Exceptional Late Pliocene microvertebrate diversity in northwestern Argentina reveals a marked small mammal turnover

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ABSTRACT

Despite a century of paleontological work in Neogene sequences of northwestern Argentina there is still much to learn about the biotic diversity in this area during Pliocene times. We report a rich microvertebrate assemblage recovered from Late Pliocene deposits of Uquía Formation, Jujuy Province, northernmost Argentina. Taxa represented in the studied sample include members of Bufonidae (Amphibia: Anura), Iguanoidea (Reptilia: Squamata), Passeriformes (Aves), Argyrolagidae, Didelphidae, Caviidae, Ctenomyidae, Octodontidae, and Cricetidae (Mammalia). Taphonomic attributes indicate that the bone concentration was produced by owls. The remains were disposed highly concentrated suggesting that the assemblage would have been generated in a short lapse, indicating a low time-averaging, retaining the main ecological signals of the past living community. The studied assemblage is noteworthy because it encompasses at least five new genera of cricetid rodents, illustrating the oldest record in northwestern Argentina for this diverse family of mammals. In spite of clear taxonomic differences at specific and generic levels, the structure of the assemblage is ecologically comparable to modern small mammal communities in terms of body mass distribution, trophic structure and abundance, with a dominance of cricetids over marsupials and caviomorph rodents. Striking differences in taxonomic composition between the Uquian assemblage and the coeval record from central Argentina indicate biogeographical distinctions since the Late Pliocene. The new Uquian cricetids show that the early divergence times for phyllotine genera proposed by several authors cannot be supported. The dominance of phyllotines in the assemblage as well as the record of *Microcavia* and an octodontid allow inferring arid or semiarid paleoenvironment conditions, in a more or less open habitat. The studied assemblage reflects a noteworthy faunal turnover, which implies the establishment of cricetid rodents as the dominant group in the small mammal communities. This faunal change can be associated to increasing aridity during Late Pliocene worldwide.

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1. Introduction

The main phase of the dispersive event Great American Biotic Interchange (GABI) took place during the Late Pliocene–early Pleistocene (Woodburne, 2010, and references therein). One of the continental beds that documents this span in South America is represented by the outcrops exposed at Quebrada de Humahuaca, northwestern Argentina, referred as Uquía Formation (see Reguero et al., 2007 for a synthesis). A century of paleontological work retrieved a moderate number of vertebrates from this unit, mainly medium and large mammals (De Carles, 1912; Castellanos, 1950; Prado et al., 2000; Reguero et al., 2007). However, the age of this fauna and its temporal relation with potentially contemporary fossil bearing units of Bolivia and central Argentina have not been satisfactorily resolved (MacFadden et al., 1993, 1994; Cione and Tonni, 1995; Flynn and Swisher, 1995; Prado et al., 2000; Tonni and Cione, 2000). An additional obstacle for a comprehensive knowledge of the paleofauna of Uquía

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Formation arises from the scarcity of small vertebrates. The most recent compilation indicates solely two mammals <250 g recorded, *Ctenomys* and *Microcavia* (Reguero et al., 2007: Table 2). This situation partially reflects the history of the South American paleomammalogy during most of the 20th century, strongly biased toward traditional prospection methods. The recent use of screen-washing techniques (McKenna et al., 1994) has increased the finding of microvertebrate remains in a number of Cenozoic paleontological sites in South America, improving drastically our knowledge on the diversity and evolution of Tertiary and Quaternary South American mammals (e.g., Pardiñas and Lezcano, 1995; Ortiz and Pardiñas, 2001; Goin and Candela, 2004; Voglino and Pardiñas, 2005; Ortiz et al., 2011b). Within this context, microvertebrate assemblages—as those produced by owls—are particularly valuable as a source of data of past communities and environments (e.g., Avery, 1982; Andrews, 1990; López Antoñanzas and Cuenca Bescós, 2002; Avery, 2007).

The contributions on small mammal assemblages of Northwestern Argentina are few and focused on Late Pleistocene and Holocene evidences (Ortiz and Pardiñas, 2001; Teta and Ortiz, 2002; Ortiz and Jayat, 2007; Ortiz et al., 2011a, 2011b, 2012). However, these studies allowed the recognition of major faunal changes, including biological extinctions (Ortiz et al., 2000), altitudinal shifts in the distributional range of some species (Ortiz and Pardiñas, 2001; Ortiz and Jayat, 2007; Ortiz et al., 2011b), and remarkable fluctuations in species abundance (Teta and Ortiz, 2002; Ortiz et al., 2012).

In this paper we describe a noteworthy fossil assemblage of microvertebrates recovered from Late Pliocene deposits of Uquía Formation, Jujuy Province, Argentina. Here we document the first amphibians, lizards and birds for this unit as well as novel and enigmatic marsupials and small rodents. Among the latter is documented the oldest indisputable record for cricetids in the region (see Nasif et al., 2009), with representatives of at least three tribes. The dominance of cricetids in the new Uquian studied assemblage prompted the discussion about the important turnover suffered by small mammal communities during the Late Pliocene. Finally, the biogeographical meaning of these new faunistic elements is analyzed at the light of the GABI and paleoenvironments for Late Pliocene times in Northwestern Argentina.

2. Materials and methods

The studied specimens were collected by three of the authors (PEO, MJB, and DAGL) and collaborators and are housed in the fossil vertebrate collection of the Instituto Miguel Lillo, San Miguel de Tucumán, Argentina (PVL). The material was obtained through wet and dry sieving with a 0.1 mm mesh, following the method described in McKenna et al. (1994). The taphonomic history of the sample was assessed through the analysis of bones and teeth surfaces (Andrews, 1990, and references therein). Reported measurements (in millimeters) were obtained using digital calipers and a micrometer eyepiece included in a binocular microscope. Microphotographs were processed in the LAMENOA (Laboratorio de Microscopía Electrónica del Noroeste Argentino, San Miguel de Tucumán, Argentina).

A stratigraphic section was measured in the levels where the fossil assemblage was found. This stratigraphic profile was compared with known sections of the Uquía Formation using main lithological and stratigraphic features, particularly those described in Castellanos (1950) and Reguero et al. (2007). On this basis we suggest possible correlations between these outcrops.

3. Geographic and geologic setting

3.1. Study area

The studied fossil remains were found at San Roque, 4 km SSW Humahuaca, Humahuaca Department, Jujuy Province, Argentina

(Fig. 1). This area is today under semiarid conditions, at 2900–3000 m elevation, and belongs to the Prepuna phytogeographical province (sensu Cabrera, 1976). The general landscape is characterized by steppe vegetation with scattered columnar cacti or "cardones" (*Trichocereus* spp.), low bushes, and small trees of "churqui" (*Prosopis ferox*) that can reach up to 3 m in height. The annual mean rainfall in Humahuaca town is 173 mm and the annual mean temperature is 12 °C (minimum mean 2.9 °C, maximum mean 22.5 °C; Buitrago and Larrán, 1994).

3.2. Geology

The Uquía Formation crops out in the Quebrada de Humahuaca, Jujuy Province, northwestern Argentina. A detailed description of the geology, stratigraphy, and fauna of this unit can be seen in Reguero et al. (2007). This unit is found in the context of Eastern Cordillera, usually lying unconformably over Cambrian–Ordovician sedimentary rocks and covered by Quaternary conglomerates and alluvium (Castellanos, 1950; Reguero et al., 2007). The formation is slightly faulted and folded and is mainly composed by siltstones, siltyclaystones, claystones, and sandstones interbeded with tuff and conglomerate beds related to fluvial deposits. Following the stratigraphic scheme of Castellanos (1950), Reguero et al. (2007) distinguished three units: the Lower Unit, characterized by sandy banks, thick conglomerates and a dacitic tuff; the Middle Unit, with more clayey-silt and sandy levels and a higher content of fossils; and the Upper Unit, mainly composed by levels of conglomerates. The Uquía Formation contains tuff horizons that have been dated using radimetric analyses (Marshall et al., 1982). The "Dacitic Tuff" of Castellanos (1950), which is a distinctive element of the Lower Unit, has been dated at Esquina Blanca in 3.54 Ma (Marshall et al., 1982). In the same locality Walther et al. (1998) determined for a second tuff (U1 tuff), about 180 m above the local base (Reguero et al., 2007), an age of 2.5 Ma. According to Reguero et al. (2007), this tuff coincides, in the Esquina Blanca section, with the limit between the Middle and the Upper units. The sum of evidences indicates that the age of the Uquía Formation can be referred for a span from middle Pliocene to early Pleistocene (Marshall et al., 1982; Cione and Tonni, 1995, 1996; Walther et al., 1996; Tonni and Cione, 2000; Reguero et al., 2007).

3.3. Description of the stratigraphic section

The stratigraphic section where the fossils here discussed were found begins with 10 m of well stratified reddish brown beds mainly composed of medium to coarse sandstones and pebbly conglomerates (Fig. 2). Sandstones often show planar lamination and some small lenses of conglomerates. Following this interval the sequence continues with about 70 m of light brown, reddish brown, and less pinkish very well stratified beds that show a reduction of the grain size. The lithology consists of fine to very fine sandstones interbeded with siltstones, claystones, and siltyclaystones, which constitute a fining upward pattern in some cases. Occasionally, some tuff beds are interbeded in the section and some silty sandstones show tuffaceous composition. Additionally, pebbly conglomerate lenses and conglomeratic sandstones are present but restricted to the upper levels of this interval. Sandstone and siltysandstone beds present parallel and cross lamination. Claystones locally present planar lamination and, in some cases, a massive aspect. Rootcasts are very common, more related to the finest sediments and, occasionally, to very fine to fine sandstone levels. Slickenslides are also present but occur locally in a claystone bed. The last 10 m are mainly composed of medium to fine sandstone beds with pebbles showing planar lamination, cross bedding, and cross lamination. Siltstone beds are less common and some of them present vegetal prints. The fossil assemblage was found in the upper levels of the measured section (Figs. 2 and 3), toward the top of a tabular-like bed of poorly consolidated medium to fine sandstone.
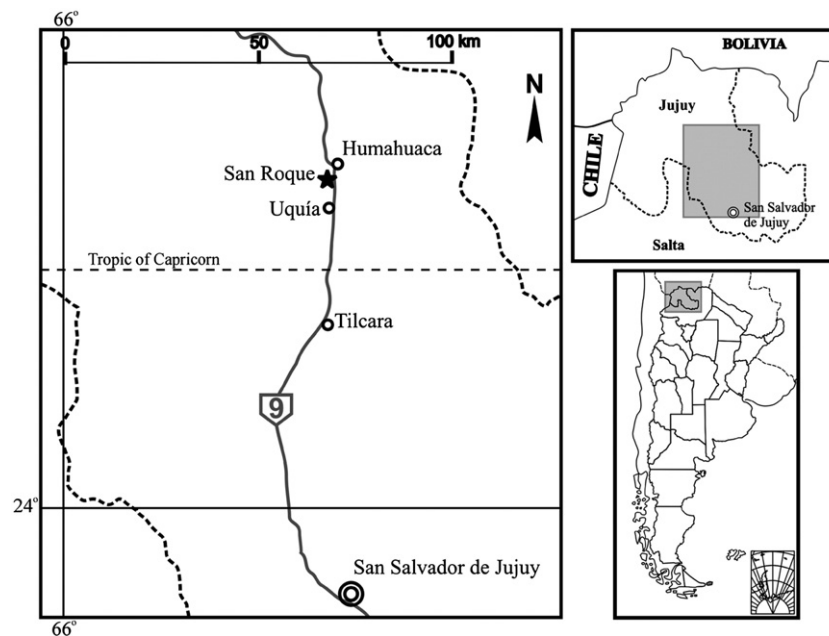
Fig. 1. Map of Humahuaca area showing the geographic location of San Roque, Jujuy Province, Argentina.

