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Redescription of the argyrolagid *Microtragulus bolivianus* (Metatheria, Polydolopimorphia, Bonapartheriiformes) based on new remains from Northwestern Argentina

M. Judith Babot and Daniel A. García-López

ABSTRACT

This work is based on new dental, cranial, and postcranial remains of the argyrolagid *Microtragulus bolivianus* (Metatheria, Polydolopimorphia, Bonapartheriiformes) and dental pieces of *Microtragulus* sp. coming from late Pliocene-early Pleistocene levels of the Uquía Formation exposed at San Roque, Humahuaca (Jujuy Province, Argentina). They were found in association with amphibians, lizards, birds, rodents, and didelphid marsupials, forming an assemblage probably generated by the trophic activity of owls. Specimens were assigned to *M. bolivianus* based on the following combination of features: M3 subcircular, with a flexus between the mesiolabial lobe and the metacone, paracone and metacone not differentiated in M4, absence of entoflexid in m1-2 and shallow entoflexid in m3, proportionally large talonid in m4, with a distinguishable distal flexid. *Microtragulus bolivianus*, initially recorded in Pliocene sediments exposed at the Bolivian Altiplano, was represented only by a mandibular fragment with one incisor and m3-m4. Based on a much more complete sample we present a detailed dental and postcranial description of the species. Since 1904 the family name Argyrolagidae and the generic names *Microtragulus* and *Argyrolagus* have been subject of several nomenclatural changes. A revision of these modifications, mainly those occurring in the last 40 years, is also presented. Furthermore, we analyze some mandibular traits of argyrolagids such as the maxillary canal (retrodental canal), a very odd feature present in all the members of the family, which could be related to the passage of a connection between the inferior alveolar and inferior orbital veins, as in some extant mammals.

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INTRODUCTION

Argyrolagidae is an odd group of small fossil metatherians, which inhabited South America during the Cenozoic. Its temporal range extends from the late Oligocene (Deseadan South American Land Mammal Age [SALMA]) to the early Pleistocene (Marplatan SALMA, Sanandresian subage). The family is only known from Argentina and Bolivia, although the closely related argyrolagoid *Khlonia* is also present in Chile (Ameghino, 1904; Kraglievich, 1931; Simpson, 1970a, 1970b; Hoffstetter and Villarroel, 1974; Wolff, 1984; Villarroel and Marshall, 1988; Goin et al., 2000, 2010; Carlini et al., 2007). Some of the most remarkable features of the group are the presence of an elongated snout, large orbits, very large palatal vacuities and wide incisive foramina, inflated tympanic bullae, procumbent lower incisors, hypsodont and highly modified molars, short, and high mandibular body, low and short coronoid process, mandibular notch long, and maxillary canal present (retrodental canal sensu Hofftsetter and Villarroel, 1974). The postcranial skeleton also shows several peculiarities such as the shortening of the forelimb, the lengthening of the tibia-fibula and metatarsals, and the reduced number of elements in the posterior autopodium, specifically the metatarsals and phalanges, all these features associated with a bipedal stance and leaping locomotor habits (Simpson, 1970a).

For more than a century, several authors studied the taxonomy, anatomy, phylogeny, and paleobiology of the group (Ameghino, 1904, 1906; Rovereto, 1914; Kraglievich, 1931; Rusconi, 1933, 1936; Simpson, 1970a, 1970b; Hoffstetter and Villarroel, 1974; Wolff, 1984; Villarroel and Marshall, 1988; Sánchez-Villagra and Kay, 1997; Goin et al., 2000; Sánchez-Villagra et al., 2000; Sánchez-Villagra, 2001; Abello et al., 2002; Carlini et al., 2007; Zimicz, 2011; Goin and Abello, 2013). There are currently five genera and 12 recognized species. Two genera are monospecific (*Hondalagus* Villarroel and Marshall, 1988 and *Anargyrolagus* Carlini, Pascual, and Goin, 2007) while *Proargyrolagus* Wolff, 1984, *Argyrolagus* Ameghino, 1904, and *Microtragulus* Ameghino, 1904 are represented by two or more species (see Table 1).

Microtragulus is the most widely distributed argyrolagid, including records in central and northwestern Argentina and the Bolivian Plateau. The current geographical record indicates a disjunct distributional pattern comprising coastal as well as highland areas. *Microtragulus reigi* is the only species known from lowland areas (the existence of *M. argentinus* remains questionable; see Discussion) and *M. catamarcensis* and *M. bolivianus* are restricted to mid and high altitudes (García-López and Babot, 2015). The oldest record of the genus, a mandibular fragment of *M. catamarcensis*, is known from ?early Miocene levels exposed at Mendoza Province, Argentina (see Garrido et al. [2014] and García-López and Babot [2015]), and the more recent records are known from the late Pliocene-early Pleistocene (*M. bolivianus*; Marplatan SALMA, probably Vorohuean subage; Ortiz et al., 2012) and early Pleistocene (*M. reigi*; Marplatan SALMA, Sanandresian subage; Cione and Tonni, 2005; Cione et al., 2015).

The genus was initially defined based on the morphology of its lower molars (Simpson, 1970a), but additional characters of the upper dentition have been recently described for this taxon (García-López and Babot, 2015). The dental features that define *Microtragulus* are the presence of a distinct ectoflexid (labial groove) separating the trigonid from the talonid and absent or vestigial entoflexid (lingual groove) in m1, trigonid with a dominant metaconid, lower ectostylid and protoconid pointing mesiolabially and separated from the ectostylid by a groove (in m1 and/or m2), reduced talonid with a distinctive tongue-like hypoconid in m1-2, well-developed entoconid, and hypoconulid absent or vestigial, and reduced m4, both in length and width, bearing a vestigial talonid separated from the trigonid by ectoflexid and entoflexid. Regarding the upper dentition, the distinctive features include a reduced StE in M1, poorly-developed paracone coalescent with metacone, reduced mesiolabial lobe in M2 and M3, and convex labial outline, particularly in M2 (García-López and Babot, 2015).

Microtragulus bolivianus is the most northern species of the genus. It was found by Hoffstetter and Villarroel (1974) in levels of the Umala Formation exposed at the locality of Viscachani (Bolivia;

TABLE 1. List of the genera and species included in the Family Argyrolagidae and their temporal and geographic distribution. Abbreviations: AR, Argentina; BO, Bolivia.

Species	Temporal distribution	Geographic distribution	References
Proargyrolagus bolivianus Wolf, 1984	Late Oligocene (Deseadan)	Salla-Luribay Basin (BO)	Wolf (1984); Sánchez-Villagra and Kay (1997)
Proargyrolagus argentinus Goin and Abello, 2013	Early Miocene (Colhuehuapian)	Puesto Almendra, Chubut (AR)	Goin and Abello (2013)
Anargyrolagus primus Carlini, Pascual, and Goin 2007	Early Miocene (Colhuehuapian)	Lower Chubut River valley, Chubut (AR)	Carlini et al. (2007); Goin and Abello (2013)
Hondalagus altiplanensis Villarroel and Marshall, 1988	Middle Miocene (Laventan)	Quebrada Honda (BO)	Villarroel and Marshall (1988); Sánchez-Villagra et al. (2000)
Microtragulus argentinus Ameghino, 1904	?Early Pliocene (Montehermosan)	Monte Hermoso, Buenos Aires (AR)	Ameghino (1904); Simpson (1970a); Tomassini et al. (2013)
M. catamarcensis (Kraglievich, 1931)	?Early Miocene - Early Pliocene	25 de Mayo, Mendoza (AR) ?Andalhuala, Catamarca (AR)	Kraglievich (1931); Simpson (1970a); Garrido et al. (2014); García-López and Babot (2015)
Microtragulus sp.	?Late Miocene	North of Tucumán (AR)	García-López and Babot (2015)
M. reigi Simpson, 1970a	Middle Pliocene – Early Pleistocene; Chapadmalan - Marplatan	Punta San Andrés, Buenos Aires (AR)	Simpson (1970a); Cione and Tonni (2005)
M. bolivianus Hoffstetter and Villarroel, 1974	?Early Pliocene - Early Pleistocene Montehermosan - Marplatan	Vizcachani (BO) San Roque, Jujuy (AR)	Hoffstetter and Villarroel (1974); Ortiz et al. (2012)
Argyrolagus palmeri Ameghino, 1904	Early Pliocene; Montehermosan	Monte Hermoso, Buenos Aires (AR)	Ameghino (1904); Tomassini et al. (2013)
A. scagliai Simpson, 1970a	Middle Pliocene; Chapadmalalan	Miramar, Buenos Aires (AR)	Simpson (1970a)
A. parodii Rusconii, 1933	Middle Pliocene; Chapadmalalan	Chapadmalal, Buenos Aires (AR)	Rusconi (1933); Simpson (1970a, b)
A. rusconii (Goin, Montalvo, and Visconti, 2000)	Late Miocene	Bajo Giuliani, La Pampa (AR)	Goin et al. (2000); García-López and Babot (2015)
Argyrolagus sp.	?Late Miocene	Caleufú, La Pampa (AR)	Abello et al. (2002)

Pliocene levels dated between 5.3-2.9 Ma [Marshall et al., 1992; MacFadden et al., 1994]) and described on the basis of scarce remains (a right incomplete mandible preserving only one incisor and m3-4). In this contribution, we present new materials of *M. bolivianus* including dental, mandibular, and postcranial elements. The materials are part of a microvertebrate fossil assemblage, probably produced by the activity of predatory birds, recovered in sediments of the Uquía Formation cropping out in the locality of San Roque, 2 km south of Humahuaca town, Jujuy Province, northwestern Argentina (Figure 1.1-3). Based on the fossil rodent assemblage Ortiz et al. (2012) suggested that xeric palaeoenvironmental conditions would have prevailed in the region by the end of the Pliocene. The presence of the argyrolagid *Microtragulus*, for which adaptations to arid environments were inferred on the basis of their morphological similarity with kangaroo rats, would reinforce this hypothesis (Ortiz et al., 2012).

In this work we provide detailed anatomical descriptions, comparisons, and a revised diagnosis of the species, which was poorly known until now. Additionally, we present an updated revision of the nomenclatural changes suffered by the taxonomic name Argyrolagidae, and examine some particular traits of the dentary of the group.

