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Occurrence of *Cyclusphaera scabrata* in Achiri (late middle-early late Miocene?, Bolivian Altiplano): paleogeographical implication

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Abstract

A palynological assemblage including the extinct araucarian dispersed pollen, *Cyclusphaera scabrata*, was analysed from the Achiri locality, Bolivian Altiplano. The fossil-yielding locality of Achiri is located in the Pacajes Province, La Paz Department, in the northwestern Altiplano, Bolivia. The Achiri locality is very well known by the fossil vertebrate faunas recovered from the Mauri Formation (M6). The palynological samples come from fine-grained and plant-rich carbonated lacustrine levels lower in the same unit. An age between late middle to early late Miocene was inferred for the palynological association studied based on local stratigraphy and radioisotopic ages obtained higher in the series. The retrieved association is mainly represented by angiosperms; although gymnosperms, bryophytes, ferns, and fresh-water algae are also documented. Compositae are the most abundant group within angiosperms, and *Polylepis* also occurred but in low percentages. The presence of *C. scabrata* in the Bolivian Altiplano expands the taxon distribution outside northern South America and provides additional evidence to infer timing and distribution routes of conifers, restricted toward the tropics during the latest Neogene. Its occurrence supports a paleoelevation of no more than 2000 m for the northern area of the Altiplano in agreement with previous results. Compositae of *Fenestrites* type and *Polylepis* occur earlier in Bolivia and *C. scabrata* later, comparing their occurrence in miocene microfloras from low to mid- latitudes of South America.

Keywords: Neogene palynomorphs; araucarian dispersed pollen; northwestern Altiplano; Mauri Formation.

1. Introduction

Nowadays, the Bolivian Altiplano as a whole is characterized by Puna vegetation, but the vegetation likely has considerably shifted in the Miocene and onwards. The precise timing and pattern of this shift is not well-constrained. In addition, Neogene palynological records from the Plurinacional State of Bolivia are pretty scarce. Graham et al. (2001) described a Miocene-Pliocene palynoflora originally presented by Berry (1922a) as the Pislepampa flora, Eastern Cordillera, Bolivia, with the following recognized microfossils: *Isoetes*, *Lycopodium*, *Cnemidaria*, *Cyathea*, *Grammitis*, *Hymenophyllum*, *Pteris*, trilete fern spores, *Danaea*, monolete fern spores, *Podocarpus*, Gramineae, Arecaceae, *Ilex*, cf. *Oreopanax*, *Cavanillesia*, cf. *Pereskia*, Compositae (three types), Ericaceae, and *Tetrorchidium*. Based on sedimentological, plant microfossil and macrofossil evidence, Graham et al. (2001) recovered evidence of a lacustrine environment bordered by elements of the Amazonian rainforest, with a cloud forest growing on the surrounding slopes. Gregory-Wodzicki (2002) analysed a new collection of the late Miocene Jakokkota flora (the upper Jakokkota flora) from a lacustrine unit, located above the lower Jakokkota flora, from a fluvial unit, first documented by Berry (1922b) and further described by Gregory-Wodzicki et al. (1998). These fossil leaf impressions, located in the northern Altiplano of Bolivia, in the Member 6 of the Mauri Formation, correspond to 24 fossil-species, mainly represented by Anacardiaceae, *Berberis*, Myrtaceae, *Zizyphus*, *Polylepis*, and several leguminosae. Based on leaf morphology for the combined flora (both lower and upper Jakokkota floras), the mean annual temperature was inferred to be $21.5 \pm 2.0^\circ\text{C}$ and the mean annual precipitation of 550 ± 180 mm. The most accurate age based into radioisotopic method (Sanidine from ash falls) of these floras is around 10.66 ± 0.06 Ma (Gregory-Wodzicki et al. 2002). The inferred elevation at that time (Late Miocene) was no more than 1600–1200 m, whereas today is almost 4000 m above sea level (ASL; Gregory-Wodzicki, 2002). Thus, based on the study of these floras, Gregory-Wodzicki (2002) suggested that a large portion of the Central Andes was covered by subtropical-dry forest with nearly half of the modern Altiplano elevation reached since the early late Miocene interval.

In this contribution, we document for the first time a palynological assemblage including the extinct araucarian dispersed pollen, *Cyclusphaera scabrata*, recovered from the northern Altiplano (Achiri locality: ACH-26 locus Cerro Pisakeri) and we discuss its correlation with palynological zonations from different sections of northern South America. The data presented here partially bridges the gap for Neogene floras from Bolivia, providing useful information to reveal the plant distribution during this period in the Central Andes region. All this, especially taking into account the difficulty of finding favorable lithologies for palynological studies in the Neogene of the Altiplano region.

