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# Spatial-temporal changes in Andean plateau climate and elevation from stable isotopes of mammal teeth

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# ABSTRACT

Paleoelevation constraints from fossil leaf physiognomy and stable isotopes of sedimentary carbonate suggest that significant surface uplift of the northern Andean plateau, on the order of  $2.5\pm1$  km, occurred between ~10.3 and 6.4 Ma. Independent spatial and temporal constraints on paleoelevation and paleoclimate of both the northern and southern plateau are important for understanding the distribution of rapid surface uplift and its relation to climate evolution across the plateau. This study focuses on teeth from modern and extinct mammal taxa (including notoungulates, pyrotheres, and litopterns) spanning ~29 Ma to present, collected from the Altiplano and Eastern Cordillera of Bolivia (16.2°S to 21.4°S), and lowland Brazil. Tooth enamel of large, waterdependent mammals preserves a record of surface water isotopes and the type of plants that animals ingested while their teeth were mineralizing. Previous studies have shown that the  $\delta^{18}$ O of modern precipitation and surface waters decrease systematically with increasing elevations across the central Andes. Our results from high elevation sites between 3600 and 4100 m show substantially more positive  $\delta^{18}$ O values for late Oligocene tooth samples compared to <10 Ma tooth  $\delta^{18}$ O values. Late Oligocene teeth collected from low elevation sites in southeast Brazil show  $\delta^{18}$ O values similar (within 2‰) to contemporaneous teeth collected at high elevation in the Eastern Cordillera. This affirms that the Andean plateau was at a very low elevation during the late Oligocene. Late Oligocene teeth from the northern Eastern Cordillera also yield consistent  $\delta^{13}$ C values of about -9%, indicating that the environment was semi-arid at that time. Latitudinal gradients in  $\delta^{18}$ O values of late Miocene to Pliocene fossil teeth are similar to modern values for large mammals, suggesting that by  $\sim$ 8 Ma in the northern Altiplano and by ~3.6 Ma in the southern Altiplano, both regions had reached high elevation and established a latitudinal rainfall gradient similar to modern.

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# 1. Introduction

The high topography in the central Andean plateau has a significant effect on atmospheric circulation, which causes a measurable change in the distribution and amount of rainfall along-strike in the central Andes. Today the central Andean plateau shows a pronounced rainfall gradient, with significantly drier conditions south of the bend at 18° to 19°S. North of the bend annual precipitation amounts to ~0.5 to 1 m/yr in the plateau and 2 to 4 m/yr in the eastern foothills, whereas south of the bend rainfall amounts average <0.25 m/yr in the plateau and 1 to 2 m/yr in the eastern foothills (Bookhagen and Strecker, 2008; Garreaud and Vuille, 2003). The oxygen (O) and hydrogen (H) isotopic composition of rainfall in the tropical Andes has been shown to be strongly dependent on both the

amount of rainfall and the degree of distillation of the vapor mass from which it is derived as water vapor moves up in elevation (Gonfiantini et al., 2001; Vimeux et al., 2005).

Prior stable isotope studies of sedimentary carbonates at ~17.5°S (Garzione et al., 2008, 2006; Ghosh et al., 2006) establish a record of paleoelevation and paleoclimate in the northern Altiplano. This study expands the spatial and temporal coverage of stable isotope data for the Altiplano to the more arid southern part where no prior data exist. We report the results of stable isotope analyses of both modern and fossil mammal teeth, which provide a record of climate and environment during the time that the animals were alive and their teeth were growing (e.g. Kohn and Dettman, 2007; Kohn, 1996).

Samples include members of three extinct orders of ungulates: Notoungulata, Pyrotheria, and Litopterna. Modern ungulate orders (Artiodactyla and Perissodactyla) were not present in South America during the time periods of interest. We assume that O and C isotopes behaved similarly in the extinct orders of ungulates as they do in

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modern ungulates. The O isotopic composition of late Oligocene to modern mammal teeth reflects surface water compositions that enable us to reconstruct latitudinal gradients and temporal changes in rainfall composition. We use these reconstructions to evaluate when modern climate conditions in the central Andes were established, which has implications for the development of the Andean plateau. In addition, we compare different aged tooth  $\delta^{18}$ O values to estimate changes in paleoelevation of the plateau through time.

# 2. Geologic and climatic setting

The Altiplano basin extends from approximately 15°S to 23°S, occupying the South American countries of Peru, Bolivia, and Chile (Fig. 1). The Andean plateau, which includes the Altiplano, Western and Eastern Cordilleras, and Puna, formed largely during the Cenozoic from subduction of the Nazca oceanic plate beneath the South American plate. Despite the plateau's location within the tropics, its climate is cool and semi-arid while the Amazon lowlands are hot and experience heavy seasonal precipitation (Garreaud et al., 2009). Evapotranspiration is significant, contributing up to 60% of water vapor that traverses ~4000 km of dense vegetation from the Atlantic Ocean to the Andean foothills (Vuille et al., 2003). The rise and adiabatic cooling of warm, moist air crossing the Subandes can produce over 6 m of annual precipitation (Johnson, 1976). Altiplano precipitation may be influenced locally by Lake Titicaca in the north and large salt lakes, like Salar de Uyuni and Salar de Coipasa, in the south (Gonfiantini et al., 2001). There is a strong latitudinal gradient in the amount of rainfall, ranging from >50 cm/yr north of 18°S to <25 cm/yr south of 20°S (Bookhagen and Strecker, 2008; Garreaud and Vuille, 2003; IAEA/WMO, 2006). West of the Andean plateau, the Atacama desert receives negligible precipitation (Miller, 1976).

