

Luciano Varela, M.Sc.

Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo, Uruguay.

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Research Interests

Vertebrate paleobiology, paleobiogeography, paleoecology, macroecology, macroevolution, functional morphology, systematics, and science education.

Education

Ongoing - Expected date Dec. 2023 - **PhD.** Biology. Department of Paleobiology, Universidad de la República (Udelar).

Advisors: Dr. Richard A. Fariña and Dr. Enrique P. Lessa.

2018 - **M.Sc.** Biology; specialization: Zoology. Universidad de la República (Udelar).

Advisors: Dr. Richard A. Fariña and Dr. H. Gregory McDonald.

2014 - **B.Sc.** (Hons.) Biology; specialization: Paleontology. Universidad de la República (Udelar).

Advisor: Dr. Richard A. Fariña.

Academic Employment

2023–ongoing: Graduate Research Associate. Employed under Agencia Nacional de Investigación e Innovación grant “Testing megafauna extinction hypotheses: an approach using ecological niche models and life history simulations.” PI. Luciano Varela.

2019–2023: PhD. Research Fellow. Comisión Académica de Posgrado, Udelar, Uruguay.

2018–2020: Graduate Research Associate. Employed under the CSIC I+D grant “Paleoecology and paleobiogeography of Pleistocene megafauna in Uruguay and the region.” PI: Richard Fariña.

2016–2018: M.Sc. Research Fellow. Agencia Nacional de Investigación e Innovación, Uruguay.

2014–2016: Graduate Research Associate. Employed under Agencia Nacional de Investigación e Innovación grant “New paleobiological approaches in the study of fossil sloths.” PI: Richard Fariña.

2012–2014: Undergraduate Researcher. Arroyo del Vizcaíno, Universidad de la República, Uruguay. Fossil preparation, collections management, and digitization.

Publications

Total citations: 378 (First author: 172; h-index 9 – Google Scholar, Oct 2023)

Number of papers: 10 first-author, 4 second-author, 8 nth-author

Students directly mentored: *

1. **Varela, L.**, Clavijo, L., Tambusso, P.S., Fariña, R.A. (2023). A window into a late Pleistocene megafauna community: Stable isotopes show niche partitioning among herbivorous taxa at the Arroyo del Vizcaíno site (Uruguay). **Quaternary Science Reviews**, 317, 108286. DOI: [10.1016/j.quascirev.2023.108286](https://doi.org/10.1016/j.quascirev.2023.108286).
2. Tamagnini, D., Michaud, M., Meloro, C., Raia, P., Soibelzon, L., Tambusso, P.S., **Varela, L.**, Maiorano, L. (2023). Conical and sabertoothed cats as an exception to craniofacial evolutionary allometry. **Scientific Reports**, 13(1), 13571. DOI: [10.1038/s41598-023-40677-6](https://doi.org/10.1038/s41598-023-40677-6).
3. **Varela, L.**, Tambusso, P.S., Zerpa, J.M.P., McAfee, R. K., Fariña, R. A. (2023). 3D finite element analysis and geometric morphometrics of sloths (Xenarthra, Folivora) mandibles show insights on the dietary specializations of fossil taxa. **Journal of South American Earth Sciences**, 104445. DOI: [10.1016/j.jsames.2023.104445](https://doi.org/10.1016/j.jsames.2023.104445).
4. **Varela, L.**, Tambusso, P.S., McDonald, H.G., Vezzosi, R.I., Fariña, R.A. (2023). Occurrence of the ground sloth *Nothrotheriops* (Xenarthra, Folivora) in the Late Pleistocene of Uruguay: new information on its dietary and habitat preferences based on stable isotope analysis. **Journal of Mammalian Evolution**, 1-16. DOI: [10.1007/s10914-023-09660-w](https://doi.org/10.1007/s10914-023-09660-w).
5. Fariña, R.A., Tambusso, P.S., **Varela, L.**, Gascue, A., Stafford, T.W. (2022). Hard Facts in an Imperfect Site: The Evidence of Human Presence in the Arroyo del Vizcaíno. Reply to Holcomb et al. **PaleoAmerica**, 8(4), 307-314. DOI: [10.1080/20555563.2022.2137927](https://doi.org/10.1080/20555563.2022.2137927).
6. Baleka, S., **Varela, L. (Shared first authorship)**, Tambusso, P.S., Paijmans, J.L., Mothé, D., Stafford, T.W., Fariña, R.A., Hofreiter, M. (2022). Revisiting proboscidean phylogeny and evolution through total evidence and palaeogenetic analyses including *Notiomastodon* ancient DNA. **iScience**, 25(1). DOI: [10.1016/j.isci.2021.103559](https://doi.org/10.1016/j.isci.2021.103559).
7. **Varela, L.**, McDonald, H. G., Fariña, R.A. (2022). Sexual dimorphism in the fossil ground sloth *Lestodon armatus* (Xenarthra, Folivora). **Historical Biology**, 34(3), 525-537. DOI: [10.1080/08912963.2021.1933470](https://doi.org/10.1080/08912963.2021.1933470).
8. Domínguez-Rodrigo, M., Baquedano, E., **Varela, L.**, Tambusso, P.S., Melián, M.J., Fariña, R.A. (2021). Deep classification of cut-marks on bones from Arroyo del Vizcaíno (Uruguay). **Proceedings of the Royal Society B**, 288(1954), 20210711. DOI: [10.1098/rspb.2021.0711](https://doi.org/10.1098/rspb.2021.0711).
9. *Lobato, C., **Varela, L.**, Tambusso, P.S., Miño-Boilini, Á.R., Clavijo, L., Fariña, R.A. (2021). Presence of the ground sloth *Valgipes bucklandi* (Xenarthra, Folivora, Scelidotheriinae) in southern Uruguay during the Late Pleistocene: Ecological and biogeographical implications. **Quaternary International**, 601, 104-115. DOI: [10.1016/j.quaint.2021.06.011](https://doi.org/10.1016/j.quaint.2021.06.011).

