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Biochronology and biostratigraphy of the Uquía Formation (Pliocene–early Pleistocene, NW Argentina) and its significance in the Great American Biotic Interchange

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Abstract

The Uquía Formation crops out in the Quebrada de Humahuaca in Jujuy province, Eastern Cordillera, NW Argentina. This unit is composed of a sequence of fluviatile sediments and water-laid air-fall tuff beds; it is approximately 260 m thick and unconformably overlain by Pleistocene conglomerates and Quaternary alluvium. The sediments have been folded into a syncline and broken by several faults that generally trend northwest–southeast. Following Castellanos stratigraphy, we characterize three units (Lower, Middle, and Upper) of the Uquía Formation. Biochronologically, the Lower Unit is assigned to the late Chapadmalalan, the Middle Unit (''Uquian fauna'') to the late Vorohuean and Sanandresian, and the Upper Unit to the Ensenadan. Biostratigraphic evidence provides a calibration of important biochronologic events in the Great American Biotic Interchange (GABI), namely, the first appearances of *Erethizon*, *Hippidion*, and proboscideans at 2.5 Ma (late Pliocene) in South America. Geological and paleobiological evidence suggest that during the late Pliocene, the area could have been a wide intermountain valley at 1400–1700 m elevation, with a more humid environment than that of the present day and some wet–dry seasonality that permitted the coexistence of forest and open areas. Uquian mammals also indicate that northwestern Argentina and the Pampean region have represented distinct biogeographical areas since at least the late Pliocene.

Resumen

La Formación Uquía aflora en la Quebrada de Humahuaca en la provincia de Jujuy, Cordillera Oriental, NO de Argentina. Esta unidad está compuesta de una secuencia de sedimentos fluviales y tobáceos; tiene aproximadamente 260 m de espesor e infrayace discordantemente a una unidad conglomerádica pleistocénica y aluviones cuaternarios. Siguiendo la estratigrafía de Castellanos hemos caracterizado las tres unidades en que subdividió a la Formación Uquía (Inferior, Media y Superior). Biocronológicamente, la Unidad Inferior es asignada al Chapadmalalense tardío, la Unidad Media (''Fauna Uquiense'') a las Edades Vorohuense y Sanandresense, y la Unidad Superior a la Edad Ensenadense. Las evidencias bioestratigráficas proveen una calibración de importantes eventos biocronológicos relacionados con el Gran Intercambio Biótico Americano: la primera aparición de *Erethizon*, *Hippidion* y proboscideos aproximadamente en los 2.5 Ma (Plioceno tardío) en América del Sur. Las evidencias geológicas y paleobiológicas sugieren que durante el Plioceno tardío el área pudo haber estado formada por un amplio valle intermontano a ~1400–1700 m de elevación y dominada por un ambiente más húmedo que el de hoy, probablemente con una estacionalidad húmedo/seca, que permitió la coexistencia de bosques y áreas más abiertas. Los mamíferos uquienses también indican que el Noroeste de Argentina y la región Pampeana representan áreas biogeográficas distintas al menos desde el Plioceno tardío.

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1. Introduction

The isolation and faunal endemism of South America changed dramatically after the establishment of the Panamanian land bridge and the corresponding immigration of taxa from North America during the late Cenozoic, resulting in what has been termed the Great American Biotic Interchange (GABI) (Marshall et al., 1979). This event occurred in several phases, beginning in the late Miocene at approximately 8–9 Ma, but the major phase of mammalian dispersal occurred during the Pliocene and Pleistocene, during the Uquian, Ensenadan, and Lujanian ages. These biochrons are relatively well calibrated at certain classic localities of the Atlantic coast of Buenos Aires (Tonni et al., 1992; Cione and Tonni, 1995; Tonni and Cione, 2001), but knowledge of this event in the northwestern part of Argentina is still poorly understood, and the "Uquian problem," as envisioned by Cione and Tonni (1995), remains unresolved. Important collections of vertebrates, age determinations, and magnetostratigraphy were made in other localities of NW Argentina (Chiquimil, Andalhuala, and Corral Quemado formations in Catamarca province) (Marshall et al., 1979; Marshall and Patterson, 1981), but they calibrated only the early phase of the GABI (Huayquerian–Montehermosan ages).

The deposits of the Uquía Formation crop out in the vicinities of Chucalesna, Esquina Blanca, and San Roque (Fig. 1) at an elevation of approximately 2800 m.a.s.l., and have produced, since 1912, a very interesting and controversial record of vertebrates that document major events of the GABI in South America during the Pliocene and early Pleistocene. However, the stratigraphy and paleontology of this unit are little known and remain obscure compared with other areas of South America, such as the Atlantic coast of Buenos Aires province, Argentina. In general, the Pliocene/Pleistocene vertebrate faunas from northwestern Argentina are not well represented or studied; even those from high elevations are rare throughout South America in general. MacFadden et al. (1994) report three high-elevation localities in the Eastern Cordillera that yield Pliocene and Pleistocene fossils in Bolivia: Viscachani, Inchasi (Pliocene), and Tarija (Pleistocene). The relationships of these faunas with the Uquian have not been studied previously.

This article reports the results of work that began effectively in 1980 but intensified in the past 10 years by various Argentinean workers studying the geology, stratigraphy, and vertebrate paleontology of late Cenozoic strata in NW Argentina. These joint efforts culminated in the field seasons of 1986, 1996, 1998, and 2002, when paleontologic and paleomagnetic sampling resulted in the biochronology and biostratigraphy proposed here and the present interpretation of the Pliocene/early Pleistocene of these strata.

Historically, the Uquía Formation played a central role in the calibration of the Uquian South American Land Mammal Age (SALMA) (Marshall et al., 1984). The dating of these faunas was addressed as early as 1982 by Marshall, Butler, Drake, and Curtis in their pioneering work on the age calibration of South American mammalian faunas. These authors published $^{40}K/^{40}Ar$ dates from two tuffaceous horizons in the Uquía Formation at Chucalesna and Esquina Blanca. These ages were the first numerical

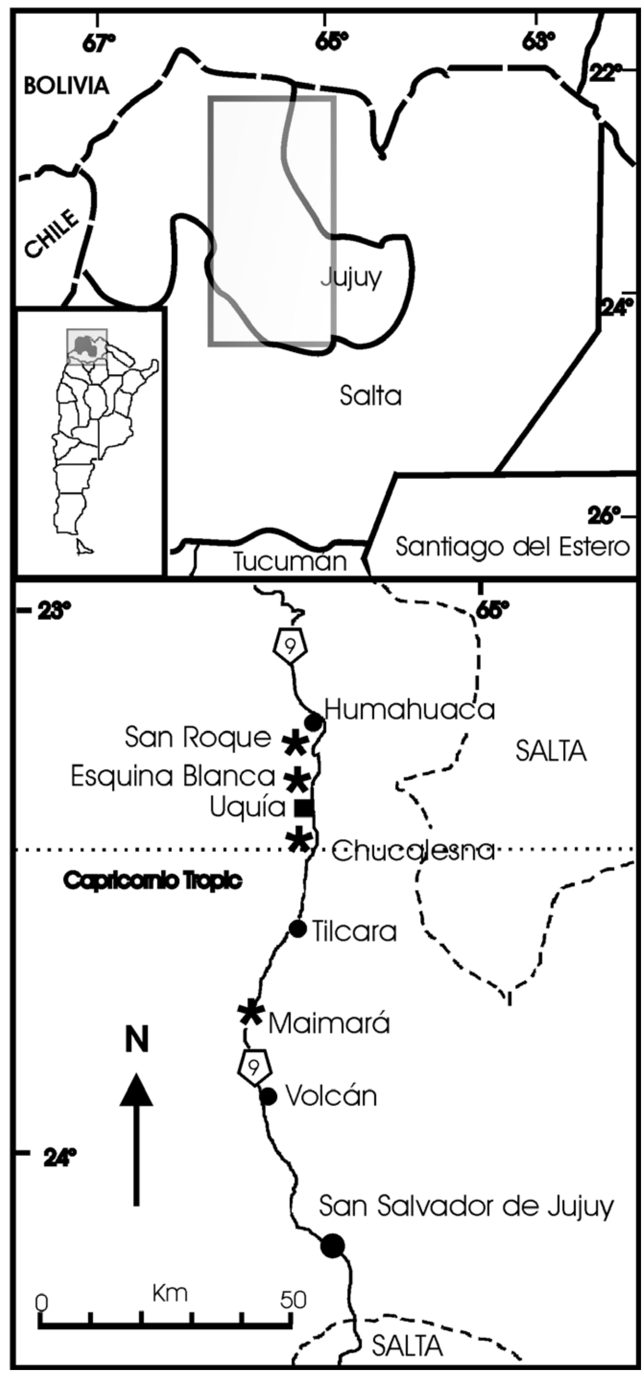

Fig. 1. General location of the Quebrada de Humahuaca area, Jujuy province, and detailed location of fossil-bearing localities (∗) discussed herein.