# 2.1. Depositional setting of fossil-bearing deposits

Though the Salla Formation was deposited in only one of several intermontane basins on the Eastern Cordillera, these deposits are unique because of their diverse suite of fossil vertebrates. The strata consist of variegated mudstones and minor sandstones over 500 m thick, interpreted to be deposited in distal alluvial floodplain and lacustrine environments (McRae, 1990). Extensive pedogenesis suggests a well-drained interfluve system (Leier et al., 2006). Radiometric <sup>40</sup>Ar/<sup>39</sup>Ar dates on interbedded tuffs constrain the age of Salla deposits to the late Oligocene (Kay et al., 1998).

Although early to middle Miocene sedimentary rocks in the northern Altiplano region have not been well-characterized in terms of depositional setting, late Miocene through Pliocene fluvial, lacustrine, and volcaniclastic rocks have been described near Callapa (Garzione et al., 2006). Depositional ages of teeth sampled in this study are constrained through <sup>40</sup> K/<sup>40</sup>Ar and <sup>40</sup>Ar/<sup>39</sup>Ar dating of interbedded tuffs and ignimbrites (Marshall et al., 1992). For teeth sampled near Achiri (BolTox1, BolTox2, and Nick1), we were unable to identify whether we sampled above or below the Callapa tuff (9.03 ± 0.07 Ma) due to poor locality information on the tuff. Therefore, we assign an 8–10 Ma age for these samples (Table 1).

Fossil teeth from south of the bend ( $\sim 18.5^{\circ}$ S) come from a 120 m thick section of Pliocene deposits near Inchasi and Puna in the Eastern Cordillera. Lithologies are dominated by fluvial gravels with mudstone interbeds (MacFadden et al., 1993). Magnetostratigraphy calibrated through  $^{40}$ Ar/ $^{39}$ Ar dating and biostratigraphy constrains fossil ages to 3.6 to 4 Ma (MacFadden et al., 1993).

In southeast Brazil, late Oligocene rocks of the Taubaté basin located near São Paulo were deposited in a continental rift setting. Along-strike equivalents in the Curitiba Basin are described as lacustrine rocks



Fig. 1. Map of South America showing fossil (circles) and modern (diamonds) tooth sample localities on the Altiplano in Bolivia and for low elevation sites in Brazil. B–B' is an approximate transect of modern precipitation data from Gonfiantini et al. (2001) and stream waters sampled along the Coroico river (Fig. 2, Table DR3).

# Table 1

Data summary for fossil teeth including location, isotopic composition, age constraints, and taxonomy.

| Locality           | Lat/long       | Modern elevation (m) | Mean $\delta^{18}O_{(VPDB)}^{a}$ | Mean $\delta^{13}C_{(VPDB)}^{a}$ | Surface Water $\delta^{18}O_{(VSMOW)}^{b}$ | Age<br>(Ma)              | Taxonomy                    | Sample number(s)        |
|--------------------|----------------|----------------------|----------------------------------|----------------------------------|--|--------------------------|-----------------------------|-------------------------|
| Northern Altiplano |                |                      |                                  |                                  |  |                          |                             |                         |
| Salla              | -17.2, -67.6   | 3785                 | -2.0 (1.6)                       | -9.0 (0.4)                       | - 3.6                                      | 25.95–25.99 <sup>c</sup> | Trachytherus                | UF 172412               |
| Salla              | -17.2, -67.6   | 3785                 | -2.9(0.9)                        | -10.4(0.5)                       | -4.6                                       | 25.95–25.99 <sup>c</sup> | Eurygenium pacegnum         | UF 90981                |
| Salla              | -17.2, -67.6   | 3785                 | 0.4 (1.7)                        | -7.8 (0.4)                       | -0.9                                       | 26.2 <sup>c</sup>        | Pyrotherium macfaddeni      | UF 132901               |
| Achiri             | -17.2, -69.0   | 3895                 | -11.0 (1.0)                      | -8.7(0.6)                        | - 13.7                                     | 8–10 <sup>d</sup>        | Toxodonta                   | BolTox1, BolTox2, Nick1 |
| Choquecota         | -18.1, -67.9   | 3840                 | -11.4 (1.0)                      | -6.4(0.4)                        | -14.1                                      | 5.5–6 <sup>d</sup>       | Plesiotypotherium achirense | Bol-05-01, Bol-05-02    |
| Copacabana         | - 16.2, - 69.1 | 3815                 | -11.1 (0.9)                      | -8.3(0.5)                        | - 13.7                                     | 0                        | Bos (cow)                   | BosCop1, BosCop2        |
| Turco              | -17.6, -68.3   | 4416                 | -6.8(0.6)                        | -9.8 (1.0)                       | - 8.9                                      | 0                        | Ovis (sheep)                | BolShp                  |
| Southern Altiplano |                |                      |                                  |                                  |  |                          |                             |                         |
| Inchasi            | - 19.7, - 65.5 | 3234                 | -8.8                             | -9.5                             | -11.2                                      | 3.6–4 <sup>e</sup>       | Posnanskytherium            | Bol-05-03 to Bol-05-08  |
| Puna               | - 19.8, - 65.5 | 3274                 | -7.0(0.5)                        | -8.0(0.5)                        | -9.2                                       | 3.6–4 <sup>f</sup>       | Promacrauchenia             | Bol-05-09               |
| Puna               | - 19.8, - 65.5 | 3274                 | -8.2(0.9)                        | -9.4(0.5)                        | - 10.5                                     | 3.6–4 <sup>f</sup>       | Posnanskytherium            | Bol-05-10               |
| Ollague            | -21.1, -68.1   | 3717                 | - 7.8                            | -14.8                            | - 10.1                                     | 0                        | Tayassu (peccary)           | AMNH 247728             |
| Uyuni              | -20.9, -66.5   | 3839                 | -6.9                             | -8.0                             | -9.1                                       | 0                        | Equus (burro)               | B1-P2                   |
| Uyuni              | -21.4, -66.5   | 4116                 | -8.8 (1.0)                       | -9.2 (0.7)                       | -11.2                                      | 0                        | Equus (burro)               | B2-RM3                  |
| Brazil             |                |                      |                                  |                                  |  |                          |                             |                         |
| São Paulo          | -23.5, -46.6   | 751                  | - 1.3                            | -8.4                             | -2.7                                       | 24.5–29 <sup>g</sup>     | Notoungulata                | BZ1, BZ2, BZ3, BZ4, BZ5 |