10. Tambusso, P. S., **Varela, L.**, Góis, F., Moura, J. F., Villa, C., Fariña, R. A. (2021). The inner ear anatomy of glyptodonts and pampatheres (Xenarthra, Cingulata): Functional and phylogenetic implications. **Journal of South American Earth Sciences**, 108, 103189. DOI: [10.1016/j.jsames.2021.103189](https://doi.org/10.1016/j.jsames.2021.103189).
11. Beri, Á., Martínez-Blanco, X., **Varela, L.**, di Pasquo, M., de Souza, P.A. (2020). Sampling biases and Paleozoic sporomorphs diversity dynamics in Western Gondwana strata. **Journal of South American Earth Sciences**, 98, 102457. DOI: [10.1016/j.jsames.2019.102457](https://doi.org/10.1016/j.jsames.2019.102457).
12. **Varela, L.**, Tambusso, P. S., Fariña, R. A. (2020). Unexpected inhibitory cascade in the molariforms of sloths (Folivora, Xenarthra). **Fossil Imprint** 76(1), 1-16. DOI: [10.37520/fi.2020.002](https://doi.org/10.37520/fi.2020.002).
13. Di Giacomo, M., Batallés, M., **Varela, L.**, Tambusso, P.S., Clavijo, L., Fariña, R.A. (2020). Keeping old giants at the service of a local community: The Arroyo del Vizcaíno collection (Sauce, Uruguay). **Geological Curator** 11 (4): 263-274. DOI: [10.55468/GC1496](https://doi.org/10.55468/GC1496).
14. Fariña, R.A., Di Giacomo, M., Batallés, M., Tambusso, P.S., **Varela, L.** (2020). Conocimiento presente para la sociedad: la mirada de la paleontología en un caso de vínculo con la comunidad. **Tecnología y Sociedad**, 2020, 9: 69-93.
15. **Varela, L.**, Tambusso, P.S., McDonald, H.G., Fariña, R.A. (2019). Phylogeny, macroevolutionary trends and historical biogeography of sloths: insights from a Bayesian morphological clock analysis. **Systematic Biology**, Volume 68, Issue 2, March 2019, Pages 204–218, DOI: [10.1093/sysbio/syy058](https://doi.org/10.1093/sysbio/syy058).
16. Tambusso, P.S., **Varela, L.**, McDonald, H.G. (2018). Fusion of anterior thoracic vertebrae in Pleistocene ground sloths. **Historical Biology**, 1-8. DOI: [10.1080/08912963.2018.1487419](https://doi.org/10.1080/08912963.2018.1487419).
17. Fariña, R.A., **Varela, L.** (2018). Comment on “Isotopic insight on paleodiet of extinct Pleistocene megafaunal Xenarthrans from Argentina” by H. Bocherens, M. Cotte, RA Bonini, P. Straccia, D. Scian, L. Soibelzon and FJ Prevosti, Gondwana Research, Volume 48, Issue 1, Pages 7–14. **Gondwana Research**, 58, 241-242. DOI: [10.1016/j.jgr.2018.03.004](https://doi.org/10.1016/j.jgr.2018.03.004).
18. **Varela, L.**, Tambusso, P.S., Patiño, S.J., Di Giacomo, M., Fariña, R.A. (2017). Potential distribution of fossil xenarthrans in South America during the Late Pleistocene: Co-Occurrence and provincialism. **Journal of Mammalian Evolution**, 1-12. DOI: [10.1007/s10914-017-9406-9](https://doi.org/10.1007/s10914-017-9406-9).
19. **Varela, L.**, Fariña, R.A. (2016). Co-occurrence of mylodontid sloths and insights on their potential distributions during the late Pleistocene. **Quaternary Research**, 85(1), 66-74. DOI: [10.1016/j.yqres.2015.11.009](https://doi.org/10.1016/j.yqres.2015.11.009).
20. Buckley, M., Fariña, R.A., Lawless, C., Tambusso, P.S., **Varela, L.**, Carlini, A.A., Powell J.E., Martinez, J.G. (2015). Collagen sequence analysis of the extinct giant ground sloths *Lestodon* and *Megatherium*. **PloSone**, 10(11), e0139611. DOI: [10.1371/journal.pone.0139611](https://doi.org/10.1371/journal.pone.0139611).
21. **Varela, L.**, Fariña, R.A. (2015). Masseter moment arm as a dietary proxy in herbivorous ungulates. **Journal of Zoology**, 296(4), 295-304. DOI: [10.1111/jzo.12246](https://doi.org/10.1111/jzo.12246).
22. Fariña, R.A., Tambusso, P.S., **Varela, L.**, Di Giacomo, M., Musso, M., Gascue, A., Bracco, R. (2014). Among others, cut-marks are archaeological evidence: reply to ‘Archaeological evidences are still missing: a

