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A LATE MIOCENE ARGYROLAGIDAE (MAMMALIA, METATHERIA, BONAPARTHERIIFORMES) FROM NORTHWESTERN ARGENTINA

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Abstract. In this contribution we present the first record of a member of the family Argyrolagidae (Metatheria) recovered from the India Muerta Formation (late Miocene) exposed near San Miguel de Tucumán, Tucumán Province, Argentina. The specimen is represented by a fragment of right maxilla with M1–4 and is referred here as *Microtragulus* Ameghino. It clearly differs from other members of the genus that preserve the upper dentition. Nevertheless, the impossibility of comparing this material with species only known by lower dentition, such as *Microtragulus catamarcensis* (Kraglievich) prevent us from establishing whether this is a new species or not. The comparisons performed allow us to identify characters from the upper dentition differing between *Microtragulus* and *Argyrolagus* Ameghino. These characters, in turn, led to the reassignment of a species previously assigned to *Microtragulus*. The new record reported here, the third known of *Microtragulus* from northwestern Argentina, broadens the geographic range of the genus, known from the Atlantic coast of Argentina and several localities of the Andean highlands and the foothills of the cordilleran range.

Key words. Microtragulus. Argyrolagus. Neogene. India Muerta Formation.

Resumen. UN ARGYROLAGIDAE (MAMMALIA, METATHERIA, BONAPARTHERIIFORMES) DEL MIOCENO TARDÍO DE LA PROVINCIA DE TUCUMÁN, ARGENTINA. En esta contribución se reporta el primer registro de un ejemplar de la familia Argyrolagidae (Metatheria) para la provincia de Tucumán, Argentina. El espécimen corresponde a un fragmento maxilar derecho con los M1–4 y proviene de sedimentos de la Formación India Muerta (Mioceno tardío) expuestos en las cercanías de la ciudad de San Miguel de Tucumán. Los rasgos dentarios permiten referir este material al género *Microtragulus* Ameghino. Si bien difiere claramente de las especies del género con las cuales puede ser comparado directamente, la imposibilidad de compararlo con *Microtragulus catamarcensis* (Kraglievich), proveniente de la Formación Andalhuala (Catamarca) impide establecer si se trata de un nuevo taxón. Por otra parte, la comparación entre éste y otros argirolágidos neógenos sirvió para identificar rasgos propios de la dentición superior que diferencian a los géneros *Argyrolagus* Ameghino y *Microtragulus* y que permitieron revisar la asignación de algunas especies. Este registro representa el tercer reporte de *Microtragulus* para el noroeste argentino y amplía el rango geográfico del género, que se distribuye tanto en localidades de la costa atlántica como en zonas de altura y aledañas a la franja andina de América del Sur.

Palabras clave. Microtragulus. Argyrolagus. Neógeno. Formación India Muerta.

THE record of Cenozoic fossil vertebrates from Tucumán Province (northwestern Argentina) ranges from the Paleocene to the early Holocene, beginning with the mammals and sauropsids from the Río Loro Formation (Soria and Powell, 1981; Soria, 1989a, b; Pol and Powell, 2011), and culminating with the Lujanian fauna recorded in levels of the Tucumán and Tafí del Valle formations (Bonaparte and Bobovnikov, 1974; Esteban, 1993; Powell *et al.*, 1993; Powell and Mulé, 1996; Ortiz *et al.*, 2000) and small rodents known from the early Holocene (Gavriloff *et al.*, 2004). The best studied regions within this province are the northwestern Tafí and Amaicha valleys and neighboring areas, in particular the Neogene units exposed at the Cumbres Calchaquíes and the valley of the Santa María River (San José, Las Arcas, Chiquimil, and Andalhuala formations; Bossi *et al.*, 1998; Herbst *et al.*, 2000). On the other hand, among the Neogene units of the eastern part of Tucumán Province, the India Muerta Formation is particularly interesting, given the limited surface of its fossil-bearing outcrops and the variety of vertebrate remains collected there.