<sup>a</sup> Value in parenthesis is the standard deviation for teeth with >4 serial samples.

<sup>b</sup> Calculated from mean  $\delta^{18}$ O of fossil teeth using Eqs. (2) and (3).

<sup>c</sup> Dated through <sup>40</sup>Ar/<sup>39</sup>Ar (Kay et al., 1998).

<sup>d</sup> Dated through <sup>40</sup>K/<sup>40</sup>Ar, <sup>40</sup>Ar/<sup>39</sup>Ar (Marshall et al., 1992).

<sup>e</sup> Dated using magnetostratigraphy (MacFadden et al., 1993).

<sup>f</sup> A lateral correlative of Inchasi samples (MacFadden, unpublished data).

<sup>g</sup> Dated by paleomagnetics, fission track, and <sup>40</sup>K/<sup>40</sup>Ar (Flynn and Swisher, 1995).

interpreted to represent a playa–lake environment, which grade upward and/or laterally into coarser-grained alluvial fan deposits (Salamuni et al., 2003).

# 3. Methods

Twenty-seven teeth ( $\geq$  12 individuals; 287 tooth enamel samples) of large-bodied herbivorous mammals representing modern and extinct ungulate orders (Notoungulata, Pyrotheria, and Litopterna) were selected for this study from localities ranging in age from ~29 Ma to modern (Fig. 1, Table 1, Table DR2). In addition, 82 stream water samples were collected in 2004-2005 from tributaries along the Coroico trunk river that drains the eastern flank of the Andes, similar in location to rain water sampled by Gonfiantini et al. (2001) along the Sapecho-El Alto transect (Fig. 1, Table DR3). We followed the approach of Garzione et al. (2000) by sampling small catchments in an effort to limit the range of elevations of rainwater. The isotopic composition of tooth samples and the 2005 water samples were determined at the University of Rochester's SIREAL laboratory according to standard methods for teeth (Higgins and MacFadden, 2004; Koch et al., 1997) and water (Coplen, 1995). 2004 stream water samples were analyzed at the University of Arizona. The data repository (DR1) contains a more detailed description of methods used.

#### 3.1. Oxygen isotopes

A definable relationship between the O isotopic composition of meteoric water and elevation exists in regions that conform to a simple Rayleigh distillation model of air mass evolution (Gonfiantini et al., 2001; Rowley et al., 2001). In the absence of a known past relationship between elevation and  $\delta^{18}$ O of precipitation, the locally defined modern relationship and a theoretical model were used to estimate large-scale changes in elevation based on  $\delta^{18}$ O of ancient meteoric water (Garzione et al., 2000; Poage and Chamberlain, 2001; Rowley et al., 2001). The effects of temporal changes in climate and atmospheric circulation (e.g. Ehlers and Poulsen, 2009) are also considered.

Gonfiantini et al. (2001) collected rainfall data along a northeastsouthwest transect from the Amazon lowlands (Sapecho) to >5000 m on the Altiplano (El Alto). Weighted mean values for 3 yr of rainfall data reported in Table 6 of Gonfiantini et al. (2001) and stream water data sampled over the same elevation transect in 2004 and 2005 define a linear regression ( $R^2 = 0.92$ ) (Fig. 2, Table DR3):

$$h = -536.4^{*}\delta^{18}O - 3201.7. \tag{1}$$

This equation indicates a  $\delta^{18}$ O value of -6.0% for low elevation (sea level) sites in the Amazon foreland, which would be consistent with partial isotopic depletion of vapor as it travels across the Amazon basin.

Stream waters are plotted with respect to the elevation of sampling (Fig. 2). The sampling elevation, as opposed to the hypsometric mean of each drainage basin, provides the best fit to the weighted mean  $\delta^{18}$ O values of rainfall. Rainfall compositions could be biased toward low elevation rainfall as cloud forest vapor masses traverse the basin floor and rain-out close to ground level as they move up in elevation. We note

6 -536.36x - 3201.7 5  $R^2 = 0.9233$ 4 Elevation (km) 3 2 1 0 -18 -16 -14 -12 -10 -4 -2 -6 δ<sup>18</sup>O (VSMOW)

**Fig. 2.** Annual weighted mean isotopic values of modern precipitation from Gonfiantini et al. (2001) (open squares) collected up the flank of the Eastern Cordillera and stream water samples collected in 2004–2005 along the Coroico river (solid diamonds) (Fig. 1, Table DR3). Stream water  $\delta^{18}$ O values are plotted against sampling elevation (see text for discussion). The linear regression (Eq. (1)) is based on these combined datasets and used for paleoelevation estimates. Uncertainty of  $\pm$  500 m (1 $\sigma$ ) is based on a bootstrap Monte Carlo simulation that incorporates both scatter in these water data and uncertainty in tooth  $\delta^{18}$ O (dashed lines).

that Eq. (1) is modified from a previous  $\delta^{18}$ O versus altitude gradient for the central Andes determined solely on the basis of rain water samples (Quade et al., 2007). Comparing the two equations, our new regression results in calculated elevations that are 200 m lower at elevations close to sea level and 300 m higher at ~4000 m. These differences are well within the uncertainty of the elevation calculations.

