Using weighted spherical harmonics to detect functional locomotor signals at the distal femoral articulation

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Abstract: The femur has been used to estimate functional and behavioral signals from fossil material at key points during primate evolution: transitions to arboreality and bipedalism. As a habitually loaded bone, its articular surfaces facilitate joint mobility and transmit forces from the axial skeleton out to distal elements. Owing to this relationship, the femur is often the focus of functional studies and is central to questions regarding locomotion. The purpose of this study is to quantify the morphology of the entire distal femoral articulation across primates to detect which morphological features are functionally associated with locomotion.

A sample of 92 surface meshes was downloaded from MorphoSource, or surface scanned. A shape analysis of the distal femoral articulation was undertaken using spherical harmonics. This Fourier-based method models continuous surfaces as a sum of 3D trigonometric functions on the surface of a sphere. The coefficients associated with the functions are used in a principal component analysis to test for shape differences between locomotor groups. Average models were generated for each group to assess morphological differences attributable to a locomotor signal.

The first three PCs explain 60.08% of the morphological variation in this sample, and distinct locomotor groups are clustered. Arboreal quadrupeds are readily distinguishable from leapers, as are leapers from slow climbers. Relative to the rest of the sample, terrestrial and suspensory clingers are less defined, likely resulting from small samples. These results indicate that a locomotor signal is discernable using the entire distal articulation and may be applicable to incomplete fossil material.

1. Background

The femur is one of the most well-studied skeletal elements with a direct role in load bearing during locomotion. Both descriptions and quantitative analyses have been used to attribute differences in morphology to locomotor modality [1, 2]. Analyses on whole femoral articular morphology are rare; consequently, functional signals related to locomotion may be overlooked.

Objective: To determine which aspects of proximal and distal femoral morphology are functionally associated with locomotor behavior in extant primates.

2. Materials and Methods

Sample:

Femora from primate species with various locomotor behaviors were downloaded from MorphoSource or scanned by the authors **(n=94)**.

Methods:

1) Proximal and distal ends were isolated in MATLAB by cropping each surface at 25% of the maximum bone length from either end.
2) A spherical harmonics analysis (SPHARM) was carried out to 30 degrees [3].
3) SPHARM coefficients describing each end were used to calculate Blomberg's K statistic to check for a phylogenetic signal [4]. Coefficients were also used as variables in a principal component (PC) analysis.
4) Nonparametric statistics were used to check for significant differences between locomotor groups.
5) Average surface models for each locomotor group were created to visualize any significant differences.

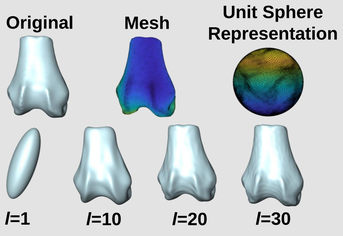


Figure 1. Sample right distal femur of *Ateles fusciceps* and its spherical parametrization (top). SPHARM models using coefficients for degrees 1, 10, 20, & 30 (bottom).

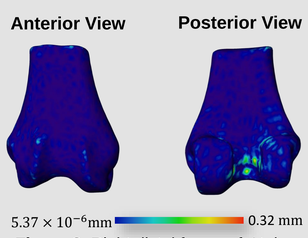


Figure 2. Right distal femur of *Ateles fusciceps* showing the typical difference between an original surface model and a 30-degree SPHARM model.

3. Results

Proximal Femur

Blomberg's K statistic= 0.52, p-value <0.05

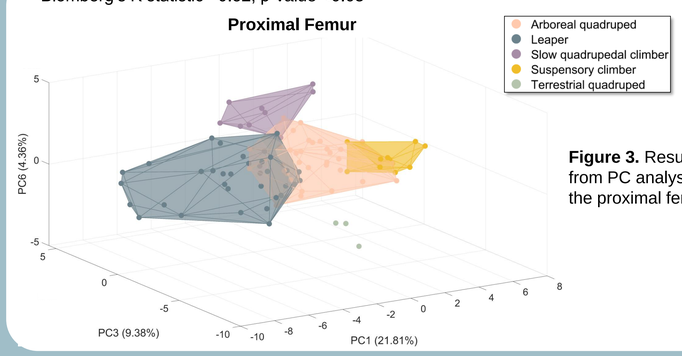


Figure 3. Results from PC analysis of the proximal femur.

Table 1. Results of nonparametric statistics for proximal femur. *P*-values were adjusted using Bonferroni correction. Bolded values indicate significance at α= 0.05. AQ= arboreal quadruped, L= leaper, SC= slow quadrupedal climber, SUSPC= suspensory climber, T= terrestrial quadruped.

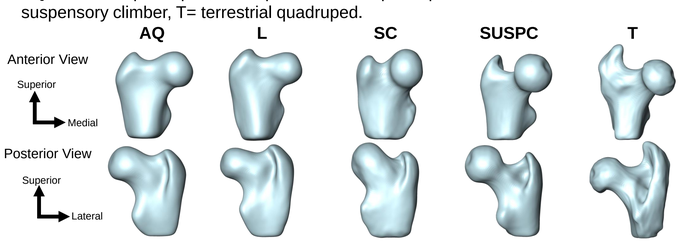
Kruskal-Wallis for Proximal Femur

PC	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
% Variation Explained	21.81	19.68	9.38	7.23	4.88	4.36	3.57	2.94	2.24
Statistic	53.31	11.23	26.12	12.43	7.93	23.86	12.53	12.51	10.95
Degrees of Freedom	4	4	4	4	4	4	4	4	4
p-value	**<0.01**	**0.024**	**<0.01**	**0.014**	0.094	**<0.01**	**0.014**	**0.014**	**0.027**