Locally, this level presents planar and cross lamination and is bounded at the sole and top by a very thin layer of silt. The assemblage consists of a high concentration of bony and dental material recovered in a small area, around 4 m² of surface and 0.3 m thick. The sedimentological features allow inferring for these levels longitudinal bar deposits, in which the fossil material would have suffered some minimum rework until it was finally buried.

4. Results

4.1. Taxonomy

The San Roque assemblage is constituted mostly by mammals (80% of all recorded taxa) and also includes one passeriform bird, one iguanoidea, and one anura. Among mammals the association is formed by marsupials (17%), caviomorph (25%) and sigmodontine rodents (58%). Considering the number of individuals, the sample is dominated by a single species of sigmodontine (Phyllotini gen. et sp. nov. 1), representing more than 50% of all recovered specimens (Table 1).

Class Amphibia Gray, 1825
Order Anura Fischer von Waldheim, 1813
Family Bufonidae Gray, 1825
cf. *Rhinella* Fitzinger, 1826
Fig. 4a, b

Referred specimens: 12 fragments of frontoparietals (PVL 6450), seven fragments of parasphenoids (PVL 6451), two pterygoids (PVL 6452), 12 fragments of prootic-exoccipital complex (PVL 6453), 67 vertebrae (PVL 6456), and seven atlas (PVL 6457).

Description: the frontoparietals have a convex lateral margin; the overall shape suggests that both frontoparietals contact each other along the sagittal plane, and consequently the frontoparietal fenestra was closed. The vertebrae are broad with a spinous medial margin.

Comments: these remains constitute the first record of an Anura for the Uquía Formation. Comparisons with living anuran groups indicate that these fossil pieces are referable to the family Bufonidae. Among the osseous synapomorphies proposed by Ford and Cannatella (1993) for Bufonidae, in the Uquian material we distinguish an "otic element", an independent ossification in the temporal region that fuses to the otic

ramus of squamosal (Griffiths, 1954). The Uquian fossils also show knobbed-shaped terminal phalanges, other feature that distinguishes Bufonidae.

Among South American bufonids, the fossils present more similarities with the genus *Rhinella*. According to Frost et al. (2006), most members of *Rhinella* have distinctive and expanded postorbital crest in older adult females. This genus differs from *Rhaebo* (*Bufo guttatus* group in Pramuk, 2006) by having a moderately prominent posterior process of the prootic (which is very prominent and notched in this last genus; see character 36 in Pramuk, 2006). *Nannophryne*, other South American genus, is clearly different from *Rhinella* and the fossils by the presence of an otic ramus of the squamosal not enlarged or overlapped with the prootic (Pramuk, 2006).

Other features that indicate strong affinities between the Uquian fossils and the genus *Rhinella* are the frontoparietal fenestra covered by the frontoparietal, the paired frontoparietal in both the parietal and frontal portions, ridges on the medial surface of parasphenoid corpus, and the presence of a spinous medial margin on the vertebrae. Nevertheless, it should be noted that most of the elements are more robust and larger than in living members of *Rhinella*, suggesting that it could be a new form with strong affinities with this extant genus.

Class Reptilia
Order Squamata Oppel, 1811
Suborder Iguanomorpha Sukhanov, 1961
Infraorder Iguania Cope, 1864
Superfamily Iguanoidea Oppel, 1811
Genus *Uquiasaurus* Daza et al., 2012
Uquiasaurus heptanodonta Daza et al., 2012
Fig. 4c

Referred specimens: complete premaxilla (PVL 6388), almost complete maxilla (PVL 6395), three right dentaries (PVL 6387, 6391, 6394), and three left dentaries (PVL 6389, 6392, 6393).

Description: heterodont dentition, including seven premaxillary, 17–18 maxillary, and between 18 and 21 heterodont teeth. The teeth are pleurodont, isodont, and cylindrical with blunt crowns. The premaxilla is overlapped laterally by the nasals. The maxilla presents a wide offset on the labial side of the posterior teeth. The ascending nasal process of the maxilla is located anterior to the
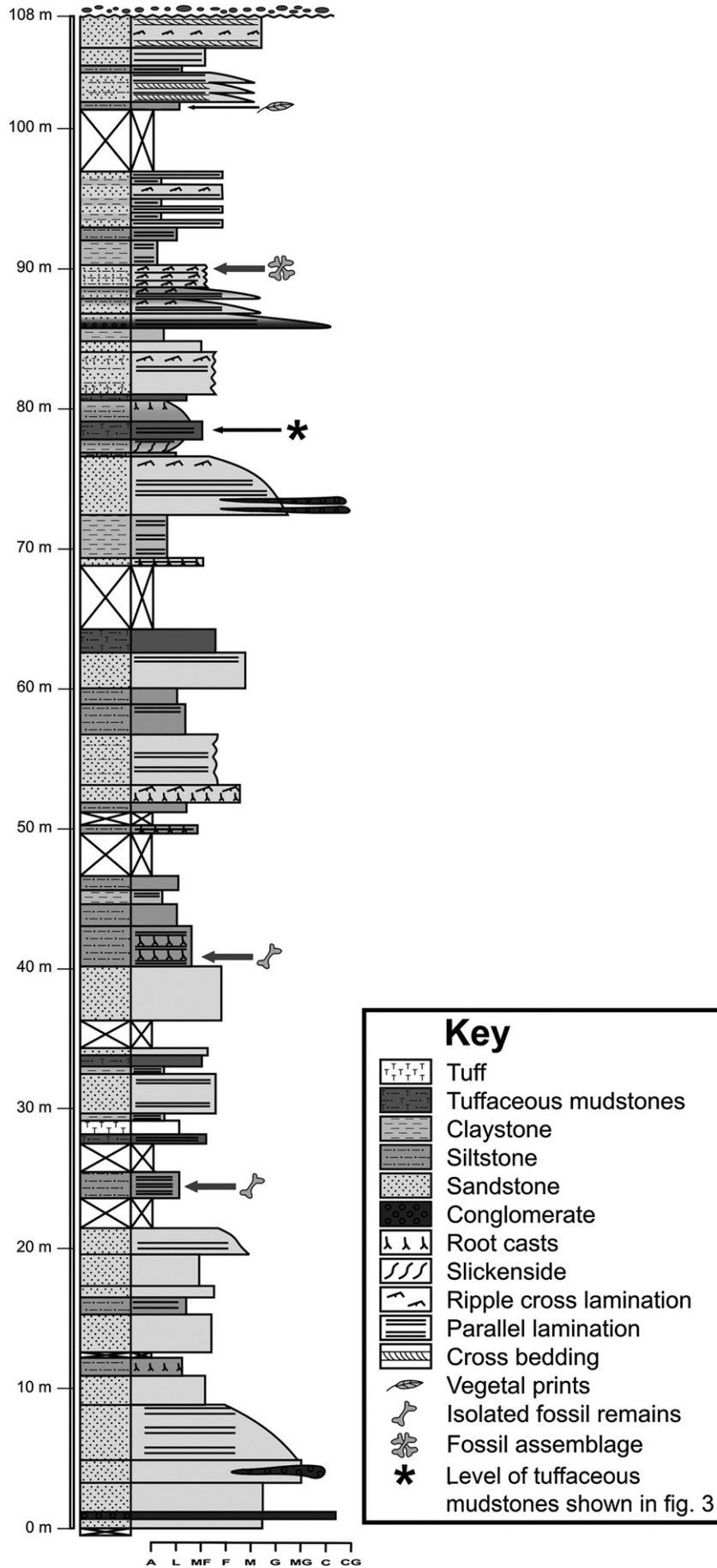
Fig. 2. Stratigraphic section of the bearing levels nearby San Roque, Jujuy Province, Argentina.
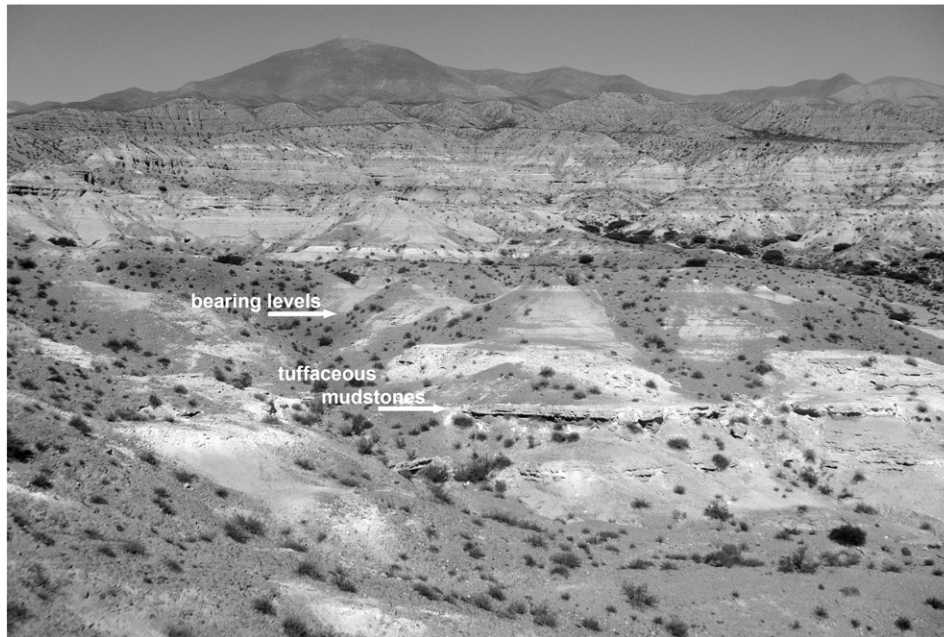
Fig. 3. Panoramic view of the fossil-bearing locality of San Roque (looking westward) showing the level containing the small vertebrate assemblage and a level of tuffaceous mudstones indicated in the stratigraphic section of Fig. 2.

midpoint of the maxilla. The dentary is a tubular and straight bone with the Meckelian canal entirely fused and no indication of a suture that has an opening anteriorly. For a detailed description of additional anatomical characters we refer to Daza et al. (2012).

Comments: these remains constitute the first record of a Squamata for the Uquía Formation The material exhibits several unique characters, such as the unusual number of premaxillary teeth and the overlapped ascending nasal process of premaxilla, which allowed the recognition of a new taxonomic entity (see Daza et al., 2012).