1.1. Geological and stratigraphical contexts

The fossil-yielding locality of Achiri is located in the Pacajes Province, La Paz Department, in the northwestern Altiplano, Bolivia (Fig. 1). The Altiplano is an extensive intramontane basin formed during the Cenozoic era, starting with the Eastern Cordillera uplifting (Suárez-Soruco, 2000). The Altiplano plateau of western South America lies within the Central Andes above the subducting Nazca plate. The extensive sedimentary archive accumulated in this area is of special interest as it reflects the Altiplano Neogene paleoclimate and surface uplift history (Garzzone et al., 2006; 2014). In the western Altiplano, the late Oligocene–Miocene Mauri Fm. unconformably overlies the Berenguela Fm. (Evernden et al., 1977). The Mauri Fm. comprises six members (M1 to M6) which include volcanoclastic rocks interbedded with volcanic flows (Sirvas and Torres, 1966). This unit was deposited in a wide fluvial and lacustrine plain in a backarc basin. The Achiri locality is well known by the fossil vertebrate faunas recovered from the Mauri Fm, M6 (e.g., Villarroel 1974; Villarroel and Marshall, 1983; Marshall et al., 1983; Hoffstetter, 1986; Saint-André, 1993, 1996; Pujos et al., 2012; Fernández-Monescillo et al., 2019; Gaudin et al., 2022). The fossiliferous levels of the Achiri locality were dated between 10.5 Ma (K-Ar, at Hako-kota; Evernden et al., 1977) and 8 Ma (K-Ar, west of San Andrés, Evernden et al., 1977). In the same area, Fernández-Monescillo et al. (2019) described a partial pathological skeleton of the notoungulate mesotheriid *Plesiotypotherium achirense* from the Cerro Pisakeri (Fig. 1) in the locus ACH-27 (Fig. 2), immediately bracketed by two 15m-distant ash layers for which they performed step-heating $^{40}\text{Ar}/^{39}\text{Ar}$ experiments on feldspar micro-populations and obtained plateau ages of 10.42 ± 0.09 Ma (ACH-TUF3, below) and 9.42 ± 0.1 Ma (ACH-TUF4, above), respectively. Accordingly, they confirmed the late Miocene age (Tortonian or late Mayoan–early Chasicoan from South American Land Mammal Ages [SALMAs] for the corresponding locus (ACH-27) and surrounding assemblages, and provided a sedimentation rate approximating 15 m per million years in the concerned time interval. The presence of several successive volcanoclastic beds, occurring throughout the sequence cropping out on the Cerro Pisakeri, suggests an almost continuous volcanic activity during the late Miocene in this area.

Extensive field explorations conducted by our team during the last decade also resulted in the discovery of older fossil-bearing levels, at the bottom of the available stratigraphic section (Fig. 2). These fine-grained and plant-rich carbonated levels (ACH-25 and ACH-26) testify to the presence of lacustrine settings in the area, in which the palynological samples were collected (ACH-25, ACH-26; Fig. 2). Interestingly, ACH-26 has yielded amphibian, bird, rodent and plant remains (Douillez et al., 2018). A late middle to early late Miocene? age can be inferred for ACH-26 and thus for ACH-25 when considering a roughly constant and low sedimentation rate throughout the whole Cerro Pisakeri section (Fig. 2).

1.2. Achiri vertebrate faunas

The late Miocene mammalian assemblage of Achiri is, together with that of Quebrada Honda (Croft, 2007), one of the most abundant and diversified faunal association during the Neogene in the Plurinacional State of Bolivia. This fauna includes several notoungulates such as the mesotheriid *Plesiotypotherium achirensense*, the small hegetotheriid cf. *Hemihegetotherium*, and the toxodontid *Hoffstetterius imperator*, a macraucheniid litoptern, the sparassodontan metatherian *Borhyaenidium altiplanicum*, and a wide array of xenarthrans with the glyptodont *Trachycalyptoides achirensense*, several Dasypodidae, a pampatheriid, and ground sloths. The latter group is documented by a megatheriine, an unidentified mylodontid, the scelidotheriine cf. *Proscelidodon* sp. and the small megatherioid “*Xyophorus*” *villarroeli* (e.g., Marshall et al., 1983; Saint-André, 1996; Pujos et al., 2012). Recently, new discoveries have permitted to: i) extend our knowledge of *Plesiotypotherium achirensense* (Fernández-Monescillo et al., 2018, 2019), ii) suggest that the extinct sloth “*Xyophorus*” spp. (including *X. villarroeli*) could correspond to an early-diverging nothrothere for which the new genus *Mcdonaldocnus* is proposed (Pujos et al., 2021; Gaudin et al., 2022), and iii) identify several rodents including the cavioids *Prodolichotis prisca* and *Cardiomys* sp., the chinchilloids *Tetrastylus* sp. and *Lagostomus* sp., and an octodontoid of uncertain affinities (Pérez et al., 2021).

2. Material and methods

Five samples were collected and processed for palynology: ACH-25, ACH-26 (PN1,2,3), ACH 14. Only two yielded palynomorphs. The two productive samples come from ACH-25 (S17°11.261', W68°00.153') and ACH-26 (S17°14.459', W69°00.255') in a dry canyon at the NW base of the Cerro Pisakeri. ACH-26 corresponds to lacustrine grey siltstone with abundant plant detritus and leaf fragments. The physical and chemical extractions of palynomorphs were performed in the Paleopalynology Laboratory at the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA) located in Mendoza, Argentina. The samples were treated with hydrochloric and hydrofluoric acids following the palynological processing techniques according to Volkheimer and Melendi (1976). No oxidation was needed. The residues were sieved with a 10 µm filter and the final slides were mounted in glycerin jelly. The specimens were examined using an Olympus BX 50 microscope. Location of the specimens on the slides, and in figure references is given by ESF (England slide finder) coordinates. The slides are housed at the Laboratory of Palynology of the IANIGLA under the catalogue numbers: 10566 (ACH-25) and 10567 (ACH-26) MPLP (Mendoza-Paleopalintoteca- Laboratorio de Paleopalínología). The palynostratigraphic analysis was based mainly on the zonation presented by Hoorn (1993) and Jaramillo et al. (2011) for the Neogene of Amazonia and Northern South America palynology.