The India Muerta Formation (Choromoro Group; Bossi, 1969) is represented by discontinuous outcrops scattered in the vicinities of the Celestino Gelsi reservoir (also known as "El Cadillal"), on the banks of the India Muerta and Vipos rivers, and near the Choromoro River. The lithology of this unit is characterized by grey, coarse- to fine-grained sandstones, either massive or with cross-bedding, and brownish siltstones (both massive and bioturbated) representing a fluvial model of meandering rivers (Bossi et al., 1998). The age of this formation has been estimated on the basis of biostratigraphical data (Peirano, 1957; Bossi, 1969, 1984; Bossi et al., 1998; Powell et al., 2012) but no absolute age dates are available yet. The fossil association recovered from the India Muerta Formation led to correlate it with the Andalhuala Formation (an important fossil-bearing unit from the Santa María River valley). Therefore, the India Muerta Formation has been referred to the Huayquerian SALMA, an age to which the Andalhuala Formation has been assigned in several contributions (e.g., Bossi et al., 1998; Powell et al., 2012). Nevertheless, it should be mentioned that the Andalhuala Formation has been recently reassigned to the Montehermosan-Chapadmalalan SALMAs (Reguero and Candela, 2011) and has been recently dated at 7.14 and 3.66 Ma (Mesinian-Zanclean, late Miocene-early Pliocene; Esteban *et al.*, 2014).

The fossil record of the India Muerta Formation is diverse and includes remains of Crocodylia, Testudines, Serpentes (Bossi, 1984; Powell *et al.*, 2012) and, among mammals, metatherians (Saprassodonta; Babot and Ortiz, 2008) and eutherians (Xenarthra, Notoungulata, and Hystricognathi; Peirano, 1957; Powell *et al.*, 2012; Madozzo Jaén and Ortiz, 2013). New mammal remains were recovered during recent fieldtrips, including the first Argyrolagidae (Metatheria) from Tucumán Province (recovered near the city of San Miguel de Tucumán; Fig. 1). This specimen, represented by a maxillary fragment with M1–4, is here described and assigned to the genus *Microtragulus* Ameghino, 1904.

Argyrolagidae includes a unique group of metatherians recorded in the Cenozoic of South America from the late Oligocene to the early Pleistocene (Simpson, 1970a, b; Hoffstetter and Villarroel, 1974; Wolff, 1984; Villarroel and Marshall, 1988; Goin *et al.*, 2000; Carlini *et al.*, 2007). This family presents outstanding convergences with other mammal groups (particularly granivore rodents) and its

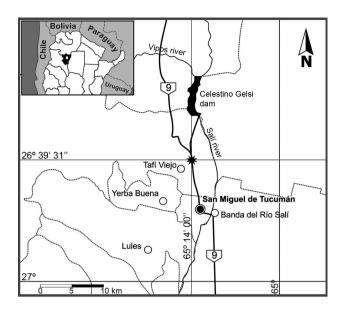


Figure 1. Map showing the geographic location of the outcrops of the India Muerta Formation where the specimen of *Microtragulus* sp. was found, north of the city of San Miguel de Tucumán. Modified from Babot and Ortiz (2008).

affinities have been widely discussed (Sánchez-Villagra, 2001; and references therein). Currently, the inclusion of argyrolagids within Metatheria is broadly accepted and their affinity with polydolopimorphian bonapartheriiforms has been supported in recent contributions (Goin and Candela, 2004; Carlini et al., 2007). After more than a century of studies, five genera are recognized for the family: Argyrolagus Ameghino, 1904; Proargyrolagus Wolff, 1984; Hondalagus Villarroel and Marshall, 1988; Anargyrolagus Carlini, Pascual and Goin, 2007; and Microtragulus; totalizing 12 species within these taxa. Microtragulus is the most diverse and widely distributed genus and two species are currently known from northwestern Argentina: Microtragulus catamarcensis (Kraglievich, 1931) (?Andalhuala Formation; Simpson, 1970a) and M. bolivianus Hoffstetter and Villarroel, 1974 (Uquía Formation; Ortiz et al., 2012).

