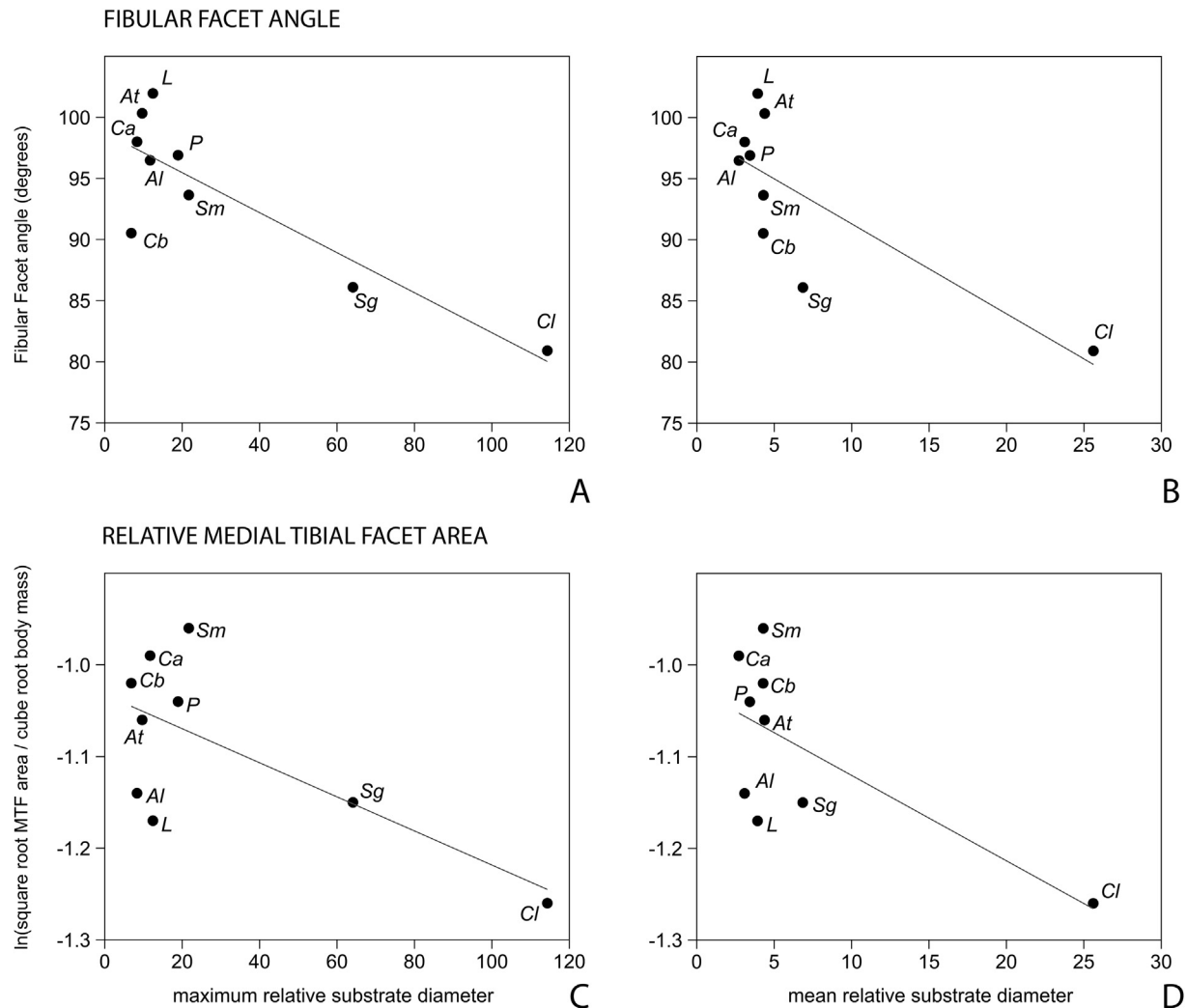


Figure 3. Correlation between relative mean and maximum substrate diameter and fibular facet angle in the Tiputini platyrrhines (A, B), as well as for relative medial tibial facet area (C, D). Each data point is the mean value for the genus (Table 1). Both sets of relationships are highly significant using phylogenetic generalized least squares (see text). Abbreviations: Al = *Alouatta*; At = *Ateles*; Ca = *Callicebus*; Cb = *Cebus*; Cl = *Cebuella*; L = *Lagothrix*; P = *Pithecia*; Sg = *Saguinus*; Sm = *Saimiri*.