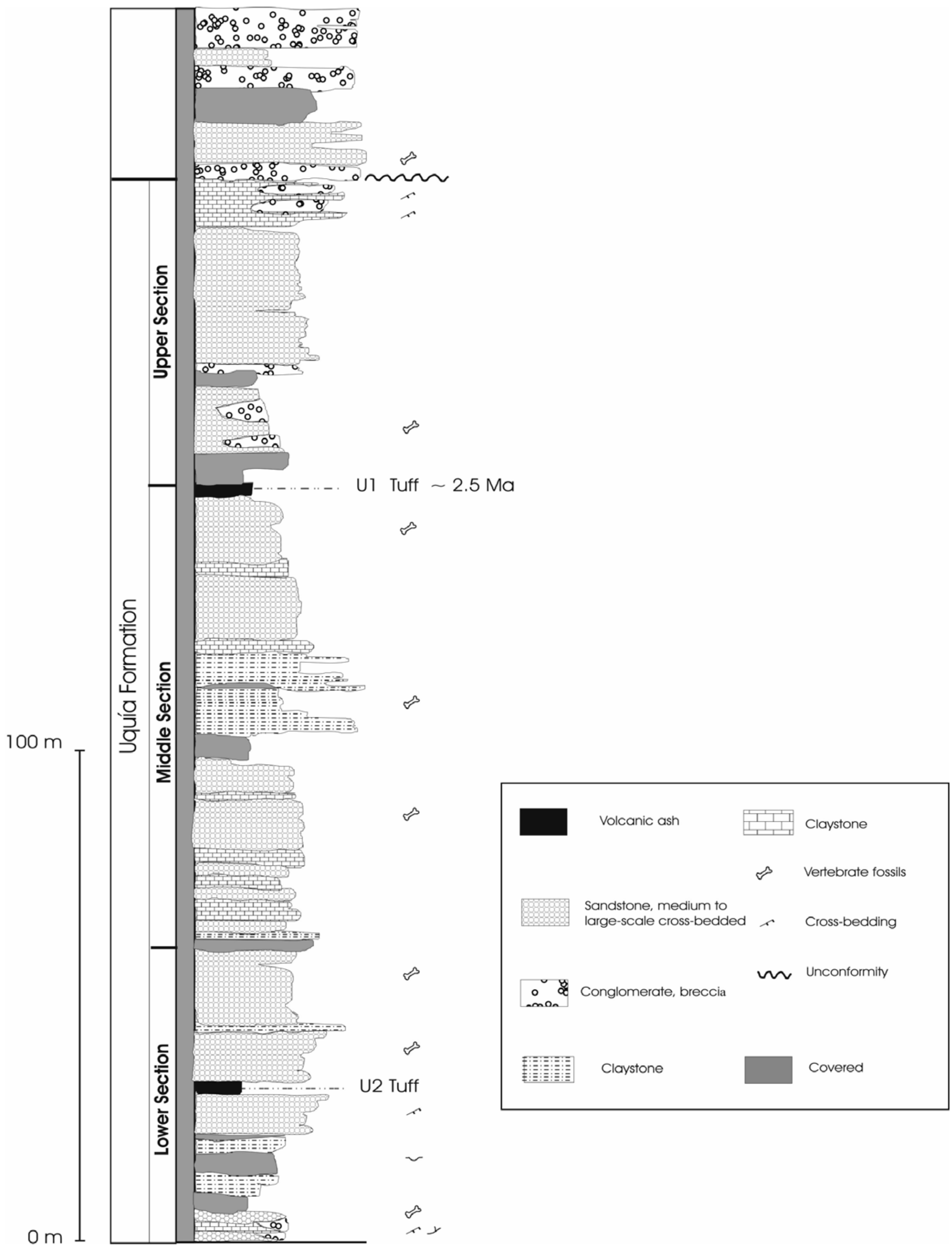

Fig. 2. Generalized stratigraphic column (stratotype) for Esquina Blanca, showing the vertebrate-bearing horizons. Radiometric ages from Walther et al. (1998). The "Dacitic Tuff" is not indicated in this column (see text).

calibration points for fossils from the Uquía Formation. The authors showed that the type section, designated by them at Esquina Blanca (Fig. 2), for the Uquian age ranges from the late Gauss to middle Matuyama, or about 2.5–1.5 Ma. Marshall et al. (1982, p. 987) state that Esquina Blanca is "the most richly fossiliferous and stratigraphically the thickest section of known Uquian beds in this area." These authors redefined the Uquian SALMA exclusively on the basis of fossil data reviewed by Castellanos (1950, 1953).

Cione and Tonni (1995, pp. 139–40) criticized the validity of the Uquian SALMA because "the Uquía Formation is not adequately fossiliferous (it is especially poor in terms of microvertebrates) and is folded and faulted and has no clear stratigraphic relationships with other fossiliferous units. Consequently, the Uquía Formation lacks a section that is adequate as stratotype of a chronostratigraphic unit.'' In turn, these authors proposed a new chronostratigraphic/geochronologic unit, the Marplatan, with three subages: Barrancalobian, Vorohuean, and Sanandresian, which are well represented by fossil faunas in the Atlantic coast of Buenos Aires province. In their contribution, the authors summarized data on the most productive and one of the most important fossil mammal-bearing sequences of the late Cenozoic of Argentina. The stage/age Marplatan is probably correlated with the Gauss and the lower Matuyama chrons (Cione and Tonni, 1995).

More than 90 years after the explorations of the naturalist Enrique de Carles, we know little about the evolution of the Miocene, Pliocene, and Pleistocene faunas in NW Argentina. The classical sequences at Chiquimil and Corral Quemado, Catamarca province, NW Argentina, which contain Huayquerian and Montehermosan faunas in superposition, have produced both radioisotopic dates and magnetostratigraphies spanning continuously from approximately Chron C4An to Chron C2Ar (Flynn and Swisher, 1995). The biogeographic and biochronologic significance of these faunas have been overshadowed by other projects and works carried out in the Atlantic coast during the last part of the twentieth century.

The aims of this study are to (1) systematically review the vertebrates from the Uquía Formation and report the first record of the porcupine *Erethizon* in South America; (2) provide a biostratigraphy of the Uquía Formation, based on its fossils and previous geochronologic data, in its type area (Esquina Blanca); (3) analyze the paleoecology of the Uquian fauna and the paleoenvironment; and (4) explore the biogeographic significance of the Uquian mammals and their importance in the history of the GABI.

The abbreviations used herein are as follows: MACN, Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia,'' Buenos Aires; MLP, Museo de La Plata; PVL, Instituto Miguel Lillo, Tucumán; FAD, first appearance datum; Ma, megannum; and GPTS, Magnetic Polarity Time Scale.

2. Historical background

In the early part of the twentieth century, the naturalist Enrique de Carles, commissioned by the authorities of the Museo de Historia Natural de Buenos Aires (MACN), explored several outcrops located in the Quebrada de Humahuaca, Jujuy province.

De Carles (1912) and Castellanos (1950) noted the presence of locally abundant fossil mammals in the outcrops of the Uquía Formation at Esquina Blanca. Description of the fauna of this unit began with the announcement of the discovery of fossil mammals (De Carles, 1912) and preliminary descriptions of some new forms (Castellanos, 1927; Rusconi, 1930; Kraglievich, 1934), as well as a review of the fauna as a whole by Castellanos (1950). Thereafter, descriptions centered on other specific taxa (Prado et al., 1998; López et al., 2002).

Several authors have discussed the age of the mammals from the Uquía Formation (Kraglievich, 1934; Castellanos, 1950, 1953; Marshall et al., 1982, 1984; Cione and Tonni, 1995; Walther et al., 1998).

Castellanos (1950) informally subdivided the Uquía Formation into three units (Secciones of Castellanos), characterizing them by stratigraphic differences and a basal distinctive tuff (''Toba Dacítica'' or ''Dacitic Tuff''); he did not establish formal limits among his three subdivisions and never figured them in any paper. He pointed out that, on the basis of the fossils collected by de Carles in 1912, and de Carles and himself in 1921–22, the ''Piso Uquiense'' (''Uquian SALMA'') should be correlated with the lower and middle units of the Uquía Formation. Kraglievich (1934), on the basis of fossils collected by de Carles and Castellanos, differentiated two faunistic assemblages and assigned them, from older to younger, to the Uquian and Ensenadan, respectively. Simpson (1940) cautioned that the Uquian fauna seemed to represent more than one age and that a single fauna, of an intermediate age (Uquian) was not demonstrated.

Pascual et al. (1965) pointed out that the Uquian SALMA is recognized ''on theoretical inferences not based on unquestionable mammal evidence from Uquía.''

3. Materials and methods

3.1. Collections

More than 200 fossil vertebrates have been collected in different expeditions since that of de Carles from the horizons from the Esquina Blanca and San Roque units. Approximately two-thirds of these fossils belong to the ''old collection,'' collected by de Carles and Castellanos at Esquina Blanca, and are housed in MACN. Most were identified to the genus and species level, though in some cases, the preservation of the specimens does not allow identification at these levels. Descriptions of these specimens were published by Castellanos (1927, 1950, 1953), Rusconi (1930), Kraglievich (1934), Mones (1991), Walther et al. (1996), and Prado et al. (2001). The identifications of the vertebrates from the Uquía Formation appear in Table 1. The most abundant forms are *Ctenomys*, *Hippidion*, and *Platygonus* (Table 2).

De Carles collected most of the fossils of the old collection at Esquina Blanca in 1912, but he did not provide any stratigraphic information for these fossils. Despite the lack of precise field data for the old collection, some constraints can be placed on many of the specimens based on information provided by Castellanos (1950, 1953) and our knowledge of the general field areas. Several lines of evidence suggest that most fossils from the old collection probably come from the Middle Unit of Castellanos (1953): (1) at Esquina Blanca, the Middle Unit is the most fossiliferous of the three units of the sequence, and it has the maximum thickness (approximately 145 m); with one exception, all the species

Table 1
List of the mammals from the Uquía Formation, Jujuy province, Argentina, and their stratigraphic ranges in Argentina/South America

- Order Proboscidea Illiger, 1929
  - Family †Gomphotheriidae Cabrera, 1929
    - Gen. et sp. indet. VO-SA
- Order Artiodactyla Owen, 1848
  - Family Tayassuidae Palmer, 1821
    - *Platygonus uquiensis* VO-SA
  - Family Camelidae Gray, 1821
    - *cf. Palaeolama* EN
  - Family CERVIDAE Gray, 1821
    - Gen. et sp. indet. EN
- Order Perissodactyla Owen, 1848
  - Family Equidae Gray, 1821
    - *Hippidion devillei* VO-SA-EN
- Order †Litopterna Ameghino, 1889
  - Family Macraucheniidae Gill, 1872
    - *Windhausenia delacroixi* VO-SA
    - *Pseudomacrauchenia yepesi* EN
    - *Macrauchenia patachonica* LU
- Order Rodentia Bowdich, 1821
  - Family Octodontidae Waterhouse, 1839
    - *Ctenomys chapadmalensis* VO-SA
    - Ctenomyinae new taxon VO-SA
  - Family Caviidae Waterhouse, 1839
    - *Microcavia* CH-R
  - Family Erethizontidae Thomas, 1897
    - *Erethizon* VO-SA
  - Family Hydrochoeridae Gill, 1872
    - *Hydrochoeropsis dasseni* VO-SA
- Order Edentata Cuvier, 1798
  - Infraorder PILOSA Flower, 1883
    - Family †Megatheriidae Owen, 1843
      - *Megatherium? uquiensis* VO-SA
      - *Pyramiodontherium? carlesi* VO-SA
    - Family †Mylodontidae Gill, 1872
      - Mylodontidae, indeterminate
      - *Scelidotherium* EN-LU
      - *Scelidotheridium* CH-VO-SA
      - *Lestodon? castellanosi* VO-SA
    - Family †Megalonychidae Zittel, 1982
      - *Sinhapalops jujuyensis* VO-SA
  - Infraorder Cingulata Illinger, 1811
    - Family †Glyptodontidae Burmeister, 1879
      - *Glyptodon* EN-LU
      - *Paraglyptodon uquiensis* CH-VO-SA
      - *Panochthus?* VO-SA
      - *Urotherium* HU-VO-SA
      - *Xiphuroides uquiensis* VO-SA
      - *Neuryurus?* sp. EN
      - Sclerocalyptinae, indeterminant
      - Doedicurinae, indeterminant
    - Family †Pampatheriidae Paula Couto, 1954
      - *Plaina* MO-CH
    - Family Dasypodidae Bonaparte, 1838
      - *Doellotatus chapadmalensis* HU-CH
      - *Chaetophractus cf. villosus* CH-R
      - Euphractinae, indeterminate

Abbreviations: HU, Huayquerian; CH, Chapadmalalan; SA, Sanandresian; EN, Ensenadan; LU, Lujanian; MA, Marplatan; MO, Montehermosan; R, Recent. †Extinct order or family.

