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# Vegetation and climate change on the Bolivian Altiplano between 108,000 and 18,000 years ago

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## Abstract

A 90,000-yr record of environmental change before 18,000 cal yr B.P. has been constructed using pollen analyses from a sediment core obtained from Salar de Uyuni (3653 m above sea level) on the Bolivian Altiplano. The sequence consists of alternating mud and salt, which reflect shifts between wet and dry periods. Low abundances of aquatic species between 108,000 and 50,000 yr ago (such as *Myriophyllum* and *Isoëtes*) and marked fluctuations in *Pediastrum* suggest generally dry conditions dominated by salt pans. Between 50,000 yr ago and 36,000 cal yr B.P., lacustrine sediments become increasingly dominant. The transition to the formation of paleolake "Minchin" begins with marked rises in *Isoëtes* and *Myriophyllum*, suggesting a lake of moderate depth. Similarly, between 36,000 and 26,000 cal yr B.P., the transition to paleolake Tauca is also initiated by rises in *Isoëtes* and *Myriophyllum*; the sustained presence of *Isoëtes* indicates the development of flooded littoral communities associated with a lake maintained at a higher water level. *Polylepis tarapacana*-dominated communities were probably an important component of the Altiplano terrestrial vegetation during much of the Last Glacial Maximum (LGM) and previous wet phases.

**Keywords:** quaternary, pollen, *Polylepis tarapacana*, Salar de Uyuni, Andes, paleohydrology, *Myriophyllum*, *Isoëtes*, *Pediastrum*

## Introduction

Paleoecological records from the Altiplano of Peru/Bolivia are important for understanding past climatic linkages between Amazonia and the Andes, as well as wider teleconnections, such as with the North Atlantic (Baker et al., 2001a). Of particular value are those few records that extend beyond the Last Glacial Maximum (LGM), which have the potential to help resolve issues surrounding the mechanisms and timing of moisture transport and the periodicity of high and low

lake stands in the tropical Andes during the Quaternary (e.g., Baker et al., 2001a, Baker et al., 2003, Betancourt et al., 2000 and Mourguiart and Ledru, 2003).

The Salar de Uyuni on the Bolivian Altiplano (20°S 68°W, 3,653 m above sea level; Figure 1) is currently the world's largest salt flat (12,106 km<sup>2</sup>), but has in the past supported a series of large intermittent paleolakes. While the timing of paleolake formation and the climates associated with them is somewhat controversial (e.g., Baker et al., 2001a and Mourguiart et al., 1998), the relatively well-documented record

from Lake Titicaca (3,810 m above sea level) located 280 km to the north (Figure 1) is directly relevant, as paleolakes in the Salar de Uyuni probably formed during periods of overflow from synchronous highstands in Titicaca (e.g., Baker et al., 2001b and Wirmann et al., 1992).

To provide an insight into pre-Holocene non-anthropogenic vegetation change in the region over Quaternary time scales, a 220-m-long core was obtained from the central area of Salar de Uyuni in 1999. The chronology developed for this sequence is based on a combination of 17 accelerator mass spectrometry (AMS) radiocarbon dates on the total organic carbon content (calibrated using Calib 4.3 for ages <24,000  $^{14}\text{C}$  yr B.P. (Stuiver et al., 1998) and using the protocol of Bard et al., 1998 for the older dates) and 14 U/Th isochron-derived ages from evaporite horizons (Baker et al., 2001a, Baker et al., 2001b, Fritz et al., 2004 and Ku, 2000). The age model suggests that the sequence extends back over 250,000 yr (Fritz et al., 2004).

In this paper, we present palynological results and their interpretations from the interval between 108,000 yr ago and 18,000 cal yr B.P. (78.30–8.25 m) of the Salar de Uyuni sequence, which was selected for its robust chronology and higher sedimentation rates when compared with earlier parts of the sequence (Fritz et al., 2004). This interval incorporates the formation and subsequent desiccation of two distinct paleolakes: Tauca (ca. 26,000–14,900 cal yr B.P.) and, tentatively, “Minchin” (ca. 47,800 yr ago to 36,000 cal yr B.P.). We acknowledge a note of caution in ascribing this interval to paleolake “Minchin,” since chronological differences exist between this study and an alternative record from Salar de Uyuni (Fornari et al., 2001; and references therein relating to dating of the “Minchin” shoreline at ca. 3,730 m).

#### *Climate and environmental setting*

The mean annual temperature and precipitation at Salar de Uyuni are, respectively, about  $5^{\circ}\text{C}$  and  $150\text{ mm yr}^{-1}$ . Potential evapotranspiration exceeds precipitation, hence Salar de Uyuni is a modern saltpan. In the past, a series of paleolakes were maintained partly through a combination of increased precipitation, decreased evaporation, and reduced overflow from Lake Titicaca into the low-lying salars. Hydrological models demonstrate that the paleolakes would have formed and evaporated rapidly as Titicaca, respectively, rose and fell relative to its outlet (Cross et al., 2001).