facet area. For MTF2, Boyer et al. (2015) quantified the shape of the medial tibial facet as the ratio of the facet perimeter to the square root of originally measured MTF area. For MTF3, Boyer et al. (2015) quantified the degree to which the MTF covers the medial side of the trochlea by taking the ratio of the dorsoplantar ‘depth’ of the entire medial trochlea (Fig. 2: Height 1) to the height of the MTF (Fig. 2: Height 2). Heights were measured orthogonal to a reference line running along sustentacular facet (Fig. 2). To compute FHLG-P Yapuncich et al. (2017) began each measurement by placing landmarks along the lateral rim of the trochlea in order to create reference line for groove position (Fig. 2). Maintaining this reference line, the specimen was then rotated until the major axis of the groove paralleled the viewing plane. Next, landmarks were placed on the most medial and lateral margins of the groove, and a second reference line was drawn through these landmarks. Distances from the medial and lateral landmarks to the first reference line were measured along the second reference line. Groove position was expressed as the ratio of the total width (medial + lateral distances) relative to the total width, plus the medial distance. More detailed measurement protocols can be found in Boyer and Seiffert (2013), Boyer et al. (2015), and Yapuncich et al. (2017).

For substrate variables, we followed Dunham et al. (2018). Specifically, we took mean, minimum, and maximum absolute substrate diameters observed for each species. We converted these metrics to relative values by dividing them by the cube root of species mean body mass. Body mass data were taken from Smith and Jungers (1997). Because Dunham et al. (2018) could not identify the sex of individual monkeys in their sample, sexes were pooled when calculating species mean body masses. All observations occurred during bouts of above-branch quadrupedalism.

Phylogenetic generalized least squares (pGLS) analyses were run in R (R Core Team, 2012) using the package ‘caper’ (Orme et al., 2012). The phylogenetic tree used in these analyses was downloaded from 10ktrees.org (Arnold et al., 2010) and is an ultrametric chronogram (i.e., branch lengths represent time in millions of years). We ran analyses using the maximum likelihood value of Pagel’s λ . This λ parameter adjusts the branch lengths to help mitigate phylogenetic autocorrelation (e.g., Nunn, 2011). Studies have shown that small sample sizes can lead to unreliable estimates of Pagel’s λ (Münkemüller et al., 2012). Therefore, we also checked to see whether misestimating Pagel’s λ would change our conclusions by rerunning analyses using $\lambda = 1$ and 0. The datasets and R code are available as supplementary information (SOM Files S1–S3).