3. Results

3.1. Palynology

The palynological association from both levels ACH-25 and ACH-26 comprises pollen grains, spores, and fresh-water algae. However, the palynomorphs recovered from the lower level (ACH 25) were very scarce, thus preventing statistical counts. This sample yielded only some psilate and verrucate trilete spores, a few angiosperms of compositae type (type 1 and 2, see below to which correspond each) and the tricolporate *Psilatricolporites crassoexinatus*.

The material recovered at the upper level (ACH-26) was quite abundant and well preserved instead, allowing to make a detailed taxonomic and relative abundance analysis based on 202 specimens counted (Fig. 3). Angiosperms are the most abundant group (90%) in the association corresponding to ACH-26, but gymnosperms, bryophytes and ferns are also documented. The fern spores retrieved included mainly laevigate monolete and trilete spores (*Laevigatosporites* sp. and *Deltoidospora* sp.; Figs. 4 A, B) and aquatic ferns (*Azolla* and *Salvinia*). Liverwort spores (Marchantiales) of *Riccia* type, similar to *Reboulisporites fuegiensis* Zamalao and Romero (Fig. 4 C), are recorded.

Gymnosperms are represented by pollen grains with coniferous affinities: *Cyclusphaera scabrata* (1%) and *Podocarpidites* sp. (0,5%). *Cyclusphaera* is a taxon with a typical Gondwanan distribution during the Mesozoic era. It corresponds to a biaperturate pollen grain with affinity to the Araucariaceae, based on early Cretaceous cones found with pollen *in situ* in Patagonia, Argentina (Del Fueyo and Archangelsky, 2005). The general distribution of the genus was reduced during the Cenozoic, and its geographical range shifted mostly toward the tropics. *Cyclusphaera* was a common element of tropical floras in South America and Africa during this time, and it became restricted to western South America by mid-Neogene times (Jaramillo et al., 2013).

Cyclusphaera scabrata was erected by Jaramillo and Dilcher (2001) from the Paleocene–early Eocene Interval of Colombia. Subsequently, Jaramillo et al. (2013) expanded the original description of the species adding new data of the exine structure obtained by transmission electron and scanning electron microscope. The Bolivian specimens (eight measured from ACH-26) have circular to elliptical amb (55 to 72 μm) with two symmetrical circular apertures with regular edges (always regular) (20 to 37 μm) occupying nearly one-third of the total grain diameter (Figs. 4 E-H). One of these specimens (Fig. 4 F) is corroded showing the granulae at the innermost portion of the sexine. The area between the aperture and equatorial margin of the Bolivian specimens is 17 to 20 μm . The aperture membrane is not present in the studied specimens. The equatorial exine thickening, of 2 μm , of *C. scabrata* given by Jaramillo and Dilcher (2001) is observed in none of the Bolivian specimens. The thickness of the exine (1 μm) is equal between the equatorial zone and the aperture. The specimens from Achiri locality (ACH-26) are slightly larger than those from the Paleogene of Colombia, in agreement with the size increase-upward trend, proposed by Jaramillo et al. (2013) in

their stratigraphic section. These authors gave a complete discussion of the worldwide spatial and temporal distributions of this taxon. The distribution of *Cyclusphaera scabrata* was even more restricted during the late Miocene–early Pliocene, recording both a drastic increase in aridity in the tropics and the expansion of C4 grasses and savannas (Zachos et al., 2001; Edwards et al., 2010).

In the Neotropics, Parra et al. (2020) described the palynology from a Neogene sequence in the Marañon Basin, north of Peru and mentioned the presence of *C. scabrata* in Zone Mar-B, corresponding to the Burdigalian stage (17.71–16.1 Ma). Sá and Carvalho (2017) and D’Apolito et al. (2021) recorded the same fossil-taxon in Miocene deposits of the Solimões Fm. in the Solimões Basin (western Brazilian Amazonia), as well as Hoorn et al. (2017) in the middle–late Miocene interval of Well 2 of Foz do Amazonas Basin (offshore Pará, Brazil). The latter authors recognize *C. scabrata* as a component of the tropical lower montane forest. The youngest record of *Cyclusphaera* (only one specimen) was reported from the Choco region in westernmost Colombia, at ca. 1.5°N, dated at 5.5 Ma (Jaramillo et al., 2013).

Podocarpaceae (represented in the association by *Podocarpidites* sp. Fig. 4D) is a southern hemisphere conifer family, which comprises evergreen, coniferous trees, and shrubs. Today, it is still a conspicuous component in angiosperm-dominated tropical forests. Tropical podocarps are most abundant in mid- to high elevation forests but also occasionally at low elevation (Cernuzak et al., 2010). The pattern of dispersal or extinction of this family during the Cenozoic was related to the availability of areas of wet climate and equable mesothermal temperatures (Morley, 2011). Thus, its presence in the palynoflora is considered as indicative of upland vegetation (mountain slopes, Andean Forest). Jaramillo et al. (2013) consider its distribution a better analogue to the pattern seen in *Cyclusphaera*.