Large-scale climatic controls on the Altiplano on all time scales are closely related to the upper air circulation (Garreaud et al., 2003). For most of the year, high-level tropospheric westerly flow across the Pacific provides air depleted in moisture, which descends along the western flank of the Andes and causes dry conditions. During the austral summer (December, January, February), however, insolation-induced convection over the Altiplano coupled with a southerly migration of the Intertropical Convergence Zone from the north results in easterly zonal flow that brings in moisture-charged air across Amazonia from the Atlantic. Wet, monsoonal conditions are

therefore experienced over the Altiplano for about 3 months a year (Zhou and Lau, 1998). Vuille et al. (2000) have demonstrated that most inter-annual precipitation variance is explained by the number of days of easterly airflow, with up to 85% being attributable to austral summer precipitation.

However, intra-seasonal variation (Garreaud, 2000) is affected by the position and intensity of the Bolivian High, which is modulated by climatic changes in the mid-latitude South Pacific. On time scales ranging from annual to glacial–interglacial, direct insolation forcing over the Altiplano or moisture changes in the humid tropical lowlands are only in part driving the climatic changes. Seasonal expansion of the equatorial easterlies in the upper troposphere, associated with anomalies caused by differential heating between the northern and southern hemispheres during glacial periods, is probably more important (Garreaud et al., 2003 and Kull and Grosjean, 1998).



**Figure 1.** Map of the Altiplano, showing the sites and major river systems referred to in the text.

Although it has been suggested that wet phases recorded at Salar de Uyuni may be linked to cold periods in the North Atlantic (Baker et al., 2001a), an investigation of both the terrestrial and aquatic vegetation response in and around the catchment should distinguish the nature of these wet phases. In addition, inconsistencies still need to be resolved between records on the Altiplano, which register contrasting signals at critical periods, such as the LGM (Baker et al., 2001a, Baker et al., 2001b and Betancourt et al., 2000).