Table 2
Abundance of different vertebrate taxa for Uquía Formation

Identification	#Specimens	%
Hippidion devillei	10	12
Platygonus uquiensis	10	12
Ctenomys chapadmalensis	10	12
Pseudomacrauchenia yepesi	8	9.5
Windhausenia delacroixi	8	9.5
Paraglyptodon uquiensis	6	7.1
Urotherium sp.	3	3.6
Plaina sp.	3	3.6
Neuryurus sp.	2	2.4
Panochthus?	2	2.4
cf. Palaeolama	2	2.4
Glyptodon sp.	2	2.4
Hydrochoeropsis dasseni	2	2.4
Chaetophractus cf. villosus	2	2.4
Doellotatus chapadmalensis	2	2.4
Chaetophractus cf. villosus	2	2.4
Xiphuroides uquiensis	1	1.2
Erethizon sp.	1	1.2
Microcavia sp.	1	1.2
Gomphotheriidae?	1	1.2
Scelidotherium sp.	1	1.2
Scelidotheridium sp.	1	1.2
Lestodon? castellanosi	1	1.2
Sinhapalops jujuyensis	1	1.2
Pyramiodontherium? carlesi	1	1.2
Megatherium? uquiensis	1	1.2

identified by de Carles and Castellanos come from the Middle Unit (Castellanos, 1950, 1953; Marshall et al., 1982); (2) only one species (*Pseudomacrauchenia yepesi*) is known from the Upper Unit (Castellanos, 1950); and (3) at Esquina Blanca, none of the specimens from the old collection pertain to species recorded in the Lower Unit of the Uquía Formation (Castellanos, 1950). Specimens from the Lower Unit come only from the new collections (PVL, MLP).

Fossil vertebrates are relatively abundant in the sequence. The principal two fossiliferous horizons are located in the middle two-thirds of the Uquía Formation, beneath the U1 Tuff (Fig. 2) of Walther et al. (1998). The fossils are usually isolated, often occurring as fragmentary dentitions and postcranial elements dispersed randomly within the sequence.

3.2. Geochronology

As mentioned previously, the Uquía Formation contains at least three volcanic tuffs (“Dacitic Tuff” of Castellanos, 1953; U1 and U2 tuffs of Walther et al., 1998) that are amenable to isotopic dating. Isotopic ages determined for some volcanic units interbedded with strata in the Chucalesna and Esquina Blanca (situated about 4 km from each other) sequences provide important calibration points for the Uquía Formation and outline its general age parameters. Marshall et al. (1982) sampled the Dacitic Tuff, the stratigraphically lowest tuff to be dated, in Chucalesna (#LGM 205) and Esquina Blanca (#LGM 202). These authors report four ^{40}K–^{40}Ar age determinations from the same horizon from Chucalesna (#LGM 205); however, they consider only two of them (KA 3835R, 2.86 ± 0.08 and KA 3836, 2.78 ± 0.09 Ma) because they "appear to be reliable estimates of the age of this tuff" (Marshall et al., 1982, p. 987). Three ^{40}K–^{40}Ar analyses on glass separates from the Dacitic Tuff (#LGM 205) yield ages of 3.29 ± 0.10 (KA 3835), 2.86 ± 0.08 (KA 3835R), and 3.40 ± 0.04 Ma (KA 3835R2, see Marshall et al., 1982). The two older determinations were dismissed by Marshall et al. (1982) as anomalously old, due to possible contamination, despite their similar ages. On the basis of those determinations, we consider that the most statistically reliable estimate of the age of the Dacitic Tuff at Chucalesna should be an average of these four glass and biotite determinations, or 2.9766 ± 0.073 Ma (∼3.0 Ma), older than the 2.82 Ma date proposed by Marshall et al. (1982). In addition, the Dacitic Tuff (#LGM 202) at Esquina Blanca was dated by the same authors at 3.54 ± 0.04 Ma, which is also more consistent with older dates from Chucalesna than the younger ones. Interestingly, these isotopic ages of the Dacitic Tuff are slightly older than the ^{40}Ar/^{39}Ar age determination of 2.896 ± 0.006 Ma for the Ayo Ayo Tuff (Marshall et al., 1992) at the top of the Umala Formation at Viscachani, Bolivia, which overlies a fauna of Chapadmalalan age (including, for correlation, Inchasi fauna, MacFadden et al., 1993).

Recently, Walther et al. (1998) determined two fission-track ages on zircon of 2.5 Ma from the U1 Tuff, approximately 180 m above the local base, and the U2 Tuff (date not reported), at approximately 30 m, which overlie the Dacitic Tuff at Esquina Blanca (Fig. 2).

To determine the paleomagnetic characteristics of the sediments of the Uquía Formation, Walther et al. (1996, 1998) sampled 48 paleomagnetic sites at San Roque and 29 at Esquina Blanca. These authors establish that the sequence spans from early Matuyama (Chron C2r) to late Gauss (Chron C2A) ages. The correlation presented by Walther et al. (1996, 1998) is partially consistent with the magnetostratigraphic results of Marshall et al. (1982), who found that the Uquía Formation is dominantly reversed and correlates to the early Matuyama chron between about 2.5 and 1.5 Ma. Walther et al. (1996) point out that the magnetostratigraphy of the Uquía Formation suggests two lines of interpretations: (1) the sequence correlates to the early Matuyama/late Gauss age and (2) the middle section of the sequence, of reversed polarity, is of Matuyama age. The older subzone of normal polarity correlates with the Olduvai event and the younger with the Jaramillo event. The upper section of normal polarity correlates with Brunhes. On the basis of biochronologic data obtained from the mammals of this sequence, these authors prefer the former interpretation.

4. Eastern Cordillera: tectonic history and paleoelevations

The Uquía Formation is located in the southern part of the Eastern Cordillera. In Argentina, the Eastern Cordillera is situated to the northwest (Fig. 3) between 22°05′ and 27°00′S and 64°40′ and 66°10′W; it represents the southern extremity of the same mountain range known from Bolivia and southern Perú. The Eastern Cordillera is generally defined as a large area of moderate relief and internal drainage in the highlands of the central Andes; it is an inactive fold-and-thrust belt. The ranges and intermontane valleys of the Eastern Cordillera bound the Altiplano to the east and the Subandean fold-and-thrust belt to the west (Fig. 3).

In a wider context, geological and geophysical evidence indicates that the principal phase of Andean uplift occurred during the late Cenozoic. However, it is difficult to estimate precisely the elevation of the Eastern Cordillera at a given time, though it seems the mountain belt had attained at least half its present elevation of approximately 4000 m prior to 15 Ma (Alpers and Brimhall, 1988). Benjamin et al. (1987) estimate, using fission-track analysis, that the uplift of Eastern Cordillera in Bolivia accelerated during the late Cenozoic from rates of 0.1–0.2 mm/yr during the middle Miocene to as much as 0.7 mm/yr during the Quaternary. It is almost certain that the paleoelevation of the Uquía area, with its current elevation of 2800 m, would have been lower in the Pliocene. Using the uplift rates of Benjamin et al. (1987), we can estimate that the Uquía area was 1400–1700 m at the time of deposition; however, it might have been lower, considering the interpretation of the environment and the composition of the fauna. This paleoelevation is consistent with estimates of other paleofaunas and paleofloras from the Eastern Cordillera (MacFadden et al., 1994; Gregory-Wodzicky, 2000; Graham et al., 2001) (Table 3). The paleoelevation of the Uquian fauna is also consistent with paleoelevations estimated using other paleoaltimeters. Kennan et al. (1997) estimate that remnants of the 10 Ma erosion surface that caps the Eastern Cordillera formed at an elevation of 1000–1500 m.

Jordan and Alonso (1987) note that in the northern Altiplano during the late Cenozoic, tectonic subsidence permitted sediment accumulation between the magnetically thickened centers, producing localized basins at high elevations. The Pliocene phase of the Andean Orogeny (so-called Diaguita phase or "Movimiento T-IV" of Yrigoyen, 1979) resulted in the elevation of the Andes and the oriental orographic system, among other events. After the Diaguita diastrophic phase began in the NW of Argentina, a distinct sedimentary regime along the north-south directed intermontane valleys between the orographic ranges compounded by the Puna–Eastern Cordillera and Subandean belts system to the west. One consequence of the uplift of the Andes was the establishment of a topographic barrier to the moisture-rich northeastern winds, resulting in the formation of a rain shadow effect along its western side.

5. Geology and stratigraphy of the Uquía Formation

The succession of fossil mammals and geochronologic data described herein were recovered from the Uquía Formation in the Quebrada de Humahuaca, with principal exposures found at Esquina Blanca, San Roque, and Chucalesna (Fig. 1). The unit is best exposed in Esquina Blanca

