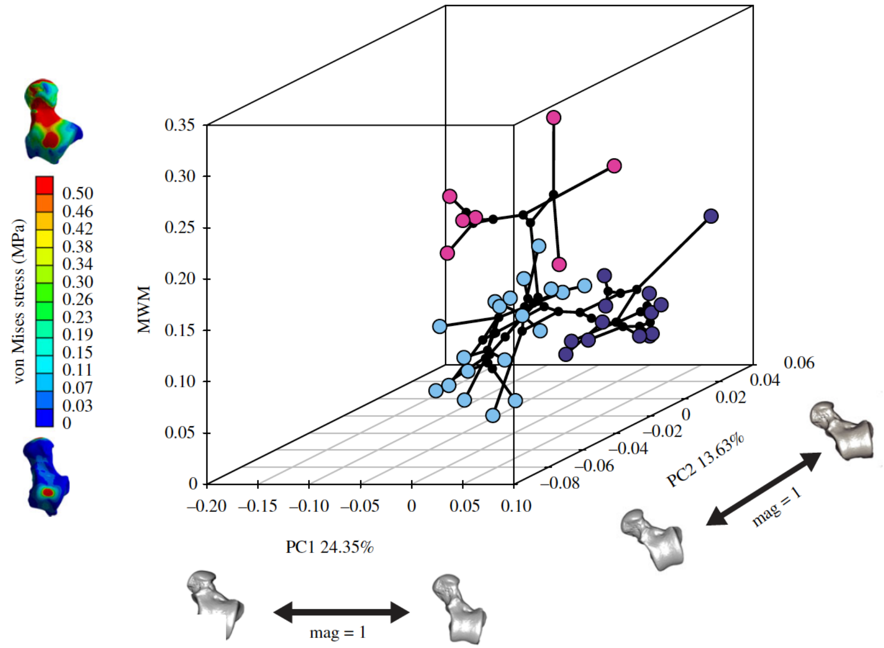
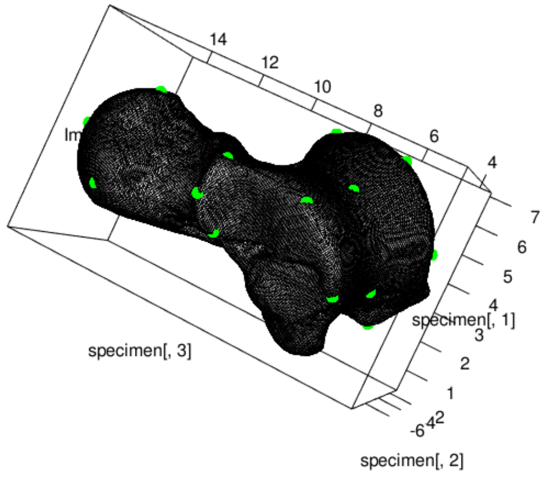
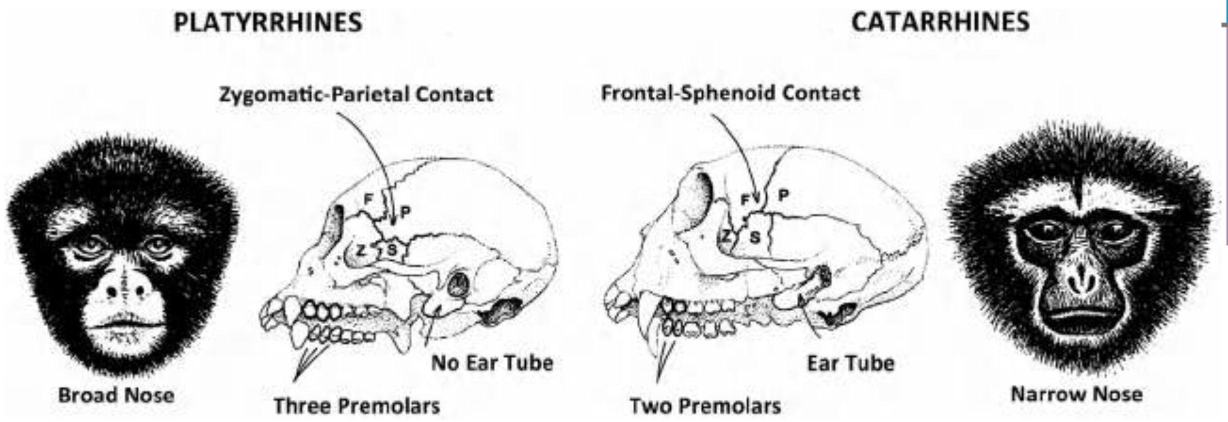
Elucidating *Paralouatta*'s semi-terrestriality using the virtual morpho-functional toolbox