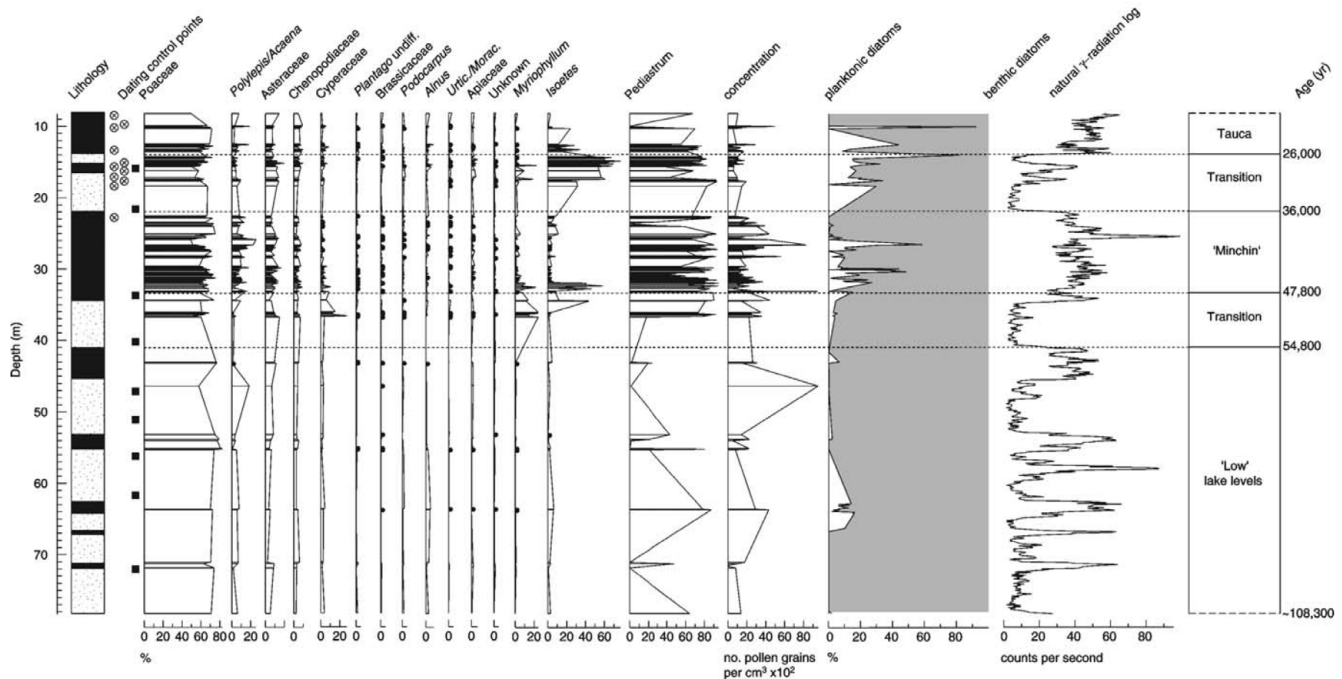
## Methodology

One hundred and thirty 0.5 cm<sup>3</sup> volumetric sediment samples were taken from the core, most of which were concentrated in intervals previously identified by natural gamma radiation data as representative of paleolakes (Baker et al., 2001a). Some gaps in the sedimentary record resulted from fluid circulation problems during drilling, especially during the transition from hard evaporites to underlying lacustrine mud. For example, the topmost 2 m of lacustrine sediment from paleolake Tauca (above 10 m depth in the sequence) was mostly lost; consequently, there are only four pollen samples spanning the time interval 22,450–16,560 cal yr B.P. Where possible, the sampling interval was 10 cm within the lake muds. Below 41-m depth (54,800 yr ago), where the sediments are dominated by evaporites, the sampling interval was sometimes up to 8 m; only 16 samples were analyzed from this interval.

Processing followed standard protocols for pollen preparation (Berglund and Ralska-Jasiewiczowa, 1986 and Stockmarr, 1971). Over 300 terrestrial pollen grains and spores were counted for each sample, or (rarely) counts were terminated when >2,000 of exotic *Lycopodium* spores had been recorded. Aquatic taxa, such as *Isoetes*, *Myriophyllum* and *Pediastrum*, were counted but excluded from the main sum. Pollen was identified using appropriate palynological atlases (e.g., Heusser, 1971, Hooghiemstra, 1984 and van der Hammen and González, 1960) and the reference collection at the Florida Institute of Technology (>3,000 types). Both terrestrial and aquatic taxa were investigated to provide proxies for changes in paleotemperature and hydrological conditions, including lake level variation.

## Results

Pollen concentrations rarely exceeded 4,000 grains/cm<sup>3</sup> and were generally below 2,000 grains/cm<sup>3</sup>. Terrestrial spores of ferns and their allies were extremely rare. Preservation of the pollen was consistently good. Although the organic content of the sediments was generally low, only 5 of the 130 samples analyzed could not be counted; these were presumed to be evaporite sediments or oxidized lake muds. The pollen diagram was divided into five zones according to three major hydrological phases and two transitions (Figure 2).



**Figure 2.** Percentage pollen diagram of the main terrestrial and aquatic taxa, and log of natural gamma radiation, major lithologies, and planktonic and benthic diatom percentages at Salar de Uyuni (Fritz et al., 2004) plotted against depth. Crossed circles denote calibrated radiocarbon dates; infilled squares denote U/Th dates. Lithologies: shading denotes lake muds; evaporite deposits are stippled.

## 78.8–41.6 m (ca. 108,300–54,800 yr ago)

Frequencies of Poaceae pollen in this interval were >55%, levels that were mirrored throughout the rest of the sequence. *Polylepis/Acaena* pollen occurred at frequencies of 5–10%, with a peak abundance of ca. 20% at 46.4 m, corresponding with one of the highest pollen concentrations of the entire record (>8,000 pollen grains/cm<sup>3</sup>). Asteraceae (5–10%) and Chenopodiaceae (ca. 5%) were a constant component of the pollen spectrum. *Alnus* pollen attained an abundance of ca. 5% at 63.65 m.

*Myriophyllum* pollen was rare, with *Isoëtes* spores also scarce, except at 63.65 and 43.0 m, where *Isoëtes* attained ≥5%. The alga *Pediastrum* showed marked variations in abundance, with major declines at ca. 71, 55 and 46.4 m. This latter event corresponded with the highest percentages and concentrations of *Polylepis/Acaena* pollen.

## 41.6–33.38 m (ca. 54,800–47,800 yr ago)

Organic lake sediment samples were investigated from the central part of a 7-m-thick salt bed that underlay paleolake “Minchin” sediments. *Polylepis/Acaena* pollen occurred in relatively low abundances (ca. 2%); however, increased abundances of Asteraceae, Chenopodiaceae and, particularly, Cyperaceae and *Myriophyllum* (>20%) pollen were noticeable. *Pediastrum* also increased markedly. Subsequently, another 3 m of evaporites was deposited in a second evaporitic phase; an organic sample from this interval included a brief peak in *Isoëtes* spores and relatively abundant *Polylepis/Acaena* pollen (ca. 13%).