Institutional abbreviations. GHUNLPam, Facultad de Ciencias Exactas y Naturales de la Universidad Nacional de La Pampa, La Pampa, Argentina; JUY-P, Museo de Geología, Mineralogía y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy, San Salvador de Jujuy,

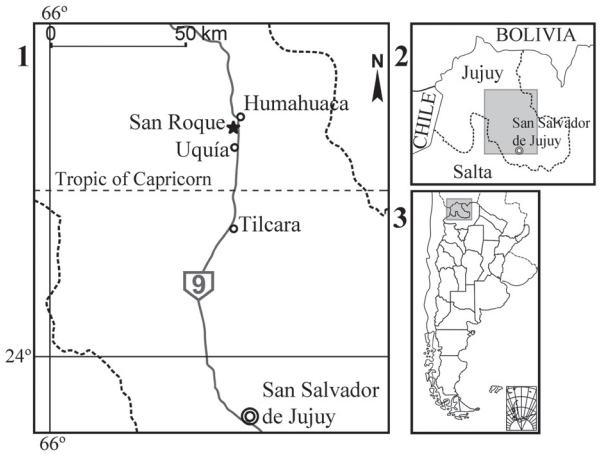

FIGURE 1. 1. Location map of the fossiliferous levels of the Uquía Formation exposed at San Roque, Humahuaca (Jujuy Province, Argentina). Relative location of the prospected area in: **2**, Jujuy Province; and **3**, Northwestern Argentina. Modified from Ortiz et al. (2012).

Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MLP, Museo de La Plata, Buenos Aires, Argentina; MMP, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Buenos Aires, Argentina; MNHN-BOL-V, Museo de Historia Natural, Colección Paleontología de Vertebrados, La Paz, Bolivia; MPEF-PV, Museo Paleontológico "Egidio Feruglio", Sección Paleontología de Vertebrados, Trelew, Argentina; PVL, Colección Paleontología de Vertebrados Lillo, Instituto Miguel Lillo, Tucumán, Argentina.

Anatomical abbreviations. M/m, upper/lower molar; P/p, upper/ lower premolar; St, stylar cusp.

MATERIALS AND METHODS

The nomenclature of molar cusps follows the proposal of Goin et al. (2010) and Goin and Abello (2013) who analyzed the changes in molar morphology from *Praedens* and *Klohnia* (as basal Argyrolagoidea) to *Proargyrolagus* and *Anargyrolagus*. The arrangement of molar cusps in *Microtragulus bolivianus* (Figure 2) is based on this hypothesis and in García-López and Babot (2015). Cusp names are used as if they were actually present, although according to the condition of typical euhypsont teeth, the cusped surface is quickly worn away after tooth eruption (sidewall hypsodonty sensu Koenigswald, 2011). Their relative position is inferred by the occlusal relief and tooth outline. The designation of the first lower incisor as i1 follows Goin and Abello (2013). Up to now, there is no supporting evidence for Hershkovitz (1995) scheme in Argyrolagidae and hence, the identity of incisors is still under discussion (e.g., Sánchez-Villagra and Kay, 1997; Sánchez-Villagra, 2001).

We assume that in *Microtragulus bolivianus* the premolar immediately anterior to the first molar is the third premolar, based on basal members of the group that preserve the complete dental series *(Proargyrogalus and Anargyrolagus;* Sánchez Villagra et al. [2000]; Carlini et al. [2007]; Goin and Abello [2013]). The anatomical terms used for crania and mandibles follow Wible (2003, 2007). The postcranial description is based on general anatomical contributions (Nomina Anatomica Veterinaria; Schaller, 1992) and specific works related with metatherian morphology (de Muizon, 1998; Szalay, 1994).

SYSTEMATIC PALEONTOLOGY

Infraclass MARSUPIALIA Illiger, 1811
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, by original designation.

Microtragulus bolivianus Hoffstetter and Villarroel, 1974
Figure 2, Figure 3, Figure 4, Figure 5, Figure 6, Figure 7

Holotype. MNHN-BOL-V-011707 (= GB-0001), right mandibular fragment with i1 and m3-m4 (GB refers to the currently nonexistent GEOBOL [Servicio Geológico Boliviano] collection).

Referred Material. JUY-P-0065, fragment of right maxilla with M3-M4; JUY-P 50, edentulous fragment of right maxilla preserving the zygomatic process; JUY-P-0066, right mandibular body with i1, alveoli of i2 and p3, and complete m1-4; JUY-P-0067, right mandibular body with complete i1 and i2, alveolus of p3, and complete m1-4; JUY-P-0068, anterior fragment of right mandibular body with i1 and alveoli of i2 and p3; JUY-P-0069, almost complete right humerus except for the proximal third; JUY-P-0070, almost complete left humerus except for the proximal third; JUY-P-0071, distal half of left humerus; JUY-P-0072, distal end of right humerus; JUY-P 59, proximal half of right ulna; JUY-P 60, proximal half of left ulna; JUY-P 61, proximal fragment of radius; JUY-P 52, right proximal epiphysis and right distal end of tibiofibula; JUY-P-0073, complete left calcaneus;JUY-P-

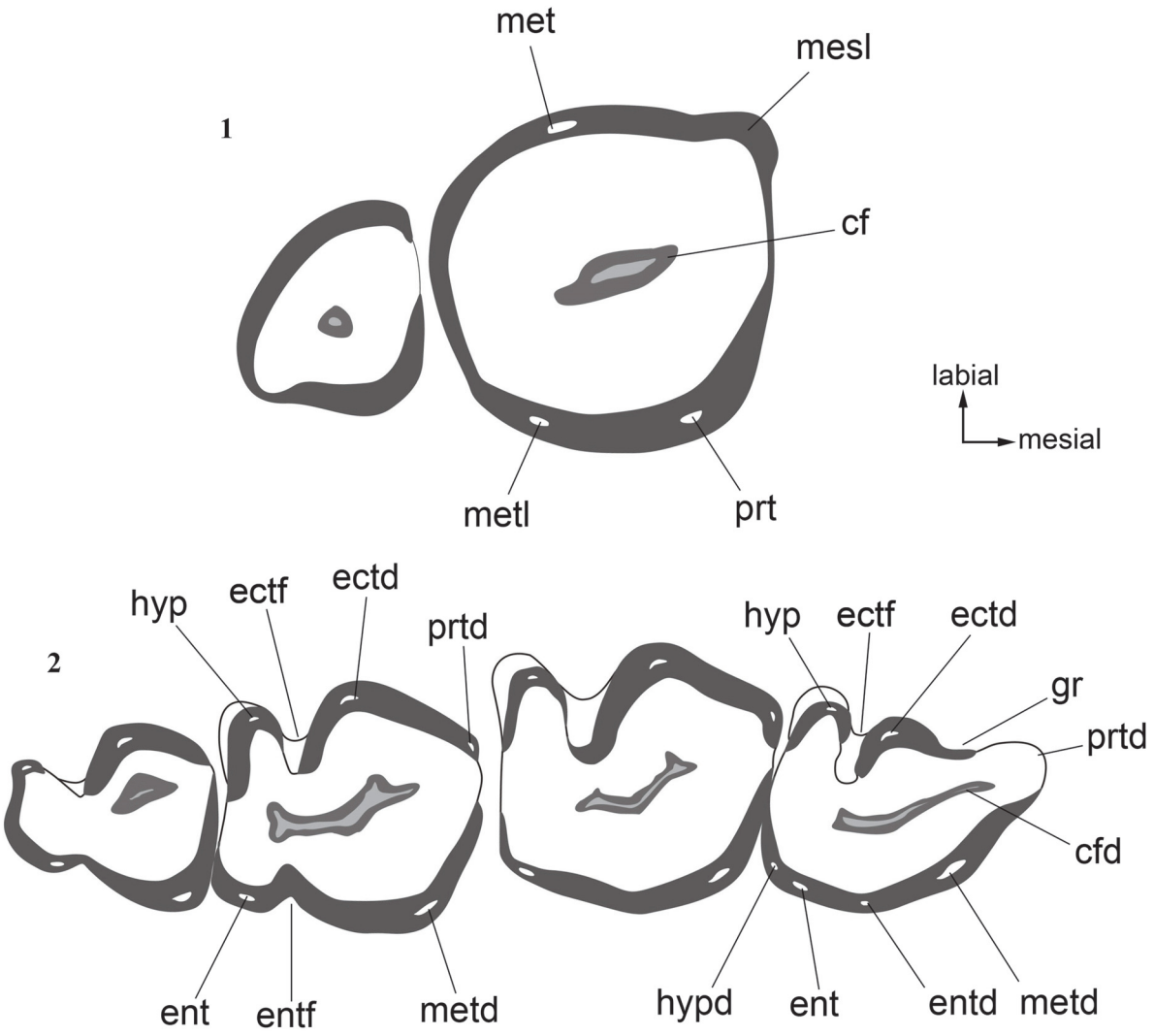

FIGURE 2. Line drawings (occlusal view) of *Microtragulus bolivianus* showing the anatomical nomenclature used in the text. **1**. Right M3-4. **2**. Right m1-4 (image reflected). Abbreviations: cf, central fossa; cfd, central fossid; ectf, ectoflexid; ectd, ectostylid; ent, entoconid; entd, entostylid?; entf, entoflexid; gr, groove; hyp, hypoconid; hypd, hypoconulid; mesl, mesiolabial lobe; met, metacone; metd, metaconid; metl, metaconule; prt, protocone; prtd, protoconid.

0074, body of left calcaneus; JUY-P-0075, right astragalus; JUY-P 55, complete right metatarsal III; JUY-P 56, lot containing proximal and distal portions of right metatarsal IV (not associated); JUY-P 57, distal portion of left metatarsal IV; JUY-P 58, lot containing three ungueal phalanges.

Range and Occurrence. The holotype comes from Viscachani, 94 km SE of La Paz, Bolivia; Umala Formation (Pliocene levels dated between 5.3–2.9 Ma [Marshall et al., 1992; MacFadden et al., 1994]). The materials studied herein come from San Roque (26º 14’ 32’’ S, 65º 21’ 55’’ W; 2940 m), 4.4 km SSW of Humahuaca town, Humahuaca Department, Jujuy Province, Argentina; Uquía Formation (late Pliocene-early Pleistocene; Marplatan SALMA, probably Vorohuan subage; Ortiz et al., 2012).

