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Last Glacial mammals in South America: a new scenario from the Tarija Basin (Bolivia)

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Abstract The chronology, sedimentary history, and paleo-ecology of the Tarija Basin (Bolivia), one of the richest Pleistocene mammalian sites in South America, are revised here based on a multidisciplinary study, including stratigraphy, sedimentology, geomorphology, paleontology, isotope geochemistry, and ^{14}C geochronology. Previous studies have indicated a Middle Pleistocene age for this classic locality. We have been able to obtain a series of ^{14}C dates encompassing all the fossil-bearing sequences previously studied in the Tarija Basin. The dated layers range in age from about 44,000 to 21,000 radiocarbon years before present (BP), indicating that the Tarija fauna is much younger than previously thought. Glacial advances correlated to marine isotopic stages (MIS) 4 and 2 (ca. 62 and 20 ka BP, respectively) are also documented at the base and at the very top of the Tarija–Padcaya succession, respectively, indicating that the Bolivian Altiplano was not dry but sustained an ice cap during the Last Glacial Maximum. The results of this multidisciplinary study enable us to redefine the chronological limits of the Tarija sequence and of its faunal assemblage and to shift this paleontological, paleo-climatological, and paleoecological framework to the time interval from MIS 4 to MIS 2.

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Introduction

Knowledge of mammalian evolution in South America during the Pleistocene is predominantly based on the abundant fossils from Argentina, Brazil, Peru, Ecuador, and Bolivia (Marshall et al. 1984). One of the richest fossil faunas, complemented by a stratigraphic framework, is that from Tarija in Southern Bolivia (Takai et al. 1982; MacFadden et al. 1983; Marshall et al. 1984; Marshall and Sempere 1991). The Tarija fauna was, until now, considered a reference site for the late Ensenadan mammal age (late Early to Middle Pleistocene; MacFadden et al. 1983; Marshall and Sempere 1991). During this time, South America experienced one of the most dramatic faunal changes since the beginning of the Great American Biotic Interchange (Stehli and Webb 1985; Cione and Tonni 1999), with the massive dispersal of Northern taxa, which included equids, camelids, cervids, proboscideans, and

large carnivores to South America. At the same time, some South American endemics migrated northward.

A previous calibration of the age of the Tarija sedimentary sequence, based on magnetostratigraphy and fission track dating of a tephra in the middle-upper part of the sequence, indicated a time span from 1 to 0.7 Ma (MacFadden et al. 1983). A younger age of ca. 0.2 Ma (late Middle Pleistocene) was provided by dating a tephra layer in the upper part of the sequence with electron spin resonance (Takai et al. 1982).

Despite the long sedimentary record, encompassing several climatic cycles, and the abundant fossil vertebrate material, a thorough study of the geological, environmental, and faunal variation in time and space of the Tarija Pleistocene Basin has never been attempted.

In this study, we present results of new multidisciplinary investigations that have been carried out in the Tarija and nearby Padcaya Pleistocene basins (hereafter referred to as Tarija–Padcaya Basin) during successive fieldworks from 2001 to 2004. This paper focuses on sedimentation processes, paleoenvironmental conditions, mammal fossil fauna, and their response to Pleistocene climatic changes in the framework of new high-resolution radiometric dates. Because the chronological and geological context of the Tarija fauna has changed so significantly based on these studies, we believe that this report is both a timely and valuable contribution to the South American vertebrate paleontology.

Materials and methods

Key sections across the Tarija–Padacaya Basin were studied to sample the entire Pleistocene succession. The basin (Fig. 1) has an irregular shape, reaches almost 90 km in length, and 50 km at maximum width. It is located near the Bolivian–Argentinean border, on the southeastern side of the Andean Cordillera, at intermediate latitude (21°S) and altitudes (about 2,000 m above sea level [a.s.l.]). Detailed stratigraphic and sedimentological analyses were carried out utilizing the architectural method proposed by Miall (1985, 1990, 1996). For each studied section (Fig. 2), the lateral facies variation has been carefully investigated so that the sections are representative of a large area. We focused our attention on the sequences studied by MacFadden et al. (1983), namely, Santa Ana, San Blas (here San Jacinto), and San Pedro (here Monte Sur) and those studied by Takai et al. (1982, 1984), namely, Ancon Grande, Rujero, and Tolomosa. It should be noted that in naming the studied section we adopted the current local toponyms. In comparing our results with previously published data, we observe, that although every effort was made to locate and thoroughly examine each of the sequences reported in the literature, it is not possible to ensure that one is dealing exactly with the same bone bed of previous authors.

Fieldwork in 2002 and 2003 resulted in the collection of some hundreds fossil mammal remains from eight sites within the Tarija–Padcaya Basin. The fossils are housed at the Museo Nacional Arqueologico–Paleontologico of Tarija. The preliminary systematic analysis of the collected material allowed the identification of 26 mammalian taxa belonging to 14 families. The stratigraphic distribution of the Monte Sur and Rio Rujero taxa is reported in Table 2.

As collagen was not suitable for direct dating of the megafaunal remains, several peat layers in various logs were sampled for accelerator mass spectrometry (AMS) radiocarbon dating at the Gröningen and Miami (Beta Analytic) Laboratories. Conventional ages and geographic coordinates of each dated sample are reported in Table 1. The dated layers encompass the entire fossil-bearing sequences exposed within the Tarija–Padcaya Basin (Fig. 2), including the sedimentary sequences previously studied by MacFadden et al. (1983) and Takai et al. (1982, 1984). Although most of the fossils sampled from the exposed sequences consist of isolated dental and skeletal elements, complete or partial skeletons in anatomical connection were encountered in several cases. This fact, along with the absence of traces of a prolonged transport of most of the bones, clearly indicate that the fossil remains were not reworked from older sediments and can be unambiguously associated to the stratigraphic context of the dated peat layers.

A geochemical isotopic investigation on horse (*Equus*) and gomphothere (*Cuvieronius*) bones and teeth was performed to assess paleoclimatic and paleoenvironmental variations. Specimens were collected at Monte Sur and Rio Rujero from the logs depicted in Fig. 2a,b.