## 33.38–22.6 m (ca. 47,800–36,000 yr ago)

These sediments represent deposits of paleolake “Minchin.” Of the two major paleolakes investigated, this had the most polliniferous sediments (generally >2,000 pollen grains/cm<sup>3</sup>) and the most complete core recovery. *Polylepis/Acaena* pollen abundance across this interval was generally >10%, occasionally reaching 15–20%. The peak in *Polylepis/Acaena* at the base of the interval corresponds with the second highest pollen concentration in the sequence (>8000 grains/cm<sup>3</sup>).

A peak in *Isoëtes* spore abundance (>40%) followed the *Polylepis/Acaena* peak and was accompanied by a marked rise in *Myriophyllum* pollen abundance (ca. 20%). Subsequently, *Isoëtes* and *Myriophyllum* frequencies stabilized at ca. 5% along with *Pediastrum* (>60%). At 24 m, all three of these taxa show a marked decline.

## 22.6–14.0 m (36,000–26,000 cal yr B.P.)

This interval between the deposits of paleolakes “Minchin” and Tauca contained two minor lacustrine muds, interbedded with halite. These brief lacustrine phases have been dated at 33,400–31,800 and 30,800–28,200 cal yr B.P., respectively. *Polylepis/Acaena* pollen maintained frequencies of ca. 5%, with Asteraceae (>10%) and Chenopodiaceae (ca. 10%) pol-

len also well represented. During both of these minor lacustrine phases, *Myriophyllum* reached frequencies of ca. 20%, *Isoëtes* ≥50%, and *Pediastrum* ≥60%.

## 14.0–8.0 m (26,000–14,900 cal yr B.P.)

The sediments of this interval corresponded to the deposits of paleolake Tauca, which had consistently low pollen concentrations (ca. 1,000 pollen grains/cm<sup>3</sup>). *Polylepis/Acaena* pollen was ca. 5% throughout most of the interval, but prior to a coring gap at 10.35–12.51 m, values increased to >15% then quickly declined. This decline also corresponded with reductions in frequencies of *Isoëtes* (to ca. 25%) and *Pediastrum* (to 40%) and a marked increase in pollen concentration for this interval, briefly reaching >3,000 grains/cm<sup>3</sup>. Due to this coring gap, there were only two subsamples taken above 10 m. Values of *Polylepis/Acaena* showed a brief recovery (to >15%), corresponding with a high pollen concentration (ca. 4,000 grains/cm<sup>3</sup>), before rapidly declining again. These samples also show a dramatic decline in values of *Isoëtes* (to <5%) and *Pediastrum* (to ca. 5%).

## Discussion

### *The Polylepis/Acaena dilemma?*

The pollen of *Polylepis* and *Acaena*, two closely related genera in Rosaceae, is difficult to distinguish. Fragmentary *Polylepis* woodlands in the high Andes today hint at their past importance at elevations above 3,600 m, with different species surviving across a wide moisture gradient (Figure 3), but all are intolerant of saline or poorly drained conditions (Figure 4; Kessler, 1995a and Kessler, 1995b).

By contrast, the genus *Acaena* is mostly herbaceous, with some species having a suffrutescent stem base or producing underground stolons that give rise to mat-like vegetative growth (Hensen, I., personal communication, 2004). There are 3–4 species of *Acaena* known in Bolivia, none of which occur in the area of distribution of *Polylepis tarapacana* (Beck, S., personal communication, 2004). *Acaena* is typically found in rather warm and humid valleys (Fjeldså, J., personal communication, 2004). Thus, while *Acaena* can certainly be mixed together with *Polylepis* in the eastern Cordilleras and in the montane valleys, this is probably unlikely in the semi-deserts of western Bolivia (Kessler, M., personal communication, 2004).

*P. tarapacana* is the only species in the genus found adjacent to Salar de Uyuni. A shrub or tree up to 3 m in height, *P. tarapacana* is adapted to the most extreme conditions of altitude (4,000–5,200 m), aridity (100–500 mm mean annual precipitation), and nightly hard frosts (Figure 4; Kessler, 1995a and Kessler, 1995b). It is therefore highly probable that the *Polylepis/Acaena* type pollen signal observed at Salar de Uyuni is dominated by *P. tarapacana*.