Compositae are the most abundant group within angiosperms in the Achiri association (77.2% in ACH-26). They are represented by four morphological types similar to Asteraceae: i) prolate tricolporoidate grains (19 to 26 µm, polar axis), echinae short (~2µm) (Figs. 4, I–J) Compositae type 1 similar to *Senecio*); ii) roughly similar to C. type 1 but differs in the size of the echinae which are more than 5µm long (Fig. 4, L Compositae type 2 similar to *Baccharis*); iii) tricolporate, echinate, fenestrate larger than 30 µm (Fig. 4, K Compositae type 3 similar to *Taraxacum*) and iv) small fenestrate pollen grains (20–24 µm) *Gomphrena* type and *Vernonia* type (similar to the morphotype *Fenestrites*; Figs. 4, M, N). Compositae first appear in South America in the late Oligocene–early Miocene interval and do not become frequent or diverse until the middle to late Miocene (Graham et al., 2001). Barreda et al. (2010) based on the broad distribution patterns of basal Asteraceae and allied families during the Oligocene in the Southern Hemisphere, suggested an Eocene origin of the clade. A significant diversification of Asteraceae occurred during the Early Miocene (Barreda et al., 2010).

Tricolporate pollen grains corresponding to *Polylepis/Acaena* group occurred (Fig. 4 O, P). They have an endoaperture with a zone of 35–42 µm (diameter); the sexine (ectexine) covers the endopore, forming a chamber with prominent flaps (pouchlike

extensions); and the exine is 1.5 μm thick microverrucate. The genus *Polylepis* consists of shrubs or trees native to the mid- and high-elevation tropical Andes (Simpson, 1979). *Polylepis* appears to be the highest natural occurring arborescent angiosperm genus in the world, since some members of the genus are components of the upper montane forest, but others occur in woodlands at elevations as high as 5200 m (Simpson, 1979). High pollen values of *Polylepis/Acaena* and Compositae, are considered to be diagnostic of a sub-puna shrubland (Hansen et al. 1984). Today *Polylepis* is commonly found in Bolivia in the Yungas (Paramo), southern Puna and northern Puna (Ortuño et al. 2011). In the late Miocene of the Bolivian Altiplano, Gregory-Wodzicki (1998, 2001) recorded *Polylepis* as one of the most abundant forms among fossil dicot leaves from Jakokkota flora. Martínez et al. (2020) recorded the presence of *Polylepis* from El Descanso Fm (Central Andean Plateau, Peru) in both studied Members (B and C). Going to east, Hoorn et al. (2017) recorded the first occurrence of *Polylepis-Acaena* in much younger strata from a well in the Foz do Amazonas Basin (5.8 Ma; Brazil). The presence of this pollen type, despite its low abundance (*ca.* 2%), points to the onset of subpuna vegetation (following Hansen et al. 1984) since the late Middle to early late Miocene in Bolivia.

Psilatricolporites crassoexinatus Hoorn (1993), an angiosperm of unknown affinity, is also present (Fig. 4 S). It was previously recorded in the Miocene–Pliocene Solimões Fm. (Hoorn, 1993; Nogueira et al., 2013) and the Miocene–Pliocene Novo Remanso Fm. from central Amazonia (Guimaraes et al., 2015). In addition, Polycolporate endocingulate pollen grains occur (Fig. 4 Q), corresponding to Polygalaceae (similar to *Xanthophyllum*). Polygalaceae have a cosmopolitan distribution and include trees, shrubs, lianas, herbs, and parasites (Banks et al., 2008). The pollen assemblage also includes tricolpate reticulate pollen grains (probably of Brassicaceae affinity, Fig. 4R) and a reticulate tricolporate of unknown affinity (Fig. 4T).

Freshwater algae referable to *Botryococcus* are retrieved (6%), further testifying to a lacustrine environment.

Finally, abundant organic matter mainly conformed by biostructured phytoclasts, cuticles, and abundant woody remains (bigger than 100 μm in length), complete the palynological association of both levels (ACH-25 and ACH-26), giving account of local vegetation which was much more diversified at that time in terms of types.

3.2. Palynostratigraphy

We correlate our data from Achiri to the palynological zonation from the Llanos Basin in Colombia (Jaramillo et al., 2011) and coeval floras from low to mid- latitudes of South America. The palynostratigraphic scheme from Colombia has been applied also to correlate outcrops and cores in the Miocene of Peru, southern Colombia, and Brazil (Boonstra et al., 2015; Hoorn et al., 2017; Jaramillo et al., 2017, Parra et al., 2020). The Achiri association can be correlated with a part of the *Fenestrites spinosus* Zone T16 (12.7 to 7.1 Ma), from the Cenozoic of Los Llanos, Colombia (Jaramillo et al., 2011)

due to the occurrence of this taxon in both associations. Nevertheless, *Cyclusphaera scabrata* had thus far its last appearance datum (LAD) in this scheme in Zone T-13 of Los Llanos, Colombia, i.e. in the late early Miocene (17.7 to 16.1 Ma). However, Jaramillo et al. (2013), based on unpublished data from western Colombia, mentioned a youngest record of this taxon as young as 5 Ma-old. In Achiri, *C. scabrata* occurs 58 meters below the tuff ACH-TUF-3 (Fig. 2) dated as 10.42 ± 0.09 Ma (Fernández-Monescillo et al., 2019). The sedimentary dynamics seems to be fairly steady and constant over the complete sequence measured at Cerro Pisakeri (Fig. 2), with fluviolacustrine and floodplain deposits, accumulated with a mean sedimentation rate of 15 m per million years at the top (between ACH-TUF-3 and ACH-TUF4). This in turn allows for hypothesizing a probable age between late middle to early late Miocene? for the palynological association studied.

The presence of *C. scabrata* in the Neogene of Bolivia expands the known distribution of the taxon outside northern South America and corresponds to the southernmost record of the specie during the Miocene (a complete distribution of the taxon is available in Jaramillo et al., 2013).