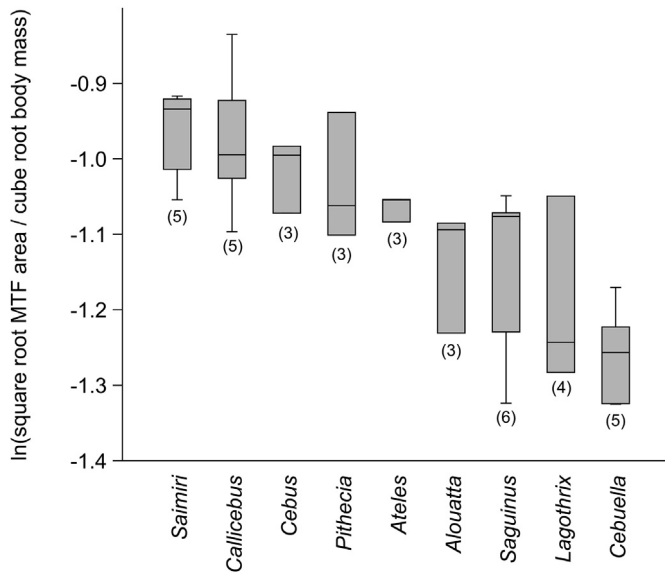


Figure 4. Variation in MTF0 values in each genus. Data points are individuals. Number of individuals per plot given in parentheses below box. Multiple species represented. See SOM Table S2 for included species. See SOM Table S1 for individual data points. Black line within box is median. Box itself includes 75% quartiles. Whiskers encompass 100% of data.

3. Results

Assessed with pGLS regression, fibular facet angle (Ffa) was negatively correlated with both relative mean and relative maximum substrate diameters (Fig. 3; Table 2), indicating that as Ffa becomes more obtuse, substrate diameter becomes relatively smaller. Body mass standardized medial tibial facet area (MTF0) was negatively correlated with relative mean and relative maximum substrate diameters, indicating that as MTF area becomes relatively larger, substrate diameter becomes relatively smaller. We only report results of analyses using the maximum likelihood value of Pagel's λ in Table 2. However, when two variables were found to be significantly correlated, we also tested whether they were significant using $\lambda = 1$ and 0. In no case did changing λ cause a previously significant result to become non-

Table 2
Results of pGLS analyses of data from Table 1 p-values in bold are significant at $\alpha \leq 0.05^a$.

Morphology	Relative substrate ^b	Pagel's λ	slope	p (slope)
Ffa	rmeanD	1	−0.5960	0.022
Ffa	rminD	1	−3.3200	0.503
Ffa	rmaxD	1	−0.1450	0.005
MTF0	rmeanD	0.34 ^a	−0.010	0.036
MTF0	rminD	0.65	0.02	0.814
MTF0	rmaxD	0.68 ^a	−0.002	0.033
MTF1	rmeanD	1	0.0010	0.737
MTF1	rminD	1	0.0340	0.629
MTF1	rmaxD	1	0.0004	0.644
MTF2	rmeanD	1	0.0030	0.254
MTF2	rminD	1	0.0520	0.246
MTF2	rmaxD	1	0.0006	0.362
MTF3	rmeanD	0.532	−0.0004	0.885
MTF3	rminD	0.521	0.0090	0.851
MTF3	rmaxD	0.366	0.0001	0.813
FHLGP	rmeanD	0	0.0010	0.382
FHLGP	rminD	0	0.0210	0.299
FHLGP	rmaxD	0	0.0002	0.375

^a Analyses that fixed Pagel's λ at 1.0 were significant at the same level.

^b Substrate diameters made relative by dividing absolute values (meanD, maxD, minD) by cube root of body masses in Table 1.

significant. All other pGLS regressions between morphological features and relative substrate diameter variables were non-significant (Table 2). Removing callitrichids from the sample renders all correlations non-significant, though trends of the same sign remain for Ffa vs. mean and maximum relative substrate diameter.

4. Discussion and conclusions

4.1. Functional interpretation of talar variables

Pedal inversion is often implied as a mechanical requirement for prehensile grasping of relatively small diameter substrates (e.g., Lewis, 1980; Dagosto, 1985; Gebo, 1986a, b). Therefore, negative correlations of fibular facet angle (Ffa) and relative medial tibial facet area (MTF0) with relative mean substrate diameter are consistent with a prediction of the hypothesis of Boyer and Seiffert (2013) and Boyer et al. (2015), that variation in these talar features is driven by degrees of pedal inversion. Although our results are derived from specific observations of platyrrhine talar morphology and substrate use, they support the general hypothesis that even more obtuse fibular facet angles and relatively larger MTFs in strepsirrhines reflect habitual use of more strongly inverted foot postures than anthropoids (e.g., Gebo, 1986a, b). Finally, our results are consistent with the suggestion of Dagosto (1988) that the origin of strepsirrhine ankle features reflect a basal increase in body mass (and the correlated use of relatively smaller substrates).