Class Aves Linnaeus, 1758
Order Passeriformes (Linnaeus, 1758)
Passeriformes indet.
Fig. 4d, e

Referred specimens: distal half of left humerus (PVL 6464), proximal fragment of right carpometacarpus (PVL 6465), proximal fragments of two left carpometacarpus (PVL 6466, 6501), distal fragment of left ulna (PVL 6467), distal fragment of right tibiotarsus (PVL 6468), two distal fragments of left tarsometatarsus (PVL 6469, 6500), and one ungual phalanx (PVL 6470).

Description: the humerus exhibits a well-developed hook-like dorsal supracondylar process. The dorsal condyle is narrow and well extended proximally. The ventral condyle is wide and its distal edge is convex. The brachial fossa is triangular and deep. The ventral epicondyle is located caudally and projects distally to the distal border of the ventral condyle. Proximal to the condyles, there is a marked and pointed tubercle probably related with the insertion of the M. extensor metacarpi radialis. The carpometacarpus presents a large and protruding extensor process, as high as the trochlea, and a deep fovea carpalis caudalis limited proximally by a small but prominent tubercle. The ulna has a rounded and distally prominent ventral condyle, separated from the dorsal condyle by a clear intercondylar sulcus. Both condyles in the tibiotarsus are narrow and elongated, with the supratendinal bridge located just above the intercondylar area. The differences in length among the trochleae metatarsorum II–IV are conspicuous. The ungual phalanx is very small and exhibits a clear neurovascular sulcus running along most of its length.

Comments: several humeral traits support the assignment of this element to Passeriformes (e.g., the development and position of the ventral epicondyle, the presence of the tubercle for the insertion of the M. extensor metacarpi radialis, and the features of the supracondylar process). Although the other elements recovered do not preserve diagnostic characters, their general morphology suggests that these remains could also belong to this group. This record
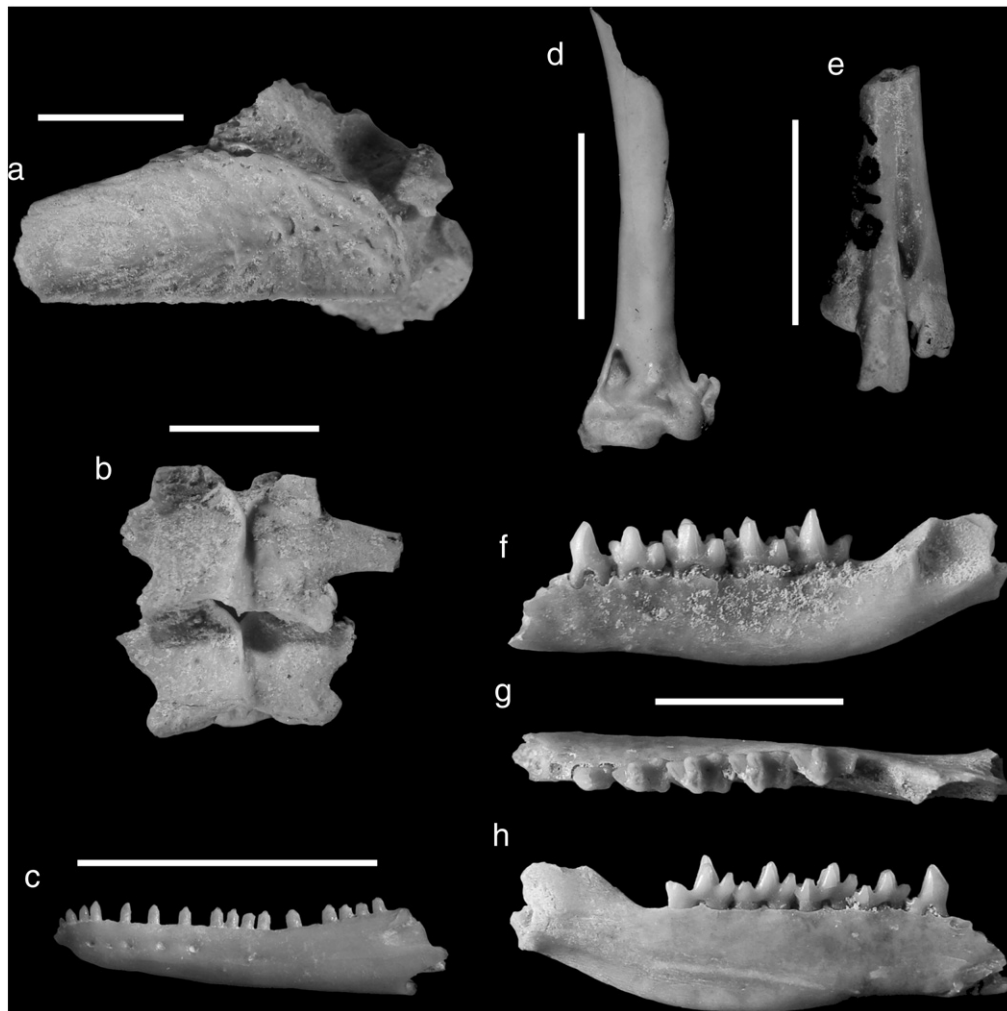
Table 1
NISP, NISP%, MNI, and MNI% for the taxa registered in the San Roque fossil assemblage, Uquía Formation, Province of Jujuy, Argentina.

Taxa	Uquía Formation (Late Pliocene)			
	NISP	NISP%	MNI	MNI%
Amphibia				
Anura				
Bufonidae				
cf. *Rhinella*	107	36.27	9	13.24
Reptilia				
Squamata				
Iguanoidea				
Uquiasaurus heptanodonta	8	2.71	3	4.41
Aves				
Passeriformes				
Passeriformes indet.	9	2.71	2	2.94
Mammalia				
Didelphimorphia				
Thylamyini indet.	4	1.36	2	2.94
Polydolopimorphia				
Microtragulus bolivianus	11	3.73	3	4.41
Rodentia				
Cricetidae				
aff. *Abrothrix*	4	1.36	2	2.94
aff. *Akodon*	10	3.39	5	7.35
Phyllotini gen. et sp. nov. 1	111	37.63	29	42.65
Phyllotini gen. et sp. nov. 2	5	1.69	3	4.41
Phyllotini gen. et sp. nov. 3	1	0.34	1	1.47
Sigmodontinae indet.	1	0.34	1	1.47
Caviidae				
Microcavia sp.	5	1.69	2	2.94
Ctenomyidae				
Ctenomys sp.	19	6.44	5	7.35
Octodontidae				
aff. *Neophanomys*	1	0.34	1	1.47
Total	296	100	68	100

Fig. 4. Fossil remains of anurans, lizards, birds, and marsupials recovered in the San Roque assemblage, Uquía Formation, Jujuy Province, Argentina. a, cf. *Rhinella*, right frontoparietal in dorsal view (PVL 6450); b, cf. *Rhinella*, intermediate vertebrae in dorsal view (PVL 6456); c, *Uquiasaurus heptanodonta*, left dentary in lateral view (PVL 6389); d, Passeriformes indet., distal half of left humerus in anterior view (PVL 6464); e, Passeriformes indet., distal fragment of left tarsometatarsus in anterior view (PVL 6469); f, Thylamyini indet., left mandible in lateral view (PVL 6375); g, Thylamyini indet., left mandible in occlusal view (PVL 6375); h, Thylamyini indet., left mandible in medial view (PVL 6375). Scale bar: 5 mm.

indicates an earlier presence of passers in South America than previously hypothesized (see Noriega, 1998, and references therein).

Class Mammalia Linné, 1758
Infraclass Metatheria T. H. Huxley, 1880
Supercohort Marsupialia Illiger, 1811
Order Didelphimorphia Gill, 1872
Family Didelphidae Gray, 1821
Thylamyini Hershkovitz, 1992
Thylamyini indet.
Fig. 4f, g, h; Table 2

Referred specimens: right maxilla with M1–3 (PVL 6376), right mandible with p2–m4 (PVL 6374), right mandible with m1–2 (PVL 6377), and left mandible with p3–m4 (PVL 6375).

Description: the mandible is deep and convex ventrally. In the upper molars the metacone is higher than the paracone and the stylocone is as large as the metastyle on M1 and M2, but is the largest stylar cusp on M3. The stylar cusp C is vestigial. The paracingulum does not contact with the preprotocrista. The ectoflexus is absent on M1 and deepens toward the M3. The lingual side of the trigon is wide and exhibits a tiny paraconule and metaconule on M3. On the lower molars the protoconid is dominant and the paraconid is the smallest cusp. The paracingulum is well developed and the talonid is shorter than the trigonid. The

hypoconid is dominant and is not labially projected. The entoconid is conical and almost as high as the hypoconid. The hypoconulid is low, situated close (not twinned) to the entoconid, and distally located.

Comments: based on Voss and Jansa (2009) and personal observations we include the Uquian remains in Thylamyini, discarding affinities with Didelphini, Metachirini, and Marmosini. The similarities with Thylamyini include the paracingulum unlinked with the preprotocrista on M3 (both structures in continuity on some Marmosini), the p2 and p3 subequal in height (p2 higher on some Didelphini, Metachirini and Marmosini), the hypoconid not labially salient on m3 (labially salient on Metachirini and some Marmosini), and a conical entoconid higher than hypoconulid on m1–m3 (subequal to or smaller than the hypoconulid on some Marmosini). Despite the numerous characters analyzed, a generic and specific assignation requires comprehensive comparisons that will be addressed on future contributions.

Order Polydolopimorphia Ameghino, 1897
Suborder Bonapartheriiformes Goin and Candela, 2004
Superfamily Argyrolagoidea Ameghino, 1904
Family Argyrolagidae Ameghino, 1904
Genus *Microtragulus* Ameghino, 1904
Microtragulus bolivianus Hoffstetter and Villarroel, 1974
Fig. 5; Table 2

Table 2
Dental measurements of Didelphimorphia and Polydolopimorphia recovered from San Roque, Jujuy Province (Uquía Formation, Late Pliocene). Intervals are indicated when the measurements are based on two specimens.

Character/measurement	Thylamyini indet.	*Microtragulus bolivianus*
Length M1–M3	5.57	–
Length M1	1.81	–
Width M1	1.50	–
Length M2	1.74	–
Width M2	1.83	–
Length M3	1.94	1.51
Width M3	2.10	1.41
Length M4	–	0.87
Width M4	–	0.71
Length i1	–	1.35–1.66
Width i1	–	0.59–0.70
Length i2	–	0.92
Width i2	–	0.63
Length p2	1.22	–
Width p2	0.58	–
Length p3	1.08–1.11	–
Width p3	0.65	–
Length p3–m4	7.63–7.87	–
Length m1–m4	6.70–6.73	5.77–6.44
Length m1	1.39–1.58	1.50–1.68
Width m1	0.90–0.94	1.14–1.27
Length m2	1.63–1.78	1.53–1.88
Width m2	1.08	1.49–1.61
Length m3	1.66	1.44–1.68
Width m3	1.22	1.34–1.47
Length m4	1.92	1.14–1.49
Width m4	1.06	1.08–1.19

Referred specimens: fragment of left maxilla with M3 and M4 (PVL 6261), right mandible with i1, alveoli of i2 and p3, and complete m1–4 (PVL 6259), right mandible with i1–2, alveolus of p3, and complete m1–4 (PVL 6260), anterior fragment of right mandible with i1 and alveoli of i2 and p3 (PVL 6265), four fragments of humeri (PVL 6443, 6444, 6445, 6446), two calcanei (PVL 6447, 6448), and complete right astragalus (PVL 6449).