Phosphate ($\delta^{18}Op$) and carbonate ($\delta^{18}Oc$ and $\delta^{13}Cc$) have long been considered potentially useful tools for paleoclimatic and paleoenvironmental studies in continental areas. In fact, the $\delta^{18}Op$ and $\delta^{18}Oc$ in bioapatite are directly related to the oxygen isotope composition of the environmental waters ($\delta^{18}Ow$) and, in turn, positively correlated to the mean local temperature (e.g. Longinelli 1984; Sanchez-Chillon et al. 1994); $\delta^{13}Cc$ is instead controlled by the proportion of C_3 and C_4 plants in the diet (e.g. Sullivan and Krueger 1981). C_3 plants (trees, shrubs, and grass) are generally typical of temperate and cold environments, whereas C_4 plants (mostly grass) grow better under warm and arid conditions. Therefore, the $\delta^{13}C$ measured in skeletal remains can provide useful information on the milieu features. $\delta^{18}O$ in carbonate ($\delta^{18}Oc$) and phosphate ($\delta^{18}Op$) and $\delta^{13}C$ in carbonate of biogenic apatite were measured, according to the conventional methods (Lee Thorp and Van der Merwe 1987; Crowson et al. 1991). We are aware that the use of bone remains, rather than just
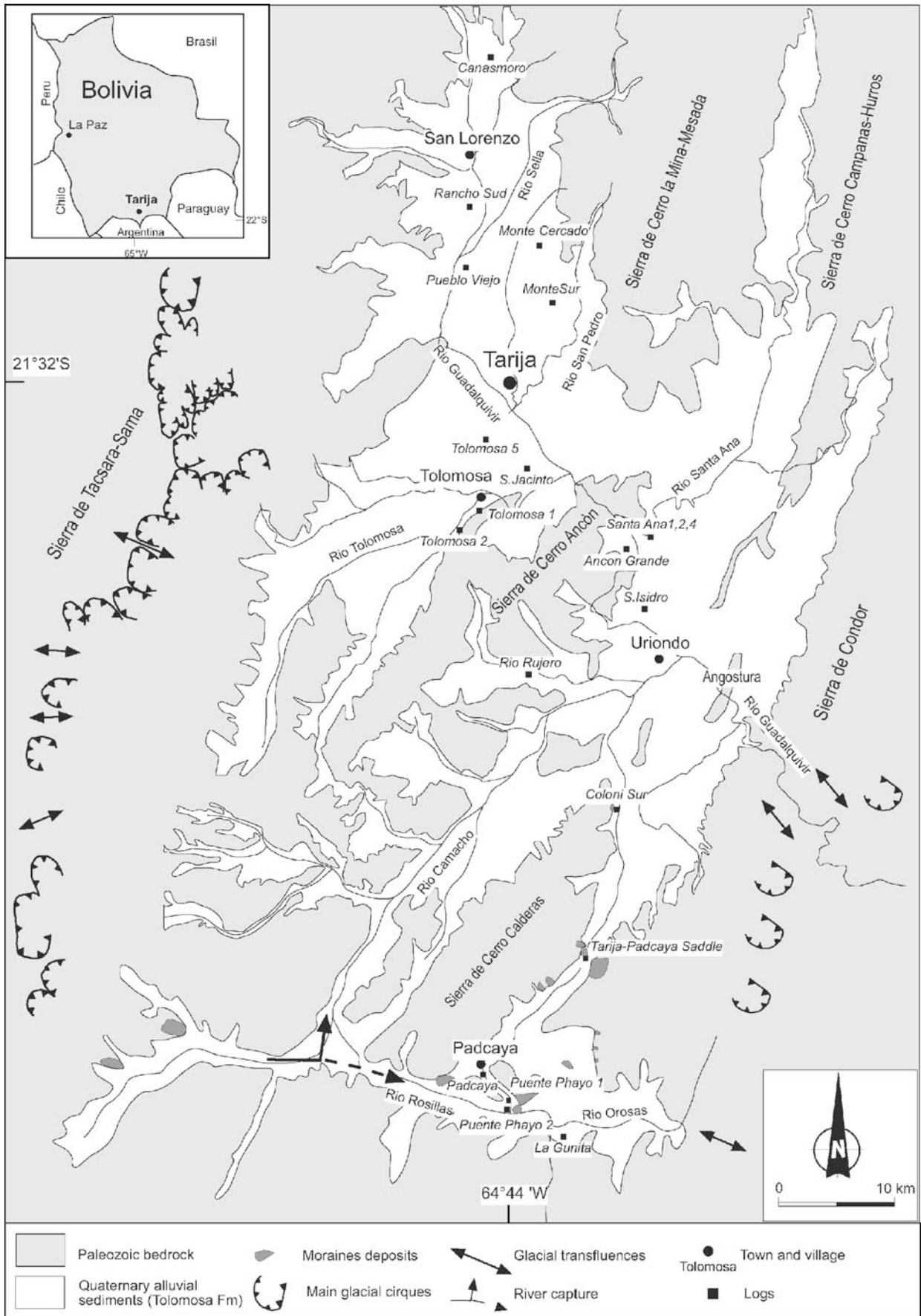
◀ **Fig. 1** The Tarija–Padcaya Basin: (*1*) Quaternary alluvial sediments (Tolomosa Fm); (*2*) glacial deposits; (*3*) Paleozoic bedrock; (*4*) main glacial cirques; (*5*) glacial transfluence; (*6*) river capture; (*7*) towns and villages; (*8*) stratigraphical logs

teeth, could impart an error due to possible taphonomic or diagenetic modifications, but our main purpose in this case was to achieve the most detailed stratigraphic sampling, to assess climatic changes throughout the sequence. In a plot
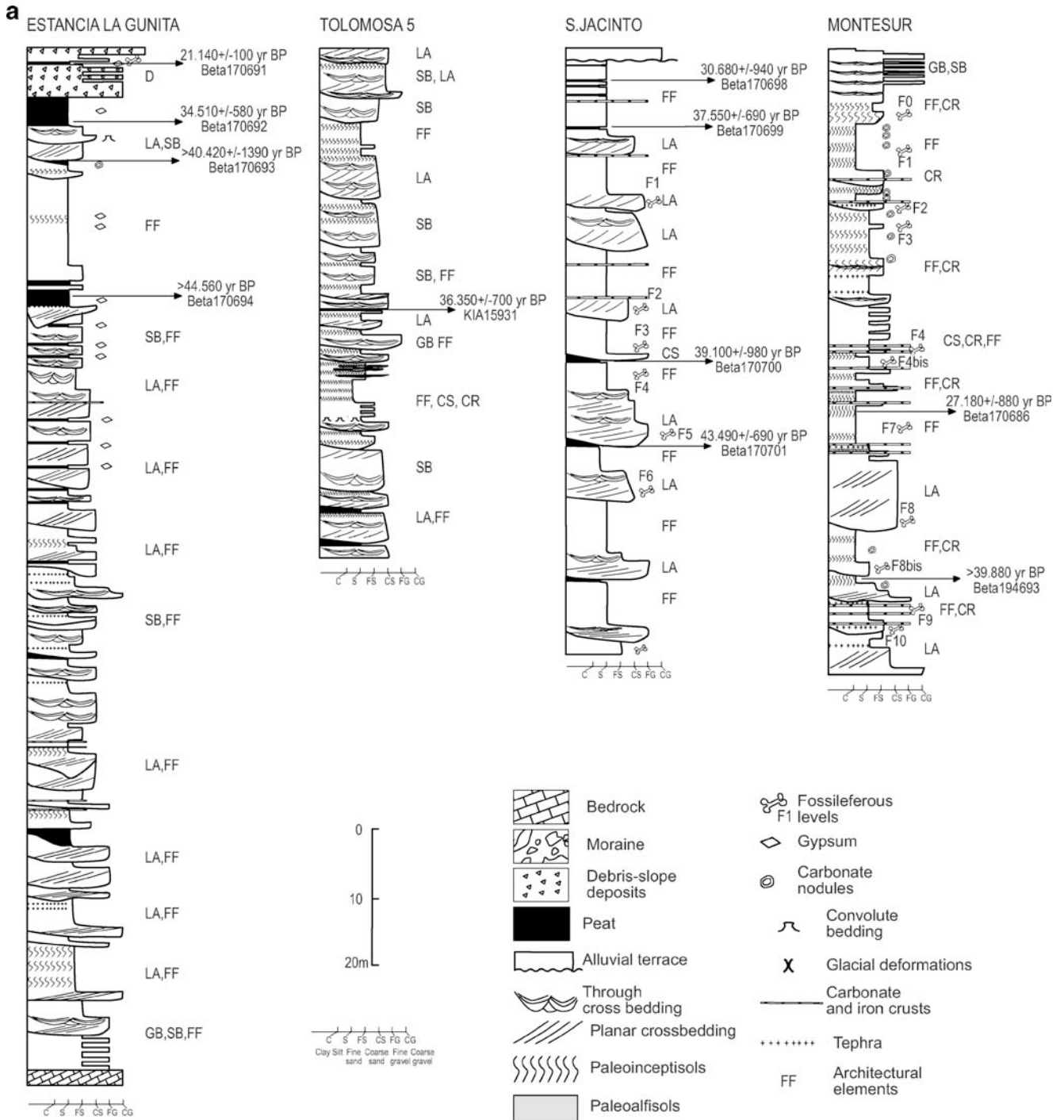