Boyer and Seiffert (2013), Yapuncich and Boyer (2014), and Boyer et al. (2015) reasoned that a more obtuse Ffa and relatively larger MTF would be biomechanically important features supporting foot inversion if the talus, itself, was involved in the inversion movements (i.e., if its plantar surface is rotated to face somewhat medially during inversion). In this configuration, a more obtuse Ffa can maintain compressive stress and avoid shearing stress at greater extremes of pedal inversion (Boyer and Seiffert, 2013; Fig. 10). Similarly, Gebo (1986a, b, 1993, 2011) argued that a more obtuse Ffa allows the fibular facet to take on a greater weight-bearing role, particularly during vertical postures. Gebo and other researchers also noted that a more obtuse Ffa increases ankle mobility during abduction and adduction of the foot (Lewis, 1980; Gebo, 1986a, b, 1993, 2011; Dagosto, 1985, 1986, 1988). Abduction during dorsiflexion and adduction during plantarflexion may be particularly important to an animal locomoting on a relatively small diameter supports (Lewis, 1980; Dagosto, 1985, 1986). Boyer and Seiffert (2013) proposed a detailed kinematic rationale supporting this functional interpretation. The strength of the relationships between Ffa and specific movements at the talocrural joint (inversion versus abduction) could be more extensively evaluated with additional data, including loading patterns and kinematic data for joint angles on different kinds of supports.

A relatively larger MTF in strepsirrhines (compared to anthropoids) has been linked to a correspondingly elongated medial malleolus and is argued to be important to “hold the talus secure” (Gebo, 1993:141) during abducted and inverted foot postures on vertical supports (Dagosto, 1985, 1988; Gebo, 1986a, b, 1993, 2000, 2011). Yapuncich and Boyer (2014) and Boyer et al. (2015) downplayed the role of vertical postures when contrasting the relative MTF areas of anthropoids and strepsirrhines, placing more importance on the use of relatively small, medially positioned supports of any orientation. As with Ffa in Boyer and Seiffert (2013), the link between MTF area and small diameter support use requires that the talus itself is involved in inversion so that the MTF is oriented more horizontally and experiences greater compressive stress (Yapuncich and Boyer, 2014; Boyer et al., 2015). Recovering a significant relationship between MTF0 and relative substrate size

within the TBS sample emphasizes that vertical postures in and of themselves do not explain expanded MTF areas.

Dunham et al. (2018) also collected substrate orientation data. These data reveal that 1) there is very little interspecific variation in substrate orientation with the exception of *Cebuella*, which tends to use more vertically oriented supports, whereas 2) the higher support angle of *Cebuella* combined with smaller MTF area induces a (non-significant) trend that is opposite the expected direction. Specifically, the facet is relatively small in *Cebuella* instead of relatively large (Table 1). While there are important biomechanical differences for vertical support use in callitrichids and strepsirrhines, the available data provide no evidence that substrate orientation drives MTF size. Nevertheless, we recognize that different primate communities (especially ones with different taxa) could present different patterns. For instance, it is possible that a strepsirrhine community could show a correlation between MTF area and substrate orientation.

It may seem problematic that MTF1, another variable reflecting medial tibial facet relative area, and relative substrate diameter were uncorrelated here. However, Boyer et al. (2015) addressed why the tendency for the ectal facet (the denominator of the variable) to scale with positive allometry (Yapuncich et al., 2014) is likely to obscure the expected trend. Likewise, while MTF2 and MTF3 are related to the relative area of the medial tibial facet, and tend to distinguish prosimians from anthropoids, there are many conceivable talar morphologies that maintain constant MTF0 and MTF1, but allow MTF2 and MTF3 to vary.