Emended Diagnosis. *Microtragulus bolivianus* differs from *Proargyrolagus* by the presence of euhypsodont teeth, simplified occlusal structure, and reduced dental formula (which is also a difference with *Hondalagus* and *Anargyrolagus*). Additionally, *M. bolivianus* differs from the species of *Hondalagus*, *Anargyrolagus*, and *Argyrolagus* by the following combined features: M3 subcircular in outline and with a single labial cusp (metacone); M4 proportionally smaller than M3 and without differentiated cuspidal relief; lower molars with talonid

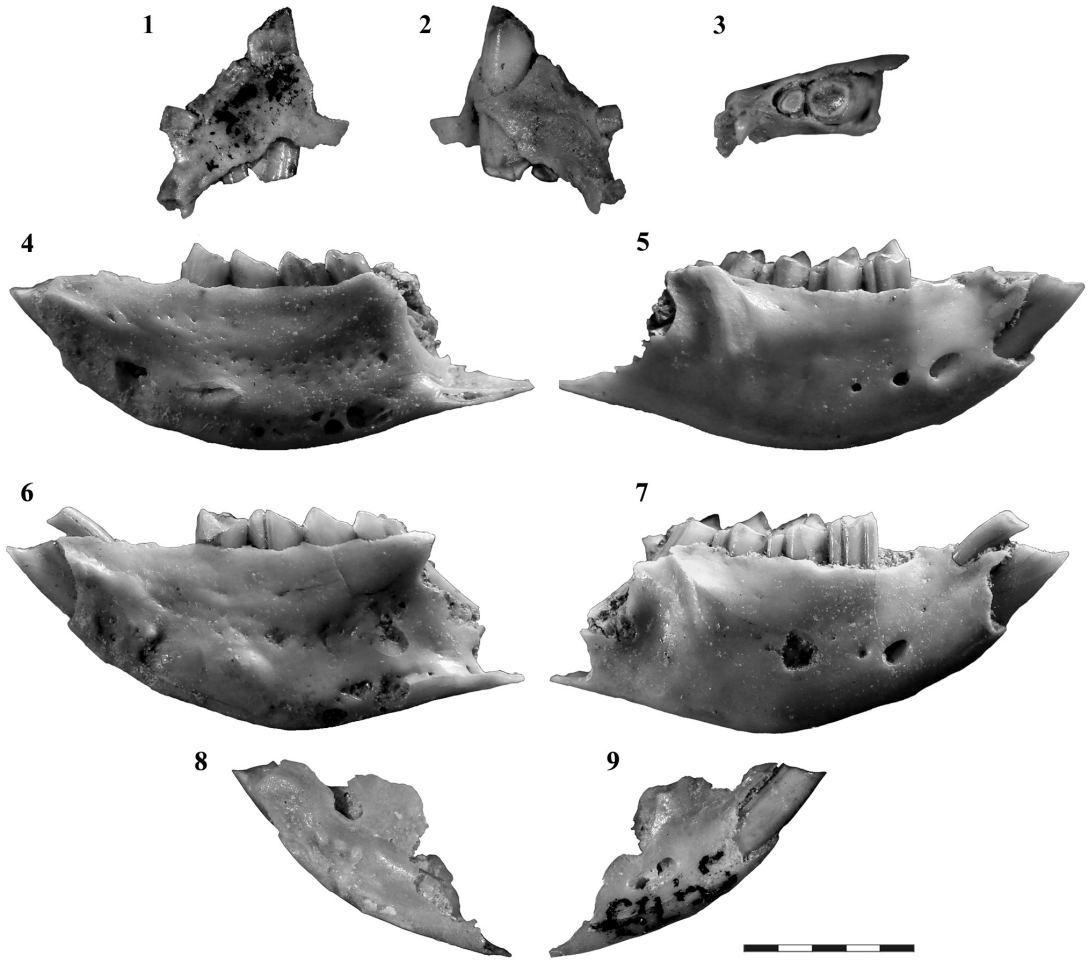

FIGURE 3. *Microtragulus bolivianus*. **1-3**. JUY-P-0065, fragment of right maxilla with M3-M4 in: 1, lateral; 2, medial; and 3, occlusal views. **4-5**. JUY-P-0066, right mandibular body with i1, alveoli of i2 and p3, and complete m1-4 in: 4, medial; and 5, lateral views. **6-7**. JUY-P-0067, right mandibular body with complete i1 and i2, alveolus of p3, and complete m1-4 in: 6, medial; and 7, lateral views. **8-9**. JUY-P-0068, anterior fragment of right mandibular body with i1 and alveoli of i2 and p3 in: 8, medial; and 9, lateral views. Scale bar equals 5 mm.

proportionally shorter than the trigonid, reduced or absent entoflexid; and proportionally smaller m4. Within *Microtragulus*, *M. bolivianus* differs from *M. reigi* by the absence of an entoflexid in m2, and a shallower entoflexid in m3; and from *M. catamarcensis* by a proportionally larger m4 and the presence of a well-marked entoflexid in m3.

Description

Maxilla. This bone is represented by two poorly preserved fragments characterized by the presence of several sulci, crests, and foramina (Figure 3.1-3). A deep sulcus is present in the medial side above M4; this sulcus becomes progressively shallower towards the anterior side, and its trajectory matches with the infraorbital canal for the passage of the maxillary nerve (a derivate of the maxillary branch of the trigeminal nerve) and accompanying vessels. This condition is inferred from the observation of the specimen GHUNLPam 8549 (holotype of *Argyrolagus rusconii*), which preserves the infraorbital foramen connected to a medial sulcus of the maxilla. Other specimen referred to *Microtragulus* sp. (PVL 6594; García-López and Babot, 2015), shows similar structures. Given this arrangement, we infer that a proper infraorbital canal is absent, being replaced by a sulcus (corresponding to the medial wall of the canal) connected anteriorly to a foramen piercing the maxilla anterior to the orbit. This modified condition is probably

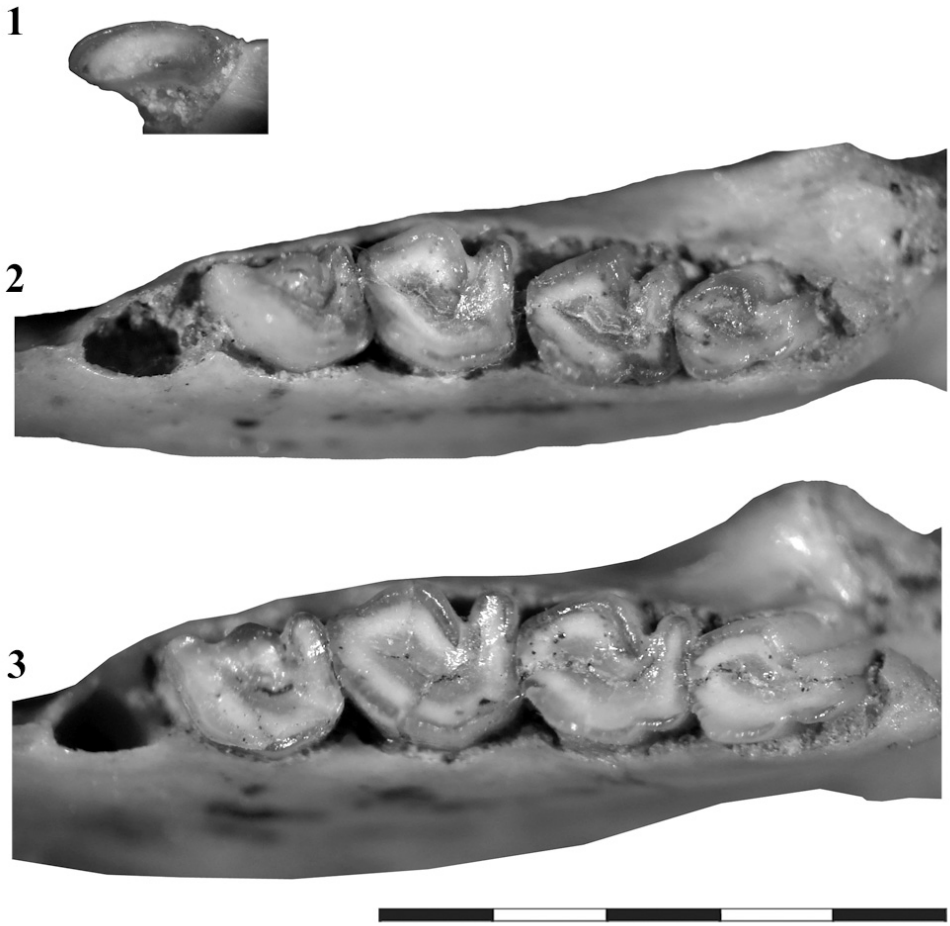

FIGURE 4. *Microtragulus bolivianus*, right lower dentition in occlusal view. **1**. JUY-P-0066, detail of i1. **2**. JUY-P-0066, m1-4. **3**. JUY-P-0067, m1-4. Scale bar equals 5 mm.

related to the great development of the palatal vacuities typical of this family.

The specimen preserving the zygomatic process (JUY-P 50) probably corresponds to a juvenile individual, judging by the posterior position of the process (above the alveolus of the last present molariform, which is very large). This would indicate that M4, which is the smallest molar, was not yet fully erupted at the time of death of the individual.

Mandible. The mandibular body is short and high and strongly convex ventrally. The point of maximum height is located at the level of m2 (Figure 3.4-7); in the labial side, it measures 5.65 mm in JUY-P-0067 and 4.94 mm in JUY-P-0066.

In lateral view the body exhibits the mental foramina. In JUY-P-0066 there are three foramina, which are progressively smaller toward the posterior side; the first one is located at the level of p3. The second one is placed at the level of the mesial border of m1, and the third opening is located at the level of the mesial border of m2 (Figure 3.5). Only two foramina are visible in JUY-P-0067, although the surface where the third foramen should be is actually broken (Figure 3.7). These openings present the same location than the first and second apertures in JUY-P-0066. Nevertheless, the second foramen is proportionally smaller in this case. The specimen JUY-P-0068 (Figure 3.9) shows a different arrangement: the two preserved foramina open together inside a larger aperture (feature also present in *Proargyrolagus bolivianus*; Wolf, 1984). Other apertures are several tiny vascular openings scattered all over the lateral surface of the mandibular body.

The lateral side of the mandibular body also preserves a blunt but conspicuous coronoid crest. This structure projects anteroventrally towards the level of the anterior half of m4.