Fig. 2 a Logs with fossiliferous beds (*F#*) and ^{14}C ages of key measured sections of the Tarija–Padcaya Pleistocene sequence. Labeling of fossiliferous beds refers to each section and is not base for correlation among logs. **b** Logs with fossiliferous beds (*F#*) and

^{14}C ages of key measured sections of the Tarija–Padcaya Pleistocene sequence. Labeling of fossiliferous beds refers to each section and is not base for correlation among logs. *Symbols* as in (**a**)
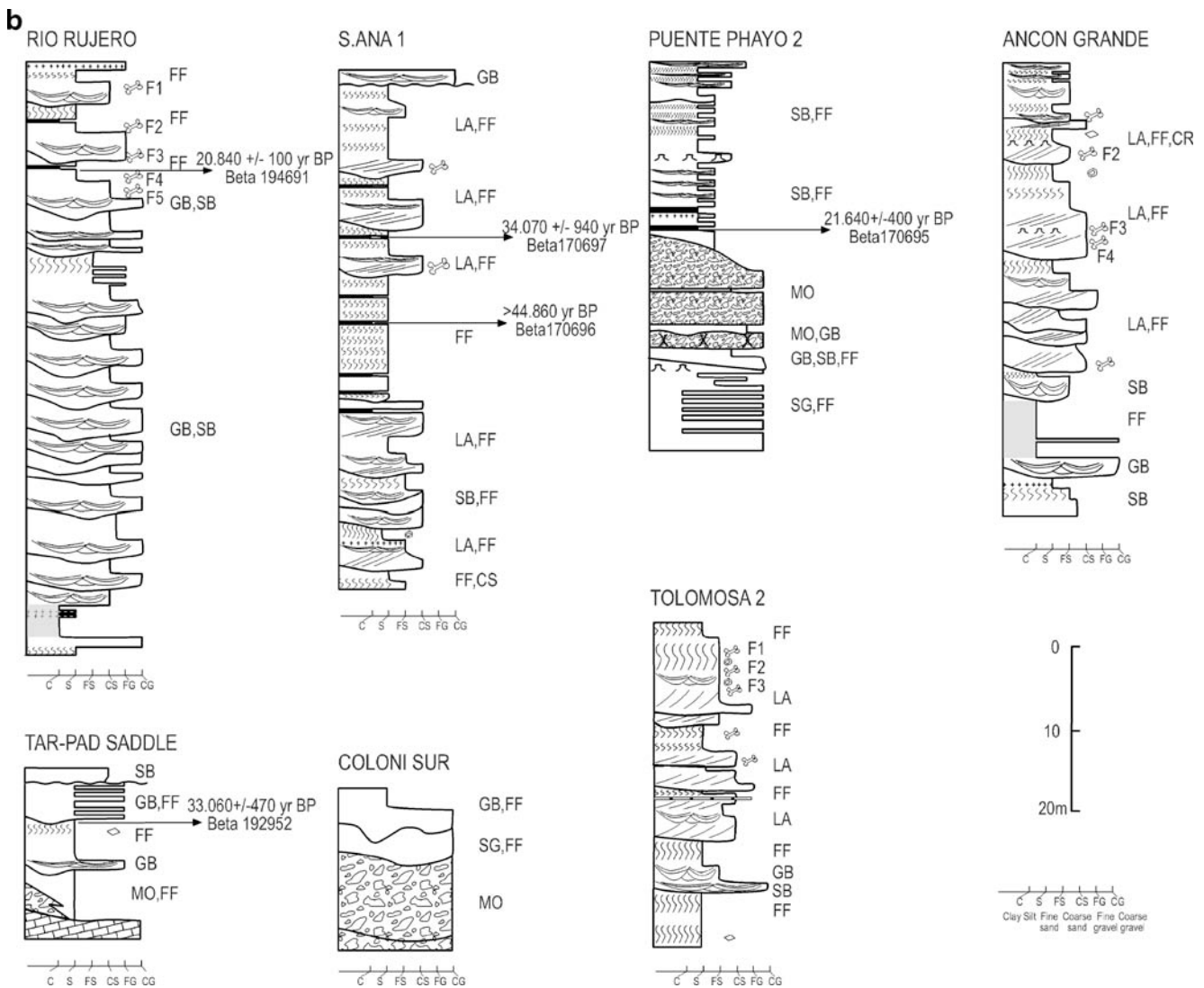
Fig. 2 (continued)

of $\delta^{18}Op$ vs $\delta^{18}Oc$, both samples fell within the error of the correlation lines proposed by Zazzo et al. (2004), and therefore, all the specimens could be considered reliable.

Stratigraphic setting and paleoenvironments

The Tarija–Padcaya Basin can be divided into the northern Tarija sector and the southern Padcaya sector drained, respectively, by the Guadalquivir and the Orosas rivers. During the Late Pleistocene, the Rio Guadalquivir captured the Rio Camacho, the westernmost part of the Orosas River basin (Fig. 1). The lower part of the sequence, which unconformably rests on the bedrock, is made of coarse grained alluvial fan deposits that are interlayered with a buried pedosequence of red, leached, and argic B horizons (paleoalfisols) in the Ancón Grande and Rio Rujero logs (Fig. 2b). These soils, developed under a forest cover, associated with a warm and

moist climate without seasonal contrasts. A very deeply weathered paleoxeralf soil, also affecting the bedrock, has been observed in the southern part of the Tolomosa River Basin. This tropical soil is the only one that evolved under a long-lasting warm and humid climate.