A laterally positioned flexor hallucis longus groove (FHLG-P) has also been proposed to be an osteological correlate of abducted and inverted foot postures on small diameter vertical supports (Gebo, 1986b, 1993; Dagosto, 1988, 2011). Through quantitative assessment, Yapuncich et al. (2017) found that the groove became more medially positioned as body size increased within strepsirrhines and anthropoids (though not within platyrrhines). The authors related these trends to the use of abducted foot postures on relatively larger and vertical supports, arguing that a more laterally positioned groove remains within the line of action of the FHL tendon over a greater range of abduction (Yapuncich et al., 2017; Fig. 11). Finding a correlation between FHLG-P and relative substrate size would have added support to the functional hypothesis proposed by Yapuncich et al. (2017), but the absence of such a relationship is not surprising, given that there was no correlation between FHLG-P and body size within platyrrhines. In general, anthropoids do not exhibit much variation in flexor hallucis longus groove position (Gebo, 1986b; Yapuncich et al., 2017), and genera in Dunham et al.'s (2018) sample represent only 7% of the sampled range of variation observed across extant euarchontans, compared to the 47% of total range of variation that the TBS genera sampled represent for fibular facet angle (Yapuncich et al., 2017). Additionally, the lack of extensive usage of vertical supports by most platyrrhines may explain the absence of a relationship between FHLG-P and relative substrate size in the current sample. A strepsirrhine sample similar to the TBS dataset would provide a more robust test of the hypothesized relationship between FHLG-P and relative substrate size.

4.2. Other behaviors affecting talus form

This study provides additional evidence for functional hypotheses that link variation in fibular facet angle (Ffa) and relative medial tibial facet area (MTF0) with pedal inversion (Boyer and Seiffert, 2013; Boyer et al., 2015). Though significant correlations for these variables were driven by callitrichids, we believe these correlations are valid expressions of the selective mechanisms influencing variation in Ffa and MTF0 for a number of reasons. First,

since callitrichids use relatively large tree trunks more frequently than other platyrrhines at Tiputini (Youlatos, 2009; Dunham et al., 2018), they are expected to use relatively everted foot postures more frequently as well. Second, the presence of claws should aid in avoiding abducted and inverted postures on vertical supports (e.g., Gebo, 1986b), since the ability to cling with claws is not contingent on the included angle of the digits (Cartmill, 1974). Third, though removing callitrichids renders correlations non-significant, negative trends for Ffa (i.e., in the direction predicted by the inversion hypothesis) remain with both maximum and mean relative substrate diameter, suggesting that variation in inversion tendencies affect Ffa even among non-callitrichid platyrrhines.

If Ffa variation primarily reflects functional differences, there must be other aspects of postural behavior (besides support size and inversion tendencies) affecting the residual variance in Ffa among non-callitrichids. One possibility is that a greater tendency for antipronograde activities requiring more foot mobility influences increased Ffa in *Ateles* and *Lagothrix* (e.g., Fleagle and Mittermeier, 1980; Cant et al., 2003), and that more frequent use of terrestrial behavior (reflecting larger relative substrate sizes) drove decreases in Ffa of *Cebus* (e.g., Barrett et al., 2018).

When reassessing the relationship between MTF0 and relative substrate size without callitrichids, the correlation is not significant and the trend is no longer negative. The absence of a relationship may indicate that while inversion tendencies (related to support size) are a valid explanation for MTF0 differences between callitrichids and other platyrrhines, other aspects of postural behavior influence MTF0 values within non-callitrichid platyrrhines. Again, greater tendencies for suspensory postures may have allowed evolution of smaller facet areas relative to body mass in *Lagothrix* and *Ateles*. However, in this scenario, we have no explanation for why *Alouatta* is more similar to *Lagothrix* in relative facet size than to *Ateles*. Furthermore, it is difficult to identify any behavioral traits that would explain the MTF0 differences between *Saimiri*, *Cebus*, *Pithecia*, and *Callicebus* (e.g., Fleagle and Mittermeier, 1980). Looking at intrageneric variation in MTF0 provides an alternative view, suggesting there are not actually any consistent differences in MTF0 among these four taxa (Fig. 4). The range of average MTF0 values in these four genera is 0.08 log units. However, the average interspecific standard deviation in a genus is 0.08 or more, indicating that variation within each group encompasses the differences between groups. The intraspecific standard deviation based on individuals is similar at 0.06 log units. The ranges of individual variation of the specimens comprising each genus also show extensive overlap (Fig. 4). If MTF0 is most correctly interpreted as uniform among these four genera, then whatever selective pressures are dominating their MTF0 variation must also be relatively uniform, even if relative substrate size and inversion tendencies differ.