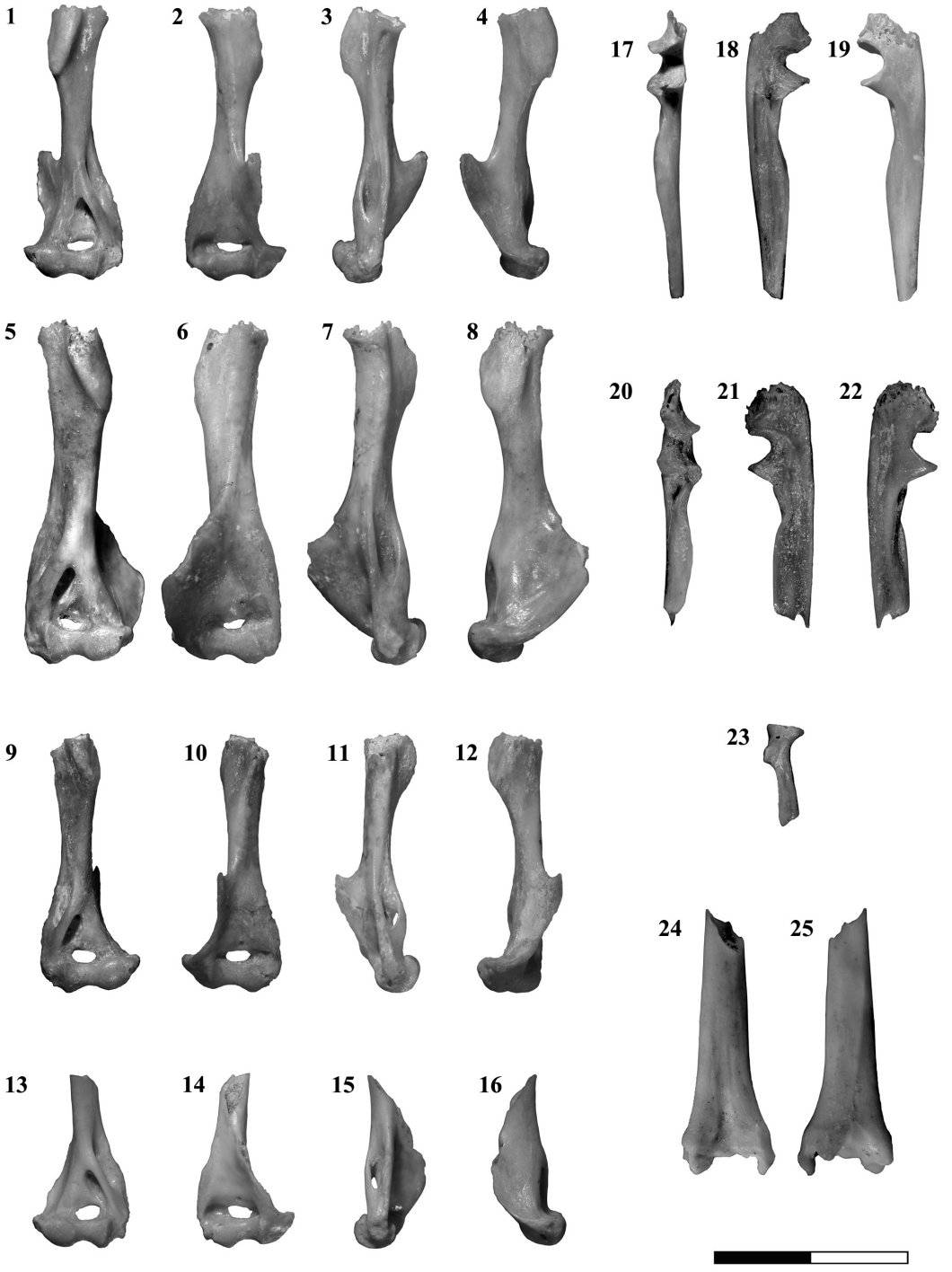

FIGURE 5. *Microtragulus bolivianus*, fore and hindlimb bones. **1-4**. JUY-P-0069, right humerus almost complete except the proximal third in: 1, anterior; 2, posterior; 3, medial; and 4, lateral views. **5-8**. JUY-P-0070, left humerus almost complete except the proximal third in: 5, anterior; 6, posterior; 7, medial; and 8, lateral views. **9-12**. JUY-P-0071, distal half of left humerus in: 9, anterior; 10, posterior; 11, medial; and 12, lateral views. **13-16**. JUY-P-0072, distal end of right humerus in 13, anterior; 14, posterior; 15, medial; and 16, lateral views. **17-19**. JUY-P 59, proximal half of right ulna in: 17, anterior; 18, lateral; and 19, medial views. **20-22**. JUY-P 60, proximal half of left ulna in: 20, anterior; 21, lateral; and 22, medial views. **23**. JUY-P 61, proximal fragment of radius. **24-25**. JUY-P 52, distal end of right tibiofibula in: 24, anterior; and 25, posterior views. Scale bar equals 10 mm.

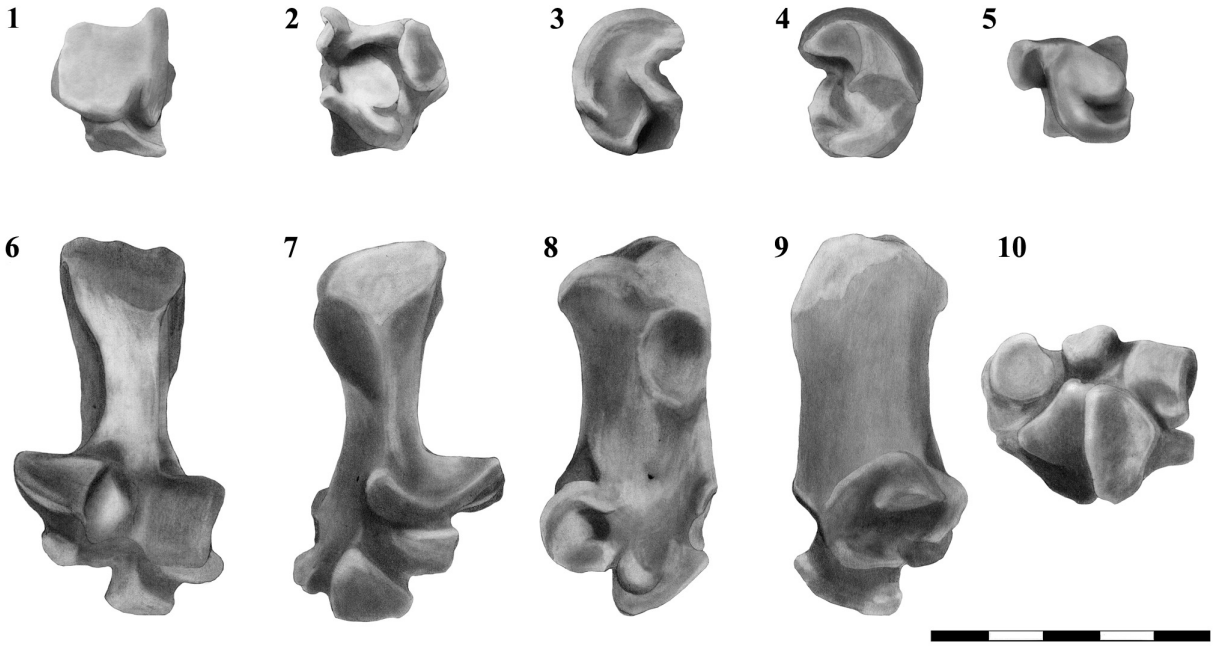

FIGURE 6. *Microtragulus bolivianus*, astragalus and calcaneus. **1-5**. JUY-P-0075, complete right astragalus in: 1, dorsal; 2, plantar; 3, medial; 4, lateral; and 5, distal views. **6-10**. JUY-P-0073, complete left calcaneus in: 6, dorsal; 7, plantar; 8, medial; 9, lateral; and 10, distal views. Scale bar equals 5 mm.

In medial view, the mandible shows an unfused symphysis, the borders of which are not well defined. However, the surface is easily recognized by the presence of several shallow depressions and low tubercles. It extends to the level of the anterior portion of m2. Both specimens JUY-P-0066 and JUY-P-0067 bear several tiny nutritious foramina and fenestrations towards the posteroventral portion of the body (Figure 3.4, 6). The angular process is partially preserved; its anterior end is located at the level of the talonid of m4. The visible portion of this process indicates that it was strongly inflected forming a well-developed concavity facing upwards, as in other argyrolagids (Rusconi, 1933; Simpson, 1970a; Sánchez-Villagra et al., 2000). Two foramina are visible above the process: the dorsal one is the proper mandibular foramen and the aperture located immediately below is interpreted here as an accessory opening of this canal. These secondary openings are also present in the holotype of *Microtragulus bolivianus* as well as in other argyrolagids. The maxillary canal (see Discussion) is not preserved in the specimens recovered from Uquía Formation but is clearly present in the holotype of *M. bolivianus* (Hoffstetter and Villarroel, 1974).

Dentition. The dentition is euhypsodont and deeply implanted in the maxilla and dentary. The teeth are prismatic, with central dentine surrounded by a layer of enamel. The teeth are also partially surrounded by a thin layer of cementum that thickens in the area of the sulci. All the recovered dental pieces (except the only i2 of the sample studied herein) show a central fossa/fossid. This structure is particularly conspicuous in i1, where the layer of enamel surrounding the inner cavity is clearly present (Figure 4.1). This feature, described for *Hondalagus* (Villarroel and Marshall, 1988), is also present in *Argyrolagus* (Simpson, 1970b) and *Microtragulus* (García-López and Babot, 2015), and probably in *Anargyrolagus* MPEF-PV 5291.

Upper dentition. M3 is sub-quadrangular (Figures 2.1, 3.3) and larger than M4 (L=1.51 mm and W=1.41 mm). The intraalveolar portion of the crown is slightly curved, vertically implanted, and divergent with respect to the intraalveolar portion of M4. The layer of enamel is continuous, although it is thinner in the mesiolabial area. The labial side is clearly higher than the lingual one, which is about the same level of the alveolar border. In the labial edge there is a poorly developed mesiolabial lobe and a distal elevation that we interpret here as the metacone (metacone + StD after Goin and Abello, 2013). The lingual side is rounded and bears the protocone and the metaconule, which is very

FIGURE 7. *Microtragulus bolivianus*, metatarsal III and IV and phalanges. JUY-P 55, complete right metatarsal III and JUY-P 56, distal portion of right metatarsal IV (not associated) in: **1**, anterior; and **2**, posterior views. Scale bar equals 10 mm. **3-5**. JUY-P 58, ungual phalanges in lateral view. Scale bar equals 5 mm.

reduced and located slightly labially in relation to the protocone. The central area of the occlusal surface bears a mesiodistally elongated and slightly oblique fossa.

The M4 is simplified in relation to M3; it is small (L=0.87 mm and W=0.71) and in occlusal view the crown is roughly triangular (Figures 2.1, 3.3). The labial edge is convex and lacks flexi and cusps. Lingually, there are no proper cusps but the presence of a protocone can be inferred, following the arrangement in the precedent molar. The metaconule is absent. The enamel distribution is irregular; it is absent in the mesiolabial side of the tooth and very thin in the distolingual part. As in other Argyrolagidae, the occlusal surface of M4 is mesioventrally directed, contrasting with the distoventrally orientation of the preceding molar. A subcircular fossa occupies a central position in the occlusal surface.

Lower dentition. The i1 is kidney-shaped (the labial border is convex and the lingual one is concave), labiolingually compressed, procumbent, and deeply implanted (the intraalveolar section extends up to the level of m1) (Figures 3.4-9, 4.1; Table 2). The tooth shows a continuous layer of enamel. In lateral view, the occlusal surface is concave; the mesial side is acute and high, and the distal one is blunt and low. It shows a small and oval fossid near the medial area of the lingual wall.

The second incisor is located immediately behind i1 (Figure 3.6-7). It is smaller and oval in outline. Although hypsodont, this tooth is not deeply implanted since the length of its alveolus is ventrally limited by the alveolus of i1. In lateral view, the crown is mesially orientated. In contrast to i1, i2 is surrounded by a thick layer of cementum. The occlusal surface presents a well-developed wear facet facing labially.

The third premolar is not preserved in any of the specimens of *Microtragulus bolivianus* here studied. Its alveolus is separated from i2 by a short diastema, whose mesiodistal length is about the same length of the alveolus of i2. The alveolar size and shape suggest that this tooth was markedly smaller than the first molar (as in other argyrolagids) and not deeply implanted (Figure 4.2-3).