Multiple Comparisons of Mean Ranks for Proximal Femur

Group Comparison	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
AQ vs L	**<0.01**	1	1	1	1	1	1	1	1
AQ vs SC	1	1	**0.041**	1	1	**<0.01**	**<0.01**	0.053	1
AQ vs SUSPC	0.071	**0.043**	0.17	**0.049**	1	1	1	1	1
AQ vs T	1	1	0.080	1	0.23	0.41	1	1	0.14
L vs SC	0.13	1	0.18	0.88	1	**<0.01**	**0.038**	**<0.01**	1
L vs SUSPC	**<0.01**	0.31	**0.040**	**<0.01**	1	1	1	1	1
L vs T	1	1	**0.032**	1	0.30	1	1	1	**0.043**
SC vs SUSPC	**0.037**	1	**<0.01**	1	0.92	0.083	0.28	**0.039**	1
SC vs T	1	0.82	**<0.01**	1	1	**<0.01**	1	1	0.39
SUSPC vs T	0.082	0.17	1	1	0.22	0.46	1	1	**0.020**

Figure 4. Average proximal SPHARM models (right femur) for each locomotor group. AQ= arboreal quadruped, L= leaper, SC= slow quadrupedal climber, SUSPC= suspensory climber, T= terrestrial quadruped.



Distal Femur

Blomberg's K statistic= 0.59, p-value <0.05

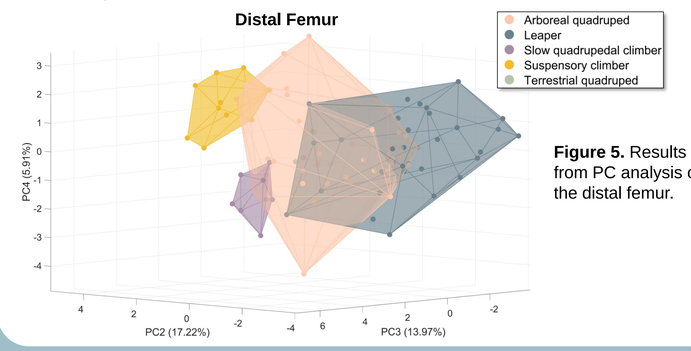


Figure 5. Results from PC analysis of the distal femur.

Table 2. Results of nonparametric statistics for distal femur. *P*-values were adjusted using Bonferroni correction. Bolded values indicate significance at α= 0.05. AQ= arboreal quadruped, L= leaper, SC= slow quadrupedal climber, SUSPC= suspensory climber, T= terrestrial quadruped.

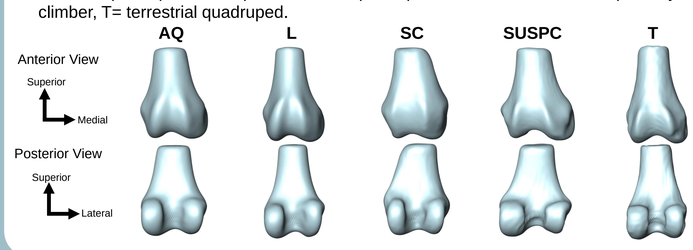
Kruskal-Wallis for Distal Femur

PC	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
% Variation Explained	29.30	17.22	13.97	5.91	4.70	3.52	2.54	2.50	1.79
Statistic	10.25	36.65	16.43	23.71	15.32	16.43	8.38	1.99	11.82
Degrees of Freedom	4	4	4	4	4	4	4	4	4
p-value	**0.036**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.079	0.74	**0.019**

Multiple Comparisons of Mean Ranks for Distal Femur

Group Comparison	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
AQ vs L	0.11	**0.013**	0.46	1	1	0.77	1	1	1
AQ vs SC	1	1	1	0.062	0.15	**0.027**	1	1	1
AQ vs SUSPC	1	**0.015**	0.19	**0.010**	0.83	1	0.062	1	1
AQ vs T	0.74	1	1	1	1	0.50	1	1	0.086
L vs SC	0.40	**<0.01**	0.16	**<0.01**	**<0.01**	0.62	1	1	0.83
L vs SUSPC	1	**<0.01**	**<0.01**	0.082	1	1	0.12	1	1
L vs T	1	0.20	1	1	1	0.080	1	1	**0.026**
SC vs SUSPC	1	1	1	**<0.01**	**<0.01**	1	1	1	1
SC vs T	0.63	1	1	1	0.32	**<0.01**	1	1	0.82
SUSPC vs T	1	1	0.82	0.60	1	0.14	1	1	**0.040**

Figure 6. Average distal SPHARM models (right femur) for each locomotor group. AQ= arboreal quadruped, L= leaper, SC= slow quadrupedal climber, SUSPC= suspensory climber, T= terrestrial quadruped.



4. Discussion and Conclusion

Average SPHARM models of the proximal end show differences in the femoral head, greater trochanter height, and lesser trochanter position which reflect degree of joint mobility and habitual positioning [5, 6]. Shape differences at the distal end were found in the flaring of the epicondyles and patellar groove depth, both of which impact the mobility and stability of the joint [7, 8]. This research supports the use of SPHARM models for quantifying the shape of long bone articulations and their application to primate behavioral reconstructions.

5. References

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Any questions?
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