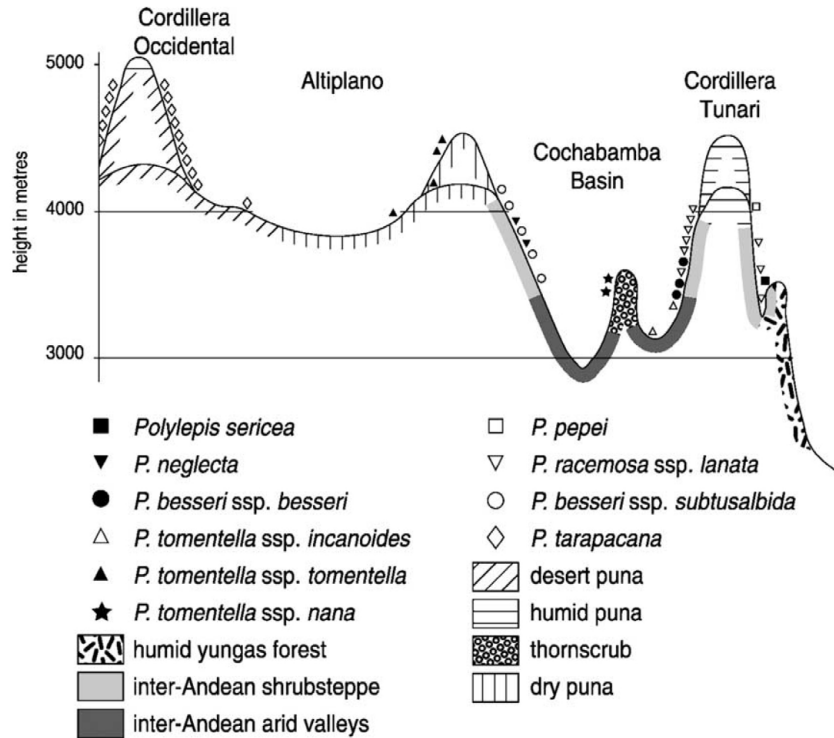


Figure 3. Diagrammatic profile of the Altiplano showing the ecological distribution of different *Polylopes* species (adapted from Fjeldså and Kessler, 1996).



Figure 4. Stand of *P. tarapacana* on the western slope of Volcán Sajama (4,400 m). Note the concentration of the trees in humid depressions on the valley floor and the greater density of trees on north-exposed slopes (left side). The light, salty areas in the valley bottom are naturally devoid of forest (Photo I. Hensen, 1991).

#### Reduced pollen concentrations

Despite generally low pollen concentrations during glacial phases, a major component of the vegetation during these times was probably *P. tarapacana*. Although species of *Polylopes* are anemophilous, initial findings suggest rather poor pollen dispersal (Salgado-Laboriau, 1979; Fjeldså, J., personal communication, 2004) that would not be representative of

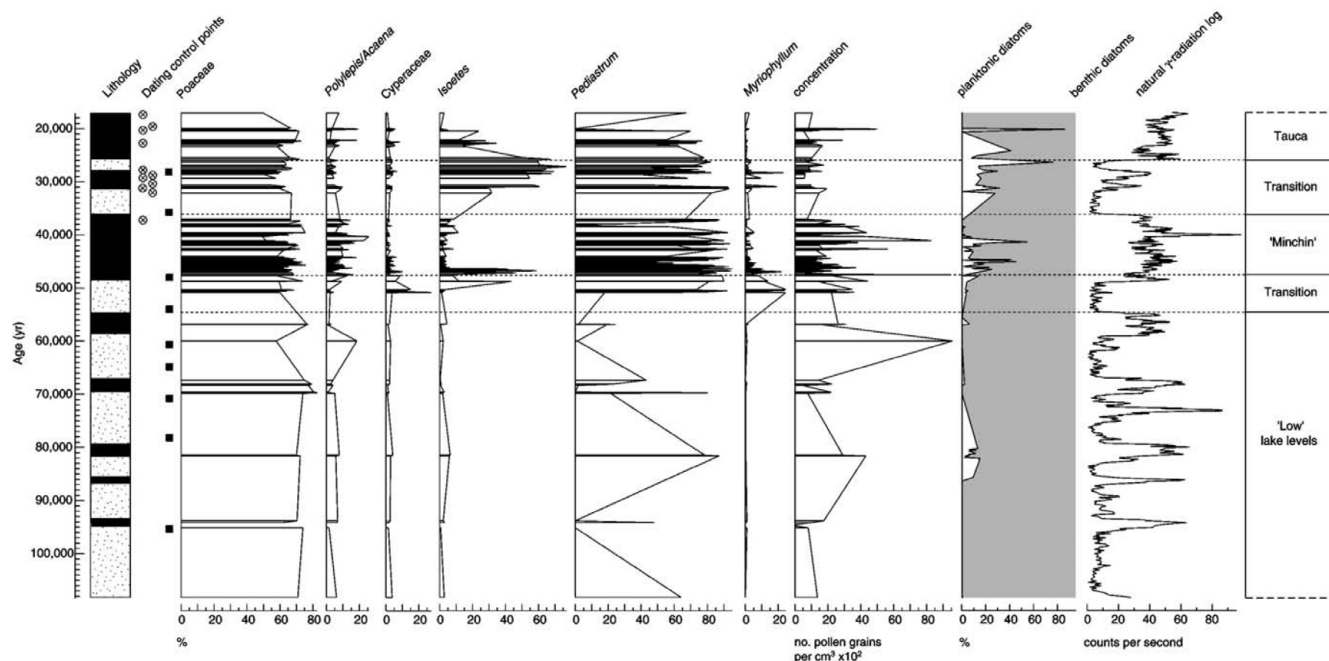
long distance transportation, particularly at a time of low pollen production. Combined with the environmental response of *P. tarapacana* to saline conditions or lake level fluctuations, *Polylopes* pollen abundances can thus be used as a proxy for the distance of individuals and population size from the lake (or coring site). At the LGM, reduced vegetation abundance (including *Polylopes*) is probably representative of both the local and regional signal.