At Coloni Sur and Puente Phayo 2 (Fig. 2b), at the contact with the bedrock, there are ground and surface moraines, although the lateral relationships with the aforementioned logs and facies is unknown. Upward, at least two superimposed ground and lateral moraines, separated by outwash deposits, are present at Puente Phayo 2 at about 1850 m a.s.l. The moraine ridges are mostly made of very coarse gravels and boulders, suggesting that the glacial advance affected the outwash deposits.

The till deposits and the lateral moraine ridges are covered with fine grained alluvial deposits (sandy bedforms, SB; lateral accretion, LA; flood plain facies, FF and to a lesser extent, gravel bedforms architectural elements),

Table 1 ^{14}C-dated organic levels of the Tarija–Padcaja succession

Site/log	Coordinates	Material	Laboratory number	[14]C conventional age (BP)
M. Sur	21°29′08″S, 64°42′30″W	Paleosoil humic substance	Beta 170686	27,180±880
M. Sur	21°29′08″S, 64°42′30″W	Paleosoil humic substance	Beta 194693	>39,880
S. Jacinto	21°38′21″S, 64°45′57″W	Peat	Beta 170698	30,680±800
S. Jacinto	21°35′05″S, 64°43′02″W	Peat	Beta 170699	37,550±690
S. Jacinto	21°35′05″S, 64°43′02″W	Peat	Beta 170700	39,100±980
S. Jacinto	21°35′05″S, 64°43′02″W	Peat	Beta 170701	>43,490
S. Ana 1	21°36′50″S, 64°38′50″W	Peat	Beta 170697	34,070±940
S. Ana 1	21°36′50″S, 64°38′50″W	Peat	Beta 170696	>44,860
Tolomosa 5	21°38′21″S, 64°45′57″W	Peat	KIA 15931	36,530±700
Estancia La Gunita	21°50′73″S, 64°45′27″W	Peat	Beta 170691	21,140±100
Estancia La Gunita	21°50′73″S, 64°45′27″W	Peat	Beta 170692	34,519±580
Estancia La Gunita	21°50′73″S, 64°45′27″W	Peat	Beta 170693	>40,420±1390
Estancia La Gunita	21°50′73″S, 64°45′27″W	Peat	Beta 170694	>44,560
Puente Phayo 2	21°50′75″S, 64°45′25″W	Peat	Beta 170695	21,640±400
Tarija–Padcaya Saddle	21°47′08″S, 64°39′38″W	Paleosoil humic substance	Beta 192952	33,060±470
Rio Rujero	21°42′25″S, 64°45′01″W	Paleosoil humic substance	Beta 194691	20,840±100

and the whole sequence is typical of a meandering to wandering and, possibly, anastomosing, river system (Models 5, 6, 7, and 8 of Miall 1996). These are particularly well represented in the Monte Sur, S. Jacinto, and Rio Rujero logs (Fig. 2a,b), which represent the most fossiliferous sequences. Part of the wide alluvial plain was characterized by relative stability as indicated by peat beds deposited in small lakes and swamps. Local intercalations of slope debris layers have been observed at many foot slopes. There are also some gypsum intercalations, frequently associated with peat layers, suggesting that the shallow lakes underwent severe drying. Mammalian fossils have only been found within this upper and finer part of the Tarija–Padcaya alluvial sequence.

The part of the sequence with the paleoalfisols could correspond to the interstadials at the beginning of the Last Glaciation (marine isotopic stages [MIS] 5 and 4), whereas the deeply weathered paleosoil (paleoxeralf) might represent MIS 5e. The older glacial deposits belong to the cooler stages of MIS 4. An alluvial plain was established in the basin from the end of MIS 4 and persisted up to the beginning of MIS 2. There is a long gap in the sedimentation from 21 to 11 ka before present (BP), where the older age is at the base of the Late Glacial–Early Holocene valley filling. Almost coeval sedimentary gaps are recorded in the Titicaca and Coipasa Salàr lacustrine sequences between 18 and 14 ka BP (Mourguiart et al. 1997; Argollo and Mourguiart 2000; Fornari et al. 2001; D'Agostino et al. 2002), whereas in the Tauka and Uyuni lakes, ^{14}C dates on organic sediments show a similar gap between 20 and 16 ka BP (D'Agostino et al. 2002). Glacial erosion features on top of the Tarija sediments, U-shaped valleys, and glacial transfluences on the watersheds suggest that this sedimentary gap was due to the presence of a glacial sheet. The glacial advance was caused by the eastward overflow of a thick ice cap that accumulated

on the Altiplano. The limited elevation of the Cordilleran Ridges and the very fast glacial retreat prevented the accumulation of glacial deposits in the Altiplano. The main moraine fronts should be found to the east of the Tarija basin, but this problem is outside the scope of this paper. Moraine deposits from local glaciers are well represented at the feet of the higher relief of the Altiplano but only formed during the stadials of the Late Glacial (Clapperton 1993; Clapperton et al. 1997). Rare and thin moraines have also been found on the western slopes of the Tarija basin, associated with short advances before the Altiplano glaciers melted out. The uppermost part of the Tarija sequence, made of coarse-grained sediments (GB and minor SB; Model 2; Miall 1996), corresponds to the glacial outwash deposited during the retreat. The coarseness of the sediments prevented a detailed chronological assessment. Minor fluvial terraces were deposited during the subsequent incision of the river valley.

Radiocarbon dates

The radiocarbon dating of the peat layers, which are intercalated among the vertebrate-bearing strata (Fig. 2), allowed us to provide a fine-scaled chronological constraint to the age of the Tarija fauna. We obtained 16 new AMS dates from eight sequences (Table 1). In some cases (e.g. S. Jacinto), up to four superposed and progressively younger dates were obtained, revealing a generally undisturbed stratigraphic context. Few ^{14}C dating are older than 44 ka BP, whereas most of them vary between 43 and 21 ka BP (Table 1; Fig. 2a,b). The new radiocarbon dates invalidate all previous chronological assessments of the Tarija mammal fauna (MacFadden et al. 1983; Takai et al. 1982) and clearly indicate a Late Pleistocene age for the entire fossiliferous sequence. According to these new chrono-

Table 2 Stratigraphic distribution and abundance of mammal taxa at Monte Sur and Rujero sites

	Xenarthra indet.	Dasypus sp.	Pampatherium sp.	Glyptodontidae indet.	Glyptodon cf. reticulatus	Neothoracophorus sp.	Tardigrada indet.	Mylodontidae indet.	Scelidotheriinae	Lestodon cf. armatus	Megatherium cf. tarijense	Erethizontidae (Coendou sp.)
M. Sur												
F0					•							·
F1		·	•		•						•	
F2	•		•	·	•		•	·	•		·	
F3	·				•		·	•		•	·	
F4	·				·						•	
F4bis	·				•		•		·			
F4ter												
F7bis							·		•			
F8							·					
F9												
F10												
Rujero												
F1			•		•							
F2					•					·		
F3					•							
F4					•					•		
F5	·				•	•	·			•		