In this contribution we describe a new record of *Micro-tragulus* from the India Muerta Formation, we compare it with other records of Argyrolagidae, and discuss the taxonomy and geographic distribution of the genus.

Institutional abbreviations. GHUNLPam, Facultad de Ciencias Exactas y Naturales de la Universidad Nacional de La Pampa, La Pampa, Argentina; MACN-PV, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Colección Paleontología de Vertebrados, Buenos Aires, Argentina; MHNSR-PV, Museo de Historia Natural de San Rafael, Colección Paleontología de Vertebrados, Mendoza, Argentina; MLP, Museo de La Plata, Buenos Aires, Argentina; MMP, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Buenos Aires, Argentina; PVL, Colección Paleontología de Vertebrados Lillo, Tucumán, Argentina. *Other abbreviations.* M/m, upper/lower molar; P/p, upper/ lower premolar; SALMA, South American Land Mammal Age; St, stylar cusp.

MATERIALS AND METHODS

Comparisons were made directly with material housed in different collections of fossil vertebrates (see below). When the material was not available, we used information available in the literature.

The terminology used here is the usual in recent works carried out on the Argyrolagidae (e.g., Zimicz, 2011; Goin and Abello, 2013) with the addition of some terms for practical purposes, such as mesiolabial lobe (StA + epiconular shelf) equivalent to the anterobuccal lobe or projection of Simpson (1970a). Although this nomenclature usually refers to molar cusps (*i.e.*, protocone, paracone, metacone, etc.), given the hypselodont condition of most of these taxa that show teeth with sidewall hypsodonty, the surface of the cusps (the primary occlusal surface) has been worn away early during the ontogeny of the animal (see Koenigswald, 2011). In this sense, the observed relief is the product of "balanced wear" and not the presence of the cusp *per se*. However, this relief apparently remains constant through the most of the life of the animal and the elevations are evidently homologous to the ontogenetically precedent cusp. In this context, we maintain the specific terms referred to topographically equivalent cusps for descriptive and comparative purposes.

SYSTEMATIC PALEONTOLOGY

Infraclass METATHERIA Huxley, 1880 Order Polydolopimorphia Ameghino, 1897 Suborder Bonapartheriiformes Goin and Candela, 2004 Superfamily Argyrolagoidea Ameghino, 1904 Family Argyrolagidae Ameghino, 1904

Genus *Microtragulus* Ameghino, 1904

Type species. Microtragulus argentinus Ameghino, 1904.

Microtragulus sp. Figure 2

Referred material. PVL 6594, fragment of right maxilla with M1–4.

Geographic occurrence. National Route 9, at the junction with the access to the Celestino Gelsi reservoir (kilometer 1313 to 1314; 26°39′31″S; 65°14′00″W), Tafí Viejo Department, Tucumán Province, Argentina (Fig. 1).

Stratigraphic occurrence. India Muerta Formation (Choromoro Group), late Miocene (Bossi, 1969, 1984; Bossi *et al.*, 1998).

Description

Maxilla. The lateral surface of the fragment presents the base of the anterior root of the zygomatic arch, which extends from the level of the mesial edge of the M1 to the level of the distal edge of the M2 (Fig. 2.1). The base of the medial concave surface of the maxilla corresponds to the lateral edge of the palatine vacuity, which occupied most of the palatine surface, as usual for Argyrolagidae. There is a deep groove on the middle part of the medial surface; towards the dorsal edge, the alveolar capsules of the molars are visible (Fig. 2.2). The distal wall of the alveolus of the P3 is preserved at the anterior end of the maxilla (Fig. 2.3).