The other main pollen taxa in our record are Poaceae, many of which are probably derived from plants growing very close to the paleolakes. Therefore, except for *Polylopes*, most of the environmental interpretation uses semi-aquatic and aquatic plants, as well as algal abundance, which originate from the paleolakes themselves or in the immediate environs.

#### Environmental history

##### Low lake levels (ca. 108,300 to 54,800 yr ago)

The dominance of halite deposition and existing analyses of petrographic textures indicate that saltpans and shallow perennial saline lakes predominated in the basin prior to ca. 54,800 yr ago (Figure 5) and suggest that evaporation generally exceeded moisture supply. Further evidence of relatively dry conditions is provided by the dominance of benthic diatoms in the intercalated mud sediments deposited in shallow environments (Fritz et al., 2004). During this pe-



**Figure 5.** Percentage pollen diagram of selected pollen taxa, planktonic and benthic diatoms, and natural gamma radiation and major sediments from Salar de Uyuni (Fritz et al., 2004) plotted against age. Crossed circles denote calibrated radiocarbon dates; infilled squares denote U/Th dates. Lithologies: shading denotes lake muds; evaporite deposits are stippled.

riod of generally low lake levels, a brief increase of *Isoetes* ca. 80,000 yr ago corresponds with moderate percentages (5–20%) of planktonic diatoms (Fritz et al., 2004) when precipitation may have increased, creating a temporary deeper lacustrine episode. *Isoetes* is frequently found in flooded littoral marshes and in erosion channels leading into lakes (Paduano et al., 2003; Nuñez, P., personal communication, 2003); thus, its presence is consistent with an increase in precipitation at this time. However, such hydrological transitions appear to have been too rapid or too saline (or both) to provide suitable shoaling conditions for *Myriophyllum*. The varying percentages of *Pediastrum* are consistent with its wide distribution across a broad salinity range, although it is not adapted to hypersaline conditions (Hutchinson, 1967).

Pollen concentrations over this interval were generally higher than after 54,800 yr ago, which may have resulted from pollen sources being closer to the center of the basin. *Polyalepis/Acaena* pollen was generally common through this interval, except during episodes of high salinity; *Polyalepis* is intolerant of saline conditions, including salt spray (Kessler, 1995a and Kessler, 1995b). We hypothesize that *Polyalepis* was migrating to and from the lake(s) in response to fluctuating salinity, rather than temperature variation. A particular peak abundance of *Polyalepis/Acaena* pollen ca. 60,000 yr ago may be an exception, as it occurred when *Pediastrum* was rare. Perhaps, during a warm phase, *Polyalepis* was able to colonize well-drained areas sheltered from salt spray close to the saline waters of the lake.

#### *The transition to paleolake “Minchin” (ca. 54,800 to 47,800 yr ago)*

Mud deposits from within this evaporite-dominated interval suggest rising lake levels and the formation of shoaling conditions suitable for *Myriophyllum*. However, the lake level may not have been high enough to create flooded, fringing marshes, which would have been suitable for *Isoetes*. An intermediary niche may have been occupied by the development of a *Cyperaceae* community. *Polyalepis* was probably in the process of colonizing the immediate catchment when unfavorable saline conditions resumed.

A sample with high abundances of *Isoetes* spores (ca. 40%) at ca. 49,000 yr ago is indicative of the increased water level heralding the onset of paleolake “Minchin.” This event would appear to mark the passing of a hydrological threshold, possibly when precessional forcing of insolation became dominant (Baker et al., 2001a and Baker et al., 2001b), though it might also be linked to geomorphological/tectonic changes at the southern outlet of the Titicaca Basin, providing greater connection between the two basins (Fritz et al., 2004).