	Felidae indet.	Smilodon sp.	Canidae (large sized)	Tayassuidae (Platygonus ?)	Camelidae indet.	Lamini (Large sized)	Lama sp.	Palaeolama sp.	Cervidae indet.	Macrauchenia cf. patachonica	Equide indet.	Equidae (hippidiforms)	Equus sp.	Cuvieronius hyodon
M. Sur														
F0							·							
F1	·						·				·		•	•
F2		•	•		•		•	•	•		•		•	·
F3				·			•	•	•	·	·		•	•
F4											·	·	·	•
F4bis							·	·			•	·		•
F4ter					·	·	·	·		·	·	·	·	
F7bis					·	·		·		·	·			
F8						·								•
F9		·				·							•	•
F10												• ·		
Rujero														
F1														
F2					·									·
F3													·	·
F4							•	•					•	·
F5					•		•						•	•

The small circle means number of remains equal to 1 and the big circle greater than 1

logical constraints, Tarija correlates with the Bruhnes chron of the magnetostratigraphic scale. Based on the very high sedimentation rates, it is our opinion that the magnetic inversions recognized by MacFadden et al. (1983) in the lower part of the Tarija sequence might correspond to either one or both of the two short magnetic excursions (Laschamps and Mono Lake) recorded worldwide in Last Glacial sequences (Condomines 1978; Liddicoat and Coe 1979; Kent et al. 2002). Furthermore, problems of remagnetization of the sediments cannot be excluded.

Vertebrate paleontology

Monte Sur and Rujero are the richest fossiliferous sites among the eight ones we surveyed. Xenarthra, with four families and seven genera, represent almost half of the entire fauna at these sites, both in quantity and in diversity (Table 2; Fig. 3). Herbivores such as *Cuvieronius* (Proboscidea), *Glyptodon* (Xenarthra), *Equus* (Perissodactyla), and *Lama* (Artiodactyla) are common and abundant remains. Other taxa show a more limited distribution, either stratigraphically or geographically. Carnivores and micromammals (e.g. rodents) are indeed poorly represented due to taphonomic and ecological biases.

Eleven fossil beds have been distinguished at Monte Sur (Fig. 2a). We describe the fossil sequence from the stratigraphic base to the top. From level MS-F10 to MS-F2, there is an evident increase in the number of species represented in each fossil bed. This trend reverses from level MS-F1 to MS-F0 and diversity seems to decrease. At the family level, lower beds are dominated by equids (both *Equus* and hippidiforms), gomphotheriids, and camelids, whereas xenarthrans are rare to absent and only represented by undetermined tardigrades (ground sloths). From level MS-F4 upward, xenarthrans increase their diversity, with the appearance of dasypodids, glyptodontids, and megatherids, whereas among artiodactyls, there appear cervids and a tayassuid. At the genus level, it is interesting to note that upper levels (MS-F4bis to MS-F2) are characterized by the co-occurrence of *Glyptodon*, *Lama*, and *Equus*, whereas hippidiforms are not recorded. In contrast, *Glyptodon* and *Lama* are not recorded in lower levels where, in addition, hippidiforms are dominant over *Equus*. This pattern seems indicative of more arid conditions during the interval corresponding to levels MS-F4bis to MS-F2 of age slightly younger than 27 ka BP.

Level MS-F2 at Monte Sur is the richest in both number of species represented and fossil abundance. This level's fossil assemblage thus provides an excellent portrait of the faunal diversity at Tarija. Taxa recorded from MS-F2 are *Pampatherium* sp., *Glyptodon* cf. *reticulatus*, *Lestodon* cf. *armatus*, *Megatherium* cf. *tarijense*, *Smilodon* sp., Canidae

(large sized), *Lama* sp., *Palaeolama* sp., Cervidae, *Macrauchenia* cf. *patachonica*, *Equus* sp., and *Cuvieronius hyodon*. The occurrence of specialized grazers such as *Glyptodon*, *Lama*, and *Equus* suggests an open environment. On the other hand, *Macrauchenia*, deer, and *Cuvieronius* imply that trees and shrubs were also present. The giant ground-sloth *Lestodon* probably indicates local humid and marshy environments, although a recent morphofunctional study suggests a more grazing diet for this taxon (Bargo et al. 2006).

Stable isotope analyses

Preliminary results (Table 3) for *Equus*, which is present in nearly all the Monte Sur and Rujero successions (Fig. 4), indicate an overall depletion in mean $\delta^{18}Op$ at Monte Sur throughout the series, reaching the lowest $\delta^{18}Op$ value at level MS-F2 that could be associated with a decrease in mean temperatures towards the Last Glacial Maximum. Carbon isotopes show a general trend towards more positive $\delta^{13}C$ values throughout the sequence, with a main positive peak at level MS-F4bis (younger than 27 ka BP; Fig. 4), probably indicating a more arid phase. Similar reconstructions at Rujero, which is correlated to the central-upper part of the Monte Sur succession, confirm the trend with analogous variations.

The isotopic patterns obtained are consistent with those expected during the climatic shift from MIS 3 to MIS 2.

Systematic differences in the isotopic composition of both O and C between *Equus* and *Cuvieronius*, opposite to what previously reported from the same area (MacFadden 2000), have been observed and will be described elsewhere (Pellegrini et al., in preparation).

Discussion and conclusions

The Tarija–Padcaya sequence consists of Late Pleistocene glacial and fluvial deposits. Till and lateral moraines are found at the base of the sequence and, to a lesser extent, at the very top. They are interlayered with coarse-grained outwash sediments deposited during the glacier advances and retreat (MIS 4 and 2). This implies that the Bolivian Altiplano sustained an ice cap, contrary to previous climatic and paleoenvironmental reconstructions that indicated a dry environment.