Dentition. All molars are hypselodont (as in all other genera of the family, except *Proargyrolagus*) and their labiolingual length is greater than the mesiodistal length, except in the M1 and M4 (Tab. 1). The outline of the M2-3 is subquadrangular, with subparallel mesial and distal walls, and markedly convex labial walls (in occlusal view) which are clearly higher than the lingual ones (Fig. 2.1–3). This is the same condition observed for specimens of Microtragulus reigi Simpson, 1970a and M. bolivianus. On the other hand, the M1 is more irregular in outline, given the great development of the mesiolabial lobe, and the M4 is subtriangular. The layer of enamel is discontinuous on the lateral walls of all teeth; it is absent on the mesiolabial corner and on the distal wall of each molar (Fig. 2.3). A thin layer of cementum is also present, partially coinciding with the mesial and lingual distribution of the enamel. Each molar presents a narrow aperture at the center of the occlusal surface. These aper-

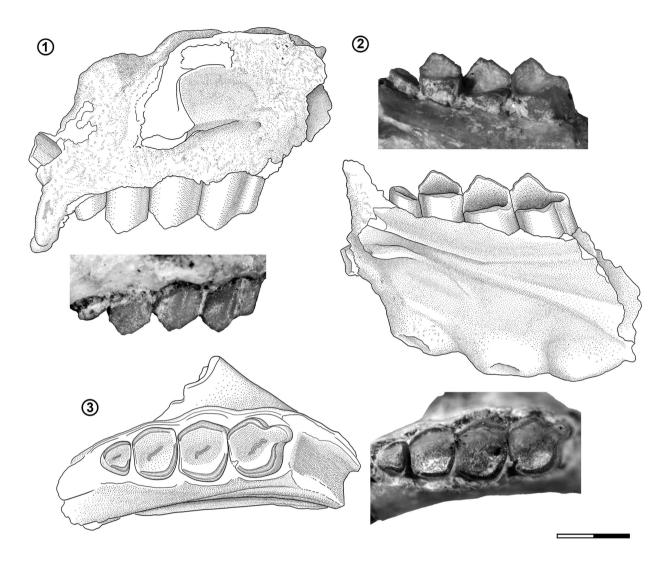


Figure 2. Microtragulus sp., PVL 6594, right maxillary fragment with M1-4; 1, lateral view; 2, medial view; 3, occlusal view. Scale bar= 2 mm.

tures are long and mesiolabially-distolingually oriented, and are here interpreted as fossae given the thin layer of enamel that surrounds them. These structures are similar in all molars and have been observed also in most studied specimens of *Argyrolagus* and *Microtragulus* with only few exceptions, probably related to the state of preservation in the corresponding material.

As already mentioned, the M1 is clearly different from the other molars because of the great development of a mesially projected mesiolabial lobe. This structure is similar to that observed in *Microtragulus* and *Argyrolagus*, more developed than in *Hondalagus*, and less differentiated and proportionally smaller than in *Anargyrolagus*. A main cusp is located distally to the mesiolabial lobe and is here inter

 TABLE 1. Dental measurements (in mm) of the specimen PVL 6594,
 Microtragulus sp.

L 1.76 1.40 1.24 0.88		M1	M2	МЗ	M4
	L	1.76	1.40	1.24	0.88
W 1.52 1.64 1.36 0.84	W	1.52	1.64	1.36	0.84

Abbreviations: L, mesiodistal length; W, labiolingual length (width).

preted as the paracone. Distally, a small elevation is associated with a StE. The paracone of the M1 is the higher point of the tooth and presents a sharp apex, as in *Argyrolagus* (*e.g.*, *A. scagliai* Simpson, 1970a, MMP 785-S [holotype]; *Argyrolagus* sp., MMP 1413 M, MLP 86-VI-20-17) and *Microtragulus* (*M. reigi*, MMP 691-S). The only evident lingual cusp is the protocone, although there is a small distal bulge on the enamel layer that may correspond to a vestigial metaconule.