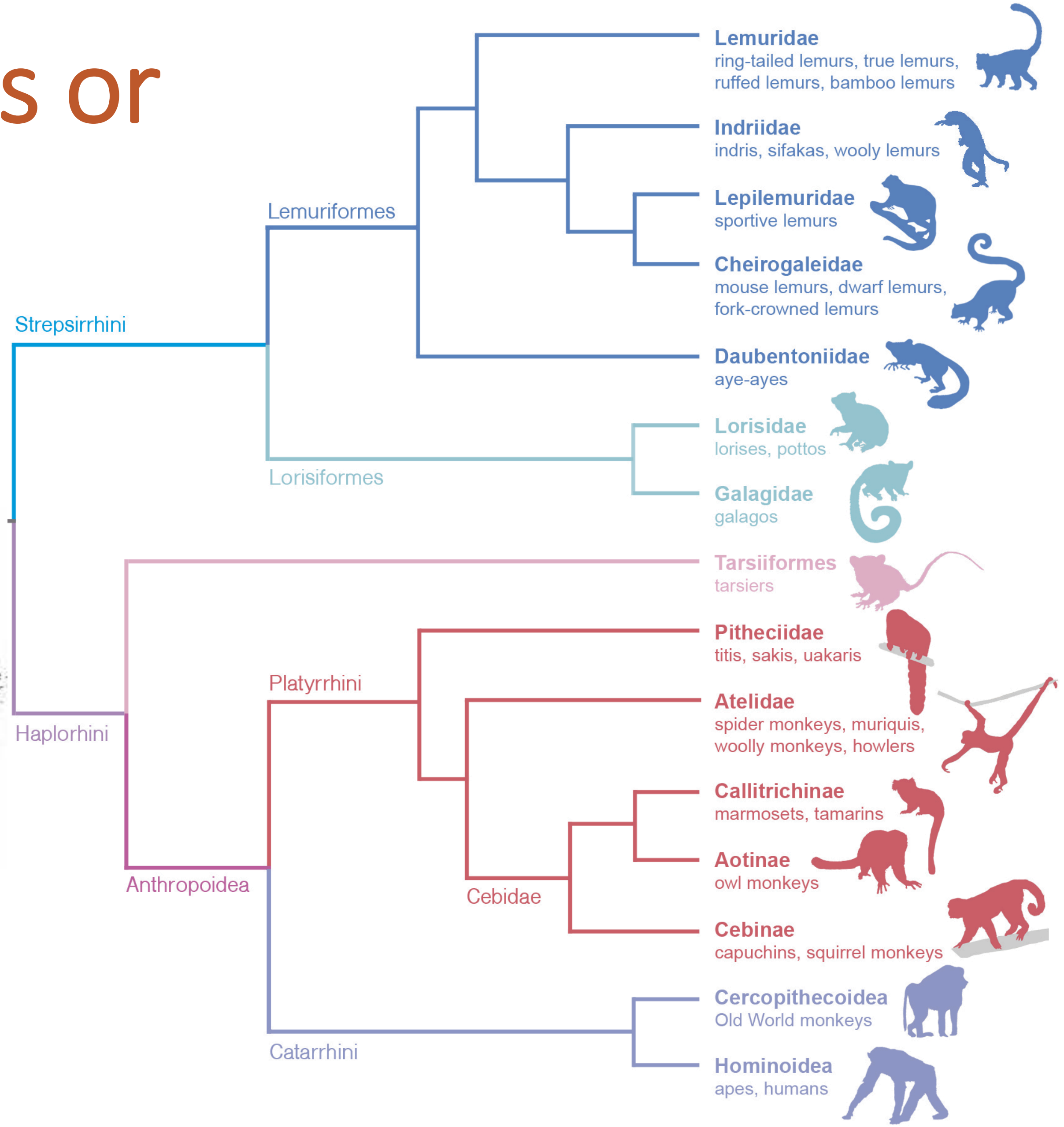




PÜSCHEL, TA, MARCÉ-NOGUÉ, J, GLADMAN, J, PATEL, BA, ALMÉCIJA, S, & SELLERS, WI

New World monkeys or platyrrhines





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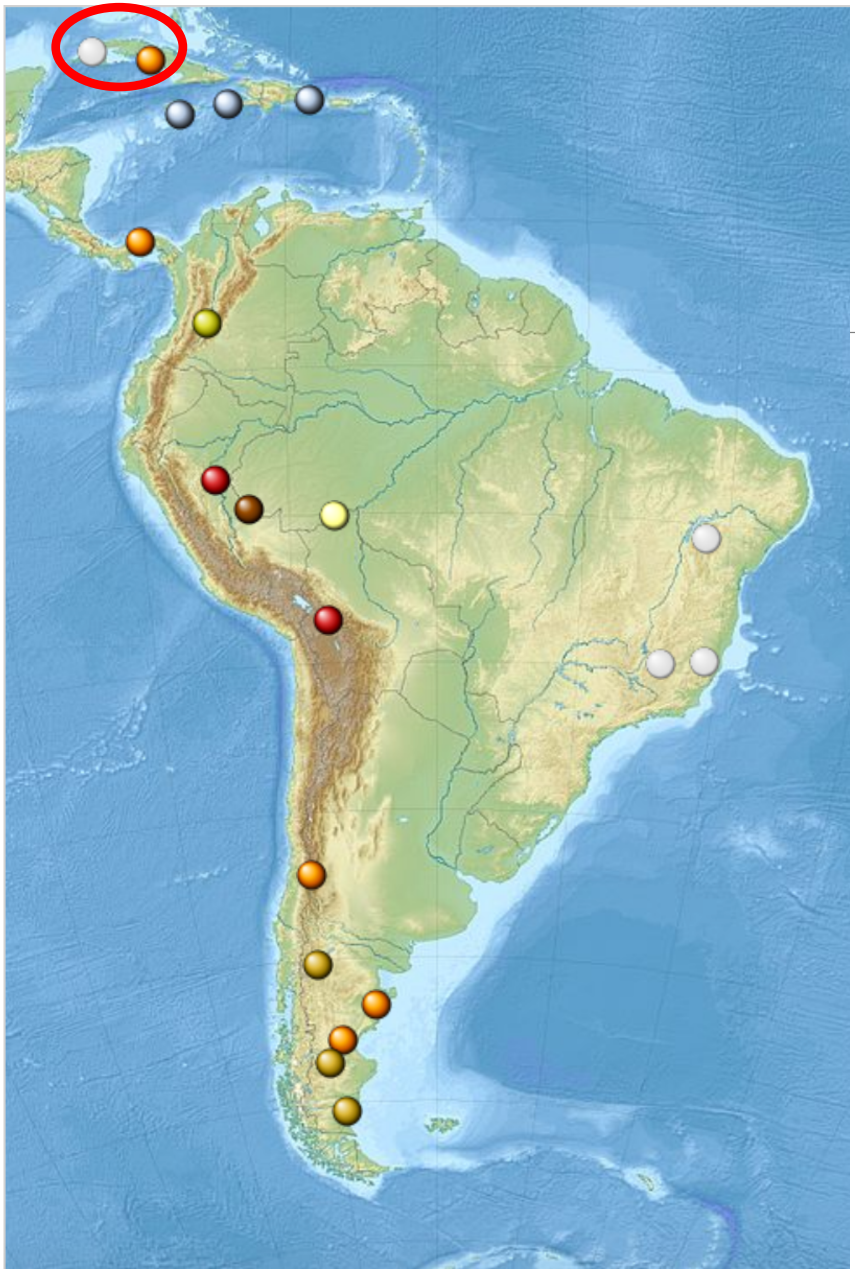
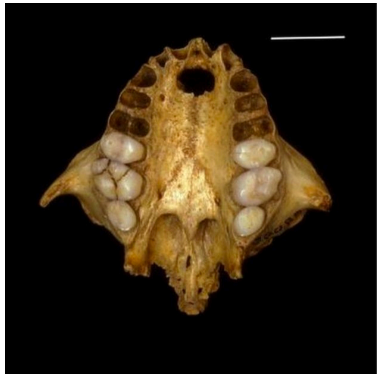
Püschel, T. A. Morpho-functional analyses of the primate skeleton: applying 3D geometric morphometrics, finite element analysis and phylogenetic comparative methods to assess ecomorphological questions in extant and extinct anthropoids. PhD dissertation (2018), Manchester.



Fossil localities

	Divisaderan	**42-36 Ma** Late Eocene
	Deseadan	**29-21 Ma** Oligocene
	Hemingfordian & Colhuehuapian	**21—17.5 Ma** Miocene
	Santacrucian-Friasian	**17.5 – 15.5 Ma** Miocene
	Laventan	**13.8 - 11.8 Ma** Miocene
	Hayquerian	**9—6.8 Ma** Miocene
	Pleistocene	**2,588,000 to 11,650 years ago**
	Holocene	**11,650 years ago - present**

Caribbean monkeys



Xenothrix

Antillothrix

Paralouatta

Insulacebus

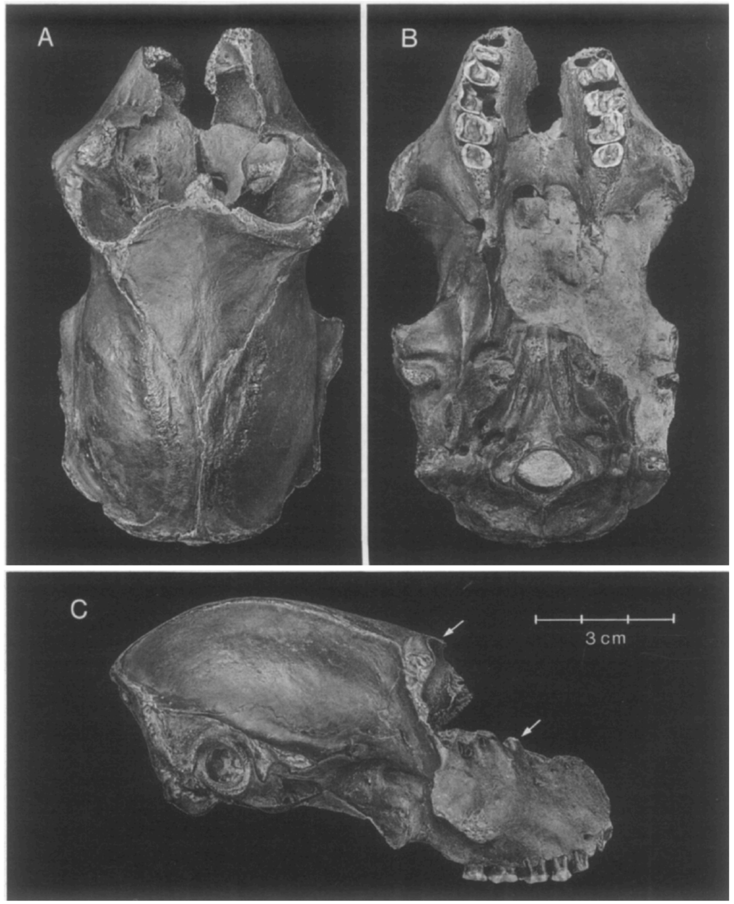
Woods, R., Turvey, S. T., Brace, S., MacPhee, R. D. E., and Barnes, I. (2018). Ancient DNA of the extinct Jamaican monkey Xenothrix reveals extreme insular change within a morphologically conservative radiation. *PNAS* 115, 12769–12774. doi:10.1073/pnas.1808603115.

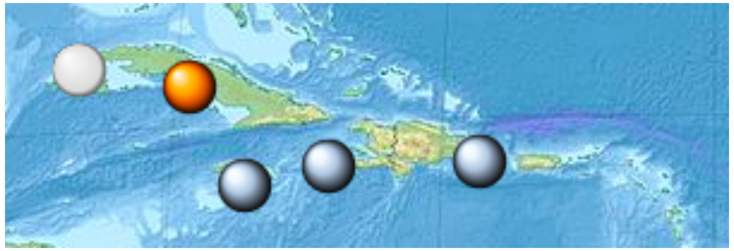
Rosenberger, A. L., Cooke, S. B., Rímoli, R., Ni, X., and Cardoso, L. (2010). First skull of Antillothrix bernensis, an extinct relict monkey from the Dominican Republic. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20101249. doi:10.1098/rspb.2010.1249.