Martínez et al. (2020) studied the plant fossil record from the Descanso-Yauri Basin, Southern Peru including palynological (pollen and spores) and macrofossil samples from two lithostratigraphic units (Members B and C) of more than 88 localities. The members were previously dated using radiometric methods: Member B, dated to *ca.* 18.7 to 9.1 Ma (early to late Miocene), and Member C, dated to *ca.* 4.8 to 3.9 Ma (early Pliocene). The palynoflora of Member B is composed of common montane forest indicators such as *Podocarpus*, *Hedyosmum*, *Bocconia*, *Mutisia*, and *Cyatheaaceae*, as well as higher elevation taxa such as *Calamagrostis*, *Polylepis*, and *Valeriana*. Part of Member B correlates to the Achiri palynoflora, having in common Podocarpaceae and *Polylepis*. Parra et al. (2020) carried out a detailed palynostratigraphic research of the Marañon Basin (western Amazonia, Peru) based on the identification of qualitative changes in palynomorphs through the intervals sampled in six exploration wells. They recognized six palynozones spanning the early Miocene– early Pliocene time interval (Mar- A-F). Accordingly, the Achiri palynoflora may be coeval to Mar-C (latest Burdigalian to late Langhian) and part of Mar-D (late Serravallian) from Marañon Basin. However, there are no common species in both associations. Tcheumeleu et al. (2020), recorded palynomorphs, fossil plants, microfossils (charophyte oogonia and ostracod fragments), mollusks, and vertebrates from the Middle Ipururo Fm, at the the Shumanza Section, Subandean Zone of Northern Peru. The Peruvian association includes palynostratigraphic markers as *Grimsdalea magnaclavata*, *Palaeosantalaceaepites cingulatus*, *Echitricolporites spinosus*, and *Fenestrites longispinosus*, pointing to a late Miocene–early Pliocene age for the TAR-27 locality (10.06–3.72 Ma). They concluded the persistence of a steady lowland rainforest (with absence of characteristic high-altitude taxa such as *Podocarpus*, *Hedyosmum*, *Jamesonia*, or *Polylepis*) close to the Andes between 10 and 8 Ma. The marker taxa recovered in Peru were not recognized in the Achiri palynoflora with the exception of Compositae of *Fenestrites* type, present in both palynofloras but with different species.

The Asteraceae zone which corresponds to the middle Tortonian–late Messinian period is very uncommon in the Brazilian Amazon palynofloras and there are only three records of the Asteraceae zone coming from three boreholes of the southwestern part of the Amazonas state (Leandro et al., 2019). In summary, we can conclude that an association of *Compositae-Polylepis-Cyclusphaera* characterizes the Achiri palynoflora which can be dated from the late middle to early late Miocene?. In this sense, Compositae of *Fenestrites* type and *Polylepis* occur earlier in Bolivia and *Cyclusphaera scabrata* later, comparing their occurrence in other miocene microfloras of the region.

4. Conclusions

The presence of *Cyclusphaera scabrata* at the bottom of the Achiri section (late middle to early late Miocene?) greatly increases the southernmost distribution of this taxon during the Neogene, farther to the South. This data also provides a useful additional contribution to infer the timing and distribution routes of conifers towards a more restricted location in the tropics during the latest Neogene. The occurrence of *Cyclusphaera*, of Araucariaceae affinities, together with Podocarpaceae pollen confirms the effective presence of conifers as components of the upland vegetation (Andean Forest) in the northwestern Bolivian Altiplano, during the late middle to early late Miocene. We assume for the extinct *Cyclusphaera* taxon similar environmental conditions of closely-related extant species of *Araucaria*. In this sense, *Araucaria angustifolia* grows today at a similar latitude (20°S) at high elevations between 1500 and 1800 m near Rio de Janeiro, Brazil (Ledru and Stevenson, 2012) and in adjacent areas of eastern Paraguay and northeastern Argentina. This taxon generally occurs at 800 m to 1800 m in the north and at 500 m to 1200 m near its southern limits (Veblen et al. 1995). Thus, considering that conifers need high levels of rainfall in temperate regions, and that they barely tolerate to drought, we can suggest an elevation of no more than 2000 m for the northern area of the Altiplano in agreement with the results of Gregory-Wodzicki (2002) and Boschman (2021). Besides, the occurrence of abundant Compositae pollen associated with incipient presence of *Polylepis* in the Achiri microflora are indicative of the sub-puna shrubland vegetation. *Botryococcus* and aquatic fern spores (*Azolla* and *Salvinia*) embody the freshwater communities related to the lacustrine environment. We hope that these first results will trigger new field efforts, in order to better bridge the existing gaps in the Neogene palynological record of the Bolivian Altiplano.