4.3. Evolutionary implications

Our results suggest that relative support size (and inferred degree of pedal inversion) have a noticeable effect on fibular facet angle (Ffa), though other behavioral factors likely contribute to Ffa variance in platyrrhines. These findings therefore strengthen the suggestion of Boyer and Seiffert (2013) that relatively acute fibular facet angles in the tali of the ancestral euprimate and early strepsirrhines (including basal adapiforms) reflect use of relatively larger supports and more everted foot postures. The trends toward increasingly obtuse fibular facet angles within strepsirrhines (including various adapiform lineages) likely represent parallel instances of increasing specialization for small branch use (Boyer and Seiffert, 2013). This interpretation is consistent with Dagosto's (1988) suggestion that the appearance of a strepsirrhine

'suite' of pedal features may correspond to the evolution of larger body sizes in strepsirrhines and selection of these features for grasping relatively small substrates with an inverted foot.

Quantitative evolutionary trends in MTF area have also been interpreted as reflecting changes in specialization for pedal inversion (Boyer et al., 2015). In particular, the parallel trends of increasing MTF area in both basal strepsirrhine and haplorhine lineages reported by Boyer et al. (2015) were interpreted as reflecting parallel increases in specialization for the small branch niche. The correlation between MTF area and relative substrate size in TBS platyrrhines strengthens this interpretation, though MTF0 appears to respond to inversion differences more coarsely than Ffa in this sample.

4.4. Future directions

The results of this study add evidence supporting functional hypotheses relating talar fibular facet angle (Ffa) and relative medial tibial facet area (MTF) to pedal inversion tendencies, but it is clear that additional behavioral factors must be involved. It is possible that inversion tendency is not always the strongest determinant of Ffa and MTF0 values depending on the taxonomic group under study. Experimental data are needed to more rigorously test these hypotheses. Relative substrate diameter data for strepsirrhine communities (with collection methods modeled after Dunham et al., 2018) would help test the generality of the inversion hypothesis for these talar variables.

Finally, the link between pedal inversion and talar variables we have proposed here is only valid if the tendency for pedal inversion also correlates with relative substrate size. While it is possible that such data could also be gleaned from videos of wild animals, our sense is that studies seeking direct correlations between substrate geometry and foot posture would be better executed in controlled laboratory settings. These highlighted future directions would provide a great deal of information that could be leveraged to meet Ripley's challenge.

Acknowledgments

We wish to acknowledge National Science Foundation grants that supported this work. In particular D.M.B. was supported by BCS-1552848; DBI-1661386 and DBI-1701714. J.W.Y. and L.J.S. were supported by BCS-1640453 and BCS-1640552. Thanks to the Ecuadorian government for permission to conduct research at the Tiputini Biodiversity Station. Special thanks to the Universidad San Francisco de Quito, Tomi Sugahara, Diego Mosquera, Gabriela Vinuesa, Tony Di Fiore, Max Snodderly, Krista Milich, Laura Abondano, Natalia Camargo, Sam Rettke, Savannah Perez, Jacopo Cantoni, Laura Gómez, Cristian Alvarado, Renee Peters, and TBS staff who provided invaluable scientific and logistical support in Ecuador.

Supplementary Online Material

Supplementary online material to this article can be found online at <https://doi.org/10.1016/j.jhevol.2019.05.012>.