Description: the mandibular body is short and high. The labial side exhibits two to three mental foramina, being the first one clearly

larger than the others. The lingual side shows several nutritious foramina and large fenestrae. The upper teeth have a simplified occlusal morphology. The lower incisors are procumbent. The molars have two lobes (trigonid and talonid) separated by a deep distolabial groove (present on m1–4) and a shallow distolingual concavity (present on the m3–4). The m1 presents a mesiolabial projection which is vestigial on the m2 and absent on the m3–m4. The m4 is reduced and exhibits a shallow distal concavity on the talonid.

Comments: the almost convex lingual side on the m1–2 and the reduced talonid on the m4 allow referring the material to *Microtragulus* (see Simpson, 1970). We assign these elements to *M. bolivianus* on the basis of its similar size and the presence on the m4 of a talonid reduced bearing a deep labial groove and a shallow distal concavity. The finding of well preserved cranial and postcranial elements of *M. bolivianus* adds new information on the anatomy of this marsupial, previously known solely by a mandibular fragment with m3–m4 (Hoffstetter and Villarroel, 1974).

Infraclass Eutheria T. H. Huxley, 1880
Order Rodentia Bowdich, 1821
Family Cricetidae Fischer, 1817
Subfamily Sigmodontinae Wagner, 1843
Tribe Abrotrichini D'Elía et al., 2007
aff. *Abrothrix* Waterhouse, 1837
Figs. 6a, and 7a; Table 3

Referred specimens: right maxilla with M1–M3 (PVL 6251), right maxilla with M1–M2 (PVL 6252), left mandible without teeth (PVL 6256), and left mandible without teeth (PVL 6360).

Description: the incisive foramina reach the level of the procingulum of the M1. The mandible is relatively slender, with the masseteric crest well developed and its anterior margin does not form a knob and does not reach the mandibular margin. The capsular projection is well developed and backward oriented. The molars are simplified, hypsodont, and with planate occlusal surface. The M1 has a well developed procingulum that exhibits lateral margins roughly parallel and anterior border remarkably straight, with no trace of anteromedian flexus, and a conspicuous parastyle. The
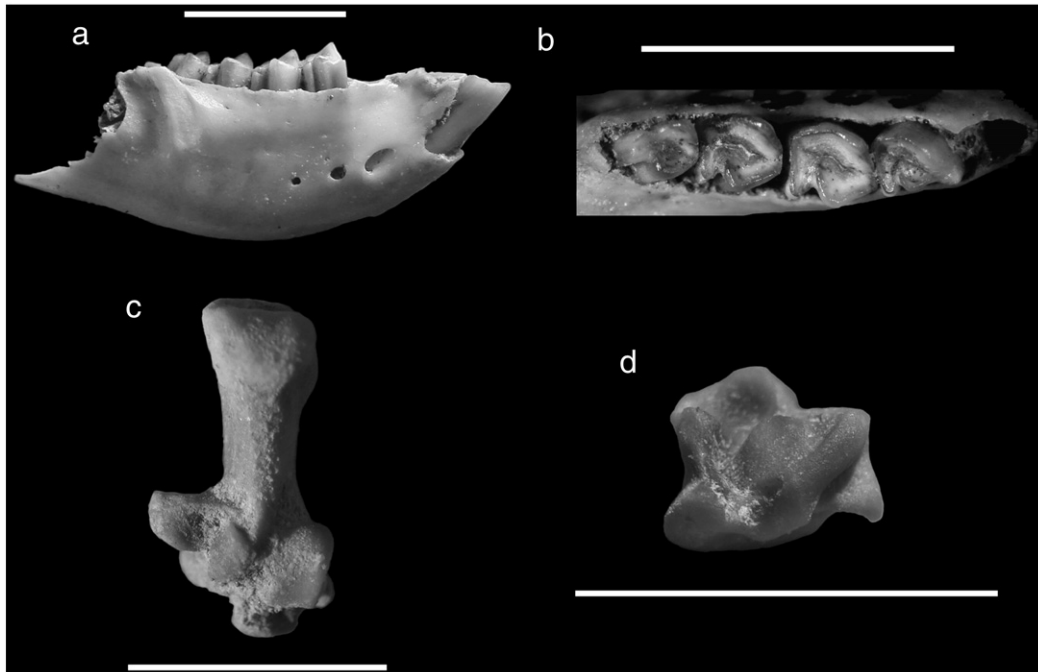

Fig. 5. Fossil remains of *Microtragulus bolivianus* recovered in the San Roque assemblage, Uquía Formation, Jujuy Province, Argentina. a, right mandible in lateral view (PVL 6259); b, detail of right m1–4 in occlusal view (PVL 6259); c, left calcaneum in dorsal view (PVL 6447); d, right astragalus in plantar view (PVL 6449). Scale bar: 5 mm.

anterior and median mures are displaced to the lingual side. In the M1 and M2 a mesoloph is observed. The M3 presents a subcircular outline and has an enamel island of central position.

Comments: many characters of the mandible and the molar morphology (such as the absence of anteromedian flexus in M1, the presence of parastyle and mesoloph in M1, the anterior and median mures displaced to the lingual side, and the M3 with a central enamel island) resemble those of larger representatives of *Abrothrix* (cf. Reig, 1987). However, the procingulum of M1 is not fan-shaped as described in the diagnosis of the tribe Abrotrichini (D'Elía et al., 2007). No member of the genera *Abrothrix* shows this feature, so that this Uquian Abrotrichini probably represents a new entity of generic rank. It is interesting to remember that abrotrichines are currently present in NW Argentina with forms distributed in forested (*Abrothrix illutea*) and high-altitude Andean areas (*Abrothrix jelskii*).

Tribe Akodontini Vorontzov, 1959
aff. *Akodon* Meyen, 1833
Figs. 6b, c, and 7b, c; Table 3

Referred specimens: right maxilla with M1–2 and zygomatic plate (PVL 6357), right maxilla with M1–M3 (PVL 6498), fragmentary left maxilla with M1 (PVL 6491), isolated M1 and M2 of the same individual (PVL 6358), two right mandibles with m1–m2 (PVL 6248, 6486), left mandible with m1–m2 (PVL 6249), fragmentary right mandible with m1 (PVL 6250), two right mandible without teeth (PVL 6263, 6359).

Description: the zygomatic plate is low, with the upper angle rounded and the anterior margin straight. The incisive foramina reach the level of the anterior wall of the protocone of the M1. The mandible is low and slender, with the diastema low and elongated. The masseteric crest is well developed, with the anterior margin
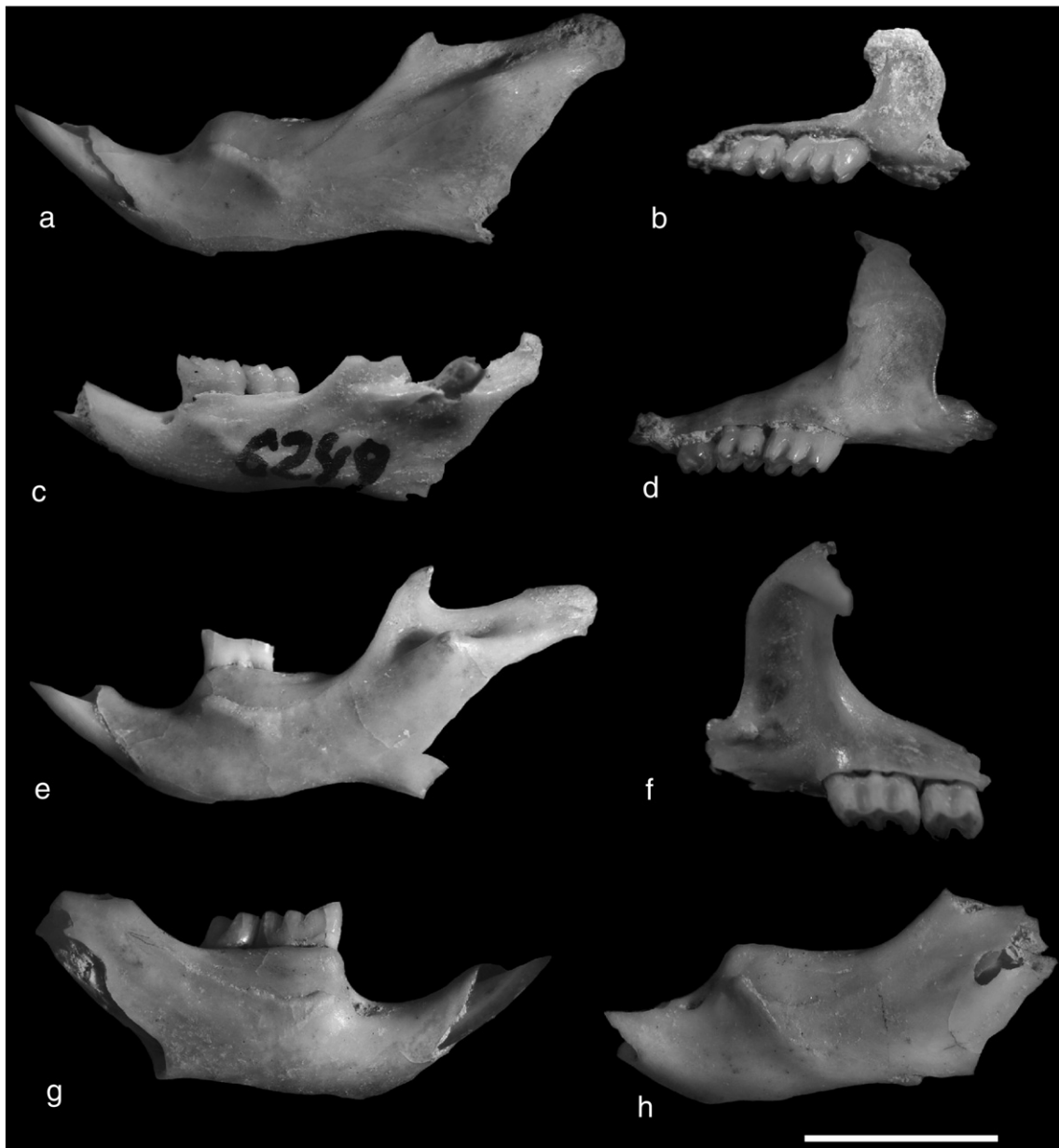