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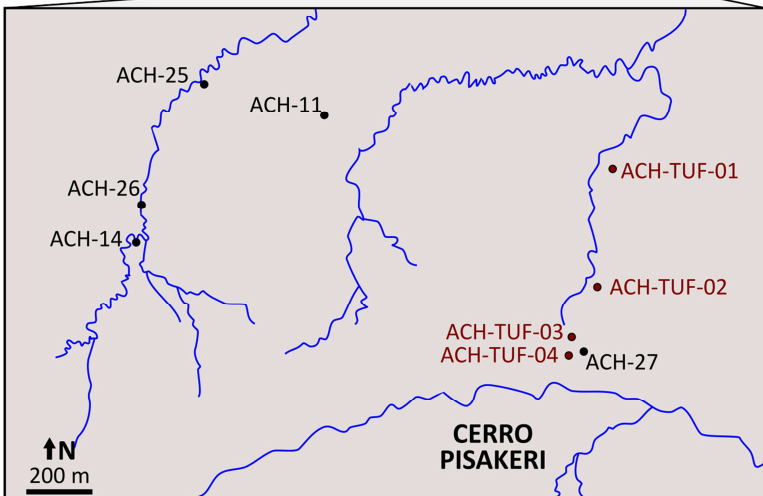
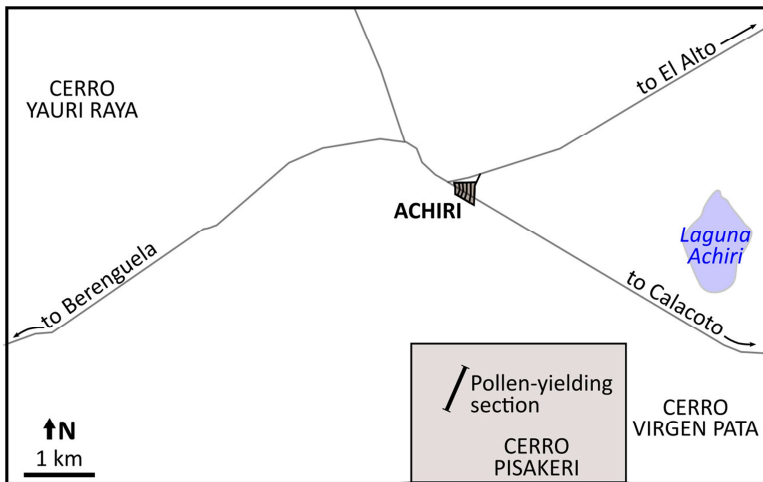
Figure captions

Figure 1. Location map of the studied area around Achiri, in the La Paz Department, Pacajes Province, Bolivia. General map of the Plurinacional State of Bolivia showing Achiri locality (present contribution); Jakokkota flora (Berry 1922b; Gregory-Wodzicki et al., 1998; 2002) and Pislepampa flora (Berry 1922a; Graham et al., 2001) (right side). Detailed map showing location of the sampled points for palynology and ash levels (left side), in the north of Cerro Pisakeri.

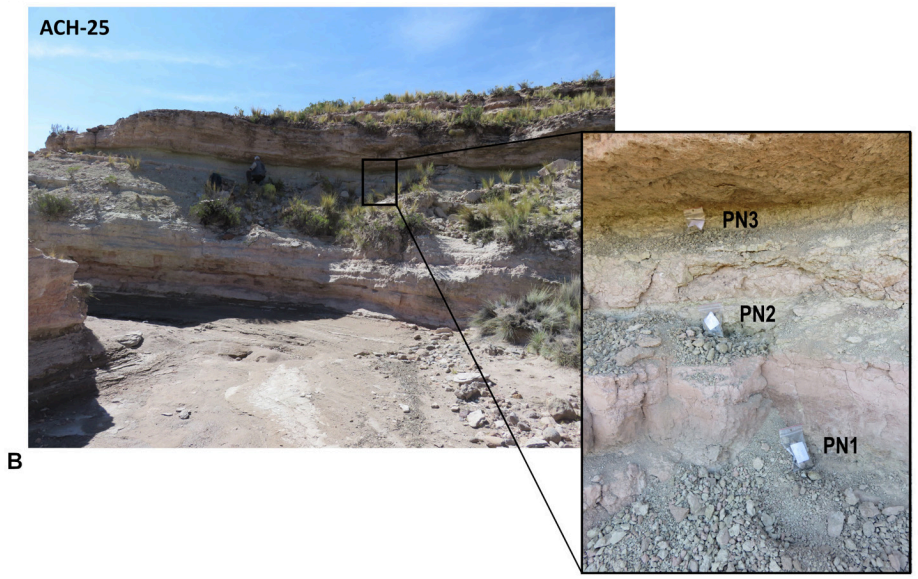
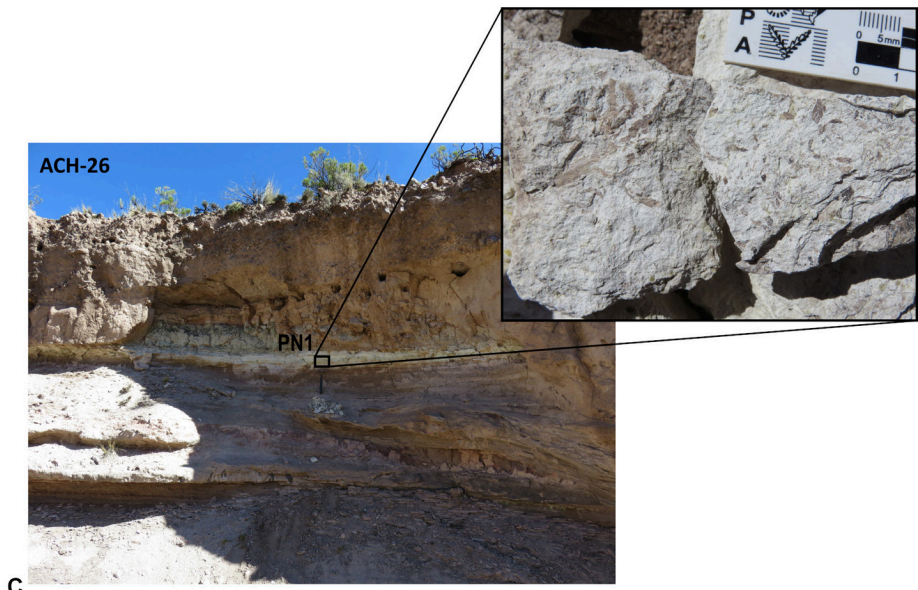
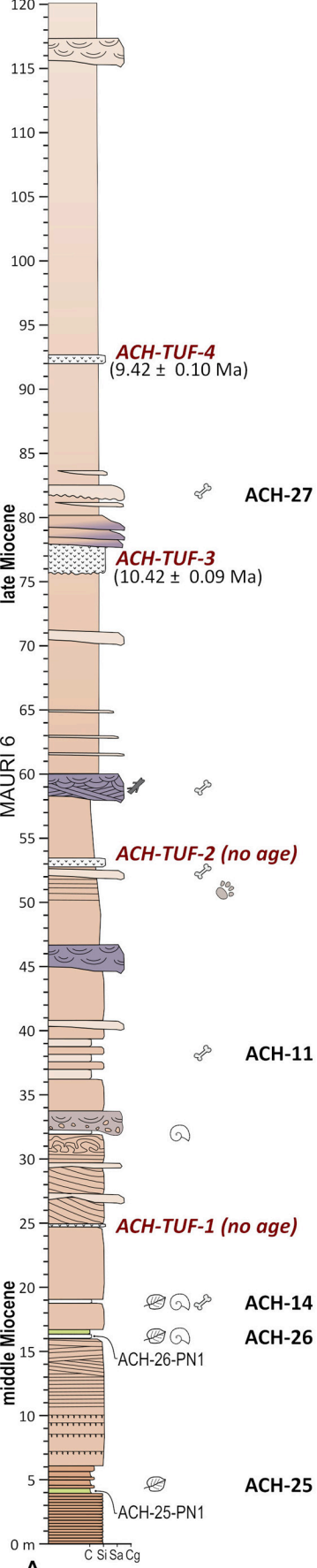
Figure 2. (A) Lithologic column of Member 6 of Mauri Fm. at Cerro Pisakeri, Achiri locality, north-western Altiplano, Bolivia. Location of the fossil and volcanoclastic levels. (B)(C) photographs showing levels sampled for palynology; ACH-25 and ACH-26 locations respectively (and details of each of them). Abbreviation: ACH-TUF, volcanic ash (tuff) samples; PN, palynological samples. ACH-14 unproductive palynological sample; ACH-11 vertebrate remains, ACH-27 locus of the partial pathological skeleton of *Plesiotypotherium achirense* described by Fernández-Monescillo et al. (2019).