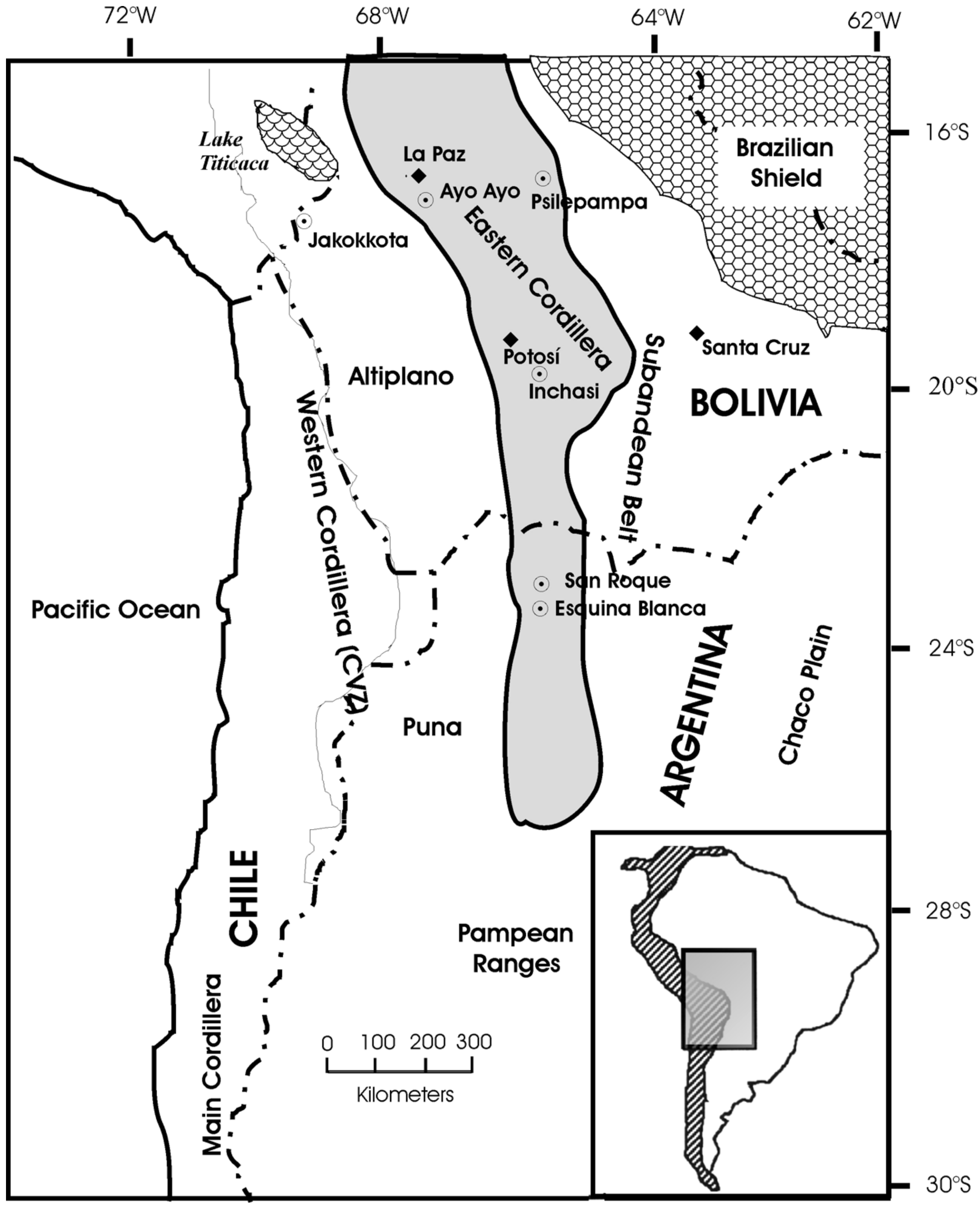

Fig. 3. Morphotectonic provinces of the Central Andes, showing the location of the Puna and Eastern Cordillera (after Jordan et al., 1983) and the Neogene localities discussed in the text.

(Fig. 4) and San Roque, located about 11 and 5 km SE, respectively, of Humahuaca at an elevation of 2700–2800 m, and thus represents the highest vertebrate fauna known from the uppermost Cenozoic of Argentina.

The thickness of the Uquía Formation ranges from 260 m in Esquina Blanca to 220 m at San Roque. At these localities, the sequence is gently folded and faulted and unconformably overlain by undifferentiated sediments of the Mesón Group of Paleozoic age (Turner, 1960). At Maimará, located 15 km south of Humahuaca (Fig. 1), the Uquía sequence overlies the folded and faulted Upper Miocene sediments of the Maimará Formation (Salfity et al., 1984).

Table 3
Estimated paleoelevations at time of deposition and modern elevations of the fauna and flora localities of the Eastern Cordillera

Locality	Current elevation (m)	Paleoelevation (m)	Source
Inchasi (fauna, Pliocene)	3220	2150	MacFadden et al. (1994)
Viscachani (fauna, Pliocene)	3900	2850	MacFadden et al. (1994)
Tarija (fauna, Pleistocene)	1950	1950	MacFadden et al. (1994)
Uquía (fauna, Plio/Pleistocene)	2800	1400–1700	This paper
Cerdas (fauna, Miocene)	3800	800	MacFadden et al. (1994)
Salla (fauna, Oligocene)	3500	<500	MacFadden et al. (1994)
Psilepampa (flora, Eocene)	3400	$1200–1400 \pm 1000$	Graham et al. (2001)
Potosí (flora, Eocene)	3300	$0–1320 \pm 1500$	Gregory-Wodzicky (2000)

Fig. 4. Photo of Esquina Blanca looking westward toward the Río Grande, showing the fossiliferous layer cropping out. The approximate contact between the underlying Upper Unit and the "Pleistocene *sensu lato* conglomerate" is indicated by an arrow.

The predominant lithology of the sequence consists of moderately to well-indurated red-brown, pinkish-tan, and light green claystone and siltstones. There are several tuffaceous horizons, which represent either primary air-falls or secondarily reworked deposits. The tuffs have fine-grained sandstone with finely laminated beds and occasional cross-bedding, interpreted to be fluvially reworked ash deposits (Fig. 2).

The Uquía Formation is unconformably covered by unnamed conglomeradic deposits, which are probably Upper Pleistocene in age.

Castellanos (1950) measured and described at least six profiles in the Uquía area (Profile 1: Chucalesna East, near Esquina Blanca and north Aparicio's Farm; Profile 8: Chucalesna West; Profile 3: Esquina Blanca South; Profile 9: Chucalesna West and south of Profile 8; Profile 5: Chucalesna East, between Aparicio's Farm and Esquina Blanca; Profile 6: Esquina Blanca), and their stratigraphy and relationships are depicted in Fig. 5.

Following Marshall et al. (1982), we characterize the stratotype of the Uquía Formation at Esquina Blanca. Marshall et al. (1982, p. 987) designate the type section at Esquina Blanca "the most richly fossiliferous and stratigraphically the thickest section of known Uquian beds exposed in this area." This section was measured by one of the authors (RNA) (Fig. 2). Although it does not contain all the lowest intervals of the formation, exposed farther south (Chucalesna) in the Quebrada de Humahuaca, the stratotype section effectively illustrates the threefold subdivision of the Uquía Formation employed herein.

The Uquía Formation at Esquina Blanca (Fig. 2) is composed mainly of braided fluvial sediments, sands, conglomeratic sands, and conglomerates with crossed structures and channels. These are light-colored sediments, whitish or grayish to yellowish. More than 90% of the pebbles are Cambrian quartzites of the Mesón Group. Some sandy banks are light green with limonitic ocher and manganese oxides. Materials are generally loose or minimally consolidated. However, the circulation of epigenetic waters partially cemented the sandy and gravy banks forming crusts. This process allowed the conservation of bone remains. Disarticulation and preservation of the bones is compatible with the fluvial environment. There are some levels of reddish clayey silts that are tight, brittle, and have "slickenside" surfaces, as well as at least one pair of thick horizons of tuffs. The tuffaceous levels reach up to 2 m thick but rapidly thin by erosion, which is why these units are well exposed in one ravine and absent in the next. The pattern of fluvial sedimentation makes correlation of the banks difficult because of the rapid lateral facies changes. Three units can be broadly distinguished. The lowest has thick conglomerate and sandy banks with a conspicuously thick Dacitic tuff. The middle unit shows thin, well-defined stratification, more sandy and clayey-silt levels, and higher fossil richness than the others. The upper unit is composed of coarse conglomerate sheets with less fine sediments. The whole set is unconformably overlain by reddish fanglomerates produced by tectonic rejuvenation of the area.

As indicated in Fig. 2, Castellanos (1950) considered the Lower Unit the basal unit of the Uquía Formation, which

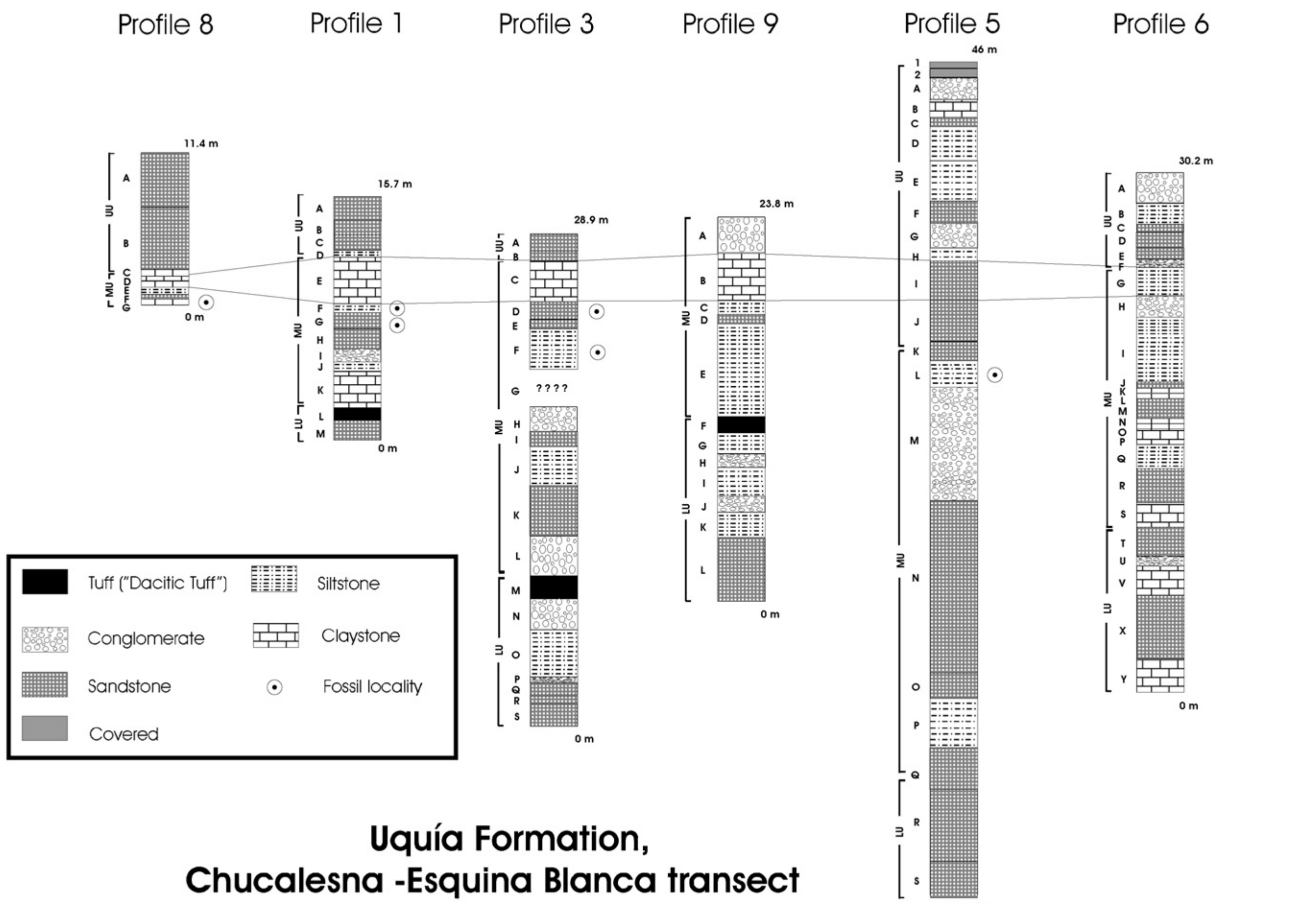

Fig. 5. Stratigraphic sections at Uquía area measured by Castellanos (1950), with the dominant lithologies, correlations between units, and position of fossil sample (⊙) horizons. Abbreviations: LU, Lower Unit; MU, Middle Unit; UU, Upper Unit.

at Esquina Blanca unconformably overlies sediments attributed to the Mesón Group of Cambrian age.

