

High diversity of harvestmen in Atlantic Rainforest and ancient geological events

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Left to right: different species of harvestmen of subfamily Sodreaninae - *S. glaucoi, S. leprevosti* [photos: Glauco Machado], *S. inscripta and S. Sodreana* Credit: Ricardo Pinto-da-Rocha

In the southern Atlantic Rainforest remnants between Rio de Janeiro State in Southeast Brazil and Santa Catarina State in South Brazil, there are some 600 species of harvestmen (*Opiliones*), arachnids that live in caves and humid forests. The number of species is considered high even for this well-known biodiversity hotspot, and most of these species are endemic.

A reconstitution of the evolutionary history of the subfamily Sodreaninae has brought to light an explanation for this peculiar distribution pattern and emergence of new <u>species</u>. Contrary to expectations, the <u>high species diversity</u> is more likely related to ancient



geological events, such as mountain range uplift and river formation, than to relatively recent climate fluctuations (i.e., those in the last 20,000 years).

The discovery is based on correlations found between evolutionary data for seven lineages of harvestmen and the influence of geological events that occurred in the region in the last 30 million years. The study was conducted in Brazil by a group of researchers at the University of São Paulo's Bioscience Institute (IB-USP) in partnership with colleagues at the Federal University of Lavras (UFLA) and the Geology Institute (IG) in São Paulo. Its results are published in the journal *Molecular Phylogenetics and Evolution*.

"Curiously, the lineages are far older than the Last Glacial Maximum 20,000 years ago, when ice sheets covered the north of the planet, changing the climate worldwide. From the evidence gleaned in our study, based on genetic analysis of harvestmen alive now, this group began diversifying well before that, about 30 million years ago. This discovery is consistent with the geological evolution of the Ribeira de Iguape and Paraíba do Sul river basins, for example," said Elen Peres, a researcher at IB-USP and first author of the article.

Given the sensitivity of harvestmen and their preference for humid habitats, Peres and her group already surmised that they must have been affected by environmental changes due to climate oscillations in the last 2 million years of the Pleistocene, but the study proved that the speciation of *Opiliones* occurred much earlier and was caused by even more ancient geological events.

Just as the evolutionary theory developed by Charles Darwin (1809-1882) grew out of his observations of a type of speciation found in the Galapagos, where different islands were home to distinct but related species of finches, in this case, the Brazilian researchers found



that the formation of the Ribeira do Iguape Valley separated entire populations, causing different species to emerge over time.

Genetic analysis

"We knew the Atlantic Rainforest remnants in the South and Southeast contained a large and highly peculiar distribution of species belonging to this family of harvestmen, but what's new from this project is that we were able to date their emergence using molecular markers," said Ricardo Pinto-da-Rocha, a professor in IB-USP's Zoology Department and a co-author of the article.

According to the study, the diversification of harvestmen species began with the geological evolution of the Atlantic Rainforest in South and Southeast Brazil, including complex transformations derived from the separation of the African and South American continents during the Upper Cretaceous, which began over 100 million years ago. This event had consequences millions of years later, including mountain range uplift and erosion as well as intense magmatism.

Approximately 60 million years ago, the process culminated in the formation of the Continental Rift of Southeast Brazil, which runs parallel with the coast for 900 km between Curitiba, Southern Brazil, and Niterói, Rio de Janeiro, and is associated with the formation of important rivers, such as the Ribeira do Iguape and Paraíba do Sul.

The article notes that the Paraíba do Sul Valley is 550-400 m above sea level and surrounded by the Serra do Mar and Serra da Mantiqueira ranges, with elevations higher than 2,000 m, constituting geographical barriers.

"The harvestman species appeared at different times between 35 million and 10 million years ago," Pinto-da-Rocha said.



The point of looking for correlations between molecular data, climate and geology was to answer a key question about the Atlantic Rainforest biome, which is how its extraordinary biodiversity came about. "It would be great to know if any specific event or series of events caused the biome's outstandingly rich biodiversity with so many endemic species," said Thadeu Sobral-Souza, a researcher at UFLA and also a co-author of the article.

Most previous research concluded that the biome's biodiversity derived from recent climate events, he added. "Studies have shown that when the climate becomes cooler or warmer, species may become either locally extinct or more widely distributed," he told. "Our study demonstrates that geology was more decisive for species diversity than recent climate oscillations, at least for this group of *Opiliones*."

Peres agreed. "Higher levels of biodiversity normally correlate with a stable climate, but the climate fluctuations of the Pleistocene occurred between about 2 million and 10,000 years ago, long after the speciation of *Opiliones*," he said.

New classifications

The genetic analysis also resulted in a new configuration of species in the subfamily *Sodreaninae*, hitherto analyzed only on the basis of morphology. Molecular analysis showed, for example, that *S. sodreana* and *S. granulata* constituted the same species, henceforth called *S. sodreana*, while *S. barbiellinii* and *S. curupira* were found to be closer to the subfamily *Progonyleptoidellinae* than to *Sodreaninae*.

"Molecular data for *S. barbiellinii* and *S. curupira* showed that the convergence was merely morphological," Pinto-da-Rocha said. "Both species have a kind of appendix that they use to capture food, and were put in the same group when this was discovered 100 years ago. However,



we discovered from the genetic analysis that this trait has appeared more than once in different families, and genetically speaking these species are closer to *Progonyleptoidellinae*."

More information: Elen Arroyo Peres et al, Phylogeography of *Sodreaninae* harvestmen (*Arachnida: Opiliones: Gonyleptidae*): Insights into the biogeography of the southern Brazilian Atlantic Forest, *Molecular Phylogenetics and Evolution* (2019). DOI: 10.1016/j.ympev.2019.05.028

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