Fig. 6. Cranial and mandibular remains of sigmodontine rodents recovered in the San Roque assemblage, Uquía Formation, Jujuy Province, Argentina. a, aff. *Abrothrix*, left mandible in lateral view (PVL 6256); b, aff. *Akodon*, right maxilla in lateral view (PVL 6357); c, aff. *Akodon*, left mandible in lateral view (PVL 6249); d, Phyllotini gen. et sp. nov. 1, right maxilla in lateral view (PVL 6382); e, Phyllotini gen. et sp. nov. 1, left mandible in lateral view (PVL 6298); f, Phyllotini gen. et sp. nov. 2, left maxilla in lateral view (PVL 6257); g, Phyllotini gen. et sp. nov. 2, right mandible in lateral view (PVL 6253); h, Sigmodontinae indet., left mandible in lateral view (PVL 6262). Scale bar: 5 mm.
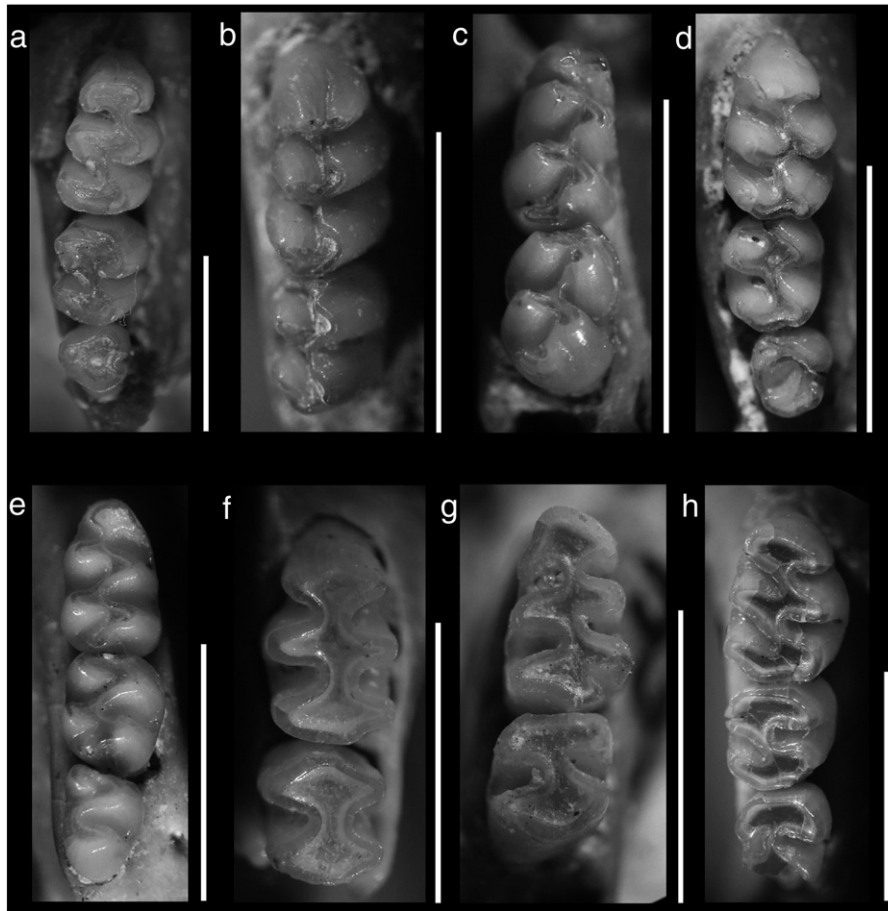
Fig. 7. Occlusal view of molar toothrow of the cricetid rodents recovered in the San Roque assemblage, Uquía Formation, Jujuy Province, Argentina. a, aff. *Abrothrix*, right upper M1–M3 (PVL 6251); b, aff. *Akodon*, right upper M1–M2 (PVL 6357); c, aff. *Akodon*, right lower m1–m2 (PVL 6263); d, Phyllotini gen. et sp. nov. 1, right upper M1–M3 (PVL 6326); e, Phyllotini gen. et sp. nov. 1, right lower m1–m3 (PVL 6295); f, Phyllotini gen. et sp. nov. 2, left upper M1–M2 (PVL 6257); g, Phyllotini gen. et sp. nov. 2, left lower m1–m2 (PVL 6264); h, Phyllotini gen. et sp. nov. 3, right upper M1–M3 (PVL 6258). The upper side of the figure corresponds to the anterior margin of the molar series. Scale bar: 3 mm.

thickened reaching the level of the procingulum of m1. The M1 exhibits a penetrant anteromedian flexus and the procingulum is more anteroposteriorly compressed than observed in the extant genus *Akodon*. The lower molars are terraced, with the cusps alternately disposed. As in the upper M1, the procingulum of m1 is also clearly antero-posteriorly compressed, and the anteromedian flexid is weakly expressed. The anterolabial cingulum arises from the anterior labial wall of the procingulum. A tiny mesolophid in m1 is present, originated from the anterior edge of the entoconid.

Comments: most of the craniodental features of the Uquian fossils, including the morphology of the zygomatic plate, the mandible, and the molars resemble those of *Akodon*, but some clear differences, such as shorter incisive foramina, a shallower diastema, the more anteroposteriorly compressed procingulum, and the position of the anterolabial cingulum in m1, preclude their unequivocal assignment to this genus. The combination of characters in these fossils indicates that they probably represent a genus of Akodontini not yet described closely related to *Akodon*.

Table 3
Dental measurements of the sigmodontine rodents recovered from San Roque, Jujuy Province (Uquía Formation, Late Pliocene). Media, standard deviation between parentheses, and sample size are given when necessary.

Character/measurements	aff. *Abrothrix*	aff. *Akodon*	Phyllotini gen. et sp. nov. 1	Phyllotini gen. et sp. nov. 2	Phyllotini gen. et sp. nov. 3	Sigmodontinae indet.
Length M1–M3	5.85	4.04–4.32	4.42 (0.0180) 24	5.10–5.26	–	–
Length M1	2.23–2.30	1.94 (0.09) 4	1.82 (0.116) 35	2.21 (0.05) 5	2.47	–
Width M1	1.37–1.49	1.51 (0. 40) 4	1.34 (0.083) 35	1.30 (0.07) 5	1.60	–
Length M2	1.63–1.75	1.28 (0.11) 3	1.28 (0.070) 31	1.45–1.48	1.40	–
Width M2	1.29–1.39	1.04 (0.05) 3	1.20 (0.085) 31	1.26–1.31	1.48	–
Length M3	1.07	0.85	0.089 (1.01) 18	–	–	–
Width M3	1.14	0.84	0.95 (0.074) 18	–	1.26	–
Length m1–m3	5.44	4.14 (0.19) 5	4.48 (0.127) 30	–	–	5.20
Length m1	–	1.78 (0.07) 5	1.93 (0.080) 38	2.03	–	–
Width m1	–	1.05 (0.06) 5	1.00 (0.05) 39	1.46	–	–
Length m2	–	1.40 (0.07) 3	1.36 (0.089) 29	1.42	–	–
Width m2	–	1.08 (0.02) 3	1.24 (0.052) 29	1.32	–	–
Length m3	–	–	1.04 (0.101) 17	–	–	–
Width m3	–	–	0.96 (0.056) 16	–	–	–

Tribe Phyllotini Vorontzov, 1959
Phyllotini gen. et sp. nov. 1
Figs. 6d, e, and 7d, e; Table 3

Referred specimens: left premaxilla and maxilla with incisor, M1–2 and zygomatic plate (PVL 6316), left premaxilla with incisor (PVL 6487), four right maxillae with M1–3 and zygomatic plate (PVL 6313, 6320, 6322, 6382), eight right maxillae with M1–3 (PVL 6318, 6319, 6326, 6327, 6339, 6340, 6362, 6379), eight left maxilla with M1–3 (PVL 6312, 6314, 6317, 6324, 6329, 6333, 6334, 6488), right maxilla with M1–2 and zygomatic plate (PVL 6328), two left maxillae with M1–2 and zygomatic plate (PVL 6323, 6325), eight right maxillae with M1–2 (PVL 6315, 6331, 6335, 6337, 6338, 6383, 6489, 6495), eight left maxillae with M1–2 (PVL 6311, 6330, 6336, 6341, 6484, 6485, 6493, 6496), right maxilla with M1 and zygomatic plate (PVL 6343), six right maxillae with M1 (PVL 6321, 6342, 6347, 6348, 6349, 6350), four left maxillae with M1 (PVL 6332, 6344, 6345, 6497), right maxilla with M2–3 (PVL 6346), left zygomatic plate (PVL 6351), three right mandibles with incisor and m1–3 (PVL 6295, 6275, 6277), four left mandibles with incisor and m1–3 (PVL 6280, 6381, 6378, 6480), two right mandibles with incisor and m1–2 (PVL 6266, 6479), ten right mandibles with m1–3 (PVL 6267, 6270, 6272, 6273, 6274, 6278, 6291, 6292, 6295, 6307), six left mandibles with m1–3 (PVL 6281, 6283, 6287, 6299, 6306, 6380), eight right mandibles with m1–2 (PVL 6269, 6271, 6288, 6290, 6294, 6303, 6309, 6483), ten left mandibles with m1–2 (PVL 6276, 6282, 6284, 6285, 6289, 6296, 6301, 6304, 6481, 6482), left mandible with incisor and m1 (PVL 6298), six right mandibles with m1 (PVL 6268, 6293, 6300, 6302, 6308, 6494), five left mandibles with m1 (PVL 6279, 6286, 6305, 6310, 6492), and left mandible (PVL 6297).

Description: the zygomatic plate is relatively broad, with its anterior margin straight or slightly convex. The incisive foramina extend posteriorly to the protocone of the M1. The masseteric crest reaches the level of the anterior border of m1 and forms a slight knob. The coronoid process has its apex exceeding the maximum height of the condyle. In the M1 of young individuals a trace of anteromedian flexus and a well developed second minor fold (sensu Hershkovitz, 1962) are observed. In the m1 a slightly developed anteromedian flexid is only present in young individuals. A moderate distoflexid (sensu Hershkovitz, 1993) is visible in the m2 of some young individuals. The m3 is proportionally large and has a very penetrating hypoflexid, more than in m1 and m2.

Comments: this small phyllotine bears a generalized morphology in the context of the tribe, without noticeable features and being only distinguishable from the living genera by a combination of characters (Ortiz et al., in press). The mandible clearly resembles that of *Calomys* but displays a markedly different dental pattern, closer to *Eligmodontia*, sharing with the latter genus the same degree of lophodonty and hypsodonty. This fossil phyllotine seems to have a putative transitional morphology between the generalized phyllotine condition, represented by *Calomys*, and the relatively specialized morphology of *Eligmodontia*. Comparisons carried out indicate that it belongs to an undescribed genus of Phyllotini morphologically related to *Eligmodontia*.

Phyllotini gen. et sp. nov. 2
Figs. 6f, g, and 7f, g; Table 3

Referred specimens: left maxilla with M1–2 (PVL 6257), right mandible with m1–2 (PVL 6253), left mandible with m1 (PVL 6254), isolated left m1 (PVL 6255), left mandible with m1–2 (PVL 6264).