6. Discussion

6.1. Chronology of ''Uquian'' mammals integrating biochronologic, biostratigraphic, and geochronologic data

Castellanos (1953) informally subdivided the Uquía Formation into three units, characterizing them by stratigraphic differences and a basal distinctive tuff (''Toba Dacítica'' or Dacitic Tuff). To provide a formal framework for the threefold subdivision of Castellanos, we delimit these units conventionally on the basis of (1) the original stratigraphic description of Castellanos (1950, 1953), (2) their mammal content, (3) the biostratigraphic assemblage zone framework depicted by Cione and Tonni (1995), and (4) the geochronology reported by Marshall et al. (1982) and Walther et al. (1996, 1998).

6.1.1. Lower Unit

As we show in Fig. 2, fossil mammals were recovered from four lithologic intervals in the Uquía Formation. The oldest mammals occur in the basal part of the Lower Unit, 30 m below the U2 Tuff. The fossils were obtained mostly from one site covering a 3 m interval and contain only a few taxa, including the dasypodid *Doellotatus chapadmalensis* and the pampatheriine *Plaina*. The Lower Unit of the Uquía Formation includes the distinctive Dacitic Tuff of Castellanos (1950) and Marshall's LGM 202. This tuff is better exposed in the Chucalesna section, where it reaches a maximum thickness of 2 m, but completely pinches out to the west in some places (San Roque), indicating an irregular deposition surface. In Esquina Blanca, this tuff is exposed on the other side of the road and pinched out at the place where the section was measured (Fig. 2).

Castellanos (1950, p. 50) established that the upper boundary of the Lower Unit at Esquina Blanca is characterized by ''un estrato de arcilla verde, endurecida, con manchones limoníticos'' (''a green clay horizon, indurated, with limonite patches''). We find that the green clay horizon is represented near the top of the first lower 40 m of the Esquina Blanca section and inclined approximately 15° (Castellanos, 1950). Fossil mammals recovered from this unit (i.e., *Paraglyptodon*, and *Scelidotheridium*; Table 3) are exclusive and common genera of the late Chapadmalalan (zone of *Paraglyptodon chapadmalensis* of Cione and Tonni, 1995). Long-ranging taxa (i.e., *Plaina* and *Doellotatus*), known to occur in both the Montehermosan and

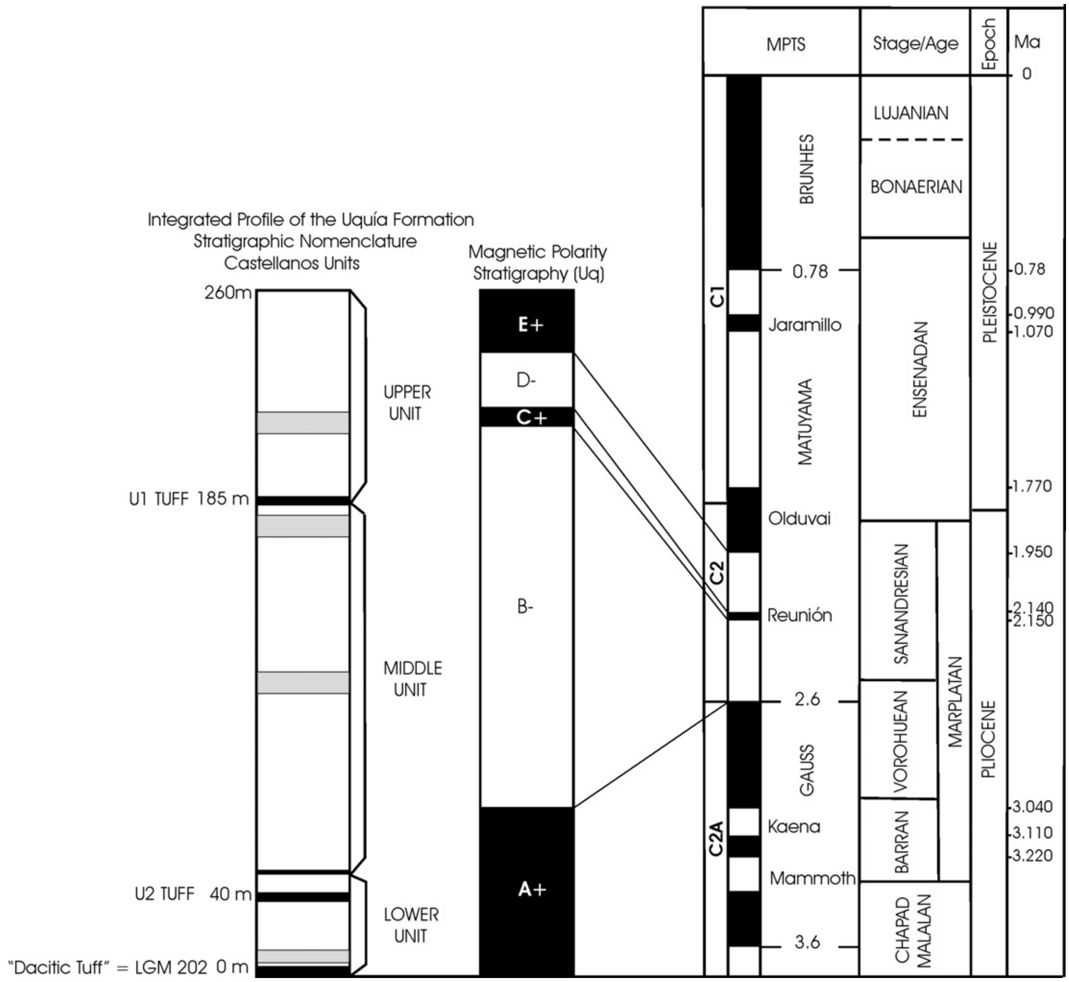

Fig. 6. Biostratigraphy and geochronology of the Uquía Formation, showing the relationships of the lithic subdivision of the formation, marker tuff beds and their isotopic ages, faunal units used herein, South American stages/ages of Cione and Tonni (1995), magnetic polarity zonation, correlation with the GPTS (Berggren et al., 1995), and isotopic time scale (Ma). Abbreviations: Barran: Barrancalobian subage.

Chapadmalalan (*Doellotatus* is also known from the Huayquerian SALMA) also occur in the Lower Unit (Table 3). Therefore, the fossil mammals from the Lower Unit of the Uquía Formation indicate an age older than the Marplatan (Fig. 6), suggesting a late Chapadmalalan age.

6.1.2. Middle Unit

Castellanos (1953, p. 51) defined the Middle Unit by "la existencia de arcillas o limos rojizos, otras veces por arena fina rojiza" ("the existence of reddish clays or muds, interbedded with reddish fine sand"). The Middle Unit of the Uquía Formation at Esquina Blanca, as considered herein, begins above this horizon (40 m) and approximately 10 m above the top of the U2 Tuff of Walther et al. (1998) and extends with a stratigraphic interval of about 145 m (Fig. 2). The best exposures of the Middle Unit are found on Esquina Blanca and San Roque. Most of the genera from the Middle Unit of the Esquina Blanca section (i.e., *Paraglyptodon*, *Platygonus*, *Urotherium*, *Pseudomacrauchenia*, and *Microcavia*) have known records in the Chapadmalalan and Marplatan of the Atlantic coast; others like *Hippidion* and *Ctenomys chapadmalensis* (=*Paractenomys chapadmalensis*) are from the Marplatan only (Table 3). The latter taxa are recorded 8–10 m beneath the U1 Tuff of Walther et al. (1998) (Fig. 2). From these horizons, a single crocodile tooth (MLP 86-V-10-18) was also recovered. In addition, in the Middle Unit of the San Roque sequence, a rodent, *Ctenomys chapadmalensis* (MLP 90-XII-4-2) and an edentate, *Chaetophractus cf. villosus* (MLP 90-XII-4-5), were recovered in 1996. Previously, Castellanos and de Carles discovered remains of *Windhausenia* sp. (MACN 5380, Catellanos, 1950) in San Roque in 1921.

Ctenomys chapadmalensis is a guide fossil of the Sanandresian (zone of *Paractenomys chapadmalensis*, Cione and Tonni, 1995) recorded at Esquina Blanca and San Roque. Other taxa recorded in this unit are the endemic macraucheniids *Windhausenia delacroixi* and *Pseudomacrauchenia yepesi*, which appear generally more derived than *Promacrauchenia chapadmalense* from the late Chapadmalalan (zone of *Paraglyptodon chapadmalensis* of Cione and Tonni, 1995). The upper limit of this unit is defined by the U1 Tuff, 185 m above the local base (Fig. 2).

Because the middle levels of the sequence are contained within the upper half of the reversed polarity zone (B-), the polarity zone must correlate with Chron C2, which includes the upper part of the Vorohuean and the Sanandresian (Fig. 6). The magnetostratigraphy and mammal evidence suggest that typical Barrancalobian taxa are not represented in the Uquía Formation. Because no unconformity is detected in the lower part of the section, the mammals are mostly found throughout, and the polarity is normal in this part of the section (no samples of reversed polarity between Chapadmalalan and Vorohuean/Sanandresian sediments), we assume that the Barrancalobian is not represented in northwest Argentina.

6.1.3. Upper Unit

The Upper Unit was defined by Castellanos (1950, p. 51) as "un conjunto de capas horizontales que se hallan en la parte alta de las formaciones donde se han encontrado restos de *Promacrauchenia*" ("a grouping of horizontal levels, which are located in the upper part of the formations where remains of *Promacrauchenia* have been found"). These horizontal beds are well exposed above the U1 Tuff; therefore, we consider this tuff the upper boundary of the Middle Unit. At Esquina Blanca, the Upper Unit is located in the last 75 m of the sequence and consists of alternating fine, light gray sandstone, quartziferous, and muscovite, and fine green sandstone that overlies pinkish claystone or dark yellow limestone, as well as sorted conglomerate and sandstone (Castellanos, 1950). Fossil mammals (i.e., *Glyptodon*, and *Scelidotherium*; Table 3) from the Upper Unit of the Uquía Formation are commonly associated with Ensenadan fauna (zone of *Tolypeutes pampaeus* of Cione and Tonni, 1995), redated by Tonni and Cione (2001) between 1.8 and <0.5 Ma.