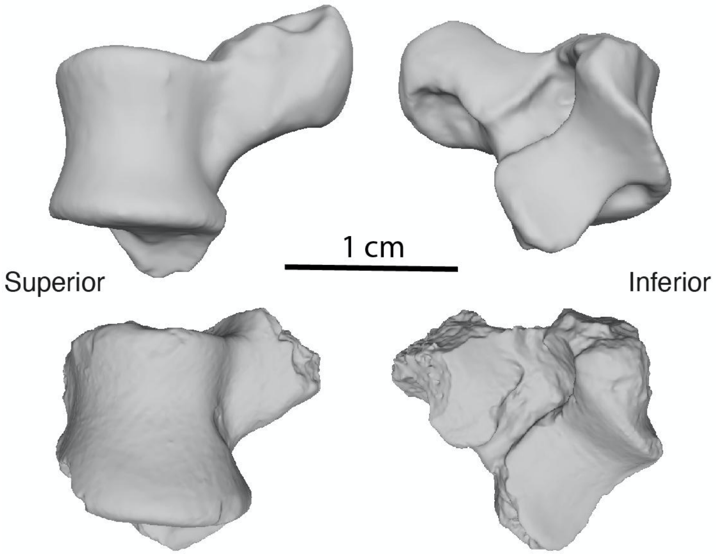
Rivero, M., and Arredondo, O. (1991). Paralouatta varonai, a new Quaternary platyrrhine from Cuba. *Journal of Human Evolution* 21, 1–11. doi:10.1016/0047-2484(91)90032-Q.

Tallman, M., and Cooke, S. B. (2016). New endemic platyrrhine humerus from Haiti and the evolution of the Greater Antillean platyrrhines. *Journal of Human Evolution* 91, 144–166. doi:10.1016/j.jhevol.2015.10.010.

Paralouatta



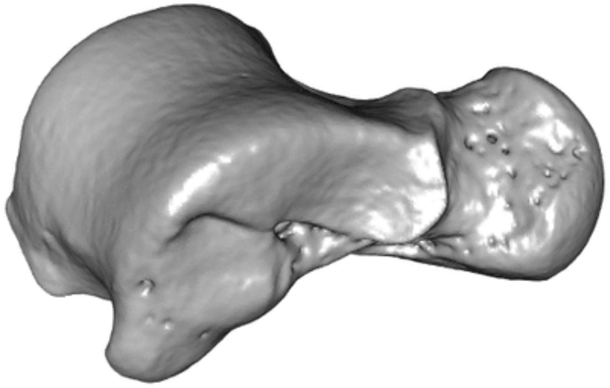


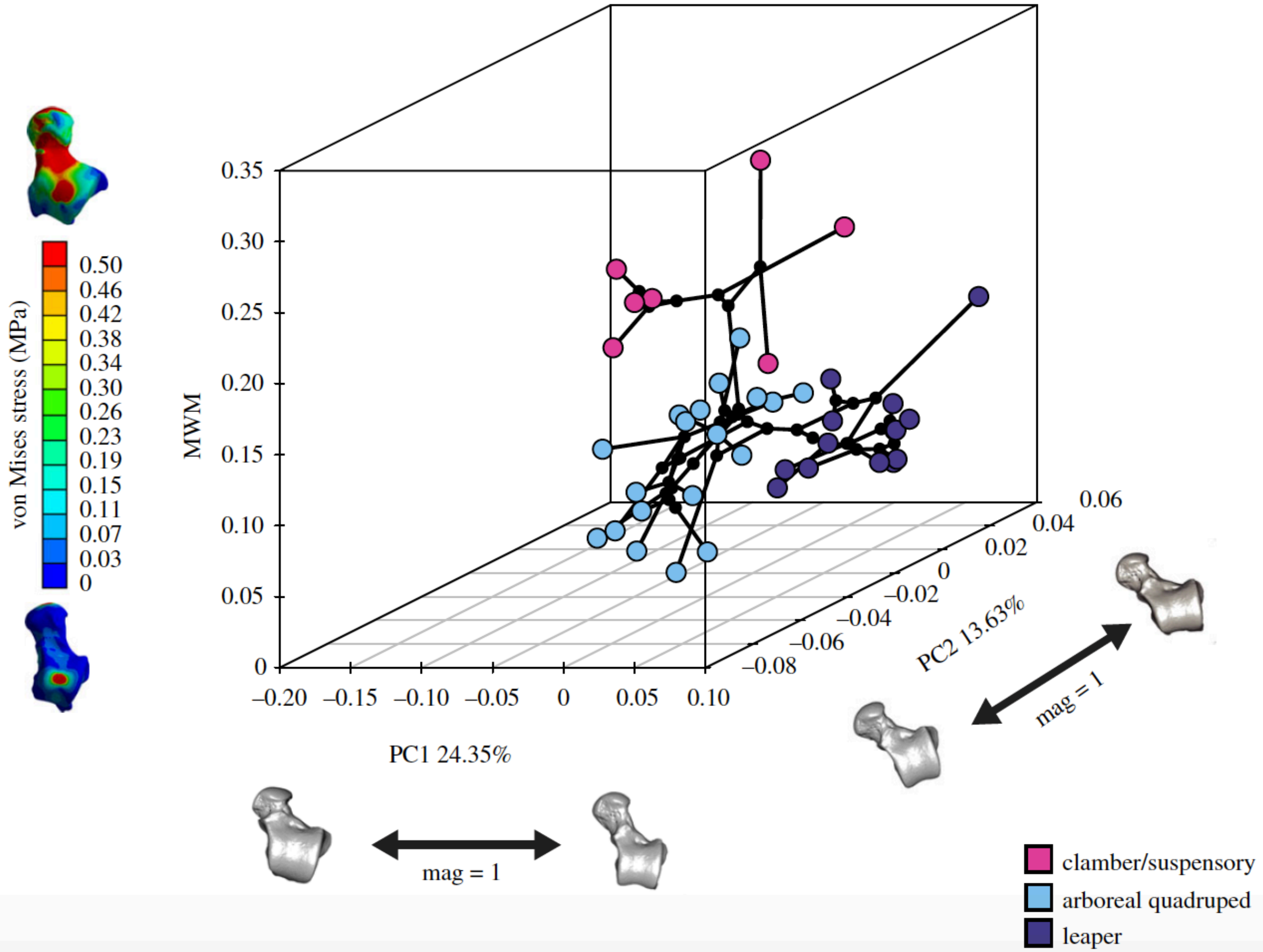


Rivero, M., and Arredondo, O. (1991). Paralouatta varonai, a new Quaternary platyrrhine from Cuba. *Journal of Human Evolution* 21, 1–11. doi:10.1016/0047-2484(91)90032-Q.

MacPhee, R. D. E., and Meldrum, J. E. F. F. (2006). Postcranial Remains of the Extinct Monkeys of the Greater Antilles, with Evidence for Semiterrestriality in Paralouatta1. *Am Museum Novitates* 3516, 1. doi:10.1206/0003-0082(2006)3516[1:PROTEM]2.0.CO;2.

Talar form and function

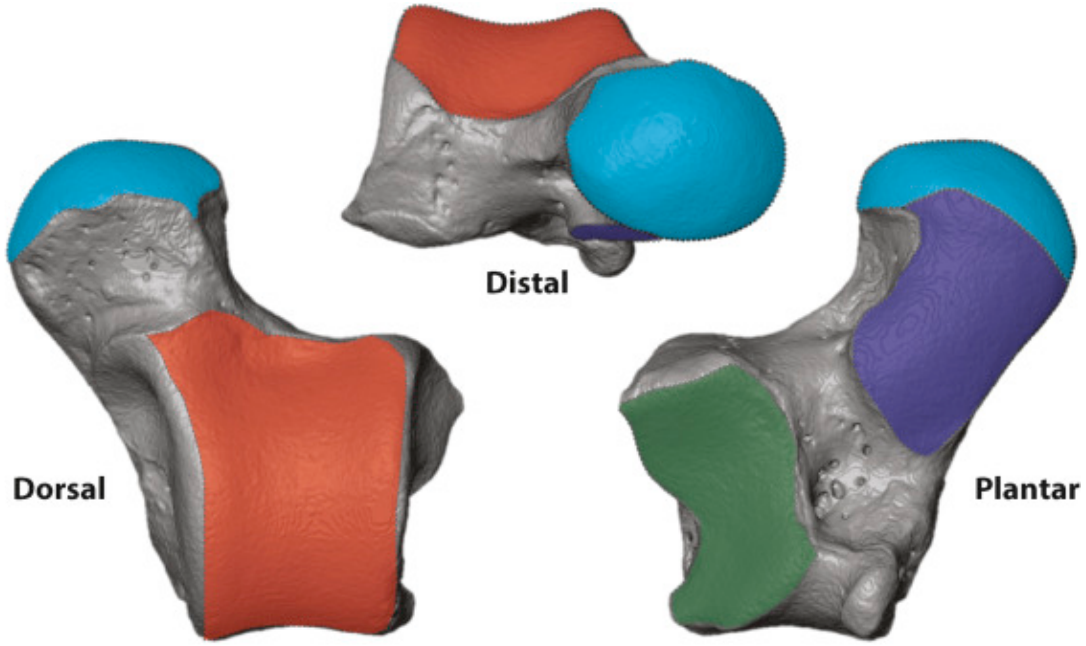




Püschel, T. A., Marcé-Nogué, J., Gladman, J. T., Bobe, R. & Sellers, W. I. Inferring locomotor behaviours in Miocene New World monkeys using finite element analysis, geometric morphometrics and machine-learning classification techniques applied to talar morphology. *Journal of The Royal Society Interface* **15**, 20180520 (2018).