The isotopic composition of meteoric water is also affected by seasonal changes in climate. In tropical settings that experience strong convective storms, an increase in the amount of precipitation during the summer monsoon results in lower surface water  $\delta^{18}$ O due to increased humidity in the air column (Rozanski et al., 1993). Studies have shown that the amount effect acting on vapor masses traversing the Amazon Basin has a significant influence on seasonal changes in surface water  $\delta^{18}$ O (Gonfiantini et al., 2001; Vimeux et al., 2005).

We use the modern relationship between elevation and the  $\delta^{18}$ O value of meteoric water with fossil teeth to evaluate temporal changes in elevation and climate. In addition, tooth  $\delta^{18}$ O values from the northern Andean plateau are compared to contemporaneous teeth from the south to constrain latitudinal changes in climate through time.

Previous studies show that teeth of large, water-dependent mammals record primary stable isotopic information from their environment (Delgado Huertas et al., 1995; Kohn, 1996; MacFadden and Bryant, 1994; Nelson, 2005). The  $\delta^{18}$ O (VPDB – Vienna Pee Dee Belemnite) values of the carbonate component of tooth enamel bioapatite can be used to calculate the  $\delta^{18}$ O (VSMOW – Vienna Standard Mean Ocean Water) values of surface water the animal was drinking. A relationship between the carbonate and phosphate component of tooth bioapatite has been defined by lacumin et al. (1996):

$$\delta^{18}O_{PO_4} = \delta^{18}O_{CO_3} * 0.98 - 8.5.$$
<sup>(2)</sup>

Using this equation, we calculate the  $\delta^{18}$ O values of PO<sub>4</sub> for fossil teeth. Equilibrium fractionation that occurs during phosphate mineralization from body fluids at constant temperature (~37 °C) has been compiled for various mammals by Kohn and Cerling (2002):

$$\delta^{18}O_{\text{BODYFLUID}} = (\delta^{18}O_{\text{PO}_4} - 23) / 0.9.$$
(3)

The oxygen isotopic composition in the body water of water-dependent, herbivorous mammals is largely determined by surface water. Though the fossil teeth we study come from extinct notoungulates, their craniodental morphology implies that they employed hind-gut fermentation, which confers strong water dependence (Kohn and Fremd, 2007). All other variations in oxygen input/output among herbivorous mammals introduces uncertainty of <1.4‰ (Kohn, 1996). Because teeth mineralize over several months to years, serial sampling along the length of a tooth can provide a continuous  $\delta^{18}$ O record of surface water that the animal ingested.

Wild animals get their drinking water primarily from running (streams) and standing (lakes) water sources. Stream water has been shown to closely reflect mean annual precipitation (Dutton et al., 2005; Quade et al., 2007). However, closed basin lakes, like those on the Altiplano, have more positive  $\delta^{18}$ O values compared to local rainfall resulting from evaporative enrichment of <sup>18</sup>O in lake water (e.g. Abbott et al., 2003).

# 3.2. Carbon isotopes

The stable isotopic composition of carbon ( $\delta^{13}$ C) from mammal teeth reflects the carbon isotopic composition of the animal's diet. For herbivores, this carbon is derived from the plant matter they consume. An enrichment of ~14‰ from plant to tooth composition results from equilibrium fractionation that occurs as plant matter is digested and during tooth mineralization for modern mammals (Cerling and Harris, 1999; Passey et al., 2005). Therefore, animals that consume a predominantly C<sub>4</sub> diet will have tooth  $\delta^{13}$ C values of near 1‰ ± 2 while those that

eat C<sub>3</sub> plants will be closer to  $-13\% \pm 3$ . Tooth compositions that fall somewhere between C<sub>3</sub> and C<sub>4</sub> plant-types may reflect a mixed diet.

Before ~7.6 Ma, C<sub>4</sub> plants were scarce or non-existent in South America (Cerling et al., 1997). As a result, older fossil teeth should have relatively low  $\delta^{13}\text{C}$  values because they are a reflection of pure  $\text{C}_3$ biomass. C<sub>3</sub> plants do show variation in isotopic values due to environmental conditions. Under water-stressed and/or high-light conditions, there is a decrease in intercellular partial-pressure relative to atmospheric, which results in more positive  $\delta^{13}$ C values (Farguhar et al., 1989) (up to -24% to -22% for C<sub>3</sub> plants). Passey et al. (2002) estimated that early Miocene ungulates consuming water-stressed C<sub>3</sub> plants would have tooth  $\delta^{13}$ C values of ~-8.5‰. Under closed-canopy conditions,  $C_3$  vegetation has more negative values (as low as -30% to -32‰) due primarily to CO<sub>2</sub> recycling (Medina and Minchin, 1980; van der Merwe and Medina, 1989). Considering that pCO<sub>2</sub> levels during the Neogene did not change significantly (Tipple and Pagani, 2007), variations in  $\delta^{13}$ C make it possible to draw additional paleoenvironmental inferences in areas that consist of predominantly  $C_3$  plants.