The mesiolabial lobe is reduced in the M2. Unlike the M1, the paracone and metacone are differentiated on the labial edge of the tooth, although they are coalescent, as usual for the genus (see below). In this case, the metacone is the main cusp and the vestigial paracone is located at its base (on the mesial slope). This condition is present in representatives of *Microtragulus* (*e.g., M. reigi,* MMP 691-S) and is a clear difference regarding *Argyrolagus* (*e.g., A. scagliai,* MMP 785-S [holotype]; *Argyrolagus* sp., MMP 1413 M, MLP 86-VI-20-17, GHUNLPam 19617). Once again, the only evident lingual cusp is the protocone, which is recognizable by a bulge of the enamel layer on the mesiolabial corner of the tooth.

The morphology of the M3 is similar to that of the M2, although the paracone is even more reduced. As in the preceding molar, this is clearly different from the condition in *Argyrolagus*, where the paracone is well-developed and well-separated from the metacone. The mesiolabial lobe and StE are moderately developed. The protocone area is identified by the same traits as in the M2, although the mesiolingual corner is slightly more quadrangular in this case.

The M4 differs in size and morphology from the rest of the molars. It is very small and subtriangular in occlusal outline. Both labial and lingual walls lack evident cusps. Additionally, as usual in the hypselodont genera of Argyrolagidae, the implantation of this molar differs from the anterior ones, so that the occlusal plane is mesioventrally oriented while it is distoventrally oriented in the preceding teeth. The relative size, shape, and lack of cusp relief represent a condition similar to that of *Microtragulus bolivianus*.

Comments on the taxonomic assignment of the specimen PVL 6594

The specimen here studied shows a variety of traits that clearly differentiate it from most of the genera known for this family. It differs from *Proargyrolagus* by the presence of hypselodont molars of simplified occlusal structure. Moreover, it differs from *Hondalagus* by the greater development of the mesiolabial lobe in the M1, the lesser development of the mesiolabial lobe in the M2, and the more triangular and less transverse M3. It also differs from *Anargyrolagus* by the simplified occlusal structure, the lack of labial grooves, and the less-developed mesiolabial lobe. Regarding *Argyrolagus*, PVL 6594 differs by the coalescence of paracone and metacone in the M2-3, the lesser development of the mesiolabial lobe (particularly in the M2 and M3), proportionally more transverse molars, markedly convex labial edge (particularly in the M2), and proportionally larger M4.

The assignment of this material to *Microtragulus* is based on the following characters: StE reduced in the M1, poorly-developed paracone, coalescent with metacone, and reduced mesiolabial lobe in the M2 and M3, and convex labial outline, particularly in the M2. Among the species of this genus, clear differences -mainly in the M2 and M3prevent the inclusion of this material in M. reigi and M. bolivianus. Regarding M. reigi, the specimen PVL 6594 presents a more quadrangular distolingual corner of the M2, subparallel mesial and distal edges in the M3 (which is also more transverse), and paracone and metacone absent in the M4. In relation to *M. bolivianus*, the specimen PVL 6594 is smaller, the M3 is more transverse and exhibits a more reduced mesiolabial lobe. Finally, the material referred as M. rusconii Goin, Montalvo and Visconti, 2000, is not included in this comparison, since this species is here reassigned to the genus Argyrolagus (see below).

The differences indicated above would be enough to refer the specimen PVL 6594 to a new species of Microtragulus. Nevertheless, we cannot discard the assignation of this new specimen to Microtragulus catamarcensis, a taxon recorded in the Andalhuala Formation (Catamarca), probably equivalent in age (at least partially) to the India Muerta Formation. Unfortunately, both the holotype of this species and a recently documented specimen recovered in Mendoza are represented only by mandibular material (Fig. 3); therefore, a direct comparison with the specimen from India Muerta is not possible. Even though PVL 6594 is relatively larger than the holotype of *M. catamarcensis*, the size variation observed in the specimens of this (see Tab. 2) and other species of argyrolagids precludes considering this difference as a valid character for the separation of two morphotypes. Thus, we choose to refer this maxilla to *Microtragulus* sp.