From the conglomeratic unit (Pleistocene "*sensu lato*" unit) that unconformably overlies the Uquía Formation (Fig. 2), an incomplete ulna (MLP 95-IX-1-1) was recovered. It was referred to *Macrauchenia cf. patachonica*, a species known only from the Lujanian age (zone of *Equus* (*Amerhippus*) *neogeus* of Cione and Tonni, 1995).

In conclusion, combined isotopic data from the Uquía Formation at Esquina Blanca indicate an overall age of 3.5–3.0 (Dacitic Tuff) to at least 2.5 Ma (U1 Tuff of Walther et al., 1998) for the "Piso Uquiense" of Castellanos (1950) or the "Uquian SALMA" of Pascual et al. (1965). The date for the Dacitic Tuff at Chucalesna is concordant with the 3.54 ± 0.04 Ma age for the Dacitic Tuff of the Lower Unit reported by Marshall et al. (1982) at Esquina Blanca, as well as with the late Chapadmalalan age assigned to the mammals from this unit in Esquina Blanca.

Our reinterpretation of the paleomagnetic data obtained from Esquina Blanca suggests that the basal part of the sequence (Lower Unit) and the basal 20 m of the Middle Unit show normal polarity (magnetozone UqA+, Fig. 6) and correlate with chron Gauss (2.581–3.580 Ma). Nearly all sediments (~140 m) included in the Middle Unit are interpreted to be of reversed polarity and occur at 60 m (magnetozone UqB-, Fig. 6). The zircon date of the U1 Tuff (2.5 Ma), on the top of this unit, also indicates reversed polarity (UqB-) and correlates with chron Matuyama (C2r.2r, 2.150–2.581 Ma) of GPTS (Berggren et al., 1995). The main horizon bearing Uquian fauna lies just 10 m below the U1 Tuff. Thus, these levels at Esquina Blanca date, to within the magnetochronologic interval, from 2.150 to 2.581 Ma. Correlation of the normal polarity zone of the magnetozone UqC+ (Fig. 6) with subchron C2r.1n ("Reunion" event, 2.140–2.150 Ma) represents the most likely correlation with the first 5 m of the Upper Unit. Overlying levels are reversed in polarity (magnetozone UqD-, Fig. 6) and correlate with chron Matuyama (C2r.1r, 1.950–2.140 Ma). This lower part of the Upper Unit (8–10 m) has scarce fossils. However, occurrences of *Glyptodon* and *Scelidotherium*, together with the geochronologic data, suggest an Ensenadan age (zone of *Tolypeutes pampaeus* of Cione and Tonni, 1995), and it seems to extend the lower limit of the Ensenadan Stage, established at 1.8 Ma on the Atlantic Coast (Tonni and Cione, 2001), to an older paleomagnetic age between 1.950 and 2.140 Ma, or possibly to 2.5 Ma (U1 Tuff) in northwestern Argentina.

Orgeira (1993) notes that the paleomagnetic age of the Uquía Formation is Gauss, older than 2.8 Ma and younger than 3.40 Ma. This age assignment coincides with our results for the Middle Unit.

Marshall et al. (1982) correlate the Chapadmalalan with the Uquian and use age determinations to date the base of the Chapadmalalan (2.5 Ma). Our results do not support this age assignment. We assign the fauna of the Middle Unit (Uquian fauna) to the late Vorohuean–Sanandresian (Fig. 6), a younger age than the Chapadmalalan. However, mammals from the Lower Unit are common in the late Chapadmalalan. The conclusions of Marshall et al. (1982) were based on dates of the tuff at the top of the Corral Quemado Formation (Catamarca, northwestern Argentina) with an average of 3.54 Ma (Butler et al., 1984). This tuff overlies Chapadmalalan fauna (including the procyonid *Chapadmalania*) (Cione and Tonni, 1996).

Biochronologically, the mammals from the Lower Unit of the Uquía Formation are similar to fauna from Inchasi (19°43′15″S; 65°28′6″W) in Bolivia, which MacFadden et al. (1993) assign to the Montehermosan. The Inchasi fauna recently was assigned to the Chapadmalalan by Cione and Tonni (1996). *Plaina* and *Paraglyptodon* occur in both the Uquía Formation (Lower Unit and the lower one-third of the Middle Unit) and Inchasi fauna. The mammals from the Lower Unit of the Uquía and Inchasi have no record of immigrant taxa. Mammals from Inchasi are also similar to those of Viscachani and Ayo Ayo, Bolivia (MacFadden et al., 1993).

The presence of *Erethizon*, the one-toed equid *Hippidion devillei*, and a gomphothere? Proboscidean in the Uquía Formation have particular significance because they represent the FADs for these taxa (see Tonni and Cione, 2000 for a different view of *Hippidion devillei*) in South America (Prado et al., 1998; López et al., 2002). The lowest stratigraphic occurrence of *Hippidion* remains lies about 10 m below the U1 Tuff (isotopically dated at 2.5 Ma and magnetostratigraphically constrained between 2.150 and 2.581 Ma). The presence of a mastodon in the Uquía Formation has particular significance, because the first appearance of immigrant mastodons should be a useful datum for a correlation within South America.

6.2. The first record of *Erethizon* (Rodentia, Erethizontidae) in South America

Of great paleobiogeographic significance is the presence in the Uquía Formation of the porcupine *Erethizon*, a genus known until now only in North America. The specimen MACN 5376 (Fig. 7) is a right mandibular fragment with a great portion of the mandibular body, preserving most of the angular region, the condyle, the base of the coronoid process, the alveoli of the p4-m3, and a significant part of the alveolus of the incisor. It was collected by Enrique de Carles in 1912 from the Middle Unit of the Uquía Formation at Esquina Blanca. MACN 5378 is assigned to *Erethizon* because its angular region is markedly inflected lingually, extending even more anteriorly than in the known species of this genus. Frazier (1981, p. 18), in reference to *Erethizon*, notes: "The most distinctive character is the inflection of the angular process." This feature is currently used to separate *Erethizon* from *Coendou* (a living Neotropical porcupine). The assignment of the Uquian *Erethizon* to any known species of this genus (White, 1968, 1970; Martin, 1974; Frazier, 1981; Hulbert, 1997) needs more material and an exhaustive taxonomic and phylogenetic revision, which is beyond the scope of this paper. However, in a general comparison, MACN 5376 differs from the known species of *Erethizon* in its angular region, which is more inflected lingually and anteriorly, a less excavated diastema, a narrower retromolar fossa, and a longer dental series relative to the estimated mandibular length. The general size of MACN 5376 (Table 4) is similar to *E. bathygnathum* (White, 1970: Table 2; Frazier, 1981, Table 3), though the alveolar length of p4-m3 is even greater than in the latter species and seems to have a shallower, less massive mandible (inferred from the depth at m3). The Uquian *Erethizon* is distinctly larger than *Erethizon kleini* (Frazier, 1981, Table 3) and larger than *Erethizon poyeri*, *Erethizon cascoensis*, and *Erethizon dorsatum* (Frazier, 1981, Table 3; Hulbert, 1997, Table 1). MACN 5376, like *Erethizon bathygnatum* and *E. poyeri*, differs from *E. dorsatum* in having an anterior projection of a line bisecting the lower cheek teeth lateral to the incisor, indicating that the tooth rows are less divergent than in the latter species. MACN 5376 also differs from *E. poyeri* in its larger m3 relative to m1–2.

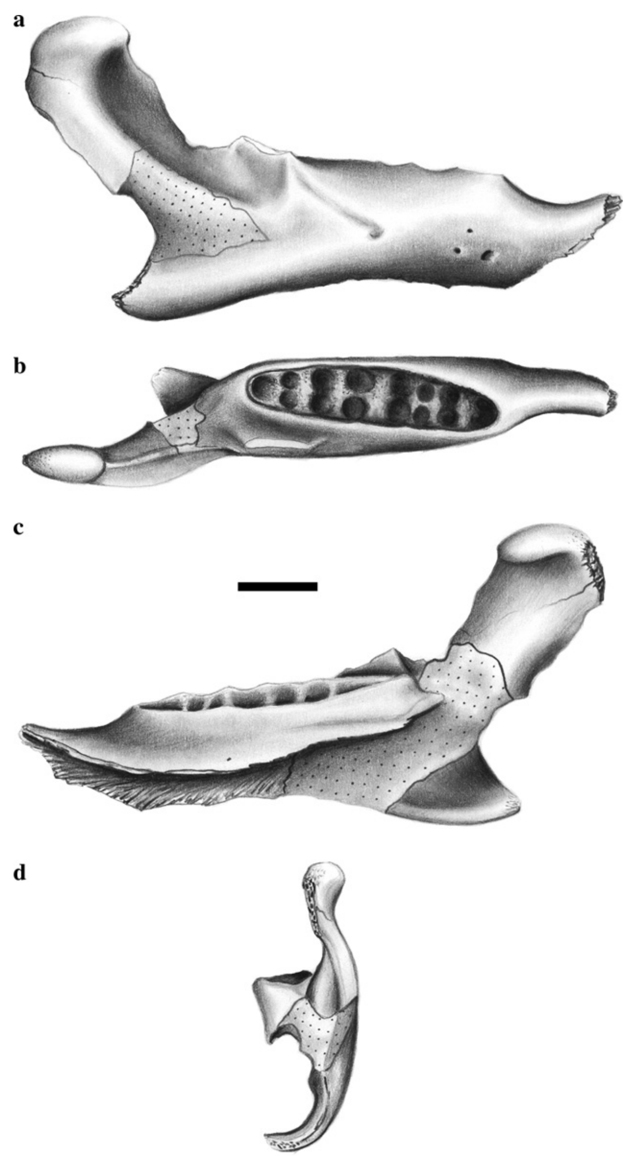

Fig. 7. *Erethizon* sp. (MACN 5376). Left hemimandible in labial (a), lingual (b), occlusal (c), and posterior (d) views. Scale 1 cm.

6.3. Paleoenvironmental and biogeographic significance of vertebrates of the Uquía Formation

In the zoogeographic classification of Ringuelet (1961), the area of Uquía belongs to the Andino Dominion of the Andino-Patagónico subregion, which includes western areas of Argentina higher than 3000 m altitude. The mean rainfall in the Eastern Cordillera at Uquía ranges from 200 to 250 mm. The main vegetation type is steppe, characterized by scattered low bushes and "cardones" (*Trichocereus terscheckii* and *Trichocereus passacana*) usually less than 1 m in height (predominantly the shrub *Prosopis ferox*, "churqui") (Cabrera and Willink, 1973). The extant mammalian herbivore fauna from Uquía is relatively depauperate, consisting of the orders Rodentia and Edentata. Among rodents *Ctenomys* ("tuco-tuco"), *Microcavia*, and *Galea* ("cuises") are common in this area. The armadillo *Chaetophractus* is also common (Cabrera and Willink, 1973).