#### 4. Results and discussion

The results of tooth analyses are reported as the mean and standard deviations of  $\delta^{18}$ O and  $\delta^{13}$ C based on serial samples of individual teeth (Table 1). Standard deviations range between 0.4% and 1.7% for all teeth. Teeth that show greater standard deviations in  $\delta^{18}$ O may reflect either: 1) different drinking water sources throughout the year with variable isotopic compositions or 2) seasonality in the isotopic composition of rainfall throughout the year forced by temperature and/or the amount effect, evidenced from the sinusoidal patterns observed in some of the teeth (Fig. 3). However, most fossil teeth lacked obvious sinusoidal patterns in  $\delta^{18}$ O (Fig. 4); possibly because animals were drinking out of standing bodies of water which tend to damp seasonal fluctuations in the isotopic composition of meteoric water.

# 4.1. Northern Altiplano

Late Oligocene teeth (UF 172412 *Trachytherus* (Fig. 3B), UF 132901 *Pyrotherium* (Fig. 3A), and possibly UF 90981 *Eurygenium*, all from the Salla Formation) show regular, approximately sinusoidal variation in  $\delta^{18}$ O, providing confidence that tooth enamel carbonate is preserving an original  $\delta^{18}$ O signal (one that has not been significantly diagenetically altered). We use the peaks and troughs of these curves for estimation of the isotopic composition of drinking water during the seasonal cycles, discussed in further detail below. Pronounced seasonal variations in the  $\delta^{18}$ O values of teeth suggest that animals drank from sources with short residence times of surface water, such as open-basin lakes (e.g. Talbot, 1990) and/or stream water, both of which reflect seasonal variations in rainfall composition.

 $δ^{13}$ C bulk values for all individuals range from -6.4% to -14.8% with an average<sup>1</sup> of -9.1%. The  $δ^{13}$ C values from all fossil and modern mammals suggest a predominantly C<sub>3</sub>-plant diet, with the possible exception of one individual from Choquecota (Bol-05-01 and Bol-05-02 *Plesiotypotherium*), which has an average  $δ^{13}$ C of -6.4%, reflecting water-stressed conditions and/or a mosaic C<sub>3</sub>/C<sub>4</sub> diet (Cerling and Quade, 1993; Kohn and Cerling, 2002). The average  $δ^{13}$ C value for late Oligocene Salla teeth is -9.1% (Table 1), indicating moderately water-stressed conditions characteristic of a semi-arid environment (Passey et al., 2002). This is consistent with contemporaneous Salla paleosols which show more positive  $\delta^{18}$ O values (-8%) than a global compilation of Cenozoic paleosols (average -9.4%) from the same study (Ekart et al., 1999). Though Salla fossil teeth and paleosols appear to reflect water-stressed conditions, we note that late Oligocene teeth

<sup>&</sup>lt;sup>1</sup> Multiple tooth  $\delta^{13}$ C and  $\delta^{18}$ O averages are calculated by taking the mean of serial samples along a single tooth to get a bulk tooth value. The average of bulk values for multiple tooth samples weighted by individual is then calculated.



**Fig. 3.** Isotopic values from serial samples along the length of two Oligocene teeth from Salla. Variation in  $\delta^{18}$ O suggests seasonality of surface water and rainfall over the time of tooth mineralization. Both  $\delta^{18}$ O (circles) and  $\delta^{13}$ C (diamonds) reported with respect to VPDB (Vienna Pee Dee Belemnite). A) UF132901 *Pyrotherium macfaddeni* tusk (26.2 Ma) from Salla, Bolivia. Sampled length represents ~3 yr of growth. B) UF172412 *Trachytherus* right dentary with three teeth (25.95–25.99 Ma) from Salla, Bolivia. Sampled length represents ~1.5 yr of growth.



**Fig. 4.** Isotopic values from serial samples along the lengths of three teeth. Lack of apparent sinusoidal variation in  $\delta^{18}$ O suggests that seasonal changes in  $\delta^{18}$ O of meteoric water are not well preserved, possibly because animals were drinking primarily from large lakes, which would buffer seasonal variation. Both  $\delta^{18}$ O (circles) and  $\delta^{13}$ C (diamonds) reported with respect to VPDB (Vienna Pee Dee Belemnite). A) Bol-05-10 *Posnanskytherium* (3.6–4 Ma) from Puna, Bolivia. B) Suborder Toxodonta Nick1 (8–10 Ma) from Achiri, Bolivia C) BosCop1 *Bos* (modern) from Copacabana, Bolivia.

from coastal Brazil (-8.4%) are also relatively positive, indicative of semi-arid conditions. The lack of  $\delta^{13}$ C values higher than -6.4% in fossils <7.6 Ma and modern teeth indicates that both modern and paleovegetation on the Altiplano is/has been primarily C<sub>3</sub>.