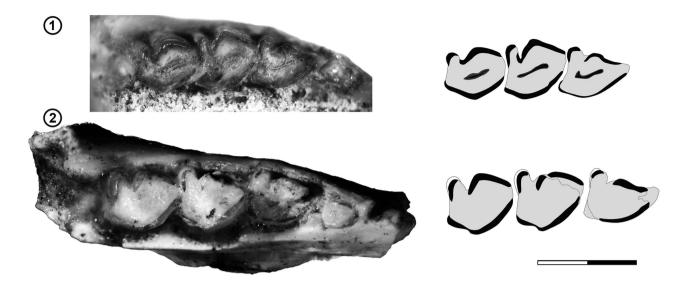


Figure 3. *Microtragulus catamarcensis.* 1, MACN-PV 5529 (holotype), detail of right dentary with m1-3 and schematic drawing of the lower molars (the images were flipped horizontally for comparative purposes); 2, MHNSR-PV 1157, fragment of right dentary with m1-3 and schematic drawing of the lower molars. Scale bar= 2 mm.

TABLE 2. Dental measurements (in mm) of Microtragulus catamarcensis.									
MACN-PV 5529 (holotype)		<i>р3</i>	m1	m2	m3	<i>m</i> 4			
Left	L		1.25	1.41	1.20	0.88			
	W		1.01	1.15	1.00	0.65			
Right	L		1.27	1.32	1.21				
	W		0.99	1.25	1.03				
MHNSR-PV 1157		<i>р3</i>	m1	m2	m3	<i>m</i> 4			
Left	L	0.66	1.45	1.43	1.38				
	W	0.46	1.10	1.30	1.18				

Abbreviations: L, mesiodistal length; W, labiolingual length (width).

Differences in the upper dentition of Microtragulus *and* Argyrolagus

Since their first mention by Ameghino in 1904, argyrolagids have been recorded at different localities of Argentina and Bolivia. The most detailed summary was given by Simpson (1970a, b) who revised the genera *Microtragulus* and *Argyrolagus* (the only known at the time), included the description of new species, revised the diagnosis of previously known taxa, described dental, cranial and postcranial characters, and commented on the affinities, paleobiology, and biogeography of the group. In spite of all the information presented by Simpson (1970a, b) the diagnosis proposed in these contributions for *Argyrolagus* and *Microtragulus* were based only on characters of the lower dentition, since mandible remains were more abundant at that time. In the present study, comparisons of specimens bearing upper dentition of *A. scagliai* (MMP 785-S; MMP 973-M), *Argyrolagus* sp. (MMP 1413-M; MLP 86-VI-20-17), *M. reigi* (MMP 691-S), and *M. bolivianus*, and particularly those with associated upper and lower dentition (MMP 785-S; MMP 691-S), allow us identifying characters of the upper teeth that distinguish the two genera.

In *Argyrolagus* the labial outline in occlusal view is mainly straight in the M2 and, to a lesser extent, the M3. This outline is more convex in *Microtragulus*. Additionally, the development of the mesiolabial lobe and StE is greater in *Argyrolagus*. Finally, the paracone and metacone are well-separated and morphologically differentiated in the M2 (particularly) and the M3 of *Argyrolagus*, while in *Microtragulus* these cusps are coalescent and closely located on those molars. According to our observations, this latter trait has no intraspecific variation and is one of the most conspicuous characters that differentiate both genera.

Revision of the taxonomic status of an argyrolagid species from La Pampa Province, Argentina

Goin *et al.* (2000) included within the genus *Microtragulus* the species *M. rusconii*, documented for the Cerro Azul Formation (late Miocene) exposed at Bajo Giuliani, La Pampa, Argentina. The direct study of the holotype and other specimens originally referred to this taxon led us to establish a new taxonomic arrangement based on characters of the upper and lower dentition. In this sense, we propose the reassignment of the species and a revised diagnosis.