Table 4
Selected mammalian stratigraphic ranges from Esquina Blanca (including Uquía Formation and Pleistocene *sensu lato* unit), Jujuy province, Argentina

	Uquía Formation			
	Lower Levels	**Middle Levels**	**Upper Levels**	**PL *s.l.***
	10-20 m -----30-40 m	50 m 100 m 185 m	190 m ---------230 m	
Gomphotheriidae gen. et sp. indet.		[-●-]		
Platygonus uquiensis		[---●-----●-●--]		
Camelidae cf. *Palaeolama*			[-●-]	
Cervidae gen et sp. indet.			[-●-]	
Hippidion devillei		[-●---●-----------●-]		
Windhausenia delacroixi		[-●-]		
Pseudomacrauchenia yepesi			[-●-]	
Macrauchenia cf. patachonica				[-●-]
Ctenomys chapadmalensis	[-●-----●----------●-]			
Ctenomyinae new taxon		[-●-]		
Microcavia sp.	[-●-]			
Erethizon sp.		?----------?		
Hydrochoeropsis dasseni		?----------?		
Megatherium? uquiensis		?----------?		
Pyramiodontherium? carlesi		?----------?		
Scelidotherium sp.			[-●-]	
Scelidotheridium sp.		[-●-]		
Lestodon? castellanosi		?----------?		
Sinhapalops jujuyensis		?----------?		
Glyptodon sp.			[-●-]	
Paraglyptodon uquiensis	[-●----------●-------●-------------●-]			
Panochthus?		?----------?		
Urotherium sp.		[-------------------]		
Xiphuroides uquiensis		?----------?		
Neuryurus? sp.			[---●-----]	
Sclerocalyptinae indet.		?----------?		
Doedicurinae indet.		[-●-]		
Plaina sp.	[-●--●-]			
Doellotatus chapadmalensis	[-●-]			
Chaetophractus cf. villosus		[-●-]		
Euphractinae indet.		?----------?		

Abbreviations: PL. *s. l.*, Pleistocene *sensu lato*. [——] FAD-LAD, ●, precise stratigraphic record.

No paleoenviromental studies of the Uquía Formation are available. However, faunistic evidence suggests that it was much more diverse than the modern tundra-like environment and that the fauna lived in a warmer, wetter climate. On the basis of tectonic aspects discussed previously, we infer that during the time of deposition of the Uquía Formation, the study area probably was a high-elevation, wide, intermountain valley. Vertebrates from the Middle Unit also provide insights into paleoenviromental conditions. The fauna is characterized by the presence of medium (peccaries, horses) and large (macraucheniids, camelids, and proboscideans) herbivores with low-crowned dentition. The undetermined Uquian camelid is a rare large form, probably close to *Palaeolama* in its size but much more robust. The metapodials of this species are longer and more robust than those of *Palaeolama* (A. Menegaz, pers. comm., 2003). Geographically, this genus was restricted during the Pleistocene to the Andean area of Perú, Bolivia, and Ecuador (Hoffstetter, 1952). *Palaeolama* has relatively short-crowned dentitions. With their relatively short tooth crowns, fossil camelids are generally believed to have been predominantly browser or browser/mixed feeders (Janis, 1990). MacFadden and Shockey (1997) regard the Pleistocene *Palaeolama weddelli* as a component of the browser guild.

The peccary *Platygonus* is one of the more frequent ungulates found in the Uquía Formation, but its paleoenviromental significance is difficult to establish because extant peccaries live in a variety of habitats, ranging from deserts to rain forests (Walker, 1983).

The only horse known in the Uquian fauna is the one-toed *Hippidion devillei* (*Hippidion ''uquiensis''* of Castellanos, 1953). *Hippidion* is characterized by unusual morphological adaptations including a retracted nasal notch. According to MacFadden (1997), the metapodials of *H. devillei* (his *Onohippidum*) are gracile and short. The Uquian horse is smaller than *Hippidion principale* and probably represents a dwarf form (M. Bond, pers. comm., 2003); its short limbs probably were adapted to a mountain habitat.

The Uquian *Erethizon* probably had a generalized diet, like the extant *Erethizon dorsatum*, and adapted to environments with some degree of seasonality, more suggestive of open areas than tropical and subtropical forests.

The endemic capybara-like *Hydrochoeropsis dasseni* suggests the presence of permanent water bodies. Today, capybaras are confined to areas with permanent standing or running water and can occur in marshes or estuaries and along rivers and streams (Redford and Eisenberg, 1992).

The mastodons have relatively short-crowned dentition, suggesting a browser or mixed feeder. However, MacFadden and Shockey (1997), on the basis of carbon isotopic data, suggest that the gomphothere *Cuvieronius* could be a poor C4 grazer.

The most surprising presence in the Middle Unit of the Uquía Formation is a crocodile. Crocodiles live in tropical and subtropical areas in warm and humid climates and near rivers. They are considered the most climate-sensitive indicators of warm and humid conditions, and this record in the Middle Unit represents the first mention of the group for the Pliocene of South America (Zulma Gasparini, pers. comm., 2003).

Marshall et al. (1982) note that Uquian fauna records the first major contingent of North American participants (14 families) in the GABI (data based largely on records from the Atlantic coast). As proposed for the arrival of Holartic mammals into the Pampean region (Cione and Tonni, 1995), in the Uquía area, immigration events probably were not sudden. The immigrant taxa recorded in the Uquía Formation indicate that immigration events could have occurred in different times during the ''Uquian'' (Marplatan) and Ensenadan ages. No records of immigrant mammals appear in the Lower Unit of the Uquía Formation (late Chapadmalalan); this is not the case in the late Chapadmalalan from the Atlantic coast. However, a new species of the Huayquerian–Chapadmalalan carnivore genus *Cyonasua* (Procyonidae) has been reported from the underlying Maimará Formation (Upper Miocene) at Maimará (Berman, 1989) in Quebrada de Humahuaca (Fig. 1). *Cyonasua* is the oldest GABI immigrant taxon recorded in NW Argentina.

The Uquian *Erethizon* represents the first record of this genus in South America. Its occurrence in the Uquía Formation indicates that it may have differentiated in South America before arriving in North America during the GABI. The presence of *Erethizon bathygnatum*, from the late Blancan of western North America, suggests that the representatives of this genus may have entered North America during the Pliocene through the Andean route, a colonization path during the GABI postulated by Webb (1978).

Finally, the records of *Erethizon* and the crocodile in the Uquía Formation reflect geographical differentiation between the northwest and Pampean regions of Argentina. Unlike the remaining groups of vertebrates recovered at the Uquía Formation (e.g., Tayassuidae, Equidae, Macraucheniidae, Camelidae, Gomphotheriidae, and Ctenomyinae), erethizontids and crocodiles are not found in the Pliocene or Pleistocene of the Atlantic coast, an area intensively prospected in the past 50 years (Tonni et al., 1992; Cione and Tonni, 1995, 1999).

The present study can serve as a chronological framework for further research dealing with the biostratigraphy of rich vertebrate fauna from northwest Argentina and Bolivia. From this detailed and precise foundation, future studies will be able to assess broad paleobiological problems, such as immigration and extinction datum planes, which will enhance our understanding of the GABI.

7. Conclusions

First, on the basis of the geochronology and biostratigraphy discussed herein, the ''Piso Uquiense'' or ''Uquian'' SALMA beds appear confined to the Middle Unit of the Uquía Formation; mammals from these levels correlate with the late Vorohuean and Sanandresian (Marplatan) of the Atlantic Coast (Buenos Aires Province). Second, the magnetostratigraphy and mammal evidence suggest that typical Barrancalobian taxa are not represented in the Uquía Formation. Third, the stage of evolution of the mammals and the geochronologic data suggest that the Lower Unit of the Uquía Formation is older than the Marplatan age. This older assemblage contains some taxa typical of late Chapadmalalan faunas elsewhere, and the fauna is assigned to the latest part of the Chapadmalalan Age. The Upper Unit contains taxa that suggest an Ensenadan age.

Fourth, the base of the Ensenadan age in NW Argentina seems older than 1.8 Ma, as established in the Atlantic coast by Tonni and Cione (2001). Fifth, the geological and paleontological evidence suggest that during the Pliocene, the Uquía area was composed of medium-elevation (1400–1700 m), wide, intermontane valleys. The environment was probably more humid than that of the present area, with some wet–dry seasonality that permitted the coexistence of forest and open areas. Sixth, *Erethizon* may have originated in South America before its arrival at North America during the GABI.

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References

Alpers, C.N., Brimhall, G.H., 1988. Middle Miocene climatic change in the Atacama Desert, northern Chile: evidence from supergene mineralization at La Escondida. Geological Society of America Bulletin 100, 1640–1656.

Benjamin, M.T., Johnson, N.M., Naeser, C.W., 1987. Recent rapid uplift in the Bolivian Andes: evidence from fission-track dating. Geology 15, 680–683.

Berggren, W.A., Kent, D.V., Swisher III, C.C., 1995. A revised Cenozoic Geochronology and Chronostratigraphy. Geochronology Time and Global Stratigraphic Correlation, Society for Sedimentary Geology, ISBN, Special Publication 54, 129–211.

Berman, W.D., 1989. Notas sobre la sistemática y paleobiogeografía del grupo *Cyonasua* (Carnívora, Procyonidae) de la Argentina. Actas VI Jornadas Argentinas de Paleontología de Vertebrados, 17–18.

Butler, R.L., Marshall, L.G., Drake, R.E., Curtis, G.H., 1984. Magnetic polarity, stratigraphy and ^{40}K–^{40}Ar dating of late Miocene and early Pliocene continental deposits, Catamarca province, NW Argentina. Journal of Geology 92, 623–636.

Cabrera, A., Willink, A., 1973. Biogeografía de América Latina. Secretaría General de la Organización de los Estados Americanos, Programa Regional de Desarrollo Científico y Tecnológico, Washington, Serie de Biología, Monografía N° 13, 1–123.

Castellanos, A., 1927. Descripción de un tubo caudal de un nuevo dedicurino en relación con sus géneros afines. Anales del Museo de Historia Natural de Montevideo, Serie II, Tomo II, 265–300.

Castellanos, A., 1950. El Uquiense. Sedimentos neógenos de Uquía (Senador Pérez) de la Provincia de Jujuy (Argentina). Univ. Nac. Litoral, Fac. Cs. Mat., Fís., Quím. y Nat. 36, 1–55.