All the lower molars are euhypsodont. The enamel distribution is mostly continuous around the tooth, with small interruptions in the mesial and distal edges of m1-3 (and a small portion of the mesial edge of m4), and the ectoflexid of all molars. Additionally, the layer of enamel of the mesial side of m2 and m3 can be absent or be very thin. The cementum has an irregular arrangement.

TABLE 2. Measurements of the lower dentition of *Microtragulus bolivianus* (in mm). * Measures taken from Hoffstetter and Villarroel (1974).

	i1		i2		m1		m2		m3		m4		m1-m4	i1-m4
	L	W	L	W	L	W	L	W	L	W	L	W	L	L
Holotype*	1.3	0.6	-	-	-	-	-	-	1.5	1.3	1.4	1.0	-	10.3
JUY-P-0066	1.35	0.59	-	-	1.50	1.14	1.53	1.49	1.44	1.34	1.14	1.08	5.77	11.01
JUY-P-0067	1.66	0.70	0.92	0.63	1.68	1.27	1.88	1.61	1.68	1.47	1.49	1.19	6.44	12.50

In most cases, it is thicker in the deepest portion of the ectoflexid and in the labial wall of the talonid. The central fossid is mesiodistally elongated (Figures 2, 4.2-3).

The first molar shows a distinct ectoflexid, which separates the trigonid from the talonid. The entoflexid is absent in m1, as in *Microtragulus catamarcensis*. This trait is present but vestigial in *M. reigi* (Simpson, 1970a) and clearly demarcated in all the other argyrolagids. The metaconid is the dominant cusp; it is a high crest-like structure mesially displaced; slightly posterior, the lingual wall of the tooth exhibits a tiny bulge that could be an accessory cusp (entostylid?; see Hershkovitz, 1971). The ectostylid is lower and presents a well-developed column in the labial wall of the tooth. Mesially, a groove separates this structure from the protoconid which points mesiolabially. The paraconid is absent. The talonid, two thirds shorter than the trigonid, is labiolingually extended with its main axis transversal to the tooth row. It has a distinctive tongue-like hypoconid and a well-developed entoconid. The hypoconulid is a vestigial structure barely distinctive in the distolingual corner of the talonid and adjacent to the entoconid.

The second molar differs from the first one in its larger size, a shallower mesial groove in the trigonid (absent in JUY-P-0066), and a wider ectoflexid. As in m1, the entoflexid is absent. The hypoconid, entoconid, and hypoconulid have the same development and arrangement than in m1.

The third molar is shorter than the preceding teeth but longer than m4. The trigonid is very similar in outline to that of m2, although both in JUY-P-0066 and in JUY-P-0067 the groove mesial to the ectostylid is absent. The talonid is well differentiated in this tooth, since a visible but shallow entoflexid lingually separates these structures. The ectoflexid is very similar to that of m2. The entoconid is more conspicuous and the hypoconulid is absent. The layer of enamel appears to be reduced in the mesial end of the trigonid in JUY-P-0066 and in the mesial and distolingual edge in JUY-P-0067.

The fourth molar is very different in shape and size from the preceding molars. It is the smallest molar, both in length and width, and the talonid is labiolingually reduced. As in m3, the trigonid is separated from the talonid by the ecto and entoflexids. The hypoconid is small and low, and the entoconid is a higher crest-like structure. The distal border of the tooth bears a shallow flexid that separates the hypoconid from the distally extended hypoconulid. This arrangement is evident in JUY-P-0067 but is masked in JUY-P-0066 given the poor development of the hypoconulid.

Postcranial Skeleton. Among argyrolagids, the postcranium is known from partially preserved remains of *Microtragulus argentinus* (cuboid, navicular, ectocuneiform, metatarsals III and IV, and caudal vertebrae), *M. reigi* (humerus, femur, calcaneus, and tibiofibula), and *Argyrolagus scagliai* (partially preserved vertebrae, scapula, humerus, radius, ulna, pelvic girdle, femur, tibiofibula, tarsals, metatarsals, and phalanges). In addition, an isolated calcaneus (not directly associated to any *Anargyrolagus* specimen, but coming from the same level and locality; A. Carlini, personal commun., 2016) was recovered at Gaiman, Chubut Province and described by Szalay (1994). Up to now, the anatomical descriptions came from the work of Simpson (1970a), which was focused on *A. scagliai*, *M. reigi*, and *M. argentinus*, and Szalay (1994) who emphasized on the morphology of the Gaiman calcaneus and the crurotarsal joint and tarsal anatomy of *Argyrolagus*. Here we present a detailed description of isolated pieces of the postcranium of *Microtragulus bolivianus*, which includes partially preserved humeri, ulnae, radii, tibiofibulae, and complete astragalus, calcaneus, metatarsals, and distal phalanges. According to our observations, there are no significant differences in the morphology of the skeletal pieces among these species. However, in the following section we include several comparisons in order to highlight inter and intraspecific variations.

Humerus. Four partially preserved humeri (two left and two right) were recovered from the Uquía fossil association (Figure 5.1-16). These elements vary in size and robustness: JUY-P-0070 (Figure 5.5-8) is larger and stouter than the other three humeri, a feature that could be related to sexual or ontogenetic variation. In anterior view the diaphysis is straight. The proximal half of the shaft appears to be twisted in relation to the distal portion although the absence of the head prevents to evaluate clearly this feature. This half bears the deltoid crest. In contrast to the general elongated shape of this structure in many mammals, in argyrolagids (e.g., *Microtragulus bolivianus*, *Argyrolagus*) the place of attachment of the M. deltoideus and M. pectoralis major is a short, raised plate-like and ovoid area facing anterolaterally. Laterally, the distal half of the humerus bears a well-developed and hook-shaped ectepicondylar crest, which faces anterolaterally and ends proximally in an acute tip. Even if this crest is not fully preserved, it appears to have a different arrangement in relation to *Argyrolagus* where it does not flare laterally (Simpson, 1970a). Medially, the distal portion of the diaphysis exhibits a large entepicondylar foramen in which the medial aperture is hidden in anterior view. The same morphology has been described by Simpson (1970a, p. 27) in *Argyrolagus scagliai*. The distal epiphysis exhibits a rounded capitulum in continuity with an ectepicondyle not expanded laterally. The trochlea is bounded medially by a sharp edge separating it from the entepicondyle. This structure is not medially expanded. The intercondylar notch is deep. Posteriorly, the supratrochlear foramen opens in the supratrochlear fossa which widens medially. Several nutritious foramina pierce the humerus. The medial wall of the entepicondylar foramen bears one (JUY-P-0069), two (JUY-0072), or three (JUY-P-0070, 0071) apertures. Other openings are visible in the proximal edge of the ectepicondylar crest, adjacent to the diaphysis, where the specimens JUY-P-0069 and JUY-P-0070 bear one foramen. Finally, foramina are also visible above the posterior side of the supratrochlear foramen (JUY-P-0070, 0071, and 0072 show one aperture and JUY-P-0069 shows two apertures).

Ulna. Two incomplete ulnae were preserved (Figure 5.17-22). The distal end is lost in both elements. The olecranon is short and stout; the anteroposterior length is greater than the proximodistal length. The anconeal process faces laterally and is not part of the anterior border of the olecranon which is well-projected anteriorly. The trochlear notch is deep. The coronoid process is prominent and its articular surface is proximally directed. Distally, the shaft exhibits a concave and triangular area related to the insertion of the M. biceps brachii**.** The radial notch is concave, facing more laterally, instead of anteriorly. It is well limited posteriorly by an acuminate process. The body is incomplete; nonetheless, it is clear that it narrowed distally. The most conspicuous feature of the shaft is the thinness of the bone and the extremely concave fossa for the M. abductor pollicis longus. This fossa is extended along almost the entire shaft and is limited anteriorly by a sharp crest which is laterally bent in anterior view. In medial view, the proximal third of the ulna exhibits a shallow fossa for the insertion of the M. flexor digitorum profundus.

Radius. The proximal end of a radius is preserved (Figure 5.23). The incompleteness of this element prevents us from determining if it is a right or a left bone. The head is round and the fovea capitis is slightly concave. The neck is conspicuous; it shows a well-developed radial (bicipital) tuberosity, as in *Argyrolagus* (Simpson, 1970a). The body has a deep posterior fossa probably related with the origin of the M. abductor pollicis longus. Laterally, this fossa is bounded by a sharp pronator crest where the M. pronator teres would be inserted.

Tibiofibula. This complex is represented by a right proximal epiphysis and a fragment of a right distal third. The proximal epiphysis is triangular in proximal view. This area exhibits the medial condyle which is subtriangular and slightly convex; the lateral one is kidney-shaped, concave, and longer anteroposteriorly. The popliteal notch is conspicuous and the intercondylar eminence exhibits both the lateral and medial tuberosities (being the lateral remarkably smaller than the medial one). The extensor sulcus is absent. Anteriorly, the material preserves part of the tibial tuberosity that is a small and smooth surface.

The distal portion of the tibia and the fibula is completely fused (Figure 5.24-25); there is no evidence of sutures distinguishing neither this pair of bones nor the diaphysis from the distal epiphysis. In anterior view this epiphysis exhibits a marked fossa, proximodistally elongated. In posterior view, the shaft has a blunt and oblique longitudinal crest. The tibia bears in its medial face a very shallow notch that indicates the position of the passage of the tendons of the muscles flexing the foot. In turn, the extensor muscles in the lateral side of the fibula pass through a deep groove (Szalay, 1994).

The joint between the tibiofibula and the tarsus includes the articulation with the astragalus

(medial) and with the calcaneus (lateral). As Szalay (1994) described for *Argyrolagus*, the crurotarsal joint is highly restricted in *Microtragulus*; both the fibular and tibial sides contact closely with the astragalus. In addition, the fibular portion joints with a large area in the calcaneus. The astragalotibial facet is formed by two well-differentiated medial and lateral facets. In the same way the medial astragalotibial facet exhibits a horizontal and vertical surface. The horizontal one is concave and anteroposteriorly elongated and the vertical is convex and located in the lateral wall of the medial malleolus. The lateral astragalotibial facet is very convex. On the fibula, the astragalofibular facet is a small surface located in the medial side of the lateral malleolus. This facet is continuous with the lateral astragalotibial facet; therefore, both facets are hard to identify. The calcaneofibular facet is concave, oval, and anteroposteriorly elongated. Its main axis is shorter than the medial astragalotibial facet. Both the morphology of the crurotarsal joint, as well as that of the tarsals is essentially the same in *Argyrolagus* and *Microtragulus*.