Tooth samples from the late Oligocene yield much higher  $\delta^{18}$ O values than <10 Ma teeth, all collected from high elevation sites (~4000 m) in the northern Andean plateau (Fig. 5, Table 1, Table DR2). Specifically, the mean tooth  $\delta^{18}$ O value of ~26 Ma individuals is -1.5% (range of 3.3%). The mean  $\delta^{18}$ O for late Miocene teeth in the northern Altiplano is -11.2% (range of 0.4‰). Modern *Bos* (cow) teeth collected near Copacabana, Bolivia have a mean  $\delta^{18}$ O value of

-11.1%, similar to late Miocene teeth<sup>2</sup> (Table 1). We convert tooth values using Eqs. (2) and (3) to calculate  $\delta^{18}$ O values for surface water for the northern Andean plateau at ~26 Ma (-3.0%) and during the late Miocene (-13.9%). The  $\delta^{18}$ O of surface water calculated from the teeth of modern *Bos* is -13.7%, essentially the same as the mean value of late Miocene teeth (Table 1).

 $<sup>^2</sup>$   $\delta^{18}$ O values from a modern sheep tooth collected near Turco (BolShp) were excluded from the comparison of late Miocene teeth to modern. The sheep's relatively positive  $\delta^{18}$ O values are typical of drought-tolerant smaller-bodied herbivores (Kohn, 1996).



**Fig. 5.** Northern Andean plateau  $\delta^{18}$ O values over time as recorded in mammal teeth. The difference between means of >25 Ma Eastern Cordillera and <10 Ma Altiplano samples is ~10‰. Each point is the mean  $\delta^{18}$ O of a unique fossil or modern tooth. Andean plateau samples are diamonds and Brazil samples are open squares. Open diamond represents a small-bodied sheep sample not included in the calculations<sup>2</sup>. *Y*-axis error bars represent 1 $\sigma$  standard deviation, a result of variation along the length of each tooth associated with seasonal changes in the  $\delta^{18}$ O values of drinking water. *X*-axis error bars represent sample age uncertainty. We do not have data between ~25 and ~10 Ma.  $\delta$  values are reported in VPDB (Vienna Pee Dee Belemnite).

The isotopic composition of modern meteoric water throughout the Andean plateau is poorly constrained. There is only one long-term record (1995–2004) from La Paz (elev. = 4071 m) in the north which reports a weighted mean  $\delta^{18}$ O value of -14.0% (IAEA/WMO, 2006). A record of rainfall amount and  $\delta^{18}$ O collected between December 1982 and December 1985 at El Alto (elev. = 4080 m) near La Paz shows a weighted mean  $\delta^{18}$ O value of -15.1% (calculated from data in Table 6 of Gonfiantini et al., 2001). These modern rainfall values are remarkably similar to our calculated water values from modern *Bos* teeth and late Miocene teeth in the northern Altiplano, suggesting that surface elevation and climate in the northern Altiplano has been similar to modern since the late Miocene.

Assuming a similar  $\delta^{18}$ O versus altitude gradient between the late Oligocene and today, we use paleo-water values derived from fossil teeth and the modern  $\delta^{18}$ O versus altitude relationship on the eastern flank of the Andes to estimate temporal changes in elevation. Elevation uncertainty is constrained using a bootstrap Monte Carlo approach based on 1000 randomly generated numbers. This error estimate includes both (1) scatter in the combined Bolivia precipitation and stream water  $\delta^{18}$ O versus altitude datasets and (2) uncertainty in tooth  $\delta^{18}O(\pm 1.4\%)$  based on variation in oxygen input/output for herbivorous mammals (Table 2 of Kohn, 1996).  $1\sigma$  error is  $\pm$  500 m at all elevations. This error estimate does not take into consideration changes in paleoclimate that may influence the paleo-lapse rate and/or the isotopic composition of lowland water vapor. Paleo-water values derived from 26 Ma teeth (-3.0%) and late Miocene teeth (-13.9%)used in Eq. (1) yield paleoelevations of  $-1590 \pm 500$  m and  $4250 \pm$ 500 m respectively (Fig. 2). The late Oligocene estimate is clearly too low, likely a result of temporal changes in atmospheric circulation and/ or climate, both of which are reasonable considering topography's effect on regional, and perhaps global, climate (Hou and Lindzen, 1992). Global circulation models (GCM) suggest that a lower elevation Andes should be associated with a decrease in low elevation rainfall amount (Ehlers and Poulsen, 2009; Insel et al., 2009; Garreaud et al., in press). Less precipitation should result in higher  $\delta^{18}$ O values associated with the amount effect (Risi et al., 2008; Vimeux et al., 2005) at low elevations as compared to today's values. Indeed, the paleo-water  $\delta^{18}$ O values that we calculated for fossil teeth from the Salla Formation ( $\delta^{18}O = -3.0\%$ ) are more positive than modern rainfall at low elevations on the eastern flank of the Andes ( $\delta^{18}O = -6.0\%$ ), as defined by Eq. (1). Sedimentary



**Fig. 6.** Photo of late Oligocene paleosol from the Salla Formation in the northern Altiplano. The presence of pedogenic carbonate indicates at least semi-arid conditions at that time. Hammer for scale.

and fossil evidence provide some evidence of past climate conditions that may explain the relatively positive meteoric water values from the Salla Formation. Paleosols contain carbonates, yet they also contain extensive root tubules (Fig. 6) indicating abundant plant productivity. The presence of contemporaneous bufonid toad fossils in the Salla Formation (Baez and Nicoli, 2004) also indicates that northern Andean plateau climate was not arid at that time. Instead, it was likely semi-arid as the mere presence of paleosol carbonates requires at least semi-arid conditions (Royer, 1999) or strongly seasonal rainfall. This is in agreement with climate modeling which suggests that a lower elevation range would be associated with a drier climate throughout the modern Subandes and Amazon Basin (Ehlers and Poulsen, 2009; Insel et al., 2009; Garreaud et al., in press).