Objectives

1. To test whether *Paralouatta* was truly semi-terrestrial or not
2. To analyse the biomechanical strength of *Paralouatta*'s tali and a comparative sample
3. To analyse *Paralouatta*'s talar morphology and a comparative sample
4. To train different ML classification algorithms using the morphometric and biomechanical data to establish *Paralouatta*'s substrate preference



Püschel, T. A., Gladman, J. T., Bobe, R., and Sellers, W. I. (2017). The evolution of the platyrrhine talus: A comparative analysis of the phenetic affinities of the Miocene platyrrhines with their modern relatives. *Journal of Human Evolution* 111, 179–201. doi:10.1016/j.jhevol.2017.07.015.

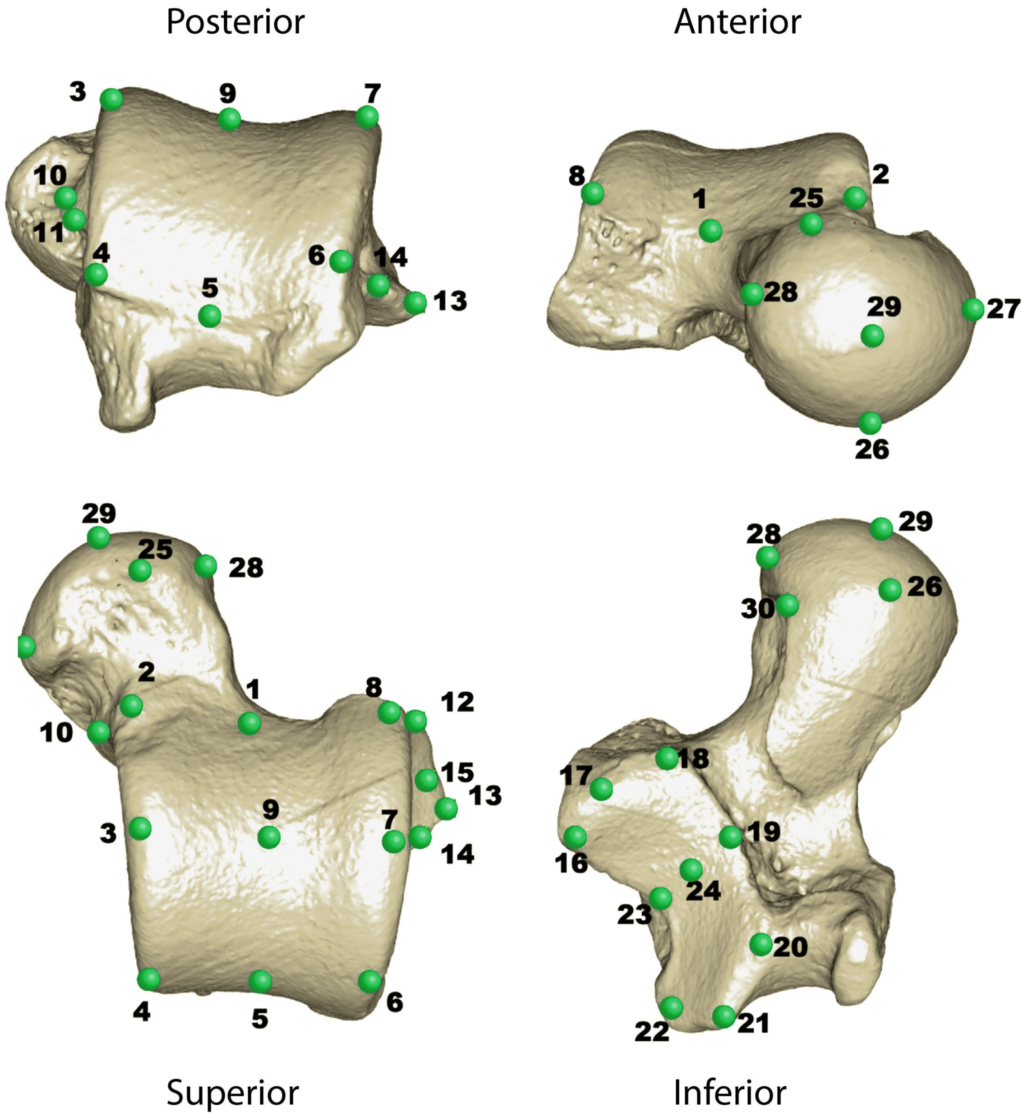
Materials and Methods

3D surface renderings of tali from 109 individuals of 85 species representing all anthropoid sub-families

Most of the 3D data are available at https://www.morphosource.org/

Thirty 3D landmarks were collected using Landmark editor v. 3.6

A generalized Procrustes analysis was performed to obtain shape variables



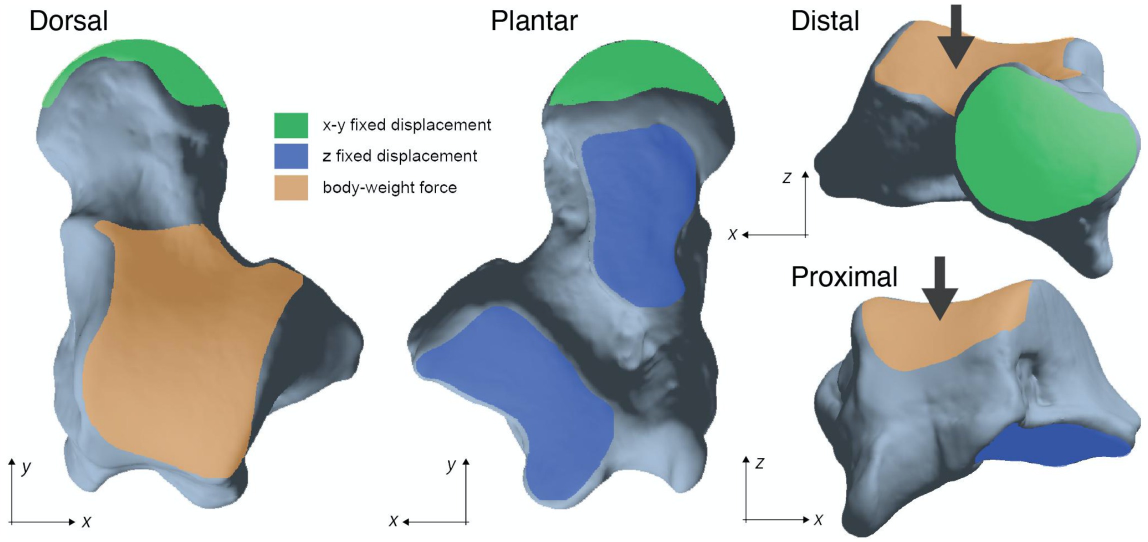
Finite Element Analysis

Models were imported into ANSYS®

We applied FEA to analyze talar mechanical strength

Homogeneous, linear and elastic material properties were used. Cortical bone values from a *Homo sapiens* talus were applied (Young’s modulus: 20.7 GPa; Poisson’s ratio: 0.3)

We applied a load on the trochlear surface of each talus in order to simulate a basic quadrupedal scenario