comment on Fariña et al. Arroyo del Vizcaíno Site, Uruguay' by Suárez et al. **Proceedings of the Royal Society B**, 281(1795), 20141637. DOI: [10.1098/rspb.2014.1637](https://doi.org/10.1098/rspb.2014.1637).

23. Fariña, R.A., Tambusso, P.S., **Varela, L.**, Czerwonogora, A., Di Giacomo, M., Musso, M., Bracco, R., Gascue, A. (2014). Arroyo del Vizcaíno, Uruguay: a fossil-rich 30-ka-old megafaunal locality with cut-marked bones. **Proceedings of the Royal Society B**, 281(1774), 20132211. DOI: [10.1098/rspb.2013.2211](https://doi.org/10.1098/rspb.2013.2211).

In Review

1. **Varela, L.**, Tambusso, P.S., Fariña, R.A. Femora Nutrient Foramina and Aerobic Capacity in Giant Extinct Xenarthrans. In review at **PeerJ**. BioRxiv Preprint DOI: [10.1101/2023.09.27.559456](https://doi.org/10.1101/2023.09.27.559456).
2. **Varela, L.**, Martínez-Blanco, X., Ugalde, R., Tambusso, P.S., *Lobato, C., Gaucher, C., Fariña, R.A. Fossil Burrows in the Camacho Formation (Late Miocene, Uruguay) Reveal a Complex Community of Ecosystem Engineers in Southeastern South America. Submitted to **Proceedings of the Royal Society B**.