A useful comparison for this surface uplift estimate based on the modern  $\delta^{\rm 18} \rm O\text{-}elevation$  relationship can be made using a model described by Rowley et al. (2001) which incorporates equilibrium fractionation during Rayleigh distillation as a function of the thermodynamics of atmospheric ascent and condensation. Given the temperature and relative humidity over the moisture source area, we input  $\delta^{18}$ O of precipitation reconstructed from fossil teeth along the vapor mass trajectory to calculate the elevation difference between sites. Relative humidity is assumed to be similar to modern  $\sim 80\%$ , with the observation that large changes in relative humidity  $(\pm 8\%)$  do not significantly affect model calculations of elevation (Rowley and Garzione, 2007). Meteoric water  $\delta^{18}$ O estimates derived from late Oligocene fossil teeth at sea level (São Paulo) and in the Eastern Cordillera are similar (-2.7% and -3.0% respectively) (Table 1), suggesting that the Altiplano was at low elevation during that time. For the late Miocene, fossil teeth are used as a proxy for the  $\delta^{18}$ O of meteoric water on the Altiplano (-13.9%) with low elevation  $\delta^{18}$ O estimated from modern rainfall at the base of the eastern flank of the Andes (-5.0%) (Gonfiantini et al., 2001). We subtract 0.5% from this value due to changes in global ice-volume from the late Miocene to present (Kohn and Fremd, 2007; Kohn and Cerling, 2002). A mean annual ambient air temperature of 26 °C based on low elevation (200 m) sites at the base of the Eastern Cordillera is used (IAEA/WMO, 2006), with an understanding that higher temperatures in the past would increase estimates of surface uplift. Based on these parameters, the model estimates surface elevations of ~4600 m during the late Miocene<sup>3</sup>. Although paleoelevation estimates are subject to large

<sup>&</sup>lt;sup>3</sup> Model ran at 26 °C and 80% relative humidity where y = elevation (m) and  $x = \delta^{18}$ O:  $y = -0.0072x^4 - 0.8033x^3 - 35.423x^2 - 793.75x - 20.239$  (Rowley et al., 2001).

uncertainties, in particular when climate is poorly constrained (Rowley and Garzione, 2007), we note that two different methods corroborate large estimates of surface uplift, on the order of the entire elevation of the plateau, between late Oligocene and late Miocene time.

The  $\delta^{18}$ O values of surface water estimated from fossil teeth in the late Oligocene Salla Formation can be compared to modern meteoric water worldwide to evaluate the likelihood that this site was at low elevation. We find that only ~8% of GNIP sites >500 m in elevation produce long-term weighted mean annual values that are higher than observed at Salla (IAEA/WMO, 2006). This is consistent with the presence of bufonid toad fossils in the Salla Formation that suggest low elevations (Baez and Nicoli, 2004) and paleobotanical evidence constraining surface elevation of the Eastern Cordillera near Potosí to less than 1250 m sometime between 21 and 14 Ma (Gregory-Wodzicki et al., 1998).

We compare seasonal variation in  $\delta^{18}$ O of modern meteoric water to variation along the length of fossil and modern teeth to evaluate paleoclimate. Long-term weighted means of monthly precipitation  $\delta^{18}$ O in the northern Altiplano at La Paz, Bolivia show variation from summer to winter of >10‰ (IAEA/WMO, 2006). The magnitude of variation becomes less pronounced eastward with low elevation, continental GNIP sites in the Amazon Basin (Porto Velho, Cuiaba, and Brasilia) showing variation of up to  $\sim 7\%$  from summer to winter months, and Atlantic coast sites in Brazil (Belem, Fortaleza, and Salvador) varying by an average of ~3.5‰ (IAEA/WMO, 2006). Variation in  $\delta^{18}$ O along the lengths of late Miocene teeth, when the Altiplano is inferred to have been high, is only ~2‰ (Fig. 4), much less than modern meteoric water at La Paz. Mammal teeth damp seasonal variation in  $\delta^{18}$ O, a result of multiple physiological factors (Kohn and Dettman, 2007). However, the large discrepancy between meteoric water and tooth value variation suggests that these animals also drank primarily from lakes, which further buffer seasonal changes. Uncertainty related to water source underscores the need to use caution when interpreting intra-tooth variability as a proxy for seasonal changes in precipitation amount. That said, the observation that late Oligocene samples from the northern Eastern Cordillera show a high magnitude of seasonal variation ~5% (Fig. 3) at a time when the Andes are inferred to have been low suggests that a low elevation Andes may have still experienced a monsoon-like climate. This is consistent with the assertion that wet summers and dry winters in South America are caused by expansion of equatorial easterlies in the upper troposphere as opposed to direct insolation over the Andean plateau (Garreaud and Vuille, 2003).

If moisture was predominantly sourced from the Atlantic in the late Oligocene as it is today, the observation that fossil teeth from the Salla Formation are not depleted in <sup>18</sup>O relative to the coastal Brazil samples suggests that the continental effect was negligible compared to today's depletions of ~3.5‰ across the continent (Vuille et al., 2003). This would require greater recycling of atmospheric water vapor by evapotranspiration, a more arid climate in the late Oligocene in the western part of the continent, and/or significant differences in atmospheric circulation; where water vapor was derived from the more proximal Pacific Ocean or a local inland seaway, both of which could contribute water vapor relatively enriched in <sup>18</sup>O. Recent GCM experiments suggest that the Pacific may provide a significant amount of moisture to the Andes if they were lower (Ehlers and Poulsen, 2009; Insel et al., 2009). However, another GCM experiment that looks at the effects of lowering the Andes suggests minimal contributions from the Pacific Ocean if the cold Humboldt Current is maintained (Garreaud et al., in press). Resolution of the discrepancies between the various model results may shed light on the plausibility of a Pacific source of water vapor during Salla deposition when the Andes were clearly lower. Regardless of the source of Andean precipitation, the relatively positive  $\delta^{18}$ O values in late Oligocene teeth require the absence of a significant topographic barrier during that time because Pacific-sourced moisture would have to traverse the Andes to reach the Salla location. The current lack of documentation of late Oligocene to early Miocene inland marine deposits precludes the determination of whether an inland seaway source was available.