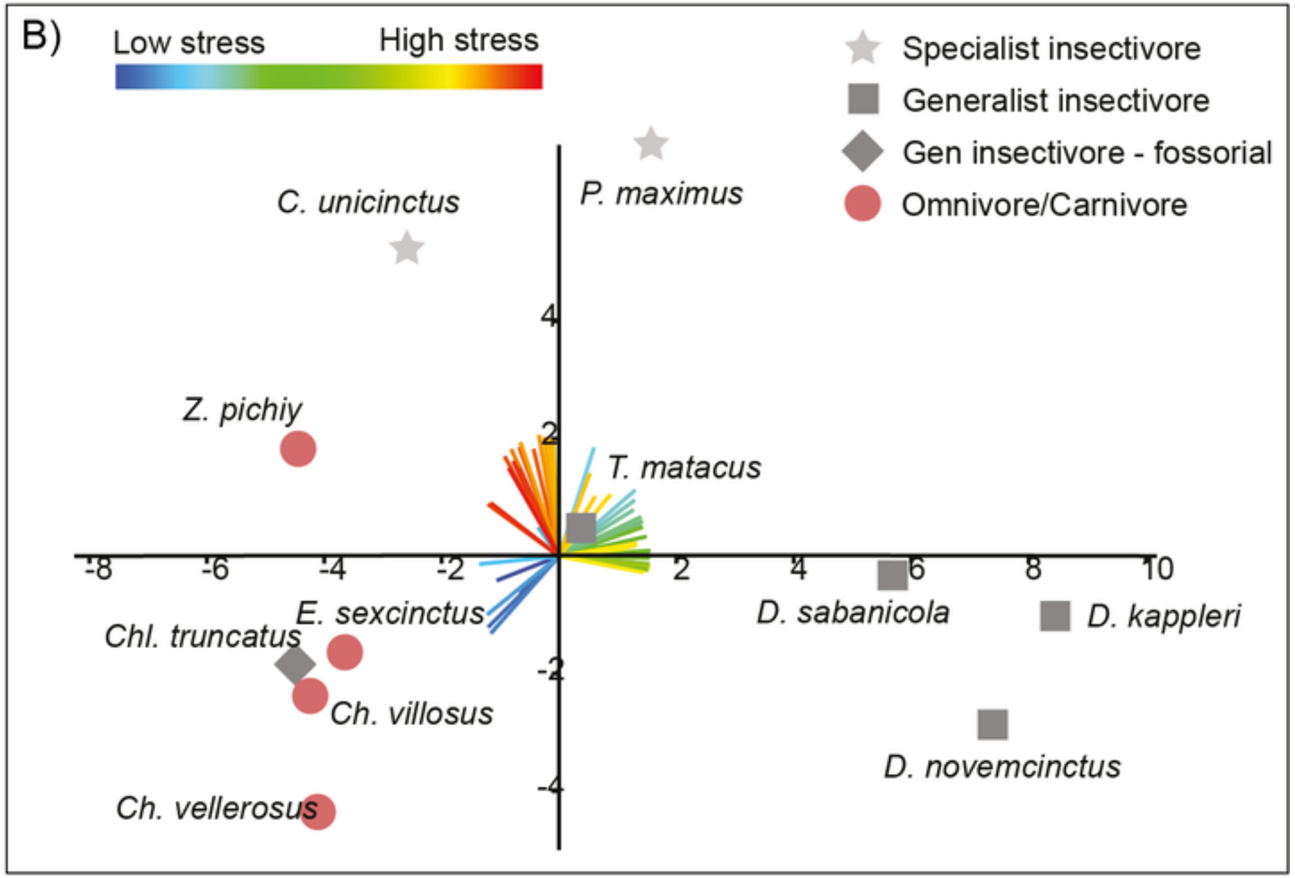


Analysis of the stress results

We computed the von Mises stress because it combines all Cartesian components of the stress tensor into a single value.

New variables corresponding to different intervals of stress values were computed following the Intervals' Method proposed by Marcé-Nogué et al. (2017a)

These interval variables were then used to analyze the FEA results. The Intervals' Method generates a set of variables, each one defined by an interval of stress values.



Marcé-Nogué, J., De Esteban-Trivigno, S. D., Püschel, T. A., and Fortuny, J. (2017). The intervals method: a new approach to analyse finite element outputs using multivariate statistics. *PeerJ* 5, e3793. doi:10.7717/peerj.3793.

Fossil Substrate Preference Classification

The extant sample was classified according to their main substrate preference based on the database of Galán-Acedo et al. (2019): a) Arboreal; b) 'Both' and c) Terrestrial

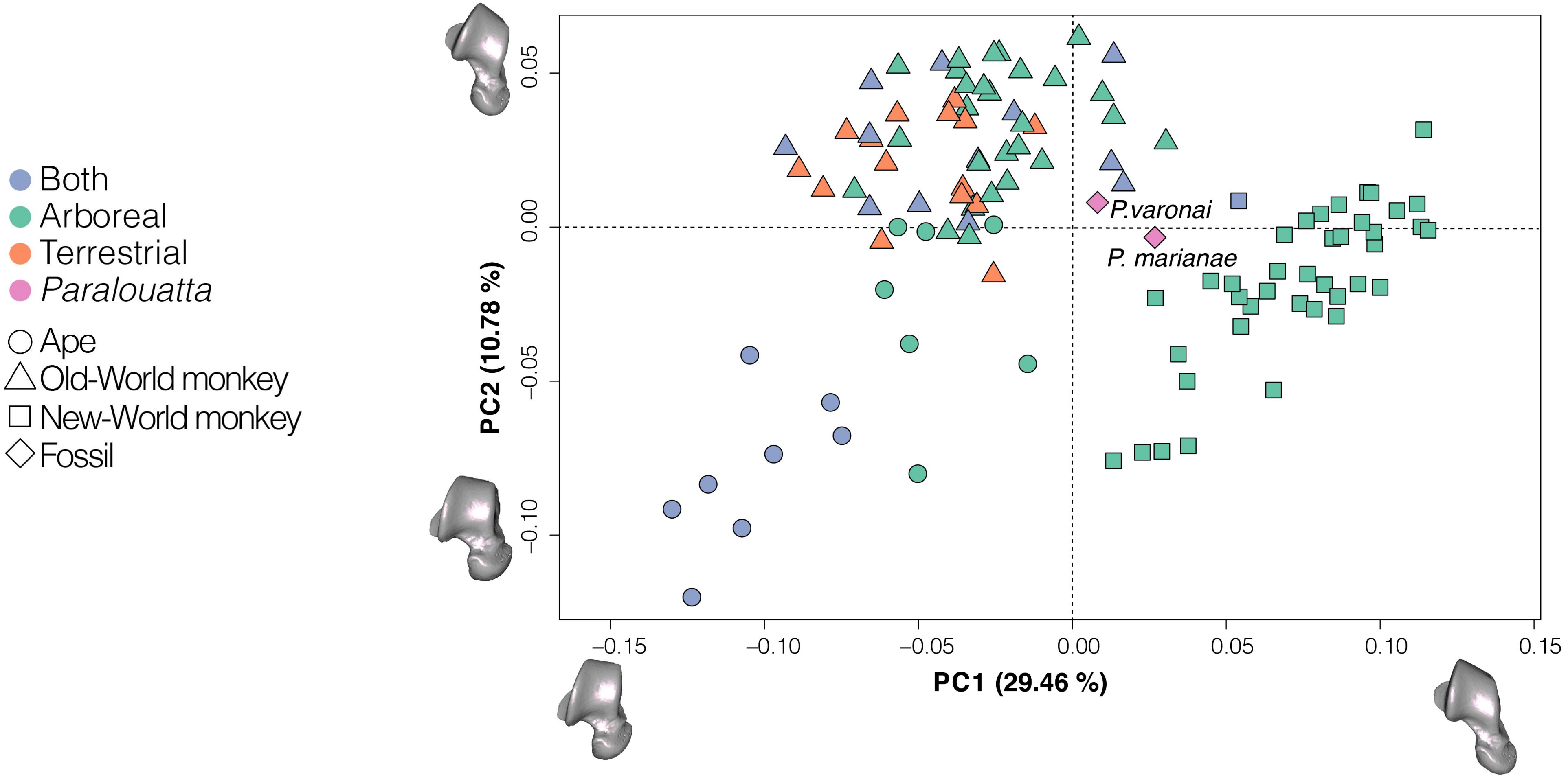
Two different datasets were analyzed and used to elucidate the main substrate preference of *Paralouatta*: (a) morphometric and (b) biomechanical data. Each one of these datasets corresponded to the PCs that accounted for 90% of the variance.