Astragalus. The astragalar body (corpus tali) is remarkably large; it contrasts with a small head, which occupies one third of the total length of the dorsal face (Figure 6.1-5). In dorsal view the body exhibits the large astragalotibial lateral facet (ATil). It is well extended, both distally and proximally, and is somewhat pulley-like, being the medial half steeper than the lateral one. The astragalar fibular facet is small and the astragalar foramen is absent. The head exhibits the dorsal portion of the astragalonavicular contact, which is proximolaterally-distomedially extended. Medially, this facet shows the astragalar distal tuber. The proximal extension of the lateral tibial contact, the ectal (calcaneoastragalar) facet, and the sustentacular and navicular facets are visible in plantar view. The ectal facet is oval and strongly concave. The main axis is roughly orientated proximomedially-distolaterally. The sustentacular facet is ribbonlike and contacts with the homonymous facet in the calcaneus; it comprises the sustentacular facet properly and the superior sustentacular facet. The first one is formed by two areas, one occupies the central exposition of the plantar face and the other is rod-like and oblique. Both are tangential and its contact is located near the proximomedial end of the rod-like area. The central area of the sustentacular facet is oval, slightly wider distally, and is almost parallel to the ectal facet. The rod-like portion of the sustentacular facet is well exposed in plantar view. It is remarkably convex, and occupies the full width of the astragalar head. A deep and narrow astragalar sulcus (interarticular sulcus) separates this facet from the calcaneoastragalar articulation. The superior sustentacular facet is represented as a deep sulcus between the plantar extension of the astragalotibial lateral facet and the sustentacular facets. The astragalar distal tuber is small and is restricted to the proximomedial portion of the plantar aspect. The astragalonavicular facet is restricted to the distolateral extremity of the head.

In medial view the dominant structure is the semicircular astragalotibial medial facet, clearly defined by a blunt dorsal edge. On the proximal and plantar corner there is a small astragalar medial plantar tuberosity located adjacent to the superior sustentacular facet. Distally this aspect exhibits the medial extension of the contact with the navicular and the astragalar distal tuber. In lateral view the astragalus exhibits the astragalofibular facet which is small, triangular, and faces laterally. The distinctive feature of the distal view is the astragalonavicular joint, which covers almost the entire surface of the head; there is no articulation between the astragalus and the cuboid.

Calcaneus. The tuber is a cylindrical lateromedially compressed structure which widens toward its posterior end (Figure 6.6-10). This end exhibits two smooth surfaces separated by a low step; one is mainly posterior and the other is more plantarly directed. In lateroplantar view the tuber shows an oval scar which was probably related to with the attachment of the M. abductor digiti quinti. A blunt crest runs anteroposteriorly in plantar view and ends in a small anterior plantar tubercle. The peroneal process is located in the laterodistal corner of the plantar aspect. This process is rounded and well developed. Adjacent to the peroneal process, and distal to it, there is a small groove for the M. peroneus longus.

The body of the calcaneus is wide and much shorter than the tuber. In dorsal view the body shows the proximal process bearing the calcaneoastragalar (or ectal) facet and the calcaneofibular facet. Both facets are separated by a shallow groove in *Argyrolagus* and *Microtragulus*, differing from the Gaiman calcaneus in which they are close together (see Szalay, 1994, figure 7.28 A, C). The calcaneoastragalar facet faces dorsally and dorsomedially and is smaller and more dorsally projected than the calcaneofibular facet (particularly visible in medial and distal views). Both in *Argyrolagus* as in *Microtragulus*, the calcaneoastragalar facet is smaller than that of the Miocene Gaiman calcaneus (Szalay, 1994). The sustentacular facet

comprises the sustentacular facet properly and the superior sustentacular articulation. As in the astragalus, the sustentacular is divided in two portions: one is proximal, oval, and distally oriented and the other is more distally located, smaller, and faces dorsomedially. The superior sustentacular facet is a small articular surface restricted to the dorsal border of the proximal part of the sustentacular facet. In distal view, this facet is smaller in *Argyrolagus* than in the Gaiman calcaneus (Szalay, 1994), a condition also present in *Microtragulus*.

The contact with the cuboid is formed by two discontinuous facets separated by a step. The proximal facet (CaCup) is smaller and somewhat triangular; the distal one (CaCud) is dorsoplantarly elongated and oval.

Metatarsals. One complete right Mt III and three fragments of the Mt IV were recovered (Figure 7.1-2). The Mt III measures 29.87 mm, slightly larger than *Microtragulus argentinus* (27 mm; Ameghino, 1904) and smaller than *Argyrolagus scagliai* (35.6 mm; Simpson, 1970a, p. 68). The Mt III exhibits a slightly concave T-shaped facet for the articulation with the ectocuneiform. Laterally a marked notch lodges a medial process for the Mt IV; medially, there is a distinctive facet which is interpreted as the contact with a vestigial Mt II, as proposed for *Argyrolagus* (Simpson, 1970a, figure 15E). The proximal end of the Mt IV exhibits a triangular convex surface which articulates with the cuboid. Laterally this bone presents a proximally projected process that probably covered partially the lateral side of the cuboid, as in *Microtragulus argentinus* MACN 12925 and *Argyrolagus scagliai* MMP 785-S (Simpson, 1970a). The only peculiarity of the diaphysis of the metatarsals is the flattened area of contact between Mt III and IV. In this last bone, the distal half of the diaphysis is thinner than in Mt III. The distal end of the metatarsals is simple. In the dorsal aspect of the head the articular surface is condylar; in plantar view this structure shows a notorious longitudinal crest.

Phalanges. Three ungual phalanges were recovered (Figure 7.3-5). They are long, slightly curved, and lateromedially compressed. The flexor tubercle is long, constricted in the middle portion, and is pierced by the ungual foramen. The articular facet is strongly concave; the dorsal border is more posteriorly projected than the ventral one.

Comparison

When compared with Oligocene and Miocene argyrolagids (*Proargyrolagus*, *Hondalagus*, and *Anargyrolagus*), *Microtragulus bolivianus* shows clear differences involving several features. Regarding *Proargyrolagus*, the main dental differences include the degree of hypsodonty, the morphology of the occlusal surface, and the dental formula. In *Proargyrolagus* the molars are hypsodont but rooted (i.e., high crown, not evergrowing; Wolf, 1984; protohypsodont in Goin and Abello, 2013) while in *M. bolivianus* the molars are euhypsodont (i.e., high crown and rootless; Hoffstetter and Villarroel, 1974). The occlusal surface of the upper molars in *Proargyrolagus* exhibits a complex outline including several distinctive cups and structures (e.g., mesiolabial lobe, paracone + StB, metacone + StD, protocone, and metaconule). In *M. bolivianus* this pattern is simplified with most of the occlusal features largely masked. Another distinctive feature of *M. bolivianus* regarding *Proargyrolagus* is related to the crown implantation in M3-4. In *Proargyrolagus* the crowns of both molars present an almost parallel implantation, while in *M. bolivianus* the intraalveolar part of the crowns is strongly divergent. This divergence determines that the occlusal surface of M3 faces ventrally and that of M4 faces mesioventrally. These differences in implantation are also visible in the lower molars. Additionally, *M. bolivianus* also lacks several dental pieces compared to *Proargyrolagus* (dental formula 2.0.1.4 for *M. bolivianus* and 3.1.2.4 or 4.0.2.4 for *P. bolivianus*; see Sánchez-Villagra and Kay [1997] for different interpretations on the lower dental formula in the Oligocene species). Finally, the euhypsodont nature of the lower molars in *M. bolivianus* also determines that the height of the mandibular body is greater in this species.

The upper teeth of the Miocene genus *Hondalagus* differ mainly in size (smaller in relation to *Microtragulus bolivianus*), outline (more transverse in *Hondalagus*), and the distinctive layer of cementum (Sánchez-Villagra et al., 2000), which is much thinner in *M. bolivianus*. *Hondalagus* has an extra anterior lower tooth (Sánchez-Villagra et al., 2000), a well-developed entoflexid in m1 and m2 (absent in *M. bolivianus*), and proportionally larger talonids (particularly in m4).

The dental formula is the main difference between *Anargyrolagus* and *Microtragulus bolivianus*, since the former presents a canine and two more premolars than *Microtragulus*. In *Anargyrolagus* M3 is more quadrangular, with a well-developed metaconule, and M4 shows a marked occlusal relief in contrast with *M. bolivianus,* which presents an almost flat occlusal surface. The first lower incisors show a clear fossettid near the medial area of the lingual wall in *M. bolivianus*,

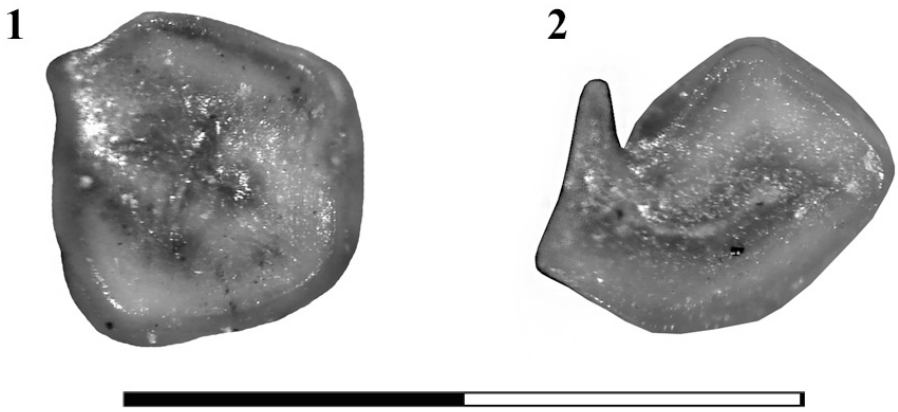

FIGURE 8. *Microtragulus* sp., upper and lower molars in occlusal views. **1**. JUY-P 53, isolated left M3. **2**. JUY-P 54, isolated left m2 or m3. Scale bar equals 2 mm.

absent in *Anargyrolagus*. This genus also contrasts with *M. bolivianus* by the higher mandibular body, the well-developed entoflexid and proportionally larger talonid in all the molars, and a proportionally larger m4.

Regarding the genus *Argyrolagus*, which includes four species (*A. scagliai*, *A. parodii*, *A. palmeri*, and *A. rusconii*), the upper dentition will be compared only with *A. scagliai* and *A. rusconii* since *A. parodii* and *A. palmeri* are represented only by lower teeth. These two species show M3 longer than wide, with the paracone present and well separated from the metacone, the occlusal outline with more distinctive corners and well-defined angles (especially in the protocone area), and the mesial border much wider than the distal one; all these features represent clear differences regarding *M. bolivianus*. Additionally, the labial wall in both species is straight in M3, contrasting with the convex wall of *M. bolivianus*. Regarding M4, in *A. scagliai* and *A. rusconii* this molar is proportionally larger and both the paracone and metacone are distinctive. Finally, the lower molars of all the species of *Argyrolagus* are characterized by a visible entoflexid (in m1-m4) and a larger talonid in all molars, particularly in m4.

