
The curious case of Cenozoic South America: Assembling the grassland biome with almost no grasses

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Résumé

Grassland ecosystems constitute one of the most prominent biomes today, covering about 40% of Earth's land surface. The assembly of the grassland biome has been of vital concern among paleontologists and evolutionary biologists for 140 years. Grassland evolution has primarily been studied using indirect lines of evidence, in particular the evolution of tall (hypsodont) cheek teeth of large mammalian herbivores, whereas direct paleobotanical data have historically been scarce. However, in recent years, phytoliths analysis has emerged as a useful tool for tracking the expansion of open habitats dominated by grassland vegetation, not least because of the potential for phytoliths to preserve in a wide range of Cenozoic deposits that do not contain other types of plant fossils. Phytolith records from North America and Eurasia have shown that grass-dominated vegetation spread in the late Oligocene or early Miocene, many million years before hypsodont ungulate herbivores evolved, supporting a link between floral and faunal change in these regions. In southern South America, hypsodont herbivores appeared and diversified in the middle Eocene (38 Ma), a pattern that was long thought to mark the spread of savanna vegetation 20 million years earlier than on any other continent. We have tested this hypothesis by analyzing early Eocene-middle Miocene (ca 49-12 Ma) phytolith assemblages from Patagonia (Argentina and Chile). In addition to 'traditional' compositional analysis of phytolith assemblages, we used a new proxy for habitat openness (reconstructed Leaf Area Index; *rLAI*) to evaluate whether habitats were open or closed, regardless of the relative abundance of grasses. The *rLAI* method relies on the fact that anticlinal epidermal cells (reflected as phytoliths) of non-grass plants change shape and size depending on light environment (with larger, more undulated cells in shaded environments) to infer light environment/habitat openness in fossil assemblages. Our phytolith assemblage compositional analysis showed that grasses were rare in Patagonia for most of the Cenozoic, and did not form grasslands until sometime after the middle Miocene. Instead woody plants, including palms, remained prominent in vegetation through the middle Miocene. However, these relatively grass-free habitats became increasingly open during

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the middle Eocene (as inferred using *rLAI*), culminating in non-analog palm shrublands roughly concurrently with the earliest hypsodont herbivores. Isotopic data from the same strata record arid climates consistent with this vegetation inference. These patterns suggest that, unlike for North America and Eurasia, hypsodonty in South America did not signal the arrival of grass-dominated habitats, but rather open systems with high availability of (likely inorganic) dietary abrasives. Our work shows that a combination of phytolith assemblage composition analysis and the *rLAI* method has great potential for reconstructing the Cenozoic emergence of not just grasslands but open habitats more generally-including vegetation types that have no modern counterpart.

Mots-Clés: Patagonia, grassland evolution, Leaf Area Index