Six well-known supervised algorithms were chosen as they correspond to a diverse range of different classification techniques

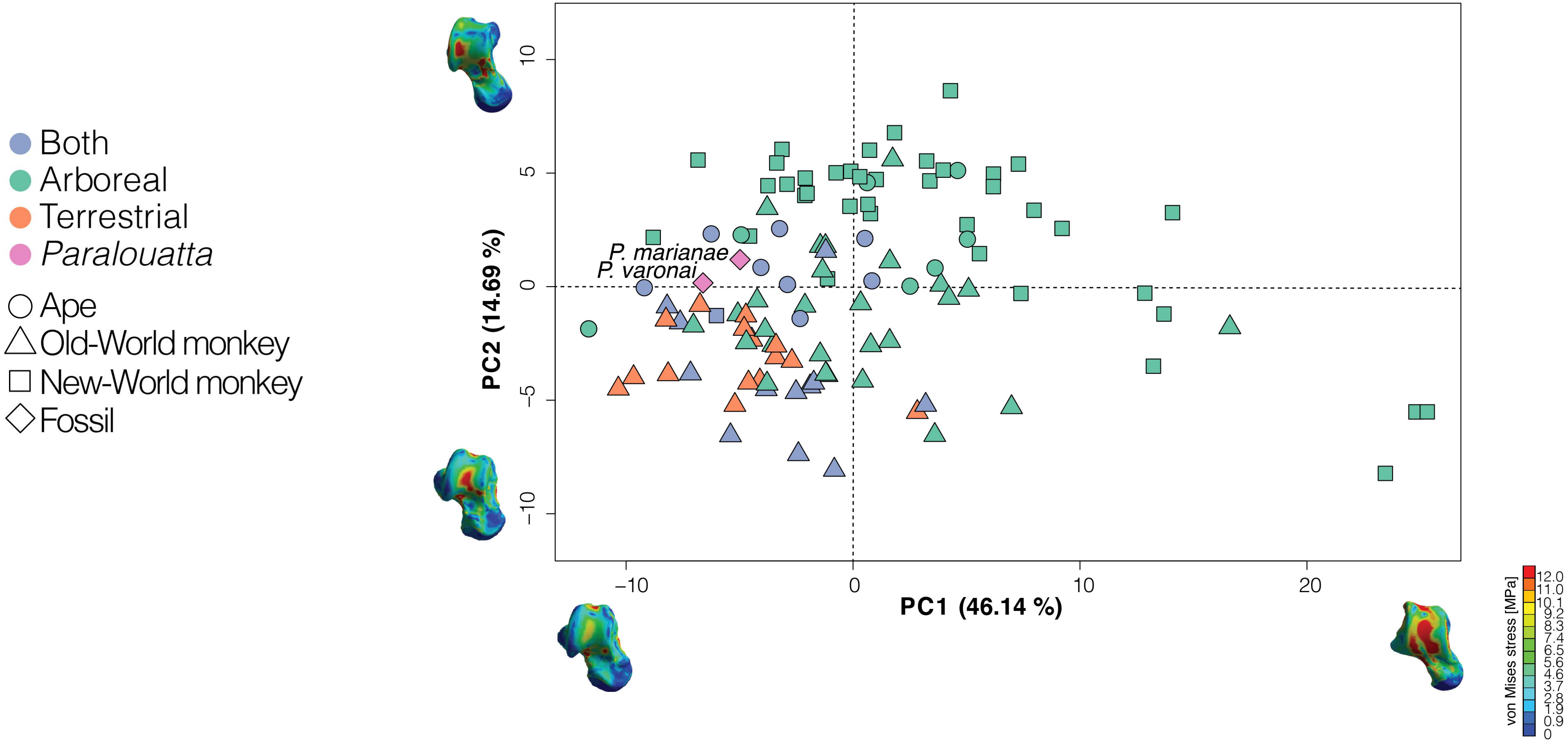
Fleagle, J. G. *Primate Adaptation and Evolution*. (Academic Press, 2013).

Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E., and Arasa-Gisbert, R. (2019). Ecological traits of the world's primates. *Scientific Data* 6, 55. doi:10.1038/s41597-019-0059-9.