The new material of *Microtragulus bolivianus* described herein can be compared more precisely with the specimens known for *M. reigi* and *M. catamarcensis*. In *M. reigi*, M3 is longer than wide, while in *M. bolivianus* the ratio between the length and the width is approximately one. Moreover, M3 in *M. reigi* has a small paracone and sharp corners (i.e., a more angled outline). Additionally, the flexus between the mesiolabial lobe and the metacone, present in *M. bolivianus*, is absent in *M. reigi*; the mesial border of the tooth is wider than the distal one; and the layer of cementum is thicker in *M. reigi*. The relative size and shape of M4 is similar between these species, but the presence of differentiated paracone and metacone in *M. reigi* is not observed in *M. bolivianus*. In the lower dentition, the morphology of the incisors is similar in both species. The molars differ in the presence of a small but distinctive entoflexid in m2-3 in *M. reigi*, and a more reduced talonid in its m4 which also lacks the distal flexid distinguishable in *M. bolivianus*.

Microtragulus catamarcensis is smaller than *M. bolivianus*, and the diastema between i2 and p3 is relatively shorter. Additionally, the talonid of m3 lacks the entoflexid, clearly present in *M. bolivianus*. The talonid in m4 has a simpler morphology in *M. catamarcensis*: the cusps are indistinguishable and the distal flexid present in *M. bolivianus* is absent.

Microtragulus sp. Ameghino, 1904
Figure 8

Referred Material. JUY-P 53, isolated left M3; JUY-P 54, isolated left m2 or m3.

Range and Occurrence. San Roque (26º 14’ 32’’ S and 65º 21’ 55’’ W; 2940 m), 4.4 km SSW of Humahuaca town, Humahuaca Department, Jujuy Province, Argentina. Uquía Formation (late Pliocene-early Pleistocene; Marplatan SALMA, probably Vorohuan subage; Ortiz et al., 2012).

Remarks. The isolated upper molar (Figure 8.1) is considered herein an M3. The tooth is subquadrangular and exhibits an irregular central fossa; the mesiolabial border is marked as an angled corner. The area of the metacone is represented by a smooth elevation and the area of the protocone is slightly more differentiated (as a subtle corner)

than the metaconular zone. The distribution of the enamel is irregular: it is clearly present in the labial wall of the tooth but is absent in the mesial side. The layer of cementum is clearly visible in the lingual and mesiolingual walls. The lower molar (Figure 8.2) is characterized by a marked reduction of the talonid, both in length as in width. This condition is similar in *Microtragulus catamarcensis* although in this species the hypoconid is U-shaped while in the isolated molar it is V-shaped. As in other members of *Microtragulus* (e.g., *M. catamarcensis* and m1-2 of *M. bolivianus*) the entoflexid is absent. The central fossid has the usual shape for Argyrolagidae, which is mesiodistally elongated.

We discard the inclusion of these molars in *Microtragulus bolivianus* based on their smaller size, the general outline of the upper molar (subcircular in *M. bolivianus* vs. quadrangular in JUY-P 53), the absence of a flexus between the mesiolabial corner and the metacone, and the angled hypoconid in the lower tooth. Nevertheless, the isolated nature and scarcity of this material prevent us from providing a specific designation.

DISCUSSION

On the Nomenclatural Problems Related to the Family Argyrolagidae and the Genera *Microtragulus* and *Argyrolagus*

Since the erection of the genus and species *Microtragulus argentinus* by Ameghino (1904) based on postcranial elements, the name of the family Argyrolagidae and the genera *Microtragulus* and *Argyrolagus* have been through extensive nomenclatural changes (see Appendix).

The basis of the conflict is that the type and only specimen of *Microtragulus argentinus* was originally included in the Family Tragulidae (Cetartiodactyla) and is represented only by postcranial elements (cuboid, navicular, and ectocuneiform, metatarsals III and IV, and two anterior caudal vertebrae) which lack diagnostic features (Hoffstetter and Villarroel, 1974). In a latter issue of the same volume, Ameghino (1904) erected the Family Argyrolagidae, which he included in Lagomorpha, and the species *Argyrolagus palmeri*, represented by a left mandibular fragment with m1-m4. This material comes from the same locality and formation than *M. argentinus* (Monte Hermoso Formation, Monte Hermoso locality, Buenos Aires), although the stratigraphical correspondence cannot be ascertained since these data remain unknown for the holotypes of *M. argentinus* and *A. palmeri*. The probability that the types of *M. argentinus* and *A. palmeri* pertain to the same species was initially noted by Carlos Ameghino and Rusconi (see Rusconi, 1936, p. 181).

After the work of Ameghino, some authors focused on this nomenclatural issue and suggested the synonymy and priority of *Microtragulus* over *Argyrolagus* (Rusconi, 1936) and even attempted to establish the use of Microtragulidae as the valid name for the family (Reig, 1955). Nevertheless, it was not until 1970 when these successive modifications were extensively and systematically reviewed by Simpson. This author proposed a conservative and arbitrary, though practical, taxonomic scheme. Based on a more complete specimen collection, he found two cranial/dental morphotypes varying in form and size. The larger morphotype included the *Argyrolagus* species (*A. palmeri*, *A. parodii*, and the then new *A. scagliai*) and, since the metatarsals assigned to *M. argentinus* are 25% smaller than those of *A. scagliai*, Simpson decided to maintain the name *Microtragulus* and associate the smaller tooth morphotypes (*M. catamarcensis* and the then new *M. reigi*) to this genus. The association was explained by the similar estimated metatarsal length of *M. reigi* (based on the metatarsal lenght/m1-m4 length ratio of *A. scagliai*), and the known measurement of *M. argentinus*. This proposal was widely accepted, although some authors continued using the name Microtragulidae (e.g., Tonni et al., 1992; Cione and Tonni, 1995; Vizcaíno et al., 2004).

By the time of his contribution, Simpson suspected that the only way to resolve the possible synonymy between the two Monte Hermoso genera was to recover associated metatarsal bones "clearly referable to *Microtragulus argentinus* and a mandible of the same individual" (Simpson, 1970a, p. 4-5). However, we now realize that this fact would be hardly the solution. As is shown in the taxonomic description above, with the exception of size, there is almost no morphological variation among the comparable postcranial elements of *M. bolivianus* and *M. argentinus* (i.e., metatarsal and tarsal bones), and *M. bolivianus* and *Argyrolagus scagliai*. Moreover, the size differences can be obviously associated to intraspecific variability, as has been reported for other species of similar size and ecological requirements (see Nader, 1978).

In this sense, we support the idea that the metatarsals referred to *Microtragulus argentinus* correspond to *Argyrolagus palmeri* and agree with the following arguments previously proposed by Hoffstetter and Villarroel (1974, p. 1947): a) the

specimens referred to these taxa are the only pieces coming from the Monte Hermoso clefts; b) the metatarsal bones do not exhibit intraspecific morphological variation among argyrolagids; and c) the metatarsal length known and estimated for the metatarsals of *M. argentinus* and *A. palmeri* can be explained by intraspecific variation. In relation to argument a), the Monte Hermoso fauna is currently one of the best studied fauna of Argentina. In the last 50 years, extensive fieldwork and different studies have focused on the resolution of this mammal age, including its mammal diversity, age, and sedimentology (Cione and Tonni, 1995, 2005; Deschamps et al., 2012; Tomassini et al., 2013 and literature therein). In this lapse, two additional specimens were found and referred to *A. palmeri* (Tomassini et al., 2013) and no specimens of a smaller morphotype referable to *Microtragulus* were found.

At this point, the two conflicts derived from this context are the validity of the name *Argyrolagus* and thus, the use of Argyrolagidae or Microtragulidae as the family name. The decision to maintain Argyrolagidae (and thus, *Argyrolagus* as type genus for the family) is supported by Article 64 of the International Code of Zoological Nomenclature (ICZN, 1999). Nevertheless, this fact would only be possible if the synonymy between *Microtragulus* and *Argyrolagus* is discarded and both generic names considered valid. This is, according to Simpson (1970a) and in our view, the most recommended scenario, since any other option would require more complicated, controversial, and hardly acceptable actions.

Anatomical Singularities of the Dentary of Argyrolagids

The dentary of argyrolagids is characterized by a high mandibular body, the presence of two to three dental foramina, an unfused mandibular symphysis extended to the level of m1 or m2, the presence of small pits and fenestrations mainly located in the posterior half of the medial side of the dentary, a robust and anteroventrally projected coronoid crest, a low and short coronoid process bearing a masseteric foramen, a well-expanded posterior shelf of the masseteric fossa and angular process, a low condyle placed above the tooth row, and other peculiar features such as a markedly long mandibular notch (ventral end of the posterior border of the coronoid process), and the presence of retromolar foramina and a maxillary canal (Rusconi, 1933, 1936; Simpson, 1970a; Hoffstetter and Villarroel, 1974; Sanchez-Villagra et al., 2000, Sanchez-Villagra, 2001; Goin and Abello, 2013). Some of these traits exhibit intrageneric variation among the basal Deseadan, Miocene, and Pliocene taxa. In *Proargyrolagus bolivianus* the mandibular body is lower than in the more recent types (Wolf, 1984; Sánchez-Villagra and Kay, 1997), probably in association with the protohypsodont condition of the molars (Wolf, 1984). The coronoid crest is longer in *Proargyrolagus* and *Hondalagus*, almost reaching the ventral border of the mandible (judging by the images from Sánchez-Villagra et al., 2000, figure 4a, c). In *Anargyrolagus*, *Argyrolagus*, and *Microtragulus* this crest shortens dorsoventrally but projects more anteriorly, towards the level of the limit between m3-m4. There is also variation among these taxa; for example, in *Argyrolagus parodii* it is stronger than in *M. bolivianus*.

Posterior and dorsal to the retromolar space the dentary of argyrolagids exhibits some noticeable traits. At the level of the alveolar border the coronoid crest expands and forms a lateral lamina (as described by Simpson, 1970a), which limits the retromolar fossa. Small foramina open in the posterior end of this concavity, clearly visible in *Anargyrolagus* (Goin and Abello, 2013, figure 4.17), *Argyrolagus scagliai* (Simpson, 1970a), *A. palmeri* (Kraglievich, 1931), *A. parodii* (Rusconi, 1933), and *Microtragulus bolivianus* (Hoffstetter and Villarroel, 1974; this paper). These openings, called the retromolar foramina, are also present in some groups of mammals such as abderitids (Rusconi, 1933; Abello and Rubilar-Rogers, 2012, figure 6.4) and humans (Schejtman et al., 1967; Kumar Potu et al., 2014). In modern mammals the retromolar foramina are related with the mandibular canal that carries the inferior alveolar nerve and vessels (Schejtman et al., 1967). Other foramina, probably related with this internal net of canals, are present at the base of the medial and lateral sides of the mandibular ramus.