Genus **Argyrolagus**

Argyrolagus rusconii (Goin, Montalvo, and Visconti, 2000) new combination

Microtragulus rusconii Goin, Montalvo, and Visconti, 2000, p.118. *Holotype.* GHUNLPam 2196.

Referred material. GHUNLPam 412, fragment of right dentary with p3-m4; GHUNLPam 8549, fragment of left maxilla with P3-M4; GHUNLPam 9073, fragment of left maxilla with P3-M2; GHUNLPam 9895, fragment of left dentary with p3-m1; GHUNLPam 12938, fragment of right dentary with p3-m4.

Geographic occurrence. Bajo Giuliani, Capital and El Guanaco departments, La Pampa Province, Argentina.

Stratigraphic occurrence. Cerro Azul Formation, late Miocene. *Revised diagnosis. Argyrolagus rusconii* differs from *Microtragulus* by the larger separation and differentiation of the paracone and metacone in the M2 and M3, the straight labial outline, and the greater development of the mesiolabial lobe in the same teeth. It also differs from this genus by the presence of a conspicuous entoflexid in all lower molars and the presence of a well-developed talonid in the m4. Within *Argyrolagus*, it differs from *A. scagliai* by the presence of a trigonid proportionally larger than the talonid in the m4, quadrangular occlusal outline of protocone and metaconule (particularly in the M2 and M3), and larger occlusal surface in the P3; on the other hand, it differs from *A. palmeri* Ameghino, 1904 by the proportionally elongated trigonid of the m1.

Comments. The specimens GHUNLPam 2275 and GHUNL-Pam 5076 were excluded from the referred material. In the case of GHUNLPam 2275 (a left maxillary fragment with M1-2), this is referred provisionally as *Argyrolagus* sp., since it bears a proportionally reduced paracone (which is larger than in *Microtragulus* but different from *A. rusconii* and other species of *Argyrolagus*). Regarding the specimen GHUNLPam 5076, it should be noted that this was mistakenly included in the argyrolagid sample, as this is a toothless fragment of a cricetid rodent dentary.

The record of Microtragulus in the late Miocene of Central and Northern Argentina

The knowledge of argyrolagids in northwestern Argentina is limited. The first taxon recognized was originally named *Argyrolagus catamarcensis* by Kraglievich (1931) and posteriorly reassigned to *Microtragulus* by Simpson (1970a). The material (MACN-PV 5529, Fig. 3.1) consists of two fragments of dentary with teeth, coming from the "*yacimientos araucanenses de Catamarca*" (Simpson, 1970a, p. 8), probably belonging to the Andalhuala Formation (G. Esteban, pers. com.). Almost a century later, two new records of *Microtragulus* were described: *M. bolivianus* from the Uquía Formation, Jujuy Province (Ortiz *et al.*, 2012), and the specimen here referred as *Microtragulus* sp.

The close geographic location and probable chronologic correspondence between the record of *Microtragulus cata-marcensis* from the Andalhuala Formation and the *Microtragulus* specimen described here from the India Muerta Formation suggest the possibility that the latter specimen might be referred to *M. catamarcensis*. If this were the case, this taxon would yield further biostratigraphic evidence for the correlation between both units, which was already proposed by Peirano (1957), Bossi *et al.* (1998), and Powell *et al.* (2012), among others. On the other hand, it is also in-

teresting to note that a specimen referred as *M. catamarcensis* (Fig. 3.2) was recently recovered in the locality of 25 de Mayo, Mendoza Province, about 800 km south of the type locality (Garrido *et al.*, 2014), suggesting a relatively broad geographic range for the species.