Book Chapters

1. Fariña, R.A., Beri, Á., **Varela, L.** (2023). Biological Diversity in Deep Time. In Encyclopedia of Biodiversity, 3rd Edition. Elsevier Science. *In press*. DOI: [10.1016/B978-0-12-822562-2.00253-X](https://doi.org/10.1016/B978-0-12-822562-2.00253-X)
2. Fariña, R.A., Tambusso, P. S., **Varela, L.**, Velazco, S., Di Giacomo, M., Gascue, A. (2021). Arroyo del Vizcaíno: Strengths and weaknesses of a very old archaeological/paleontological site in Uruguay, South America. In New Discoveries in the American Paleolithic: The Pre-16,000 Archaeological Record, Conference Proceedings. Sunbelt Publications, Inc. San Diego, CA.

Open Research Data

1. **Varela, L.**, Tambusso, P.S. (2023). 3D Models Related to the Publication: 3D Finite Element Analysis and Geometric Morphometrics of Sloths (Xenarthra, Folivora) Mandibles Shows... . MorphoMuseum, 9(2), 1-2. DOI: [10.18563/journal.m3.199](https://doi.org/10.18563/journal.m3.199).
2. **Varela, L.** (2023). 3D model related to the publication: Occurrence of the ground sloth *Nothrotheriops* (Xenarthra, Folivora) in the Late Pleistocene of Uruguay: New information on... . MorphoMuseum, 9(2), 1-2. DOI: [10.18563/journal.m3.191](https://doi.org/10.18563/journal.m3.191).
3. **Varela, L.**, *Lobato, C., Tambusso, P.S. (2021). 3D model related to the publication: Presence of the ground sloth *Valgipes bucklandi* (Xenarthra, Folivora, Scelidotheriinae) in southern Uruguay... . MorphoMuseum, 7(147), 1-2. DOI: [10.18563/journal.m3.147](https://doi.org/10.18563/journal.m3.147).

4. Brewer, P., Burton, K., Lister, A., Scott-Murray, A., Pullar, J., Steel, L., Keeble, E., Fariña, R.A. Tambusso, P.S., **Varela, L.**, Muyano, M. (2018). Darwin's Fossil Mammals [Data set]. Natural History Museum. DOI: [10.5519/0086786](https://doi.org/10.5519/0086786).

Working Papers

1. **Varela, L.**, Fariña, R.A. Isotopic Dietary Variability in the Ground Sloth *Lestodon armatus* (Xenarthra, Folivora): A Bulk-Feeding Grazer in the Late Pleistocene Pampas. Intended for **Palaeogeography, Palaeoclimatology, Palaeoecology**.
2. **Varela, L.** Sloths (Xenarthra, Folivora) Show a Unique Inhibitory Cascade Pattern Among Mammals. Intended for **Biology Letters**.

Awards and Honors

- 2021: **Stephen Jay Gould Student Research Award**. Paleontological Society.

Scholarships and Grants Awarded

- 2023: **Short-Term Fellowship**. Smithsonian Tropical Research Institute. \$ 3800
- 2021: **Student Research Grant**. Paleontological Society. \$ 1200
- 2021: **Sepkoski Grant (PalSIRP)**. Paleontological Society. \$ 1000
- 2021: **Graduate Student Research Award (GSRA)**. Society of Systematic Biologists. \$ 1000
- 2019: **Sepkoski Grant (PalSIRP)**. Paleontological Society. \$ 1000
- 2019–2023: **Ph.D. Scholarship**. CAP, Udelar, Uruguay. \$ 40000
- 2015–2018: **M.Sc. Scholarship**. ANII, Uruguay. \$ 15000
- 2011–2012: **Undergraduate Student Research Grant**. ANII, Uruguay. \$ 4000

Relevant Presentations at Meetings

- **Varela, L.**, Tambusso, P.S., Clavijo, L., *Lobato, C., *Núñez, T., Fariña, R.A. (2021). Ecological Niche Modeling of the South American Late Pleistocene Megafauna: Exploring Regionalization and Connectivity. 3rd Palaeontological Virtual Congress. Valencia, Spain.
- *Lobato, C., **Varela, L.**, Tambusso, P.S., Fariña, R.A. (2020). First Record of *Valgipes bucklandi* (Folivora, Xenarthra) Outside Brazil. 2nd Palaeontological Virtual Congress. Valencia, Spain.