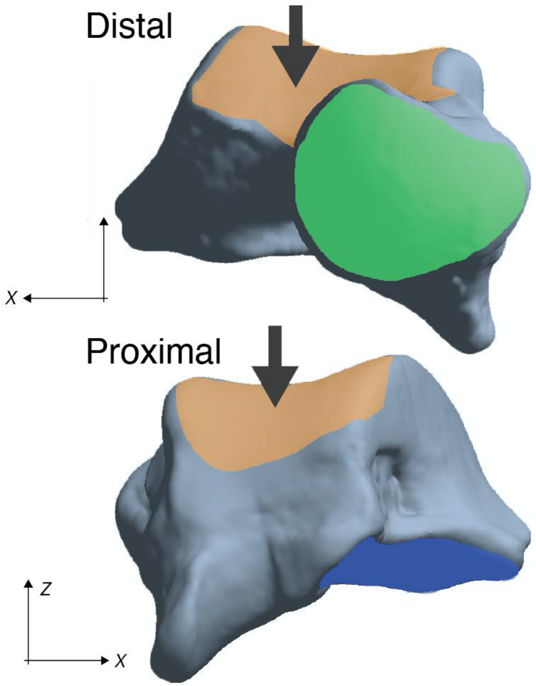
Results: Morphometric PCA

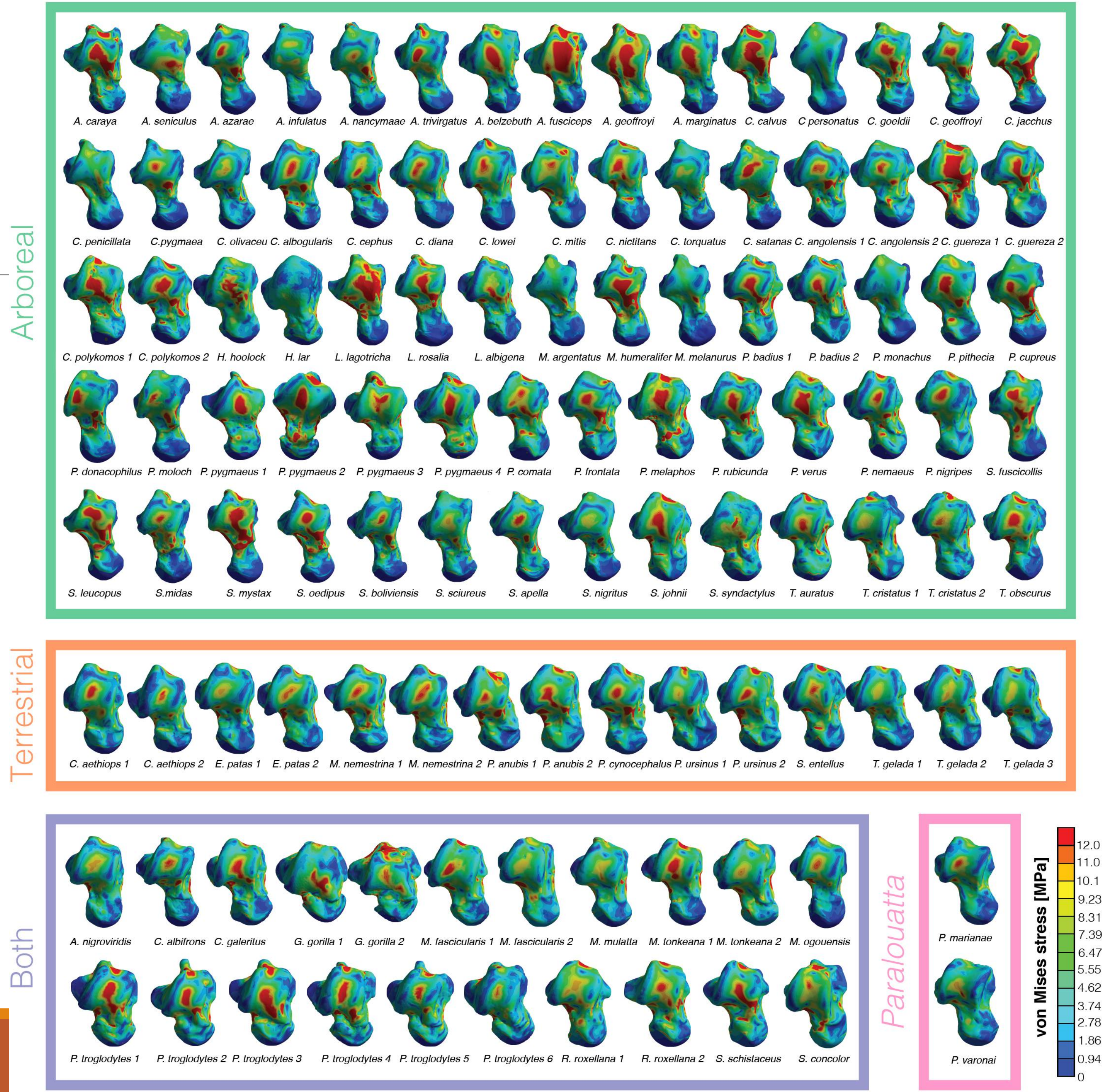


Results: Biomechanical PCA

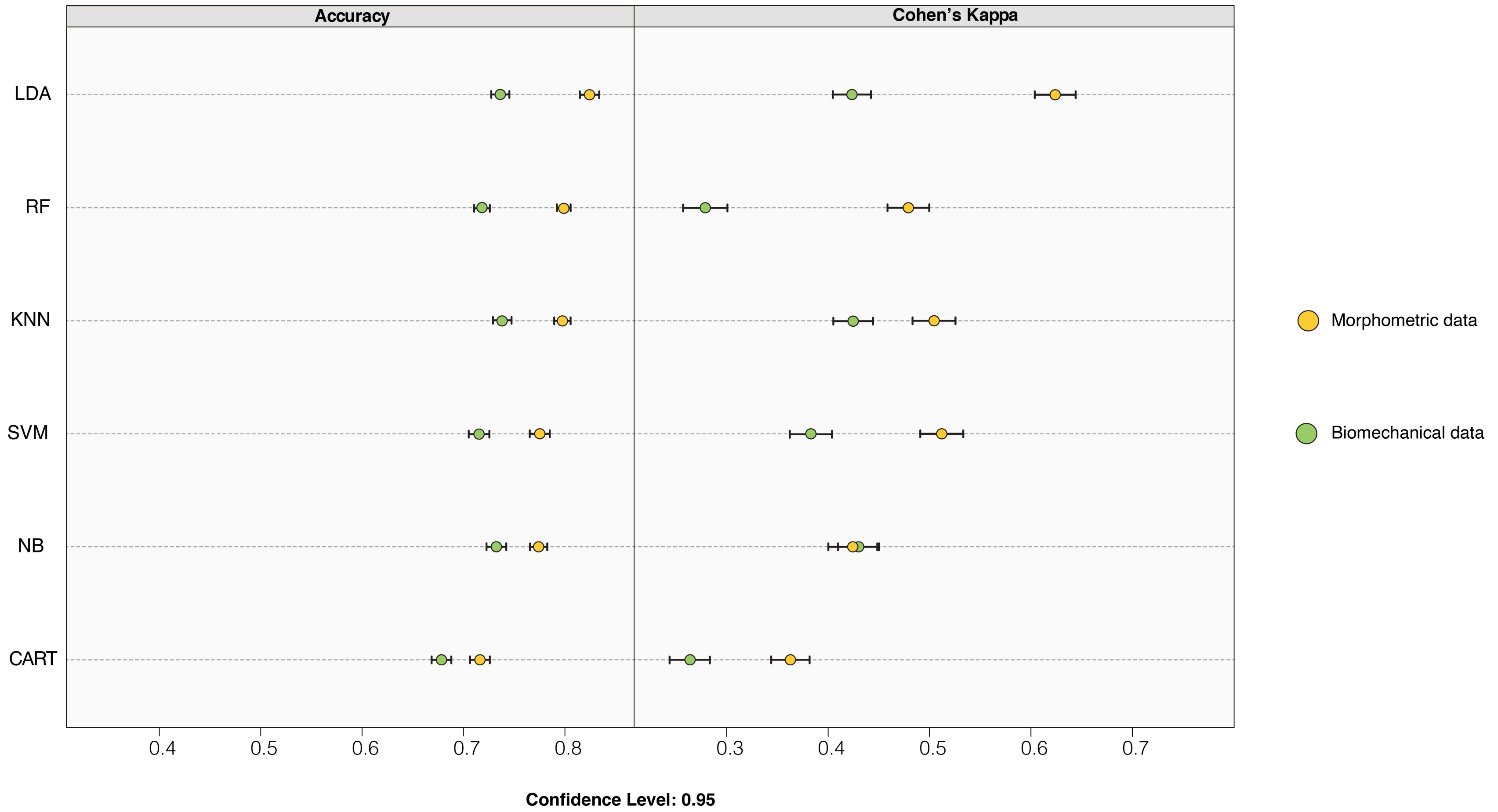


Biomechanical results

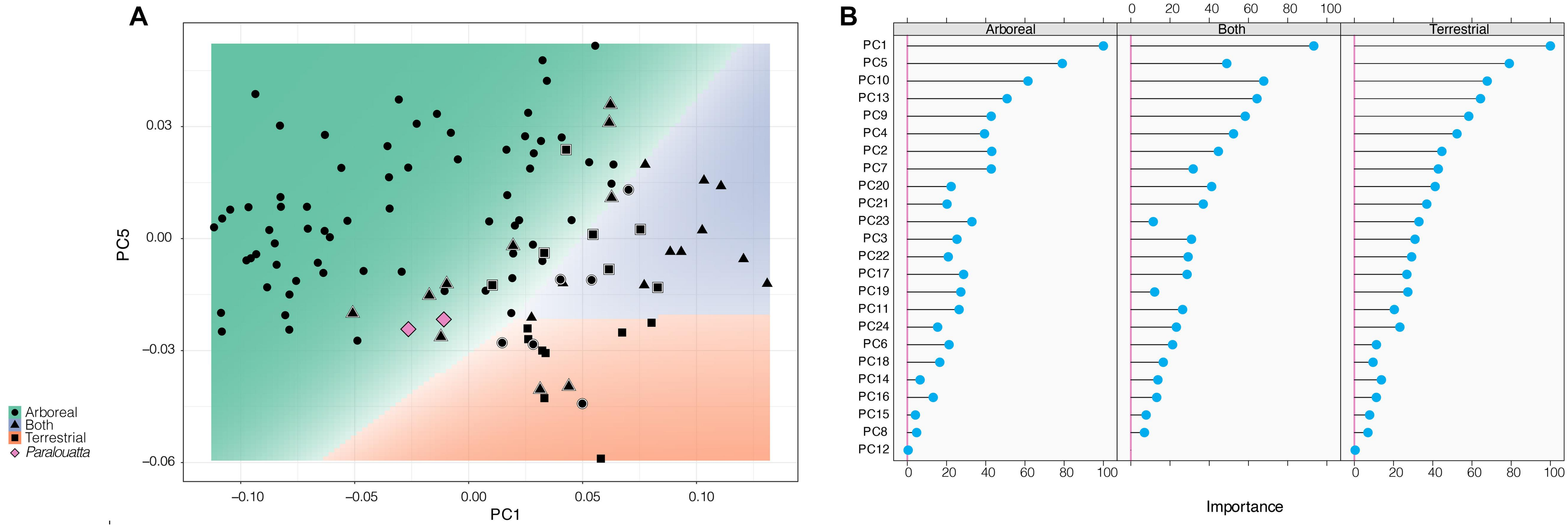




Machine-learning model comparison

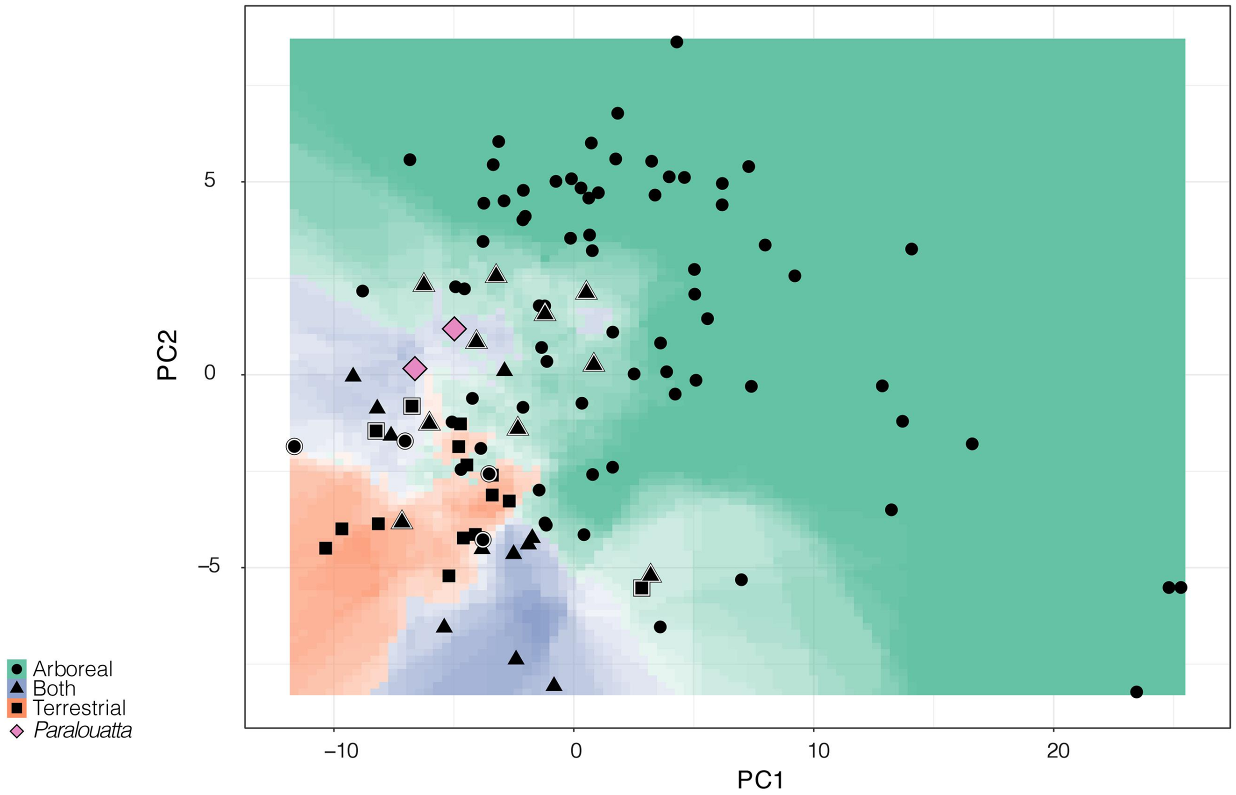


Substrate preference: Morphometric data

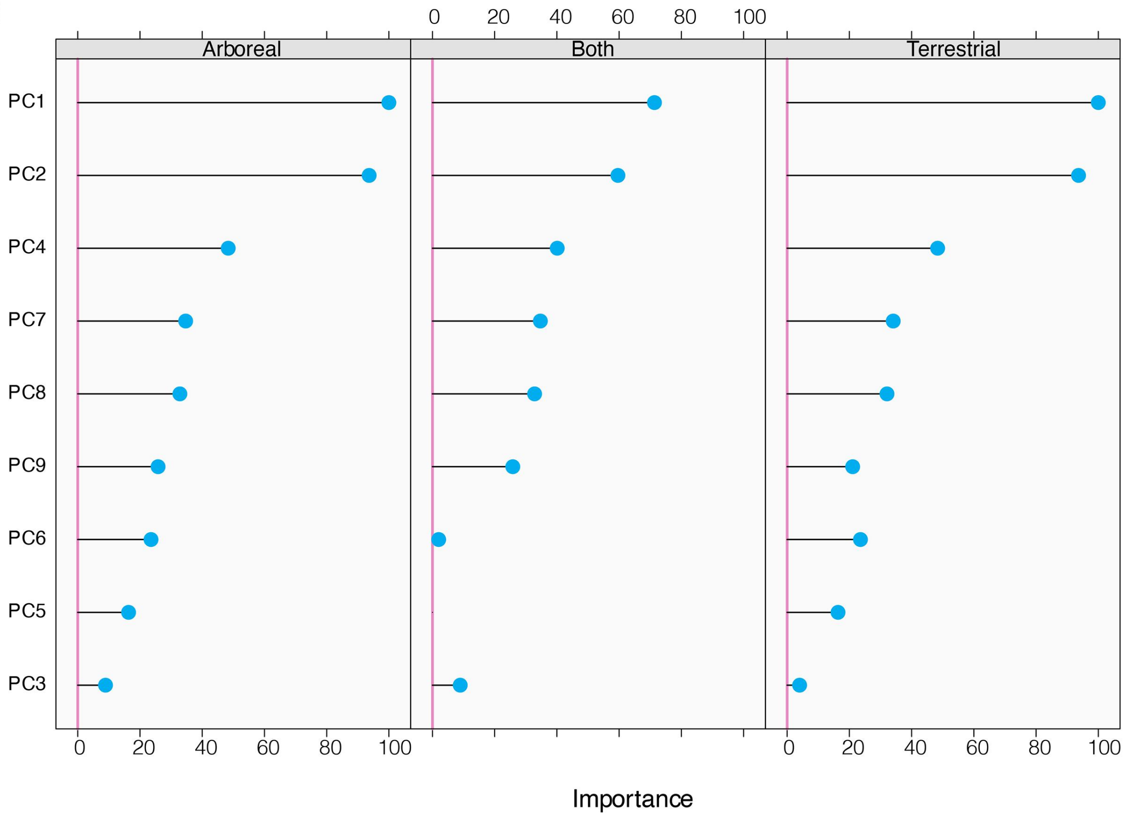


Substrate preference: Biomechanical data

C



D



Classification results

	LDA morphometric model			KNN biomechanical model		
	Posterior probabilities			Posterior probabilities		
Species	**Arboreal**	**Both**	**Terrestrial**	**Arboreal**	**Both**	**Terrestrial**
Paralouatta marianae	0.99	0.01	0.00	0.43	0.43	0.14
Paralouatta varonai	0.27	0.73	0.00	0.00	0.71	0.29

Conclusions

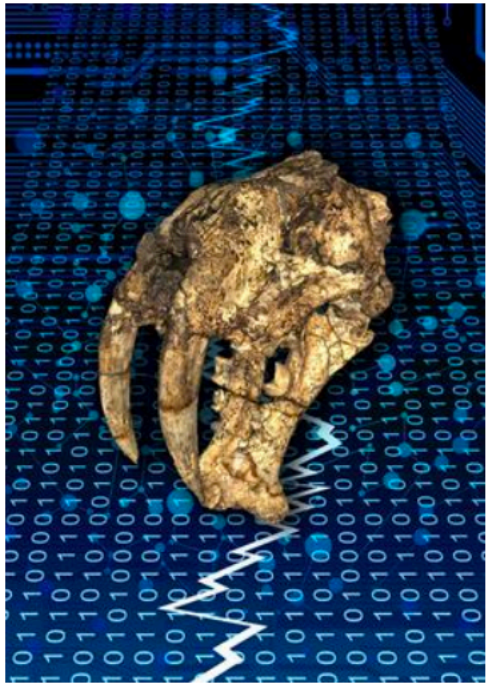
1. Both the **morphometric** and **biomechanical** data indicate **mixed** locomotor behaviors, thus indicating some levels of **terrestriality**

2. ***Paralouatta*** was probably an **island-adapted large-bodied** genus that most likely diverged from other platyrrhines during the early Miocene. This would certainly explain the similarities of *Paralouatta* to the other platyrrhines, as well as many traits that are evidently unique to this genus and that seem to be exaggerated in the later species *P. varonai*. The **talar morphology** of *Paralouatta* **combines some more primitive morphological** aspects (both anthropoid and platyrrhine) with **derived features associated to some terrestriality levels.**