Description: the zygomatic plate is high, relatively narrow, with its anterior margin straight. The incisive foramina reach posteriorly the level of the protocone of the M1. The mandible is relatively robust, with the masseteric crest surpassing the level of the anterior border of m1 but not reaching the mandibular margin. The molars present

plane occlusal surface and with the main cusps opposite and mures/murids parallel to the main axis of the teeth and of subcentral position. The labial and lingual flexi/flexids are almost opposite.

Comments: in spite of their smaller size, the general morphology of the fossils resembles that of the specialized genus *Chinchillula* in zygomatic plate, mandible, and molar pattern. However, *Chinchillula* has molars with mures/murids not so centrally situated and lacks the posteroflexid observed in the fossil material. Furthermore, the lower molars also resemble the morphology seen in *Auliscomys*, particularly the shape of the procingulum at the m1. However, the set of features is unique among phyllotines and justifies the recognition of a new taxonomic entity of generic rank.

Phyllotini gen. et sp. nov. 3
Fig. 7h; Table 3

Referred specimens: right maxilla with M1–3 (PVL 6258).
Description: the molars show the occlusal surface planate and simplified, with lophs and flexi somewhat oblique. The flexi are penetrating, reaching the midline of the teeth. In the M1 there are no evidences of both anteromedian flexus and posteroflexus. The M2 shows the anterior wall straight and the hypoflexus transverse and broad along all their longitudes. The M3 is large, with the hypoflexus transverse and very penetrating, crossing beyond the midline and more obliquely oriented than in M1 and M2.

Comments: at first glance the M1 appears as that observed in *Auliscomys* but in this genus the hypoflexus is obliquely oriented, forward directed, and their apex is pointed. Furthermore, in *Auliscomys* the M2 has a well developed anteroflexus and the M3 is conspicuously smaller than M2, showing a hypoflexus less developed. This fossil is very interesting because it also resembles *Loxodontomys*, an example of involution in molar modeling process (Hershkovitz, 1962: 93). *Loxodontomys* is sister to *Auliscomys* according molecular-based phylogenies (see D'Elía, 2003). The unique and intermediate molar morphology justify considering this material as a new genus and species of Phyllotini.

Sigmodontinae indet.
Fig. 6h; Table 3

Referred specimens: left mandible without teeth (PVL 6262).
Description: the mandible is deep and robust. The masseteric crest is well developed, with its anteriormost point forming a knob that does not reach the mandibular margin, well above the level of the mental foramen. This foramen is visible in lateral view.

Comments: the shape, position and development of the masseteric crest are not seen in any genus of Phyllotini and Akodontini. Although it is highly probable that this material corresponds to a new genus and species of Sigmodontinae, the preserved features are insufficient to a reliable taxonomic assignation.

Suborder Hystricomorpha Brandt, 1855
Family Caviidae Fischer, 1817
Genus *Microcavia* Gervais and Ameghino, 1880
Microcavia sp.
Figs. 8a, b, c, and 9a, b; Table 4

Referred specimens: right maxilla with P4–M2 (PVL 6353), right mandible with p4 (PVL 6490), left mandible with p4–m2 (PVL 6352), left mandible without teeth (PVL 6355), isolated molars (PVL 6356).

Description: the anterior margin of the P4 is situated at the same level that the anterior border of the zygomatic arch. The P4, M1 and M2 share a similar morphology, with a penetrant hypoflexus and a poorly developed external flexus. The anterior end of the masseteric crest is situated at the level of the first prism of the m1. The p4 is smaller than the m1 and m2; its first prism has an additional anterior lobe of poor transverse development. The second prism of p4–m2 has

a penetrant internal flexid. In the three lower teeth there is interprismatic cement.

Comments: all features of the Uquian specimens are typical of *Microcavia*, excepting the interprismatic cement in lower teeth, a feature only shared with one Late Miocene specimen coming from Catamarca Province, the oldest record for the genus (Nasif et al., 2007). The fossil record of *Microcavia* in northwestern Argentina is poor, restricted to the Late Miocene of Catamarca (Nasif et al., 2007), the Middle Unit of Uquía Formation in Esquina Blanca (Reguero et al., 2007), and Late Pleistocene levels of central Catamarca (Ortiz et al., 2011b).

Family Ctenomyidae Lesson, 1842
Genus *Ctenomys* Blainville, 1826
Ctenomys sp.
Figs. 8d, e, and 9c, d; Table 4

Referred specimens: right premaxilla with incisor (PVL 6474), two left premaxillae with incisor (PVL 6370, 6475), left premaxilla (PVL 6476), maxilla with right P4–M2 and left M1–M2 (PVL 6473), maxilla with right P4–M2 and left P4 (PVL 6472), left maxilla with P4 (PVL 6369), two right mandibles with incisor and p4–m3 (PVL 6363, 6471), right mandible with incisor and p4–m2 (PVL 6365), left mandible with incisor and p4 (PVL 6364), left mandible with m2 (PVL 6366), left premaxilla with incisor (PVL 6367), right mandible with p4–m2 (PVL 6368), left mandible with incisor and p4–m3 (PVL 6371), left mandible with incisor and p4–m1 (PVL 6362), left mandible without teeth (PVL 6477, 6478), and nine isolated molars (PVL 6373).

Description: the distance between the anterior margin of the alveolus of P4 and the premaxillo-maxillary suture is short, less than the P4 length. The anterior root of the zygoma is narrow anteroposteriorly and is situated at the same level than the P4. The lower diastema is less concave and longer than in living species. The masseteric crest is descending backward, more than modern *Ctenomys*. The P4–M2 and p4–m2 are kidney-shaped and the m3 is reduced.

Comments: Walther et al. (1996) indicate the presence of *Ctenomys* sp. for the Uquía Formation on the base of one specimen from San Roque and two from Esquina Blanca. They pointed out some differences between these specimens and *Ctenomys chapalmalensis*, a guide fossil of the Sanandresian (zone of *Paractenomys chapadmalensis*; Cione and Tonni, 1995), but indicated a similar "evolutionary state" on the base of several primitive features. Reguero et al. (2007) mentioned ten specimens of *Ctenomys* for the Middle Unit of the Uquía Formation, highlighting one specimen recovered in San Roque (the MLP 90-XII-4-2), and referred them to *C. chapalmalensis*. Verzi et al. (2009) described the species *Ctenomys uquiensis* for the Lower Unit of the same outcrops, on the base of two fragmentary specimens (MLP 96-II-29-1 and MLP 96-II-29-2), apparently none of those referred by Reguero et al. (2007) when cited *C. chapalmalensis*. Further comparisons are needed in order to determine if the material here studied belongs to any of the mentioned forms or it represents a new entity.

Family Octodontidae Waterhouse, 1839
aff. *Neophanomys*
Fig. 9e

Referred specimens: isolated upper molar (PVL 6361).
Description: The tooth is hypsodont, with flattened occlusal surface, and is formed by two lobes separated by the hypoflexus and a relictual mesoflexus. The anterior lobe is more transversely expanded than the posterior. There is a rounded mesofossette situated next to the level of the isthmus connecting the two lobes.

Comments: the material here presented is the first record for an octodontid in the Uquía Formation. The molar morphology resembles that of the specimen MACN A-1644 figured by Verzi and Carrín Iglesias (1999) and referred as aff. *Neophanomys biplicatus*, from Farola Monte Hermoso, Buenos Aires Province, Early–Middle Pliocene. However, the San Roque specimen is conspicuously larger
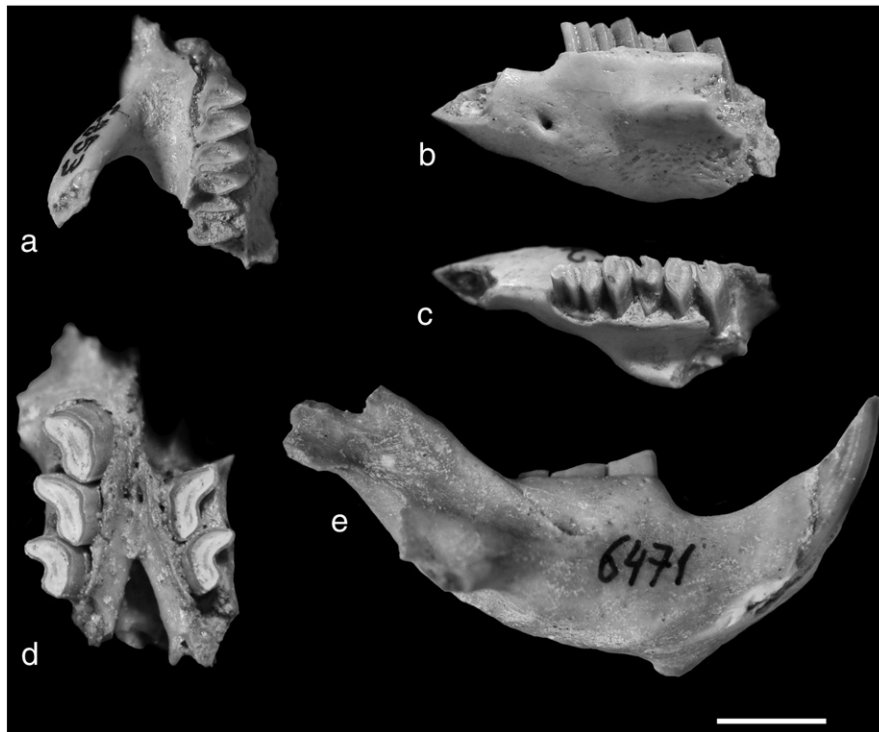

Fig. 8. Cranial and mandibular remains of the caviomorph rodents recovered in the San Roque assemblage, Uquía Formation, Jujuy Province, Argentina. a, *Microcavia* sp., right maxilla in palatal view (PVL 6353); b, *Microcavia* sp., left mandible in lateral view (PVL 6352); c, *Microcavia* sp., left mandible in dorsal view (PVL 6352); d, *Ctenomys* sp., palatal region of skull (PVL 6473); e, *Ctenomys* sp., right mandible in lateral view (PVL 6471). Scale bar: 5 mm.
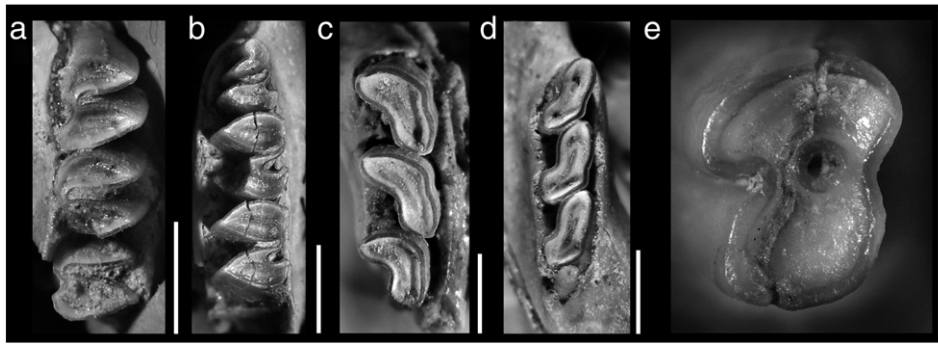
Fig. 9. Occlusal view of molariform teeth of the caviomorph rodents recovered in the San Roque assemblage, Uquía Formation, Jujuy Province, Argentina. a, _Microcavia_ sp., right upper P4–M2 (PVL 6353); b, _Microcavia_ sp., left lower p4–m2 (PVL 6352); c, _Ctenomys_ sp., right upper P4–M2 (PVL 6473); d, _Ctenomys_ sp., right lower p4–m3 (PVL 6471); e, aff. _Neophanomys_, isolated left upper molar (PVL 6361). Scale bar: 3 mm.