#### *Paleolake “Minchin” (ca. 47,800 to 36,000 yr ago)*

Pollen concentration values of these lacustrine sediments are almost double those recorded during the later paleolake Tauca phase. This may be indicative of slightly warmer temperatures and higher local productivity than during the LGM. *Polyalepis* was locally important, and the observed fluctuations



within this interval may have been primarily linked with lake level changes and the resulting variation in salinity and shoreline position. The interpretation that paleolake “Minchin” was generally shallower than Tauca is corroborated by the diatom evidence; “Minchin” not only supports high percentages of planktonic species, but also a mixture of benthic diatoms, some of which are typical of saline waters (Fritz et al., 2004).

Lithologic and gamma ray borehole data indicate that the sudden decline and subsequent recovery of *Pediastrum*, *Isoëtes*, and *Myriophyllum* at ~23 m (ca. 38,000 cal yr B.P.) was not due to evaporite deposition, but instead may mark a brief reduction in temperature. Curiously, the terrestrial response to this event was muted, reflected only by a limited decline in values of *Polylepis*. Interpretation of the topmost paleolake “Minchin” sediments was limited by a core break (recovery possibly being hampered by the presence of gypsum), causing a sampling gap between 22.6 and 18.4 m.

#### *The transition to paleolake Tauca (ca. 36,000 to 26,000 cal yr B.P.)*

This interval is characterized by salt deposition as a result of a generally arid climate, but is punctuated by two short-lived lacustrine phases; these are clearly evident in the responses of *Myriophyllum*, *Isoëtes*, and *Polylepis*, which increase at these levels. While the timing of the lacustrine phases apparently matches that of subtropical eastern North Atlantic sea-surface temperature minima (Baker et al., 2001a and Bard et al., 2000), the intervening dry episode at ca. 33,000 cal yr B.P. may be related to a period of lowered lake levels in northern Amazonia (Bush et al., 2002). Before paleolake Tauca began to infill, another major arid interval occurred causing the complete loss of ice on the nearby Sajama volcano (Thompson et al., 1998); notably, both the Sajama ice cap and paleolake Tauca have nearly the same basal age of 26,000 cal yr B.P.

#### *Paleolake Tauca and the LGM (ca. 26,000 to 14,900 cal yr B.P.)*

The gamma log (Figure 5) clearly demonstrates that the Altiplano sustained a lake continuously throughout this interval, including the LGM (ca. 23,000–19,000 cal yr B.P.). The dominance of planktonic diatoms and negative values of  $\delta^{18}\text{O}$  in the lacustrine carbonates suggest that this was the deepest of the lakes formed over the past 100,000 yr (Fritz et al., 2004), with paleoshorelines reaching an altitude of almost 3800 m (Bills et al., 1994 and Clayton and Clapperton, 1997). Blodgett et al. (1997) calculated that precipitation levels about 30% higher than present would have been necessary to support paleolakes “Minchin” and Tauca. These estimates apply even over the LGM, where snowline studies and climate modeling for this part of the tropical Andes have yielded an estimated mean annual temperature depression of 5°C (Hostetler and Mix, 1999, Klein et al., 1999 and Mix et al., 1999).

In spite of a coring gap between 10.35 and 12.51 m, the temporal proximity of the radiocarbon dates of 22,452 cal yr

B.P. (10.2 m) and 22,830 cal yr B.P. (13.35 m) suggests that high rates of sedimentation marked the onset of the LGM. Colder temperatures inducing ice development and suspended material clouding the water column may have negatively affected diatom populations and submerged aquatics, for example, *Myriophyllum*. *Isoëtes* may have survived as an emergent or in erosional gulleys. As conditions became less saline, the cold-tolerant *Polylepis* may have been able to expand closer to the lake.

A temperature minimum is suggested at ca. 23,000 cal yr B.P. that affected not only the main aquatic taxa, but also the terrestrial vegetation cover, including *Polylepis*, which would have been forced to occupy lower altitudes until 20,000 cal yr B.P. After this time, *Polylepis* demonstrates a marked recovery with the subsequent warming, as does *Pediastrum*, among the aquatic taxa. Low temperatures and a shoreline covered in glacial debris may have retarded expansion of *Isoëtes*; this is in marked contrast to the record from Titicaca, with better resolution across this interval, which shows a marked expansion in *Isoëtes* after ca. 21,000 cal yr B.P. It has been suggested that this indicates an initial warming after the LGM (Paduano et al., 2003), but could also reflect differences in the timing and rate of local glacial retreat around Titicaca and Salar de Uyuni.