References

Arnold, C., Matthews, L.J., Nunn, C.L., 2010. The 10kTrees website: a new online resource for primate phylogeny. *Evolutionary Anthropology* 19, 114–118.
 Ashton, E.H., Oxnard, C.E., 1964. Locomotor patterns in primates. *Proceedings of the Zoological Society of London* 142, 1–28.
 Barrett, B.J., Monteza-Moreno, C.M., Dogandžić, T., Zwyns, N., Ibáñez, A., Crofoot, M.C., 2018. Habitual stone-tool aided extractive foraging in white-faced capuchins, *Cebus capucinus*. *Royal Society for Open Science* 5, 181002.

Bezanson, M., 2017. Primate positional behavior development and evolution. *Annual Review of Anthropology* 46, 279–298.
 Bock, W.J., von Wahlert, G., 1965. Adaptation and the form-function complex. *Evolution* 19, 269–299.
 Boyer, D.M., Seiffert, E.R., 2013. Patterns of astragalar fibular facet orientation in extant and fossil primates and their evolutionary implications. *American Journal of Physical Anthropology* 151, 420–447.
 Boyer, D.M., Toussaint, S., Godinot, M., 2017. Postcrania of the most primitive euprimate and implications for primate origins. *Journal of Human Evolution* 111, 202–215.
 Boyer, D.M., Yapuncich, G.S., Butler, J.E., Dunn, R.H., Seiffert, E.R., 2015. Evolution of postural diversity in primates as reflected by the size and shape of the medial tibial facet of the talus. *American Journal of Physical Anthropology* 157, 134–177.
 Cant, J.G., Youlatos, D., Rose, M.D., 2003. Suspensory locomotion of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuní National Park, Ecuador. *Journal of Human Evolution* 44, 685–699.
 Cartmill, M., 1974. Pads and claws in arboreal locomotion. In: Jenkins, F.A. (Ed.), *Primate Locomotion*. Academic Press, New York, pp. 45–83.
 Dagosto, M., 1985. The distal tibia of primates with special reference to the Omomyidae. *International Journal of Primatology* 6, 45–75.
 Dagosto, M., 1986. The joints of the tarsus in the strepsirrhine primates: functional, adaptive, and evolutionary implications. Ph.D. Dissertation, City University of New York.
 Dagosto, M., 1988. Implications of postcranial evidence for the origin of euprimates. *Journal of Human Evolution* 17, 35–56.
 Dagosto, M., 1990. Models for the origin of the anthropoid postcranium. *Journal of Human Evolution* 19, 121–139.
 Dagosto, M., 1993. Postcranial anatomy and locomotor behavior in Eocene primates. In: Gebo, D.L. (Ed.), *Postcranial Adaptation in Nonhuman Primates*. Northern Illinois University Press, DeKalb, pp. 199–219.
 Dagosto, M., Gebo, D.L., 1998. Methodological issues in studying positional behavior: Meeting Ripley's challenge. In: Strasser, E., Fleagle, J.G., Rosenberger, A.L., McHenry, H.M. (Eds.), *Primate Locomotion*. Plenum, New York, pp. 5–29.
 Dunham, N.T., McNamara, A., Shapiro, L., Hieronymus, T., Young, J.W., 2018. A user's guide for the quantitative analysis of substrate characteristics and locomotor kinematics in free-ranging primates. *American Journal of Physical Anthropology* 167, 569–584.
 Fleagle, J.G., Mittermeier, R.A., 1980. Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *American Journal of Physical Anthropology* 52, 301–314.
 Gebo, D.L., 1986a. The anatomy of the prosimian foot and its application to the primate fossil record. Ph.D. Dissertation, Duke University.
 Gebo, D.L., 1986b. Anthropoid origins—the foot evidence. *Journal of Human Evolution* 15, 421–430.
 Gebo, D.L., 1987a. Functional anatomy of the tarsier foot. *American Journal of Physical Anthropology* 73, 9–31.
 Gebo, D.L., 1987b. Locomotor diversity in prosimian primates. *American Journal of Primatology* 13, 271–281.
 Gebo, D.L., 1988. Foot morphology and locomotor adaptation in Eocene primates. *Folia Primatologica* 50, 3–41.
 Gebo, D.L., 1993. Functional morphology of the foot in Primates. In: Gebo, D.L. (Ed.), *Postcranial Adaptation in Nonhuman Primates*. Northern Illinois University Press, DeKalb, pp. 175–196.
 Gebo, D.L., Dagosto, M., Beard, K.C., Qi, T., Wang, J.W., 2000. The oldest known anthropoid postcranial fossils and the early evolution of higher primates. *Nature* 404, 276–278.
 Gebo, D.L., 2011. Vertical clinging and leaping revisited: Vertical support use as the ancestral condition of strepsirrhine primates. *American Journal of Physical Anthropology* 146, 323–345.
 Jenkins, F.A., 1974. Tree shrew locomotion and the origins of primate arborealism. In: Jenkins, F.A. (Ed.), *Primate Locomotion*. Academic Press, New York, pp. 85–115.
 Jones, F.W., 1916. *Arboreal Man*. Arnold, London.
 Kinzey, W.G., 1967. Preface. *American Journal of Physical Anthropology* 26, 115–118.
 Lauder, G., 1995. On the inference of function from structure. In: Thomason, J. (Ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, Cambridge, pp. 1–18.
 Lewis, O.J., 1980. The joints of the evolving foot. Part I. The ankle joint. *Journal of Anatomy* 130, 527–543.
 McGraw, S., 1996. Cercopithecoid locomotion, support use, and support availability in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology* 100, 507–522.
 Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffrers, K., Thuiller, W., 2012. How to measure and test phylogenetic signal. *Methods in Ecology and Evolution* 3, 743–756.
 Napier, J.R., Walker, A.C., 1967. Vertical clinging and leaping — a newly recognized category of primate locomotion. *Folia Primatologica* 6, 204–219.
 Nunn, C.L., 2011. *The Comparative Approach in Evolutionary Anthropology and Biology*. University of Chicago Press, Chicago.
 Orme, C.D.L., Freckleton, R.P., Thomas, G.H., Petzoldt, T., Fritz, S.A., Isaac, N.J.B., 2012. CAPER: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2, 458.
 R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