- *Núñez, T., **Varela, L.**, Fariña, R.A. (2018). New Megafauna Fossil Remains from the Uruguayan Continental Shelf. 1st Palaeontological Virtual Congress. Valencia, Spain.
- **Varela, L.**, McDonald, H.G., Fariña, R.A. (2018). Sexual Dimorphism in the Extinct Ground Sloth *Lestodon armatus* (Mammalia: Xenarthra). 1st Palaeontological Virtual Congress. Valencia, Spain.
- **Varela, L.**, Tambusso, P.S., Fariña, R.A. (2016). Inner and middle ear 3D reconstruction of the extinct giant sloth *Lestodon armatus*. 11th International Congress of Vertebrate Morphology. Washington, DC, USA.
- **Varela, L.**, Tambusso, P.S., Di Giacomo, M., Patiño, S., Fariña, R.A. (2016). Potential distribution of fossil xenarthrans during the late Pleistocene. 11th International Congress of Vertebrate Morphology. Washington, DC, USA.
- **Varela, L.**, Fariña, R.A. (2015). Co-ocurrencia de perezosos en el sitio Arroyo del Vizcaíno, Uruguay, y sus distribuciones potenciales en el Pleistoceno tardío. V Congreso Latinoamericano de Paleontología de Vertebrados. Colonia del Sacramento, Uruguay.

Research Experience

2023–ongoing: **Principal Investigator** in the ANII I+D project “Testing megafauna extinction hypotheses: an approach using ecological niche models and life history simulations.”

2020–ongoing: Team Investigator in European Union’s Horizon 2020, Marie Skłodowska-Curie Actions, SciCoMove project. PI: Nathalie Richard and Irina Podgorny. scicomove.hypotheses.org

2018–2021: Team Investigator in the CSIC I+D project “Paleoecology and paleobiogeography of Pleistocene megafauna in Uruguay and the region.” PI: Richard Fariña.

2017–2019: Team Investigator in the NHM (UK) “Digitising Darwin’s Fossil Mammals” project. PI: Pip Brewer and Adrian Lister. [Link](#)

2017–2018: Team Investigator in the NatGeo grant “Arroyo del Vizcaíno site.” PI: Richard Fariña.

2016–2018: **Principal Investigator** in the CSIC I+D project “Three-dimensional reconstruction of the middle ear of the fossil sloth *Lestodon armatus*.”

2014–2016: Team Investigator in ANII I+D project “New paleobiological approaches in the study of fossil sloths.” PI: Richard Fariña.

2013–2014: Team Investigator in CSIC I+D project “Prospection of new fossil and archaeological sites in the Arroyo del Vizcaíno site.” PI: Richard Fariña.

2011–present: Curatorial activities at the Arroyo del Vizcaíno collection, Uruguay. Fossil preparation, collections management, and digitization.

Fieldwork and Visits to Scientific Collections

2022: One week stay at the University of Copenhagen Zoological Museum, Copenhagen, Denmark. Studying late Pleistocene Pampean megafauna, historical collections of American fossils, 3-d photography of specimens.

2022: One week stay at the Muséum National d'Histoire Naturelle, Paris, France. Studying late Pleistocene Pampean megafauna, historical collections of American fossils, 3-d photography of specimens.

2021–2023: Field work at Kiyú and Arazatí Neogene sites, Uruguay. Stratigraphic excavation, fossil burrows survey, vertebrate fossils extraction, sampling for isotopic analyses, 3-d photography of excavation areas.

2018: Field work at the late Pleistocene Aiguá site, Uruguay. Stratigraphic excavation, vertebrate fossils extraction, sampling for radiocarbon and isotopic analyses, 3-d photography of excavation areas.

2014: One week stay at the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina. Studying late Pleistocene Pampean megafauna, 3-d photography of specimens.