Although this seems to be a potential source of biostratigraphic and biochronological data, the records of Microtragulus catamarcensis are associated to a series of problems related to the lack of stratigraphic and morphological information that prevent reaching precise conclusions. The first problem is the lack of specimens of *M. catamarcensis* bearing upper and lower dentition, which precludes direct comparisons. Secondly, the bearing levels of the specimen from Mendoza Province (Garrido et al., 2014) were traditionally referred to the Aisol Formation, recently redefined and dated at 19.5 Ma (Santacrucian SALMA) (Forasiepi et al., 2014; Garrido et al., 2014). In this sense, the record of M. catamarcensis in this unit indicates that the species had a much wider temporal distribution than previously thought (spanning from the early Miocene to, at least, the late Miocene), reducing thus the biostratigraphic value of the taxon. Alternatively, an additional issue related to this record is the fact that the bearing levels of *M. catamarcensis* in Mendoza were only tentatively referred to the Aisol Formation, so the age of these strata must be confirmed (Garrido et al., 2014). In this sense, a possible scenario would be that the specimen comes from the La Huertita Formation (which overlies the Aisol Formation in neighboring localities). If this were the case, then the temporal range of the species would be restricted to the Monterhermosan or perhaps Chapadmalalan SALMAs, according to the age estimated for this younger unit (Garrido et al., 2014). This would also match with recent stratigraphic characterizations made for the Andalhuala Formation (Reguero and Candela, 2011), the probable bearing unit of the holotype of M. catamarcensis.

Thus, stratigraphical and chronological uncertainties and the fragmentary nature of the collected specimens show the need to intensify the search of small metatherians in Miocene units from northwestern Argentina, such as the Neogene outcrops in the eastern part of Tucumán Province. Likewise, it seems evident that many morphological traits that were traditionally considered as diagnostic or informative in the taxonomy of Argyrolagidae (such as size) could be subject to some variation. We can not discard the possibility that future findings will lead to a deep revision of *Microtragulus* and *Argyrolagus*, in order to corroborate if the present systematic arrangement is valid and sustainable.

The other species recorded in northwestern Argentina, *Microtragulus bolivianus*, provides relatively more accurate biogeographic data, given the more solid information related to the comparison of the material, the assignment of specimens, and their geographic and stratigraphic occurrence. The record of this species in highlands in Bolivia and northwestern Argentina indicates an environmental connection between these regions, particularly considering that the highly specialized morphology of these forms may be caused by some degree of ecological constraint (Ortiz *et al.*, 2012).

From a biogeographic point of view, *Microtragulus* shows the broadest distribution of all argyrolagid genera (Fig. 4). However, the records of these taxa are scattered



Figure 4. Map of South America showing the geographic location of Argyrolagidae records.

and restricted to middle latitudes in South America. The known distribution includes highland species recorded near the cordilleran range (*M. catamarcensis* and, particularly, *M. bolivianus*) and others from lowlands of the Atlantic coast (*M. reigi* and *M. argentinus*). This disjunct distributional pattern is evident by the absence of the genus *Microtragulus* in localities of the Pampean region (*e.g.*, La Pampa Province) where other argyrolagid taxa are abundant. It also contrasts with the pattern in *Argyrolagus*, which is only known from lowlands, mainly near the Atlantic coast. Likewise, this gap in the geographic range of *Microtragulus* shows once again the need of a revision of the systematic correspondence between the coastal and "Andean" species of this genus.

CONCLUSIONS

We report the first record of Argyrolagidae for Tucumán Province, northwestern Argentina, consisting of a maxillary fragment with M1–4 here referred to the genus *Microtragulus*. Although this specimen shows several unique characters, which would justify erecting a new taxon, it cannot be compared with some of the species of the family, such as *M. catamarcensis*, due to the lack of overlapping material. Thus its specific assignment cannot be clarified at this point.

A series of characters from the upper dentition are here identified as additional differences between *Argyrolagus* and *Microtragulus*. This new information allows validating previous references and reassigning *Microtragulus rusconii* to the genus *Argyrolagus*, establishing the new combination *Argyrolagus rusconii*.

The difficulties regarding comparisons and lack of accurate stratigraphic data highlight the need of increasing the paleomastozoological studies in the Miocene–Pliocene of northwestern Argentina. In this sense, the focus on micromammals and the application of appropriate sample techniques, such as screen washing, will be very useful for these purposes.

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