(anteroposterior diameter = 2.32 mm, transverse diameter = 1.73, against 1.55 and 1.41 mm, respectively, of the Farola Monte Hermoso specimen), so that their membership to a new taxonomic entity of generic rank should not be discarded. _Neophanomys biplicatus_ has been mentioned for the Late Miocene of the northwestern Argentina (Marshall and Patterson, 1981) and for Late Miocene–Early Pliocene levels in the central area of this country (Verzi et al., 1991, 2011). Tauber (2005) considered that the stratigraphic distribution of _N. biplicatus_ would include the Huayquerian and Montehermosan ages. A taxonomic review of the octodontids related to _Neophanomys_ is still needed.

4.2. Taphonomy

Virtually all skeletal elements were recovered, showing good preservation conditions and a relatively high integrity, being concentrated in a high areal density. Small mammal cranial and postcranial bones were the most abundant and best preserved remains in the assemblage. Weathering evidences are scarce, suggesting that the remains only would have been exposed for a short time. Taphonomic features related to pedogenetic processes such as marks produced by roots, soil acids, and microorganisms were not observed. A relatively high proportion of incisors, 44% of 92 examined, showed evidences of slight corrosion (according to Andrews, 1990), mainly concentrated at the tip of these teeth.

Table 4
Dental measurements of the caviomorph rodents _Microcavia_ and _Ctenomys_ recovered from San Roque, Jujuy Province, Argentina (Uquía Formation, Late Pliocene). Media, standard deviation between parentheses, and sample size are given when necessary. For the specimen determined as aff. _Neophanomys_ see text.

Character/measurements	_Microcavia_ sp.	_Ctenomys_ sp.
Length P4	2.77	3.07–3.54
Width P4	2.31	1.60–1.76
Length M1	2.40	3.16–3.58
Width M1	2.33	1.42–1.50
Length M2	2.45	2.72–2.85
Width M2	2.34	1.33–1.36
Length M3	–	–
Width M3	–	–
Length p4–m3	–	9.68
Length p4	2.34–2.50	2.72 (0.34) 5
Width p4	1.96	1.38 (0.19) 5
Length m1	2.90	2.74 (0.39) 4
Width m1	2.31	1.46 (0.23) 4
Length m2	3.80	2.64–3.06
Width m2	2.50	1.32–1.65
Length m3	–	0.92–0.96
Width m3	–	0.82–0.98

5. Discussion

5.1. Chronology

The main lithological features observed in the measured interval indicate a section characterized by the predominance of sandy and clayey-silt levels locally interbedded with tuff horizons, scarce occurrence of coarse-grained sediments, and relatively abundant fossil content. This lithological pattern matches with that described by Reguero et al. (2007) for the Middle Unit of Uquía Formation at the locality of Esquina Blanca, and suggests a probable correspondence with this unit. Nevertheless, since Uquía Formation is faulted and folded, and that the outcrops of San Roque and Esquina Blanca are distant by about 5 km, this relationship cannot be completely confirmed. Taking onto account this possible stratigraphic equivalence, the chronological implicances should be properly evaluated. The Middle Unit was assigned to the Vorohuean and Sanandresian subages of the Marplatan age by Reguero et al. (2007), who also indicated that the Barrancalobian subage is not represented at Uquía Formation. These authors stated that the top of the Middle Unit is marked by the "U1 tuff," dated in ~2.5 Ma, implying that this unit could be restricted to a span between around 3 Ma (i.e., the currently recognized lower limit of the Vorohuean) and 2.5 Ma. This age is coincident with the GABI 1 stage (see Woodburne, 2010), which represents the first major dispersal event between North and South America and is characterized by the arrival of a great number of Holarctic taxa to South America. Thus, if the inferred stratigraphic correlation is true, the age of the San Roque microvertebrate assemblage could be bracketed between 3 and 2.5 Ma. Nevertheless, more data are necessary to confirm this situation.

5.2. Taphonomy

Corrosion marks in the tip of incisors constitute unequivocal evidence that the genesis of the assemblage is related to the trophic activity of predator birds. The frequency of affected incisors allows including the assemblage in the second category of Andrews (1990), suggesting that the association was generated as an accumulation of owl pellets. At the same time, the good preservation and integrity of the remains allow discarding carnivore mammals or diurnal birds as producing agents, because these predators heavily broke and corrode bones and teeth (see Andrews, 1990). Owls are the most important contributors to the formation of microvertebrate fossil assemblages (Andrews, 1990; Fernández-Jalvo and Andrews, 1992; Fernández-Jalvo et al., 1998). The high concentration of bones in a very small area and the thinness of the fossiliferous level (and, to some extent, the fact that this assemblage was produced by strigiform birds), strongly suggest that the assemblage was formed in a short lapse (i.e., low time averaging). So, these faunal elements would

have been really contemporary, retaining the ecological signals of the living community (see Terry, 2010).

5.3. The Uquian small vertebrates

Excepting mammals, the finding of small vertebrates in Pliocene deposits of Argentina is an occasional fact. This is probably related to taphonomic processes (e.g., differential preservation of small and fragile bones) and the preferences of the predator involved in the accumulation. The fossil record of amphibian for the latest Neogene is relatively well known but it is nearly restricted to the Montehermosan and Chapadmalalan units from Buenos Aires province (Reig, 1958; Casamiquela, 1967; Gasparini and Báez, 1975; Cione and Báez, 2007). The finding of a bufonid related to *Rhinella* in deposits of the Uquía Formation in the central Andean region will allow having a broader view on the diversity and distribution of this group during Marplatan times. The Neogene iguanoid record in South America includes several species from the Miocene (Albino, 1996, 2008) and Pleistocene of Argentina (Van Devender, 1977; Albino, 2005, 2008 and references therein). However, excepting for a fragment assigned to Iguania indet. recovered at Saldungaray Formation (Late Miocene–Early Pliocene) of Buenos Aires Province (Deschamps, 2005), nothing was known until now about fossil lizards from Montehermosan, Chapadmalalan, and Marplatan ages. The discovery of *Uquiasaurus* in Late Pliocene increases the knowledge of the morphological diversity, evolution, and phylogenetic relationships of iguanoids (see Daza et al., 2012). Fossil passeriform birds are very rare in Neogene and Pleistocene of South America. Up to now, Pliocene deposits of Buenos Aires Province yielded only four isolated pieces assigned to suboscine passerines from the Sanandresian, Barrancalobian and Vorohuan (Tambussi, 1995; Noriega, 1998). The elements recovered at the Uquian levels show some resemblances with members of oscine passeriforms, suggesting that this group would have reached South America before previously though. Further studies on these non mammalian Pliocene small vertebrates and the finding of additional key fossils are essential to understand the historical development of these groups during the last 5 Ma. At the same time, these fossils constitute invaluable elements to infer divergence times of their respective living lineages, many of whose phylogenies are mainly based on molecular data with weak calibrations based on fossils (Santos et al., 2009; Weir et al., 2009).

The record of Late Miocene small mammals in South America is constituted almost exclusively by caviomorph rodents and marsupials (e.g., Tonni et al., 1992; Nasif, 1998; Cione et al., 2000; Goin et al., 2000; Herbst et al., 2000; Abello et al., 2002; Verzi et al., 2003; Nasif et al., 2007). The putatively Late Miocene assemblage of Caleufú, in central Argentina (Abello et al., 2002; Verzi and Montalvo, 2008; Verzi et al., 2008; see Prevosti and Pardiñas, 2009 who suggested a Pliocene age for this locality) provided a rich record of small mammals, showing a clear dominance of didelphids and small caviomorphs (octodontids, caviids, ctenomyids, and echymids). Small marsupials and caviomorphs are also continuously recorded during the Pliocene and Pleistocene (e.g., Hoffstetter and Villarroel, 1974; Goin et al., 1994; Fernández et al., 2000; Verzi and Quintana, 2005; Vucetich et al., 2005) together with cricetids (Pardiñas et al., 2002). The Montehermosan–Marplatan record of cricetids is scarce and represented by isolated remains coming exclusively from the Pampean region (Reig, 1978, 1987, 1994; Pardiñas, 1997; Pardiñas and Tonni, 1998; Steppan and Pardiñas, 1998; Pardiñas et al., 2002; Verzi and Montalvo, 2008; Prevosti and Pardiñas, 2009). These rodents underwent a particular increase in abundance and diversity just since the Ensenadan (Lower–Middle Pleistocene) (Pardiñas, 1995; Pardiñas and Lezcano, 1995; Pardiñas, 1999; Voglino and Pardiñas, 2005), then becoming the most conspicuous components of modern small mammal communities (Pardiñas et al., 2010). For example, Caleufú assemblage retrieved solely two cricetid fragments over a total sample of

2257 specimens collected (Verzi and Montalvo, 2008). In the same line of argumentation, about two centuries of paleontological work at Chapadmalal Formation outcrops produced <50 cricetid specimens over hundred of thousands of fossils (Reig, 1972; Pardiñas, 1999). The San Roque assemblage constitutes the oldest microvertebrate fossil association in South America with a clear predominance of cricetids over caviomorphs and marsupials, showing the beginning of a trend that remains today. In this context, despite the clear taxonomic differences at specific and generic levels, with only three extant mammal genera recorded, the structure of the fossil assemblage is ecologically comparable to modern small mammal communities in terms of body mass distribution, trophic structure and abundance.

5.4. Small mammal turnover

One interesting issue arises when the moment and specific causes of the striking faunal turnover in small mammal communities are invoked. Today, the assemblages from central and southern latitudes of South America have a clear dominance of cricetid rodents in virtually all types of habitats (e.g., Pardiñas et al., 2003; Vargas and Simonetti, 2004; Yahnke, 2006; Pardiñas et al., 2008; Teta et al., 2009; Ortiz et al., 2010). These rodents are key elements in the structure of the modern communities due to its role in the dynamic of the ecosystems through several trophic specializations, including its position in trophic chains and its role as seed dispersers. The Late Miocene Caleufú assemblage is clearly dominated by caviomorphs, which would have occupied the microherbivorous/granivorous trophic niche of >100 g small mammals (Verzi and Montalvo, 2008; Verzi et al., 2008). In this context, the niche occupied by smaller or tiny microherbivorous/granivorous small mammals would have virtually been empty during most of the Cenozoic (but see Antoine et al., 2012, for recently discovered tiny caviomorphs from middle Eocene). Although cricetids were already present during the Pliocene, they were inconspicuous elements in the communities, contrasting with a much richer record for caviomorphs (Reig, 1978, 1980, 1987; Pardiñas et al., 2002, and references therein). The best known record for Pleistocene deposits already shows a clear dominance of cricetids, both in Pampean and northwestern Argentina regions (Pardiñas et al., 2002, and references therein; Teta and Ortiz, 2002; Ortiz and Jayat, 2007; Ortiz et al., 2011a, 2011b). Thus, the fossil evidence indicates that this striking shift in the structure of small mammal communities would have occurred at some point between the Chapadmalalan and the Sanandresian. If this turnover was caused by the Late Pliocene global cooling and drying event (Ravelo et al., 2004; Vizcaíno et al., 2004; see Section 5.6) and how the ecosystems were affected are questions that the inaccuracies in the fossil record do not allow them to be answered yet. Interestingly, the exploitation of this new niche may have played an important role in the community structure of the newcomer placental predators that arrived in the early phase of the GABI. New fossil collections will provide a more complete picture of this noteworthy turnover and their causes.