At the base of the sequence, there are also alluvial fan deposits locally weathered to paleoalfisols and probably associated to the beginning of the Last Glaciation. The subsequent long sequence of meandering–wandering–anastomosing river sediments contains abundant mammalian fossils, peat layers, and organic horizons dated from 43 to
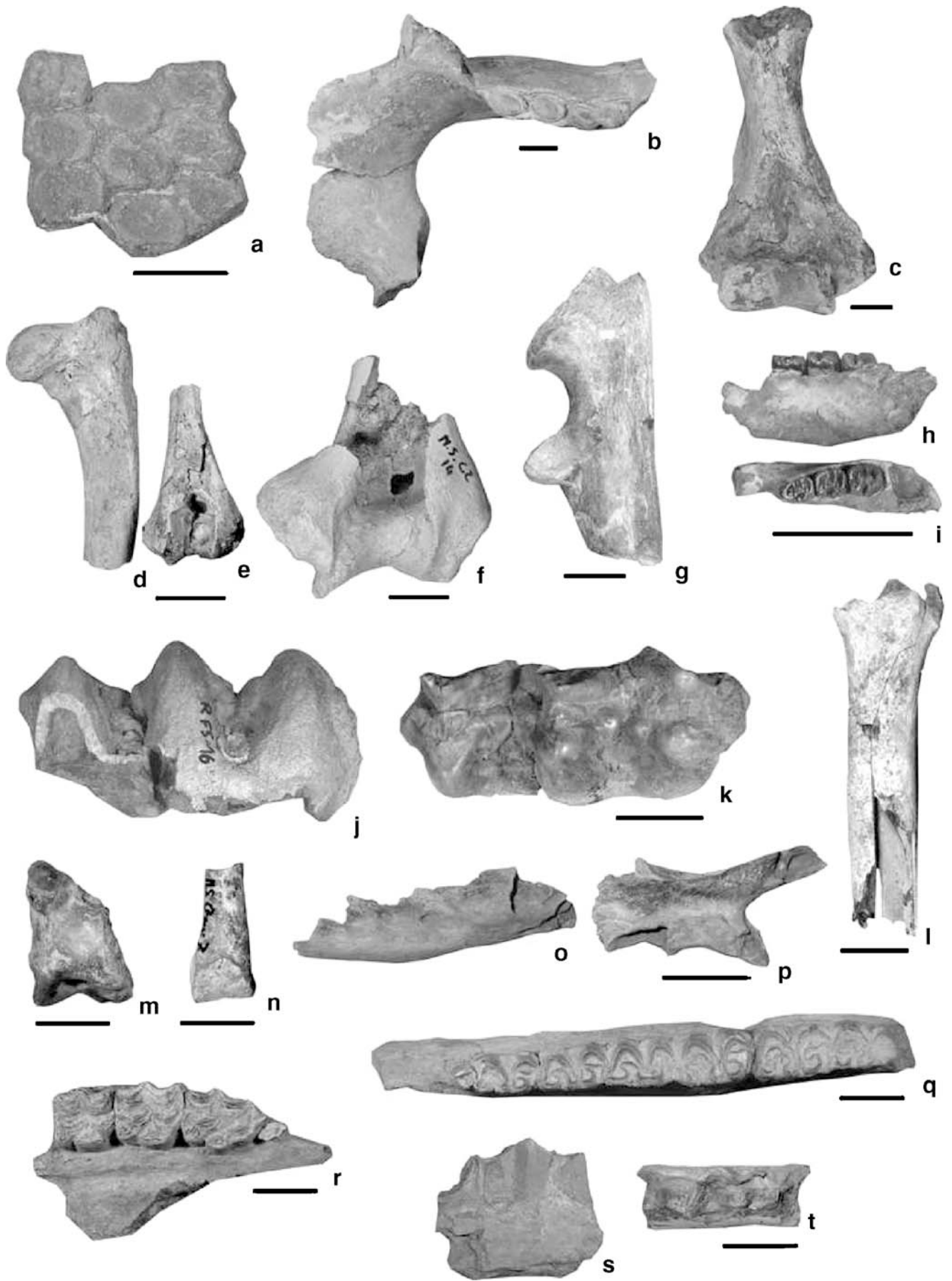
◄ Fig. 3 a R-F5-22 *Neotoracophorus*, dermal plates. **b** TOL2-5-7 *Lestodon*, mandible in occlusal view. **c** TOL2-5-10 *Glyptodon*, distal humerus. **d**, **e** MS-F2-16 Canidae (large form), proximal and distal humeri. **f** MS-F3-14 *Smilodon*, distal humerus. **g** MS-F2-13 *Smilodon*, proximal ulnae. **h**, **i** *Coendu*, right mandible in labial and occlusal views. **j**, **k** R-F5-16 *Cuvieronius*, molar in lateral and occlusal views. **l** MS-F4bis-10 *Lama*, tibia. **m** R-F2-10 *Paleolama*, astragalus. **n** MS-F7bis-7 Camelidae (large form), first phalanx. **o**, **p** MS-F3-d Tayassuidae, mandible in labial and occlusal views. **q** MS-F4-1b Equidae (hippidiform), mandible in occlusal view. **r** MS-F4bis-9 *Equus*, maxillary in occlusal view with incomplete dental series. **s**, **t** MS-F4t-1 *Macrauchenia* mandible with molar

21 ka BP. The analysis of the mammalian remains revealed a faunal change along the stratigraphic sequence. Differences in faunal composition between successive levels (e.g. relative abundance between *Equus* and hippidiforms) could be related to climatic changes. The occurrence of specialized grazers like *Glyptodon*, *Lama*, and *Equus* in the Monte Sur upper levels suggests the onset of more arid conditions after 27 ka BP. The isotopic data confirm a general cooling

and progressively more arid conditions from the base to the top of the sequence.

The new chronological data here presented prompts a revision of the biochronologic placement of the Tarija fauna. Specifically, *Macraucheniopsis*, *Megalonychops*, *Epieurycerus*, *Doedicuroides*, *Pithanotomys*, *Orthomyctera*, *Brachynasua*, and *Mesotherium*, taxa which are believed to have either last appeared in the Ensenadan faunal assemblages in South America or to have been restricted to it (Marshall et al. 1984; Tonni et al. 1992; Cione and Tonni 1995), are absent from the Tarija sequence. Conversely, the Tarija fauna, taken as a whole, shows closer similarity to the Argentinean Lujanian (i.e. Late Pleistocene) faunas, such as Mar del Plata, Santa Isabel, Arroyo Seco, Paso Otero, and Arroyo Napostá Grande (Deschamps and Tonni 1992; Prado et al. 1987; Stehli and Webb 1985; Tonni et al. 1992), than to typical Ensenadan one (e.g. Miramar; Stehli and Webb 1985). This is consistent with the new radiometric dating of the sedimentary succession here reported. Differences in the

Table 3 Results of δ^{13}C, δ^{18}Oc, and δ^{18}Op analyses in bioapatite for *Equus sp*