The observation that precipitation amount is negatively correlated with  $\delta^{18}$ O of precipitation throughout the tropical Americas, particularly at high elevation sites (Vimeux et al., 2005), suggests that the more arid southern Altiplano would have precipitation with more positive  $\delta^{18}$ O values compared to the north. We compare modern and fossil tooth enamel carbonate from a range of latitudes in the Andes to characterize latitudinal gradients in rainfall. Northern Altiplano sites are between 16°S and 18°S and southern Altiplano sites are between ~19.5°S and 21.5°S (Fig. 1). Modern and late Miocene tooth samples exhibit higher  $\delta^{18}$ O values in the southern Altiplano compared to the north (Fig. 7). The average  $\delta^{18}$ O of northern Altiplano late Miocene teeth is -11.2% (Table 1). By comparison, the average of all southern Altiplano tooth samples is -7.9%. The relative enrichment in <sup>18</sup>O from north to south is >3% for the most negative tooth  $\delta^{18}$ O values. Significantly less precipitation falls in the southern Altiplano when compared to the north (Garreaud and Vuille, 2003; Montgomery et al., 2001) which suggests that more positive  $\delta^{18}$ O values in the south are a reflection of increased aridity (i.e., evaporative enrichment of <sup>18</sup>O). Modern and late Miocene teeth from the northern Altiplano yield strikingly similar  $\delta^{18}$ O values with a range of only 0.4% for all 3+ individuals. Southern Altiplano modern and fossil teeth are also fairly consistent with a range of 1.9% for all 5+ individuals. These tooth data suggest that a pronounced gradient of precipitation amount has existed since at least 3.6 Ma, which represents the oldest fossils that we have analyzed from the southern Altiplano.



**Fig. 7.** Comparison of  $\delta^{18}$ O in fossil teeth from the northern (squares) and southern (diamonds) Altiplano. Difference between the most negative  $\delta^{18}$ O values from the north and south is ~3‰ (indicated by gray curve). Each point is the average  $\delta^{18}$ O of a unique fossil or modern tooth. Open square is small-bodied sheep sample not included in the calculations<sup>2</sup>. Error bars represent 1 $\sigma$  standard deviation, a result of variation along the length of each tooth associated with seasonal changes in the  $\delta^{18}$ O values of drinking water.  $\delta$  values are reported in VPDB (Vienna Pee Dee Belemnite).

δ<sup>18</sup>O (VPDB)

# 5. Conclusions

Modern *Bos* teeth corroborate the relationship between tooth O isotopes and meteoric water, yielding a reconstructed meteoric water  $\delta^{18}$ O value of -13.7%, similar to northern Andean plateau long-term averages of -15.1% from El Alto (Gonfiantini et al., 2001) and -14.0% from La Paz (IAEA/WMO, 2006). Based on the close agreement between meteoric water reconstructions from late Miocene fossil teeth (-13.9%) and long-term averages of modern meteoric water, the northern Andean plateau reached high elevation (similar to modern) by late Miocene time.

The oldest sampled fossils in the southern Altiplano are ~3.6 to 4.0 Ma. Comparing fossil and modern teeth from the southern Altiplano with teeth <10 Ma in the northern Altiplano reveals that southern Altiplano teeth are ~3‰ more positive. This isotopic difference suggests that by at least 3.6 Ma, a similar to modern gradient in isotopic composition was established. Assuming that this isotopic gradient is a reflection of the pronounced gradient in rainfall amount, the southern Altiplano appears to have been more arid than the north by Pliocene time, suggesting atmospheric circulation patterns similar to modern. Ideally, new paleoclimate proxy data from the middle to late Miocene would help identify the onset of this climate pattern in the central Andes.

Late Oligocene teeth from the Eastern Cordillera (Salla Formation) and the southeast coast of Brazil produce similar reconstructed meteoric water  $\delta^{18}$ O values of -3.0% and -2.7% respectively (Table 1). Little depletion in  $\delta^{18}$ O for Salla teeth suggests that the Andean plateau was at low elevation during this time, in agreement with paleosol carbonate and faunal data (Baez and Nicoli, 2004; Garzione et al., 2008; Gregory-Wodzicki, 2000). Salla teeth also show relatively positive  $\delta^{13}$ C values for a C<sub>3</sub> dominated environment (-9.1%). These observations may reflect semi-arid conditions at that time, consistent with climate predictions for a low elevation Andes based on GCMs (Ehlers and Poulsen, 2009; Insel et al., 2009; Garreaud et al., in press). Other possible explanations include a local <sup>18</sup>O-enriched source from an inland seaway or derivation of water vapor from the more proximal Pacific Ocean. Regardless of the source of Andes precipitation, the only reasonable explanation for such positive  $\delta^{18}$ O values in late Oligocene teeth is the absence of a significant topographic barrier during that time.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.epsl.2009.11.047.

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