Figure 3. (A) Bar diagram showing relative percentages of different groups of palynomorphs in the ACH-26; (B) relative percentage of the different groups among angiosperms from ACH-26.

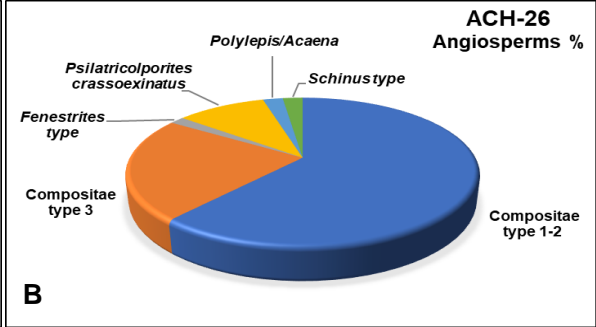
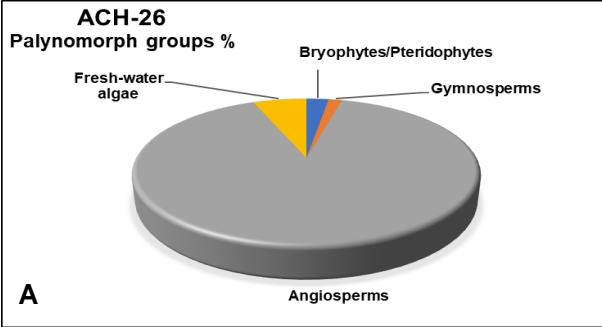
Figure 4. Palynomorphs from Achiri locality. (A) *Deltoidospora* sp. 10567B: J 29/3 (25 µm); (B) *Laevigatosporites* sp. 10567C: E32/0 (36 µm); (C) *Reboulisporites fuegiensis* Zamaloa and Romero 1990, 10567A: T30/2 (45 µm); (D) *Podocarpidites* sp. 10567B: D42/2 (55 µm); (E-H) *Cyclusphaera scabrata* Jaramillo and Dilcher 2001, (E) 10567B: V24/2 (72 µm), (F) 10567A: W29/2 (55 µm), (G) 10567B: T26/0 (70 µm each specimen); (H) 10567B: V27/4 (60 µm); (I) Compositae type 1, 10567C: J42/1 (22 µm); (J) Compositae type 1, 10567A: W44/0 (22 µm); (K) Compositae type 3, 10567C: O22/0 (37 µm); (L) Compositae type 2, 10567C: F20/1 (23 µm); (M-N) *Fenestrites* sp. 10567B: M32/3 (20µm); (O-P) *Polylepis* sp. (O) 10567B: U38/1 (39 µm), (P) 10567B: U43/0 (42 µm); (Q) Polygalaceae 10567C: T20/3 (37 µm); (R) Tricolpate reticulate indet. 10567C: S37/4 (42 µm) (S) *Psilatricolporites crassoexinatus* Hoorn 1993, 10567 A*: E32/3 (35 µm) (T) reticulate tricolporate 10567A: M40/1 (22 µm). Scale bars= 10µm.