Site/Log	Specimen	Item	δ^{13}C‰ PDB-1	δ^{18}Oc‰ V-SMOW	δ^{18}Op‰ V-SMOW	Δ ^{18}Oc–^{18}Op	Calcul. water
Monte Sur	MS-F1-2	Bone	−3.6	25.6	15.2	10.3	−9.2
Monte Sur	MS-F1-5	Bone	−4.1	29.2	18.2	11	−5.2
Monte Sur	MS-F1-6	Bone	−7.8	27.7	17.0	10.7	−6.8
Monte Sur	MS-F2-1	Enamel	−3.3	26.5	16.3	10.3	−7.8
Monte Sur	MS-F2-2	Bone	−6.9	25.7	16.0	9.8	−8.2
Monte Sur	MS-F2-3	Bone	−5.4	25.9	16.3	9.6	−7.7
Monte Sur	MS-F2-2a	Bone	−7.3	26.6	16.7	9.9	−7.2
Monte Sur	MS-F2-3a	Bone	–	–	16.2	–	−8.0
Monte Sur	MS-F3-1	Bone	−6.4	26.5	16.8	9.7	−7.1
Monte Sur	MS-F3-3	Enamel	−3.2	29.5	19.3	10.2	−3.7
Monte Sur	MS-F4bis-1	Bone	–	–	16.6	–	−7.4
Monte Sur	MS-F4bis-2	Enamel	−2.1	29.2	18.7	10.5	−4.5
Monte Sur	MS-F7bis-1	Bone	−7.9	27.1	17.4	9.7	−6.3
Monte Sur	MS-F9-1	Bone	−5.0	28.4	17.9	10.5	−5.6
Monte Sur	MS-F9-2	Bone	−4.0	28.8	18.0	10.8	−5.4
Monte Sur	MS-F9-4	Enamel	−5.8	27.5	17.5	10	−6.2
Rujero	R-F2-1	Enamel	−4.2	28.2	18.3	9.9	−5.0
Rujero	R-F2-2	Enamel	−3.8	29.2	18.7	10.5	−4.5
Rujero	R-F3-1	Bone	−5.4	27.2	17.0	10.2	−6.9
Rujero	R-F4-1	Enamel	−7.6	27.2	16.2	11	−7.9
Rujero	R-F4-2	Bone	−6.6	26.7	16.9	9.8	−7.0
Rujero	R-F4-4	Enamel	−3.7	28.6	17.7	10.9	−5.9
Rujero	R-F4-5	Bone	−8.6	27.7	17.6	10.1	−6.0
Rujero	R-F4-7	Bone	−5.8	27.0	16.8	10.2	−7.1
Rujero	R-F4-8	Enamel	−4.3	30.5	19.7	10.8	−3.1
Rujero	R-F5-1	Bone	−4.1	29.4	17.4	11.9	−6.2
Rujero	R-F5-2	Bone	−4.3	29.7	18.5	11.2	−4.8
Rujero	R-F5-3	Bone	−4.1	29.1	17.4	11.7	−6.2
Rujero	R-F5-4	Enamel	−2.8	29.4	18.5	10.9	−4.8
Rujero	R-F5-5	Enamel	−3.1	28.7	18.0	10.6	−5.4

Water composition was calculated according to horse δ^{18}Op–δ^{18}Ow calibration proposed by Sanchez-Chillon et al. (1994).

Fig. 4 Isotopic variations with time at Monte Sur (**a** and **c**) and Rujero (**b** and **d**). Mean $\delta^{18}O_p$ (**a** and **b**) show a shift towards more negative values in the upper part of the two sequences that could be associated with the cooling stage of the Last Glacial Maximum (MIS 2), whereas $\delta^{13}C$ (**c** and **d**) show a more rough pattern with a humid stage at level F7bis and a more arid interval at level F4bis
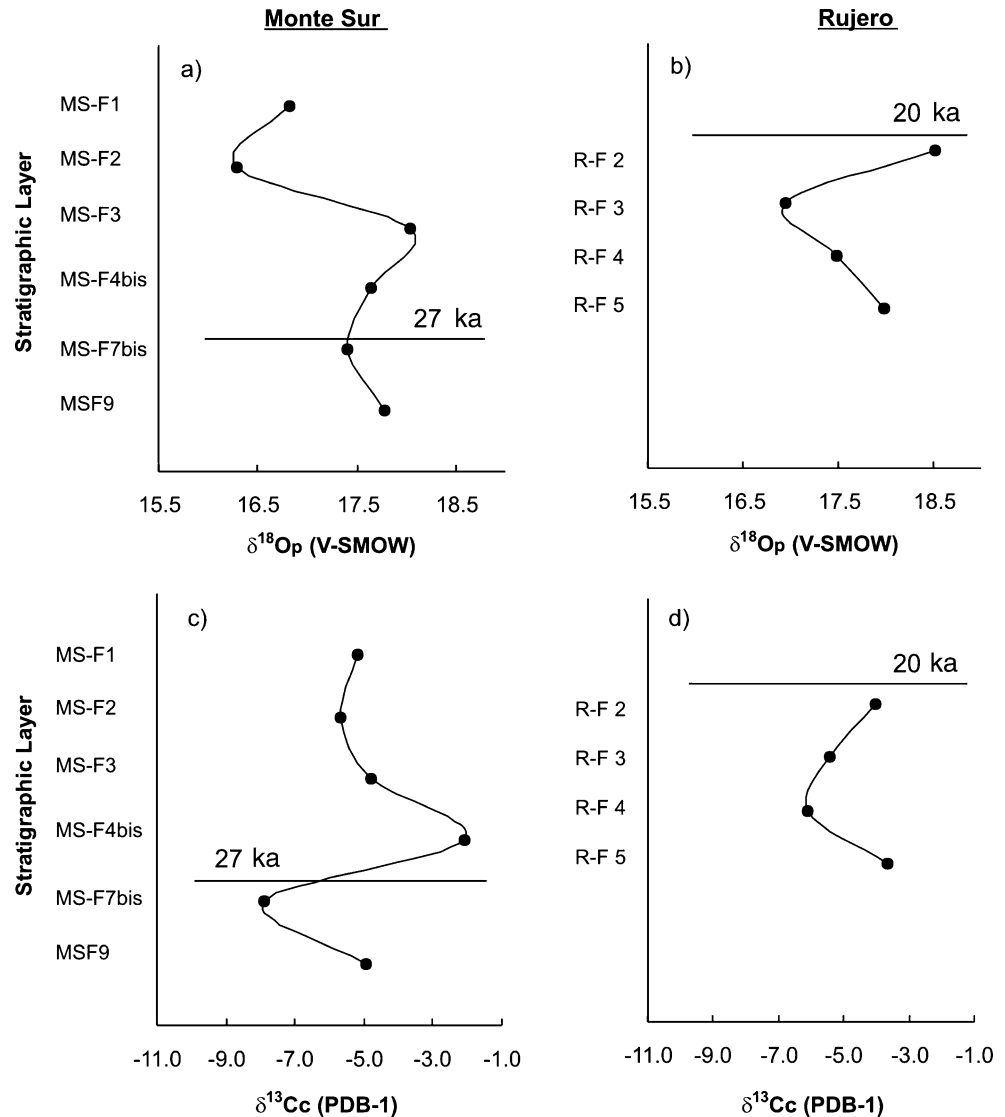
faunal composition between Tarija and other Lujanian localities should instead be interpreted as resulting from geographical and ecological factors. The extremely diversified Tarija fauna could indeed be the result of the peculiar geographic location of this basin, which is found at the edge of the Andean Altiplano and at the border with the Amazonian lowlands. Furthermore, when integrating previous studies by Hoffstetter (1963) and Marshall and Sempere (1991), the taxonomic composition of the Tarija mammal assemblage indicates a faunal link to both the southeastern plains (e.g. occurrence of *Toxodon*) and to the Andean highlands further north (e.g. occurrence of *Hippocamelus*, *Andinomys*, *Phyllotis*). As a whole, however, the fossil faunal association of Tarija shows a more marked similarity to the Andean bioprovince.