Another particular trait of the argyrolagid mandible is the presence of a short medially located canal at the base of the coronoid process and posterior to m4 (Figure 9). This canal is bounded medially by a bridge-like vertical osseous bar and laterally by the mandibular ramus. This structure was observed in *Microtragulus bolivianus* by Hoffstetter and Villarroel (1974) and named the retrodental canal. In modern mammals (e.g., Lagomorpha) it is called the maxillary canal and is the passage of a vein that connects the inferior alveolar and inferior orbital veins (Wible, 2007). Sánchez-Villagra et al. (2000) misinterpreted this trait as a common feature of Argyrolagidae and the

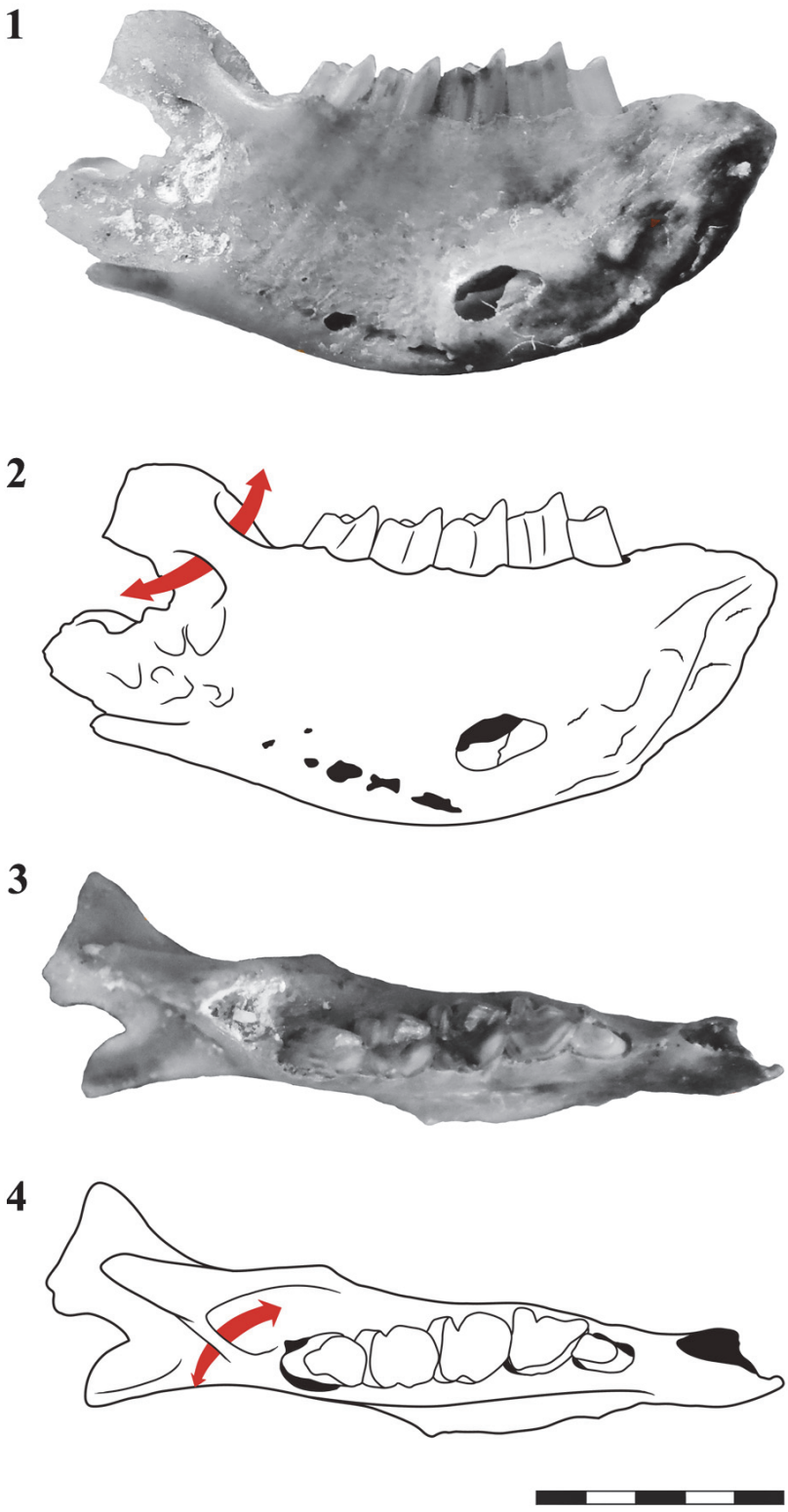

FIGURE 9. *Argyrolagus* sp. MACN 17590, left mandibular fragment with m1-4. **1-4**. Photograph and line drawing in: 1-2, medial; and 3-4, dorsal views. The arrow points the maxillary canal. Scale bar equals 5 mm.

cenolestid *Lestoros* but in this genus, as well as in other caenolestids, the canal is actually absent. Therefore, among South American extant and extinct metatherians, the maxillary canal is a unique and singular feature of argyrolagids.

CONCLUSIONS

This contribution adds new materials to the hypodigm of *Microtragulus bolivianus*, expanding on several craniomandibular, dental, and postcranial remains. The dental distinctive features of this species include M3 subcircular in outline and with a flexus between the mesiolabial lobe and the metacone (single labial cusp), M4 proportionally smaller than M3 and without differentiated cusp relief, lower molars with talonid proportionally shorter than the trigonid, entoflexid absent in m1-m2 and present but shallow in m3, and talonid in the m4 proportionally large and with a distinguishable distal flexid.

The cranial and mandibular morphology here evaluated is fairly homogeneous among the Pliocene genera. The mandibular body is short and high, and strongly convex ventrally. Many small vascular openings are scattered over the lateral and medial surface of the body. The number, size, and arrangement of the mental foramina vary among the observed specimens; two to three foramina are variably located in the anterior half of the dentary. The coronoid process is low and short, and the coronoid crest is conspicuous and projects anteroventrally towards the level of the anterior half of m4. The mandibular condyle is low, placed above the tooth row. A very peculiar feature of the anatomy of the dentary of argyrolagids is the maxillary canal, a structure probable related with the passage of the vein that connected the inferior alveolar and inferior orbital veins and probable analogue to a similar opening found in living Lagomorpha.

After reviewing all available specimens during this study we found the postcranium of argyrolagids to be fairly uniform among members of the family (e.g., *Argyrolagus*, *Microtragulus argentinus*, *M. reigi*). Therefore, several skeletal features are not useful enough for taxonomic or phylogenetic studies among Argyrolagidae. This is relevant because the first species included in the family is *M. argentinus*, a taxon founded on postcranial remains. In part because of this situation, the problems related to the validity of the names Argyrolagidae and *Microtragulus* were questioned repeatedly. At present, this nomenclatural problem has not been formally solved but a reasonable and practical proposal was provided by Simpson (1970a). This option is here considered as the most adequate, and hence, we argue in favor of maintaining the names Argyrolagidae, *Microtragulus*, and *Argyrolagus*.

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APPENDIX

Revision of the changes that occurred in the last century in the nomenclature of the Family Argyrolagidae and the genera *Microtragulus* and *Argyrolagus*.

Author and year of publication and erected family and species or used names	Comments
Ameghino, 1904 Family Tragulidae *Microtragulus argentinus*	This taxon was founded on the basis of metatarsal and tarsal bones
Ameghino, 1904 Family Argyrolagidae *Argyrolagus palmeri*	*A. palmeri* is the type species of the genus *Argyrolagus*. *Microtragulus argentinus* and *A. palmeri* were published in the same year, but *Microtragulus* has priority because was published in an earlier issue of the same volume
Kraglievich, 1931 Family Argyrolagidae *Microtragulus catamarcensis*	This author named a small dentary coming from Catamarca Province as *Argyrolagus catamarcensis*. Posteriorly Simpson (1970a) proposed the new combination *Microtragulus catamarcensis*
Rusconi, 1936 Family Argyrolagidae *Microtragulus* = *Argyrolagus*	This author suggested the synonymy but he did not consider the priority of *Microtragulus* under *Argyrolagus* and continued the use of *Argyrolagus* and Argyrolagidae (See also Rusconi, 1967)
Reig, 1955, 1958 Family Microtragulidae *Microtragulus* = *Argyrolagus*	This author established this synonymy after he and Kraglievich studied the then new specimen referred as *Microtragulus* sp. (probably the holotype of *Argyrolagus scagliai*) and began the use of Microtragulidae with *Microtragulus* as the only valid genus
Ringuelet, 1966 Family Microtragulidae *Microtragulus* = *Argyrolagus* *M. argentinus* = *A. palmeri*	This author established the priority of Microtraguidae over Argyrolagidae, *Microtragulus* under *Argyrolagus*, and *M. argentinus* under *A. palmeri*. The material there figured (but not catalogued; see p. 58) was referred as *M. argentinus* but later assigned to the neotype of *A. parodii* (Simpson, 1970b) and catalogued as MLP 62-VII-27-81
Simpson, 1970a Family Argyrolagidae *Microtragulus* (including *M. argentinus*, *M. catamarcensis*, *M. reigi*)	This author made the first comprehensive attempt in order to resolve the nomenclatural problems in the family (see text for a complete explanation)
Hoffstetter and Villarroel, 1974 Family Microtragulidae *Microtragulus* (including *M. reigi*, *M. catamarcensis*, and *M. bolivianus*	They validated the genus *Microtragulus* (including *Argyrolagus*) and proposed tentatively the erection of the subgenus *Microtragulus* and *Argyrolagus*. *Microtragulus bolivianus*is presented as *Microtragulus* (*Argyrolagus*?) *bolivianus* in the original publication. The authors did not formalize the taxonomic status of the genera included in *Argyrolagus*
Tonni et al., 1992 Family Microtragulidae *Argyrolagus palmeri*	These authors included these taxon names in a taxomic list of the mammals recovered at Monte Hermoso (Buenos Aires) and included in the Montehermosan SALMA. No explanation was given in relation to the exclusion of *M. argentinus* from this list
Cione and Tonni, 1995 Family Microtragulidae *Microtragulus* (including *M. reigi*) *Argyrolagus* (including *A. palmeri*, *A. scagliai*)	*M. argentinus* is not included among the taxa recovered at Monte Hermoso, Buenos Aires
Goin, 1995 Family Argyrolagidae *Microtragulus* (including *M. argentinus*, *M. reigi*) *Argyrolagus* (including *A. palmeri, A. scagliai*)	The author followed the proposal of Simpson (1970a)
Vizcaíno et al., 2004 Family Microtragulidae *Microtragulus reigi* *Argyrolagus scagliai*	The authors followed Tonni et al. (1992)

Author and year of publication and erected family and species or used names	Comments
Sanchez-Villagra, 2001; Goin et al., 2000; Zimicz, 2011; Ortiz et al., 2012; Goin and Abello, 2013; Tomassini et al., 2013; García López and Babot, 2015. Family Argyrolagidae *Microtragulus* (including *M. argentinus*, *M. reigi*¸ *M. bolivianus*) *Argyrolagus* (including *A. palmeri, A. scagliai*)	These authors followed the proposal of Simpson (1970a)