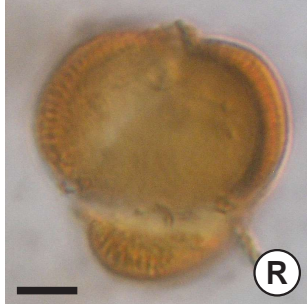
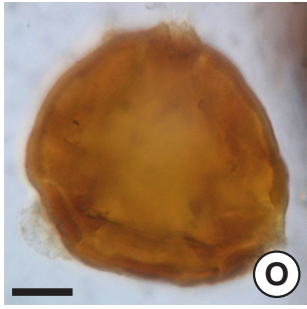
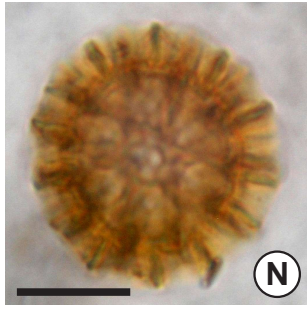
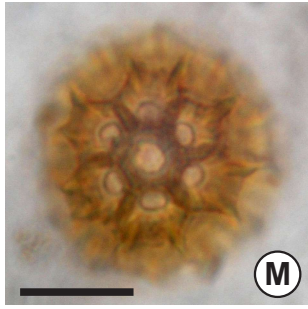
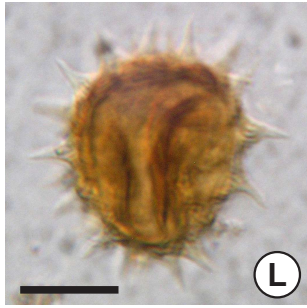
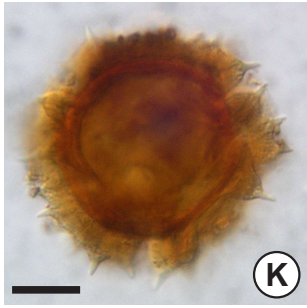
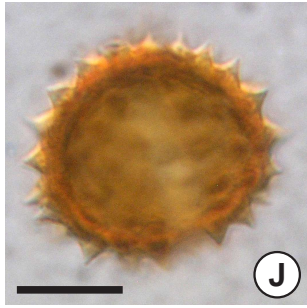
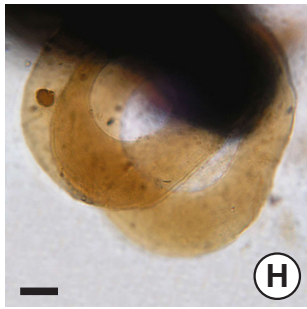
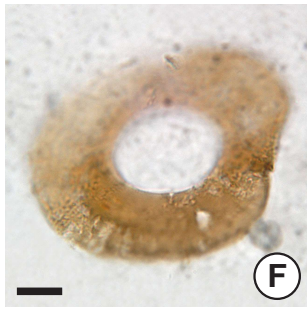
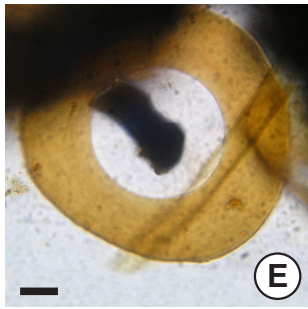
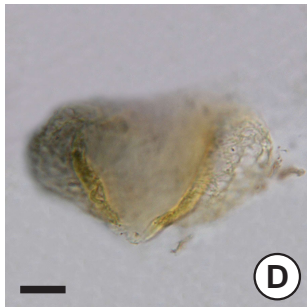
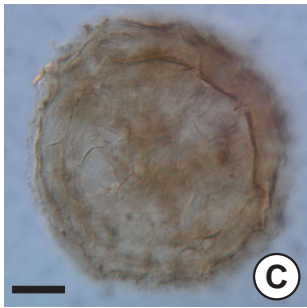
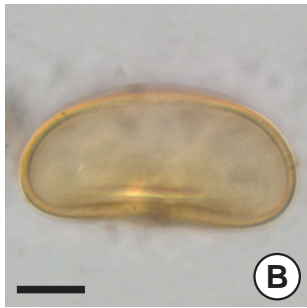
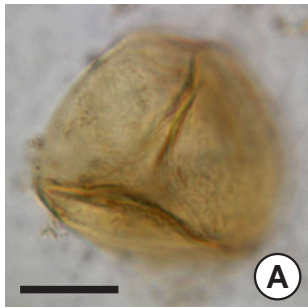


Cerro Pisakeri



	Volcanic ash
	Paleosol
	Wood
	Leaf/wood imprints
	Molluscs
	Vertebrates





PALYNOMORPHS%	ACH-26
Bryophytes/Pteridophytes	2.5
Gymnosperms	1.5
Angiosperms	90
Fresh-water algae	6
	100%

ANGIOSPERMS %	ACH-26
Compositae type 1-2	61.5
Compositae type 3	22.6
Fenestrites type	1.6
Psilatricolporites crassoexinatus	9.9
Polylepis/Acaena	2.2
Schinus type	2.2
	100%