According to the new chronological and paleoenvironmental framework here proposed, the Tarija–Padcaya Basin is one of the most promising areas for the study of faunal evolution in the Andean highlands during the Last Glacial Stage. In particular, the possibility of a detailed analysis of faunal and environmental change at Tarija is offering a unique chance to understand the ecological dynamics at work in the Central Andean Altiplano at the onset of end-Pleistocene megafaunal extinction.

References

Argollo J, Mourguiart P (2000) Late Quaternary climate history of the Bolivian Altiplano. Quat Int 72:37–51

Bargo MS, Toledo N, Vizcaino SF (2006) Muzzle of South American Pleistocene Sloths (Xenarthra, Tardigrada). J Morphol 267: 248–263

Cione AL, Tonni EP (1995) Chronostratigraphy and "Land-Mammal Ages" in the Cenozoic of Southern South America: principles, practices, and the "Uquian" problem. J Paleontol 69:135–159

Cione AL, Tonni EP (1999) Biostratigraphy and chronological scale of Uppermost Cenozoic in Pampean area, Argentina. In: Tonni EP, Cione AL (eds) Quaternary of South America and Antarctic Peninsula. Quat South Am Antarct Penins 12:23–51

Clapperton CM (1993) Quaternary geology and geomorphology. Elsevier Science, Amsterdam

Clapperton CM, Clayton JD, Benn DI, Marden CJ, Argollo J (1997) Late Quaternary advances and paleolakes highstands in the Bolivian Altiplano. Quat Int 38/39:49–59

Condomines M (1978) Age of the Olby–Laschamp geomagnetic polarity event. Nature 276:257–258

Crowson RA, Showers WJ, Wright EK, Hoering TC (1991) Preparation of phosphate samples for oxygen isotope analysis. Anal Chem 63:2379–2400

D'Agostino K, Seltzer GO, Baker PA, Fritz SC, Dunbar RB (2002) Late-Quaternary lowstands of Lake Titicaca: evidence from high resolution seismic data. Palaeogeogr Palaeoclimatol Palaeoecol 179:97–111

Deschamps CM, Tonni EP (1992) Los vertebrados del Pleistoceno Tardio–Holoceno del Arroyo Napostá Grande, Provincia de Buenos Aires. Aspectos paleoambientales. Ameghiniana 29:201–210

Fornari M, Risacher F, Feraud G (2001) Dating of paleolakes in the Central Altiplano of Bolivia. Palaeogeogr Palaeoclimatol Palaeoecol 172:269–282

Hoffstetter R (1963) La faune Pléistocène de Tarija (Bolivie). Note préliminaire. Bull Mus Natl Hist Nat Paris 35:194–203

Kent D, Hamming S, Turrin B (2002) Laschamp excursion at Mono Lake? Earth plan. Sci Lett 197:151–164

Lee Thorp J, Van der Merwe NJ (1987) Carbon isotope analysis of fossil bone apatite. S Afr J Sci 83:712–715

Liddicoat JC, Coe RS (1979) Mono Lake geomagnetic excursion. Geophys J Int 84:261–271

Longinelli A (1984) Oxygen isotopes in mammal bone phosphate—a new tool for paleohydrological and paleoclimatological research. Geochim Cosmochim Acta 48:385–390

MacFadden BJ (2000) Middle Pleistocene climate change recorded in fossil mammal teeth from Tarija, Bolivia, and upper limit of the Ensenadan land-mammal age. Quat Res 54:121–131

MacFadden BJ, Siles O, Zeitler P, Johnson NM, Campbell KE (1983) Magnetic polarity stratigraphy of the Middle Pleistocene (Ensenadan) Tarija Formation of Southern Bolivia. Quat Res 19:172–187

Marshall LG, Sempere T (1991) Fosiles y Facies de Bolivia, 1: Vertebrados. Rev Tec Yacim Pet Fisc Boliv 12:631–652

Marshall LG, Berta A, Hoffstetter R, Pascual R, Reig O, Bombin M, Mones A (1984) Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. Palaeovertebrata, Mémoire Extraordinaire:1–76

Miall AD (1985) Architectural element analysis: a new method of facies analysis applied to fluvial deposits. Earth Sci Rev 22: 261–308

Miall AD (1990) Principles of sedimentary basin analysis, 2nd edn. Springer, Berlin Heidelberg New York

Miall AD (1996) The geology of fluvial deposits. Springer, Berlin Heidelberg New York

Mourguiart P, Argollo J, Corrége T, Martin L, Montenegro ME, Sifeddine A, Wirrmann D (1997) Changements limnnologiques et climatologiques dans le basin du lac Titicaca (Bolivia), depuis 30.000 ans. Compte Rendu Academie de Science de la terre et des planets 325:139–146

Prado JL, Menegaz AN, Tonni EP, Salemme MC (1987) Los mamiferos de la fauna local Paso Otero (Pleistoceno Tardio), Provincia de Buenos Aires. Aspectos paleoambientales y bio-estratigraficos. Ameghiniana 24:217–233

Sanchez-Chillon B, Alberdi MT, Leone G, Bonadonna FP, Stenni B, Longinelli A (1994) Oxygen isotopic composition of fossil equid tooth and bone phosphate—an archive of difficult interpretation. Palaeogeogr Palaeoclimatol Palaeoecol 107:317–328

Stehli FG, Webb SD (1985) The Great American biotic interchange. Plenum, New York

Sullivan CH, Krueger HW (1981) Carbon isotope analysis of separate chemical-phases in modern and fossil bone. Nature 292:333–335

Takai F, Mizuno T, Iwasaki Y, Tanaka K, Yoshida A (1982) Tarija mammal-bearing formation in Bolivia. Res Inst Evol Biol Tokyo 3:1–72

Takai F, Arozqueta B, Mizuno T, Yoshida A, Kondo H (1984) On fossil mammals from the Tarija Department, Southern Bolivia. The research Institute of Evolutionary Biology. Tokyo, 4:1–63

Tonni EP, Alberdi MT, Prado JL, Bargo MS, Cione AL (1992) Changes of mammal assemblages in the Pampean region (Argentina) and their relation with the Plio-Pleistocene boundary. Palaeogeogr Palaeoclimatol Palaeoecol 95:179–194

Zazzo A, Lecuyer C, Sheppard SMF, Grandjean P, Mariotti A (2004) Diagenesis and the reconstruction of paleoenvironments: a method to restore original $\delta^{18}O$ values of carbonate and phosphate from fossil tooth enamel. Geochim Cosmochim Acta 68(10):2245–2258