- Rein, T.R., Harrison, T., Zollikofer, C.P., 2011. Skeletal correlates of quadrupedalism and climbing in the anthropoid forelimb: implications for inferring locomotion in Miocene catarrhines. *Journal of Human Evolution* 61, 564–574.
- Ripley, S., 1967. The leaping of langurs: a problem in the study of locomotor adaptation. *American Journal of Physical Anthropology* 26, 149–170.
- Smith, R.J., Jungers, W.L., 1997. Body mass in comparative primatology. *Journal of Human Evolution* 32, 523–559.
- Toussaint, S., Herrel, A., Ross, C.F., Aujard, F., Pouydebat, E., 2015. Substrate diameter and orientation in the context of food type in the gray mouse lemur, *Microcebus murinus*: implications for the origins of grasping in primates. *International Journal of Primatology* 36, 583–604.
- Yapuncich, G.S., Boyer, D.M., 2014. Interspecific scaling patterns of talar articular surfaces within Euarchonta. *Journal of Anatomy* 224, 150–172.
- Yapuncich, G.S., Seiffert, E.R., Boyer, D.M., 2017. Quantification of the position and depth of the flexor hallucis longus groove in euarchontans, with implications for the evolution of primate positional behavior. *American Journal of Physical Anthropology* 163, 367–406.
- Youlatos, D., 1999. Comparative locomotion of six sympatric primates in Ecuador. *Annales des Science Naturelles* 20, 161–168.
- Youlatos, D., 2009. Locomotion, postures, and habitat use by pygmy marmosets (*Cebuella pygmaea*). In: Ford, S.M., Porter, L.M., Davis, L.C. (Eds.), *The Smallest Anthropoids*. Springer, Boston, pp. 279–297.