3. This study has shown that a **combined virtual morpho-functional** approach can help to the understanding of **locomotor behaviors in other fossil taxa**. By combining morphometrics, biomechanics and ML methods it is possible to provide a broader perspective regarding the locomotor behaviors of fossils species by analyzing different aspects of their functional morphology

Publication associated with this work

frontiers in Earth Science | Paleontology



Research Topic

Evolving Virtual and Computational Palaeontology

Püschel, T. A., Marcé-Nogué, J., Gladman, J., Patel, B. A., Almécija, S., and Sellers, W. I. (2020). Getting Its Feet on the Ground: Elucidating Paralouatta's Semi-Terrestriality Using the Virtual Morpho-Functional Toolbox. *Front. Earth Sci.* 8. doi:[10.3389/feart.2020.00079](https://doi.org/10.3389/feart.2020.00079).

https://www.frontiersin.org/articles/10.3389/feart.2020.00079/full

Acknowledgments

This project was funded by the NERC (NE/R011168/1). TP was funded by the Leverhulme Trust Early Career Fellowship, ECF-2018-264, SA by the NSF-BCS 1316947, AEI/FEDER EU (CGL2017-82654-P), and BP by the National Science Foundation (BCS-1317047) and the Leakey Foundation. JM acknowledges Dr. Juan Liu and the Laboratory for the Evolution and Anatomy of Fish of the University at Buffalo. Both SA and JM-N acknowledge the CERCA Programe (Generalitat de Catalunya).

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