Elsewhere during the LGM on the Altiplano, cold, wet conditions from 25,000 to 22,000 cal yr B.P. are indicated by depleted  $\delta^{18}\text{O}_{\text{ice}}$  values, low anion concentrations, and a high regional precipitation of dust in the Sajama ice core record (Thompson et al., 1998). In Peruvian Lake Junin (11°S), similar conditions persisted, with a decrease in organic carbon and an increase in magnetic susceptibility occurring at ca. 30,000 cal yr B.P. marking the onset of the LGM, with a high magnetic susceptibility signal remaining until 22,500 cal yr B.P. (Seltzer et al., 2002).

Evidence from the Sabana de Bogotá record in Colombia (Hooghiemstra, 1984) suggests that lake level during the LGM was low; this would be expected, as northern versus southern tropical lakes on a variety of time scales have opposing climatic signatures (e.g., Fritz et al., 2001). However, less easy to explain is the interpretation of dry conditions from the lack of fossil rodent middens in the central Atacama Desert (22° to 24°S) between 35,000 and 22,000 cal yr B.P. (Betancourt et al., 2000). Although Salar de Uyuni and the Atacama Desert lie in different catchments and could have completely different hydrological histories, one would expect rodent middens to at least provide some “snap-shots” of an occasional wet episode during this period; complete lack of preservation for this interval seems improbable.

## Conclusions

The independent aquatic vegetation record from Salar de Uyuni is in accordance with existing sedimentological and diatom data. Between 100,000 and 50,000 yr ago (Figure 5), low abundances of *Myriophyllum* and *Isoëtes*, accompanied by marked fluctuations in *Pediastrum*, suggest generally very

dry conditions in a basin dominated by saltpans, reflecting reduced moisture on the Altiplano or limited connection with Lake Titicaca.

Around 50,000 yr ago, a major hydrological threshold seems to have been passed, with conditions becoming significantly wetter and lacustrine sediments becoming increasingly dominant. The transition to the formation of paleolake “Minchin” began with marked rises in *Isoetes* and *Myriophyllum*, and suggests a lake of moderate depth. After 36,000 cal yr B.P., the transition to paleolake Tauca is also initiated by rises in *Isoetes* and *Myriophyllum*; the sustained presence of *Isoetes* indicates the development of flooded littoral communities associated with a lake maintained at a higher water level.

A major increase in effective moisture on the Altiplano ca. 50,000 yr ago would be in accordance with sedimentological and seismic reflection evidence from Salar de Atacama and Lake Titicaca, respectively (Bobst et al., 2001 and D’Agostino et al., 2002). Down-cutting of the Rio Desaguadero may have been a significant factor in creating greater connection between Lake Titicaca and Salar de Uyuni, for which tectonic explanations can be invoked. Radiocarbon-dated lacustrine deposits at ca. 40,000 cal yr B.P. (C. Rigsby, unpublished data) from the upper Rio Desaguadero valley located south of Lake Titicaca and 50 m above the modern level of Lake Titicaca indicate that down-cutting postdated increases in regional effective moisture and the observed hydrological changes at Salar de Uyuni. However, this greater connection may have contributed to the higher water levels observed after 36,000 cal yr B.P.

The Salar de Uyuni record suggests that, in comparison to the paleolake Tauca phase, vegetation cover was more extensive at the time of paleolake “Minchin,” probably due to somewhat milder temperatures and lower lake levels. During the paleolake Tauca phase, there is no evidence for Salar de Uyuni being arid during the LGM (Mourguiart and Ledru, 2003), despite temperatures around 5°C lower than present. Although pollen concentrations are lower during the Tauca phase in comparison with “Minchin,” this may be an artifact related to deeper lake levels and the consequent increased distance from the pollen source rather than changes in pollen production. Discrepancies with the lack of fossil rodent middens in the central Atacama Desert (22° to 24°S) between 35,000 and 22,000 cal yr B.P. interpreted as a dry interval still need to be resolved (Betancourt et al., 2000).

The Salar de Uyuni record also indicates that *Polylepis* (most likely *P. tarapacana*) was probably an important continuous component of the vegetation at high altitude, surviving a range of climatic extremes. The intervals 50,000–36,000 yr ago and 26,000–14,900 cal yr B.P. were periods of maximum wetness and maximum insolation on the Altiplano (Baker et al., 2001a and Fritz et al., 2004), and these conditions may have been beneficial to the expansion and extent of *Polylepis* populations. Preliminary data obtained from continuous long records in Lake Titicaca reveal a similarly complex history in which *Polylepis* has been an important floral component of Altiplano communities.

Our data are consistent with the view that *Polylepis* has, at times, been a more widespread component of Upper Andean floras than it is today. Furthermore, our data underline the need for conservation of remaining *Polylepis* forest fragments not only as centers of endemism but also as examples of a nearly vanished landscape (Fjeldså and Kessler, 1996). Importantly, these fragments provide potential nuclei for ecological restoration in situ.

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