Castellanos, A., 1953. Descripción de restos de *Paraglyptodon uquiensis* n. sp. de Uquía (Senador Pérez) de Jujuy. Memorias del Museo de Entre Ríos 32, 1–30.

Cione, A.L., Tonni, E.P., 1995. Chronostratigraphy and "Land-mammal Ages" in the Cenozoic of southern South America: principles, practices, and the "Uquian" problem. Journal of Paleontology 69, 135–159.

Cione, A.L., Tonni, E.P., 1996. Reassesment of the Pliocene–Pleistocene continental time scale of Southern South America. Correlation of the type Chapadmalalan with Bolivian sections. Journal of South American Earth Sciences 9, 221–236.

Cione, A.L., Tonni, E.P., 1999. Biostratigraphy and chronological scale of upper-most Cenozoic in the Pampean area, Argentina, Quaternary of South America and Antarctic Peninsula 3, 23–51.

De Carles, E., 1912. Ensayo geológico-descriptivo de las Huayquerías del sur de Mendoza (Dep. de San Carlos). Anales del Museo Nacional de Historia Natural de Buenos Aires 22, 77–95.

Flynn, J.J., Swisher, C., 1995. Cenozoic South American land mammal ages: correlation to global geochronologies. In: W.A. Berggren, D.V. Kent, M.-P. Aubry, J. Hardenbol (Eds.), Geochronology, Time Scales, and Global Stratigraphic Correlation. Special Publ. 54, Tulsa, OK: Society for Sedimentary Geology, pp. 317–333.

Frazier, M.K., 1981. A revision of the fossil Erethizontidae of North America. Bulletin of the Florida State Museum, Biological Sciences 27, 1–76.

Graham, A., Gregory-Wodzicki, K.M., Wright, K.L., 2001. Mio-Pliocene playnoflora from the Eastern Cordillera, Bolivia: implications for the uplift of the Central Andean Plateau. American Journal of Botony 88, 1545–1557.

Gregory-Wodzicky, K.M., 2000. Uplift history of the Central and Northern Andes: a review. Geological Society of America Bulletin 112, 1091–1105.

Hoffstetter, R., 1952. Les mammifères Pléistocenes de la République de l'Equateur. Mémoires Société Géologique de France 31 (66), 314–346.

Hulbert, R.C., 1997. A new late Pliocene porcupine (Rodentia: Erethizontidae) from Florida. Journal of Vertebrate Paleontology 17, 623–626.

Janis, C.M., 1990. The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. In: Boucot, A.J. (Ed.), Evolutionary Paleobiology of Behavior and Coevolution. Elsevier, New York, pp. 241–259.

Jordan, T.E., Alonso, R.N., 1987. Cenozoic stratigraphy and basin tectonics of the Andes mountains, 20°–28° south latitude. American Association of Petroleum Geologist, Bulletin 71, 49–64.

Jordan, T.E., Isacks, B.L., Allmendinger, R.W., Brewer, J.A., Ramos, V., Ando, C.J., 1983. Andean tectonics related to geometry of subducted Nazca plate. Geological Survey of America Bulletin 94, 341–361.

Kennan, L., Lamb, S.H., Hoke, L., 1997. High-altitude paleosurfaces in the Bolivian Andes: evidence for late Cenozoic surface uplift. In: Widdowson, M. (Ed.), Paleosurfaces: Recognition, Reconstruction and Palaeoenvironmental Interpretation. Geological Society Special Publ., N° 120, pp. 307–323.

Kraglievich, L., 1934. La antigüedad Pliocena de las Faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron. Imprenta "El Siglo Ilustrado", Montevideo, 1–136.

López, G., Reguero, M., Lizuain, A., 2002. El registro más antiguo de mastodontes (Plioceno tardío) de América del Sur. Ameghiniana 38(4) Suplemento, 35R–36R.

MacFadden, B.J., 1997. Pleistocene horses from Tarija, Bolivia, and validity of the genus *Onohippidium* (Mammalia: Equidae). Journal of Vertebrate Paleontology 17, 199–218.

MacFadden, B.J., Shockey, B.J., 1997. Ancient feeding ecology and niche differentation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. Palaeobiology 23, 77–100.

MacFadden, B.J., Anaya, F., Argollo, J., 1993. Magnetic polarity stratigraphy of Inchasi: a Pliocene mammal-bearing locality from Bolivian Andes deposited just before the Great American Interchange. Earth and Planetary Science Letters 14, 229–241.

MacFadden, B.J., Wang, Y., Cerling, T.E., Anaya, F., 1994. South American fossil mammals and carbon isotopes: a 25 million-year sequence from the Bolivian Andes. Palaeogeography, Palaeoclimatology, Palaeoecology 107, 257–258.

Marshall, L., Patterson, B., 1981. Geology and geochronology of the mammal-bearing Tertiary of the Valle de Santa María and Río Corral Quemado, Catamarca Province, Argentina. Fieldiana Geology 9, 1–80.

Marshall, L.G., Butler, R.F., Drake, R.E., Curtis, G.H., Tedford, R.H., 1979. Calibration of the Great American Interchange. Science 204, 272–279.

Marshall, L.G., Butler, R.F., Drake, R.E., Curtis, G.H., 1982. Geochronology of Type Uquian (Late Cenozoic) land mammal age, Argentina. Science 216 (4549), 986–989.

Marshall, L.G., 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. Paleovertebrata, Montpellier, Mm. Extr., 1–76.

Marshall, L.G., Swisher III, C.C., Lavenu, A., Hoffstetter, R., Curtis, G.H., 1992. Geochronology of the mammal-bearing late Cenozoic on the northern Altiplano, Bolivia. Journal of South American Earth Sciences 5, 1–19.

Martin, R.A., 1974. Fossil mammals from the Coleman IIA fauna, Sumter County (Florida). In: Webb, S.D. (Ed.), Pleistocene Mammals of Florida. Univ. Press Florida, Gainesville, pp. 35–99.

Mones, A., 1991. Monografía de la familia Hydrochoeridae (Mammalia: Rodentia). Courier Forschungsinstitut Senckenberg 134, 1–50.

Orgeira, M.J., 1993. Extensión temporal de las edades mamífero cenozoicas tardías sudamericanas. Edad del istmo de Panamá. Revista de la Asociación Geológica Argentina 48, 169–174.

Pascual, R., Ortega Hinojosa, E.J., Gondar, D., Tonni, E., 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a áquellas del territorio bonaerense. Anales Comisión de Investigaciones Científicas, Buenos Aires 6, 165–193.

Prado, J.L., Alberdi, M.T., Reguero, M.A., 1998. El registro más antiguo de *Hippidion* Owen, 1869 (Mammalia, Perissodactyla) en América del Sur. Estudios Geológicos 54, 85–91.

Prado, J.L., Alberdi, M.T., Reguero, M.A., 2001. Réplica a los comentarios de E.P. Tonni y A.L. Cione sobre la geocronología, estratigrafía y paleontología de vertebrados de la Formación Uquía en el perfil de Esquina Blanca, Jujuy. Estudios Geológicos 56, 1–137.

Redford, K.H., Eisenberg, J.F., 1992Mammals of the Neotropics. The Southern Cone, vol. 2. University of Chicago Press, Chicago and London, 1–436.

Ringuelet, R.A., 1961. Rasgos fundamentales de la zoogeografía de la Argentina. Physis 22, 151–170.

Rusconi, C., 1930. especies fósiles argentinas de pecaríes (Tayassuidae) y sus relaciones con las de Brasil y Norte América. Anales del Museo Nacional de Historia Natural Bernardino Rivadavia de Buenos Aires 36, 121–241.

Salfity, J.A., Brandan, E.M., Monaldi, C.R., Gallardo, E.F., 1984. Tectónica compresiva cuaternaria en la cordillera oriental argentina, latitud de Tilcara (Jujuy). Actas III Congreso Geológico Argentino 2, 321–336.

Simpson, G.G., 1940. Review of the mammal-bearing Tertiary of South America. Proceedings of the American Philosophical Society 83, 649–709.

Tonni, E.P., Cione, A.L., 2000. Comment on "El registro más antiguo de *Hippidion* Owen, 1869 (Mammalia, Perissodactyla) en América del Sur", by Prado et al. Estudios Geológicos 56 (1–2), 1–137.

Tonni, E.P., Cione, A.L., 2001. Correlation of Pliocene to Holocene southern South American and European vertebrate-bearing units. Bollettino della Società Paleontologica Italiana 40, 167–173.

Tonni, E.P., Alberdi, M.T., Prado, J.L., Bargo, M.S., Cione, A.L., 1992. Changes of mammal assemblages in the Pampean region (Argentina) and their relation with the Plio-Pleistocene boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 95, 179–194.

Turner, J.C.M., 1960. Estratigrafía de la Sierra de Santa Victoria y adyacencias. Bol. Acad. Nac. de Ciencias Córdoba 41 (2), 163–196.

Walker, E.P., 1983. Mammals of the World (fourth ed.). In: Nowak, R.M., Paradiso, J.L. (Eds.), vol. II, University Press, pp. 569–1362.

Walther, A.M., Orgeira, M.J., Reguero, M.A., Verzi, D.H., Chernoglasov, C., Vilas, J.F., Sinito, A.M., Herrero Bervera, E., 1996. Nuevo estudio paleomagnético de la Formación Uquía de la provincia de Jujuy, Argentina. Revista de la Asociación Geológica Argentina 51, 355–364.

Walther, A.M., Orgeira, M.J., Reguero, M.A., Verzi, D.H., Vilas, J.F., Alonso R., Gallardo, E., Kelley, S., Jordan, T., 1998. Estudio paleomagnético, paleontológico y radimétrico de la Formación Uquía (Plio-Pleistoceno) en Esquina Blanca (Jujuy). Actas X Congreso Latinoamericano de Geología y VI Congreso Nacional de Geología Económica vol. 1, 77.

Webb, D., 1978. A History of Savanna Vertebrates in the New World. Part II: South America and the Great Interchange. Annual Review of Ecology System 9, 393–426.

White, J.A., 1968. A new porcupine from the Middle Pleistocene of the Anza-Borrego desert of California with notes on mastication in *Coendou* and *Erethizon*, Contributions in Science. Los Angeles County Museum of Natural History 136, 1–15.

White, J.A., 1970. Late Cenozoic porcupines (Mammalia, Erethizontidae) of North America. American Museum Novitates 2421, 1–15.

Yrigoyen, M.R., 1979. Cordillera Principal. Academia Nacional de Ciencias de Córdoba, (Segundo Simposio de Geología Regional Argentina) 1, 651–694.