5.5. Comparison with other assemblages

In order to place the San Roque assemblage in a biogeographical and temporal context, it is necessary to compare it with contemporary Bolivian and central Argentina fossiliferous deposits. Some Pliocene paleontological sites in Bolivia have shown a rich mammal fauna, such as the Umala Formation, dated between 5.4 and 2.8 Ma (Evernden et al., 1977; Lavenu et al., 1989; Marshall et al., 1992), where many fossil mammals (mainly medium to large forms) have been recognized. The record of small mammals in this unit is scarce, but the presence of the argyrolagid *M. bolivianus* and an undetermined ctenomyinae and caviinae rodents, also recorded in the Uquian assemblage, should be noted. *M. bolivianus* is the only argyrolagid known for highland regions, so its record in the Humahuaca area by the end of the

Pliocene suggests the presence of a biogeographic connection of high altitude environments between northwestern Argentina and central Bolivia. In other Bolivian units roughly contemporary to Umala Formation, such as La Paz, Mauri, and Remedios formations (Hoffstetter et al., 1972; Lavenu et al., 1989; Marshall et al., 1992), the record of micromammals is virtually null.

More similarities are observed among the San Roque sample and those recorded from the classic deposits along the Atlantic coast of Buenos Aires Province, central Argentina. These assemblages share the presence of small thylamyines, *Microtragulus*, and the caviomorphs *Microcavia* and *Ctenomys*. *Thylamys* is the most common genus of Thylamyini in Late Miocene to Pleistocene levels of the Pampean region, represented in the Pliocene by *T. contrerasi* (Mones, 1980; Goin, 1995, 1997; Goin et al., 2000). Most of the fossil record for *Thylamys* comes from lowland localities; thus, the fossil of Uquía is the first one known from highlands areas and documents that this genus was already established in the central Andes at the end of the Pliocene. Today, *Thylamys* displays an important diversity in northwestern Argentina, being represented by *T. pallidior*, *T. venustus*, *T. sponsorius*, and *T. pusillus* (Flores et al., 2007). Among the distributional range of these taxa in northwestern Argentina, that of *T. pallidior* comprises arid and open areas higher than 1500 m. Regarding Argyrolagidae, the only genus of this family in the Pampean region whose temporal range extends to the Late Pliocene (Marplatan) is *Microtragulus*, represented by *M. reigi*, also mentioned for the Chapadmalalan (Goin, 1995). On the other hand, the extant caviomorphs *Microcavia* and *Ctenomys* have a continuous record in the Pampean area since the Pliocene. While remains of *Microcavia* have been recovered since the Montehermosan, being well known in the Marplatan, the oldest record of *Ctenomys* in this area comes from this last stage, about 1 Ma after of the recently described *C. uquiensis* from the Lower Unit of the Uquía Formation (Verzi and Quintana, 2005; Verzi et al., 2008).

The pre-Quaternary record of cricetids in Northwestern Argentina is restricted to one dubious fragmented molar coming from Late Miocene levels of Catamarca Province (Nasif et al., 2009). This virtual absence is remarkable considering that these mammals are continuously recorded in central Argentina since, at least, early Pliocene times (Reig, 1978; Pardiñas and Tonni, 1998; Pardiñas et al., 2002 and references therein). So, this absence seems to be a clear bias due to sampling techniques focused mainly on the search of medium and large-sized mammals. Excepting the dubious Miocene record, all the fossils of this group in northwestern Argentina are restricted to Middle-Late Pleistocene to Late Holocene (Ortiz et al., 2000, 2011a, 2011b, 2012; Ortiz and Pardiñas, 2001; Teta and Ortiz, 2002; Ortiz and Jayat, 2007).

The clear differences in taxonomic composition between the Uquian sigmodontines and the contemporary record from central Argentina suggest biogeographical distinctions in a similar grade than that present today. Certain particularities of the Uquian assemblage reinforce this idea, such as the dominance of a small phyllotine and the remarkable absence of *Reithrodon auritus*—frequently recovered in Pliocene Pampean outcrops (Pardiñas, 1995, 1999; Pardiñas and Galliari, 2001; Pardiñas et al., 2002)—and other genera recorded for Late Pliocene in central Argentina (e.g., *Akodon*, *Abrothrix*, *Necromys*, *Auliscomys*, *Graomys*). Precisely, Pardiñas (1995, 1997) proposed that the small phyllotines, such as *Eligmodontia* and *Calomys*, would have reached the Pampean region in the Ensenadan stage (lower–middle Pleistocene), when they have their first record and become predominant. Thus, the dominance of a small phyllotine in Pliocene outcrops of northwestern Argentina contrasts with the record of this tribe for Chapadamalalan (lower and middle Pliocene) and Marplatan (upper Pliocene and lower Pleistocene) in the Pampean region, characterized by medium to large size forms.

Phyllotines and akodontines constitute the main groups of sigmodontines distributed along the Central Andean region. According to this, Reig (1986) indicated that the area of original differentiation

of these groups would have been located in the Andes of southern Peru, southwestern Bolivia, northern Chile and northwestern Argentina. Spotorno et al. (2001), based on cytogenetic data, supported the hypothesis of Reig indicating a diversification of the ancestral phyllotine from this Andean area toward the south and the north, also suggesting this same diversification pattern for several polytypical living genera such as *Calomys*, *Eligmodontia*, and *Phyllotis*. The assemblage of Uquía Formation suggests that the central Andes represented an area of high diversity for the phyllotines during Late Pliocene, with the occurrence of several extinct genera. Moreover, this scenario suggests that the early divergence times for lineages leading to living phyllotine genera indicated by several authors (e.g., Salazar-Bravo et al., 2001; Almeida et al., 2007; Steppan et al., 2007; Mares et al., 2008) have been somewhat overestimated. On the basis of the absence in Uquian sediments of currently specious and broadly distributed sigmodontines (e.g., *Necromys*, *Calomys*, *Eligmodontia*, and *Phyllotis*), our data suggest a possible significantly later diversification for these living genera that usually stated using molecular clocks. It is important to note that the oldest record for *Calomys*, *Eligmodontia*, and *Phyllotis* comes from the Ensenadan (Pardiñas et al., 2002), all in the Pampean region, providing additional support to the hypothesis that these genera would have not yet differentiated for Late Pliocene times around 3 Ma ago.

5.6. Paleoecology

The fossil evidence from Uquía Formation reported in literature suggests a warmer and more humid environment than the present conditions in the area. This evidence is based on the record of medium and large mammals such as Hydrochoeridae, Gomphotheriidae, Tayassuidae, Camelidae, Cervidae, and Equidae (e.g., Kraglievich, 1934; Castellanos, 1950; Prado et al., 1998, 2000; Walther et al., 1998; Tonni and Cione, 2000). Moreover, Reguero et al. (2007) cited a crocodile and the porcupine *Erethizon* for this unit (but see Sussman, 2011, for its recent assignation to the genus *Coendou*), evidences of warmer and wetter environmental conditions. However, the micromammal species recorded at San Roque assemblage partially contradicts this general scenario. Some small mammals, among them rodents such as the extant *Microcavia* and the octodontid aff. *Neophanomys*, suggest the presence of semiarid and open habitats. As their living species are clearly associated with open and dry environments (Tognelli et al., 2001), *Microcavia* has been considered a good indicator of eremic paleoenvironmental conditions. Furthermore, the dominance of phyllotines in the assemblage is significative because this group is today constituted by species of grazing sigmodontines, mainly dwellers of open habitats (Reig, 1986). Taking into account the whole evidence, it is possible to infer the paleoenvironment as a community dominated by xerophytic plants, in a more or less open habitat with some bare sandy or rocky soils. It is also important to note, on the base of the close faunistic association with extant genera, that this paleoecological framework reinforces the idea that argyrolagids (or, at least, *Microtragulus*) are related with open areas in xeric conditions (Simpson, 1970). Our conclusion, when compared with the contrasting previously reported environmental scenarios for the Uquía Formation, indicates the occurrence of striking climatic pulses during the deposition of this sedimentary unit, with increasingly colder and more variable climatic conditions, related to the Late Pliocene global cooling and drying event (Ravelo et al., 2004). In South America, this global cooling began ca 3.2 Ma as a growing trend that changed the warmer and more stable climates prevalent before this age and that is documented by a significant faunal turnover (Tonni et al., 1992; Ortiz Jaureguizar et al., 1995; Vizcaíno et al., 2004; Verzi and Quintana, 2005). In addition to a climate component, the composition of the assemblage can be also, although perhaps secondarily, the result of the establishment of a rain-shadow effect caused by the "Diaguita" diastrophic phase (Late Pliocene) of the Andean orogeny. This uplift of

the eastern orographic systems of Argentina, including the Puna and Eastern Cordillera, resulted in xeric conditions on intermontane valleys like Quebrada de Humahuaca (Ortiz Jaureguizar and Cladera, 2006), which began to take place during the deposition of the San Roque assemblage.

6. Conclusions

The fossil content of Uquía Formation provides new and valuable phylogenetic and biogeographic data on several clades of small vertebrates because it is situated in a key geographical and temporal context. Beyond the differences with Late Pliocene Pampean small mammal faunas that can be attributed to biogeographical causes, the association indicates a noteworthy faunal turnover, particularly illustrated by the establishment of cricetid rodents as the main compositional group in small mammal assemblages. Two hypotheses to be explored are: a) if the dominance of cricetid in the paleocommunities is a consequence of the extinction of very small caviomorphs in the Late Pliocene; b) to what extent the occupation of this empty niche affected the community of the newcomer placental predators.

Clearly, in order to understand the dynamics of the different groups of small vertebrates in central and southern South America during the Pliocene it is mandatory to increase fossil collections. Moreover, sieving techniques together with an adequate correlation among the outcrops of Bolivian, northwestern Argentina and Pampean area must be applied. The fact that a century of paleontological work on Uquía Formation retrieved no more than 200 fossils (see Reguero et al., 2007) and that with the single sample here documented we doubled this number, are proofs of the importance of the assemblages produced by owls to refine our view of past communities.

Acknowledgments

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