2014: One week stay at the Museo de la Plata, La Plata, Argentina. Studying late Pleistocene Pampean megafauna, 3-d photography of specimens.

2011–present: Field work at the Arroyo del Vizcaíno site, Uruguay. Stratigraphic excavation, vertebrate fossils extraction, sampling for radiocarbon and isotopic analyses, 3-d photography of excavation areas.

Teaching and Mentoring

Ongoing – Tomás Núñez. BSc. (Hons.) Biology, Specialization Paleontology. Universidad de la República. Advisor: **M.Sc. Luciano Varela** and Dr. Richard Fariña.

2022 - Carolina Lobato. BSc. (Hons.) Biology, Specialization Paleontology. Universidad de la República. Advisor: **M.Sc. Luciano Varela** and Dr. Richard Fariña.

2014–present: Teaching assistant, Udelar. Lab instructor, Paleontology.

Science Communication and Outreach

- Sci. Comm. Publication: **Varela, L.**, Batallés, M., Tambusso, P.S., Fariña, R.A., (2023). The strange megafauna that roamed the Earth until 12000 years ago. Under revision at **Frontiers for Young Minds**.
- Development Team Member in the science outreach project “Megafauna 3D.” megafauna3d.org
- Science outreach book: Batallés, M., Costoya, G., **Varela, L.**, Tambusso, P.S., Di Giacomo, M., Fariña, R.A. (2022). Megafauna 3D. Un libro de huesos. ISBN: 978-9915-41-026-5. [Link](#)
- Augmented Reality web app used for Megafauna 3D. Un libro de huesos. [GitHub](#)
- Lead role in the digitization of fossil specimens and sites at Udelar Paleobiology Lab. sketchfab.com/PaleoBioLAB

- Development Team Member in the science outreach project “Arroyo del Vizcaíno.” arroyodelvizcaino.org
- Talks for primary and secondary schools during visits to the Arroyo del Vizcaíno collection.
- Science outreach eBooks: Batallés, M., **Varela, L.**, Tambusso, P.S., Di Giacomo, M., Fariña, R.A. (2021). Megafauna en el Arroyo del Vizcaíno. ISBN: 978-9915-40-572-8. [Link](#)
- Augmented Reality web app used for Sci. Comm. talks and in the Arroyo del Vizcaíno exhibition. [GitHub](#)

Technical Skills

Ecological Niche Modeling, GIS, Photogrammetry, Cladistic and Bayesian Phylogenetics, Historical Biogeographical Analysis, Phylogenetic Comparative Methods, Geometric Morphometrics, Finite Elements Analysis, Bayesian isotope mixing models.

Software: AgiSoft Metashape, Beast2, Blender, FeBio, ImageJ, Maxent, Mesquite, MrBayes, Past, QGIS, R, TNT.

Workshops

2022 - **Skull collections. Series, standardization, and instruments.** Horizon 2020 Marie Skłodowska-Curie Actions, SciCoMove. Turin, Italy.

2020 - **Introduction to geometric morphometrics.** Universidad Católica del Maule. Chile.

2019 - **Latin American Evolution School.** European Society for Evolutionary Biology. PEDECIBA. Uruguay.

2019 - **Macroevolution.** Centro Universitario Regional Este. Uruguay.

2013 - **Megafauna and human presence in the Quaternary.** Faculty of Sciences. Udelar. Uruguay.

Service and Professional Affiliations

Meetings organization: Organizing committee of V Congreso Latinoamericano de Paleontología de Vertebrados. Uruguay. 2015.

Reviewer: Alcheringa (1), Boreas (1), Forests (4), Frontiers in ecology and evolution (1), Journal of environmental management (1), Journal of systematic palaeontology (2), Land (2), Nature communications (1), Naturwissenschaften (1), Palaeogeography, Palaeoclimatology, Palaeoecology (1), Papers in palaeontology (2), Quaternary (2), Zoological journal of the Linnean Society (2), Zoological Research (1). Independent project reviewer for Agencia Nacional de Promoción Científica y Tecnológica, Argentina (1).

Member: Conservation Paleobiology Network, Past Global Changes, Paleontological Society, Society of Systematic Biologists.