

## A new argyrolagid marsupial from the Early Miocene of Patagonia (Argentina)

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With 3 figures and 1 table

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**Abstract:** We describe *Anargyrolagus primus* gen. et sp. nov. (Marsupialia, Polydolopimorphia, Bonapartheriiformes, Argyrolagoidea), represented by cranial and mandibular remains collected from Colhuahuapian beds (Early Miocene) of Patagonia (Chubut Province, Argentina). This species is the oldest and most primitive argyrolagid known from Patagonia. In several aspects it resembles the cranial, mandibular, and dental features exhibited by the late Miocene species of *Argyrolagus*; however, it preserves three additional teeth of the generalized metatherian dental formula, the canine and the first two premolars. In occlusal view, its molars are more quadrangular in outline than those of *Argyrolagus* and *Microtragulus*.

**Key words:** Mammalia, Metatheria, Neogene, Patagonia, South America.

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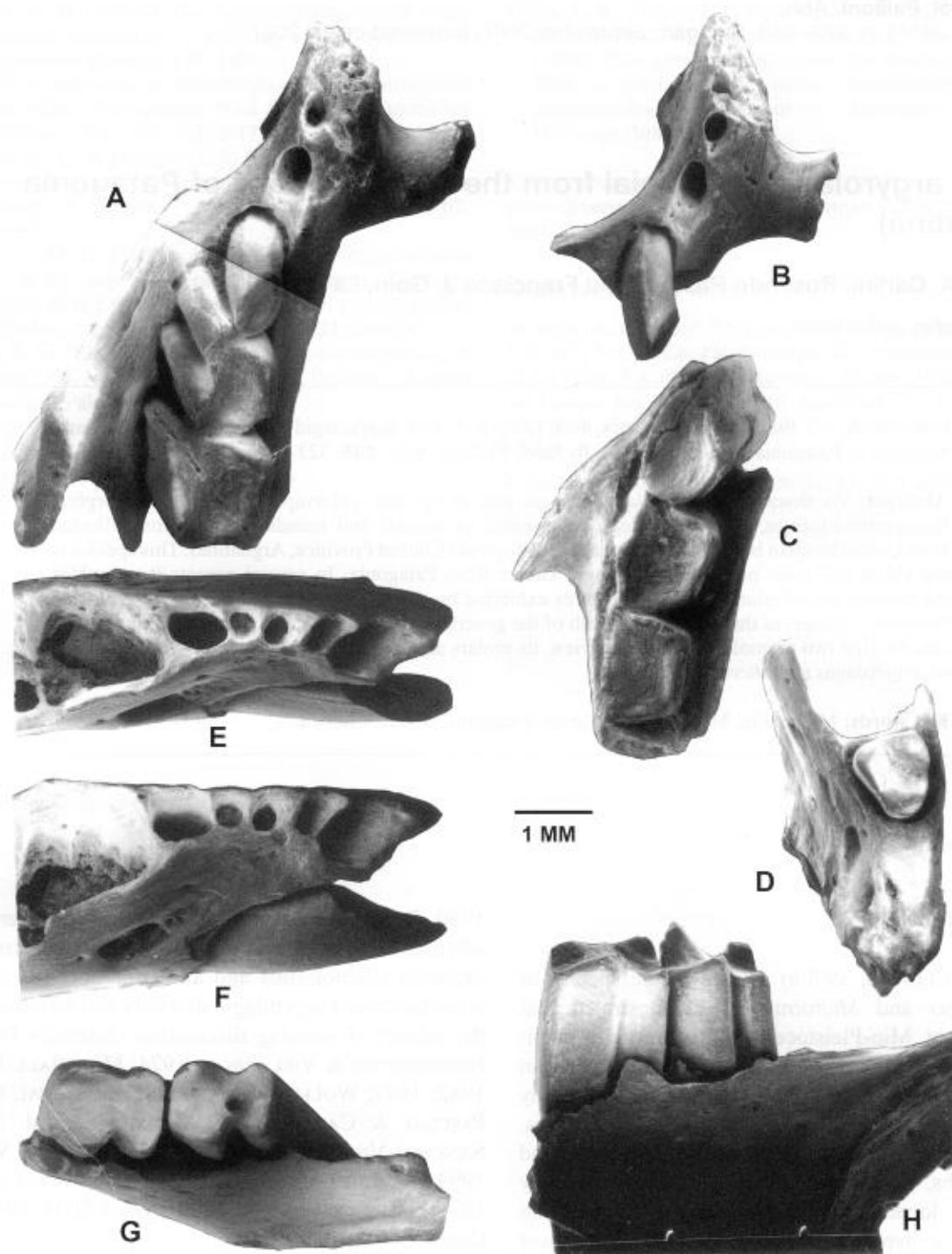
### 1. Introduction

SIMPSON'S (1970a, 1970b) studies of the species of *Argyrolagus* and *Microtragulus* demonstrated that these extinct, Mio-Pleistocene South American mammals are part of a unique clade of South American marsupials. These genera are distinguished by many derived cranial, postcranial, and dental features, among them: the disproportionate size of the fore- and hind limbs, related to a bipedal and probably ricochetral locomotion; and a rodent-like dentition including a hyperthrioped, procumbent first lower incisor. The genera included in this family are *Microtragulus* AMEGHINO, 1904, *Argyrolagus* AMEGHINO, 1904, *Proargyrolagus* WOLFF, 1984, *Hondalagus* VILLARROEL & MARSHALL, 1988, and the new genus described below.

Argyrolagids are so notably specialized, so radically unlike other South American mammals that even their marsupial affinities have been questioned (McKENNA

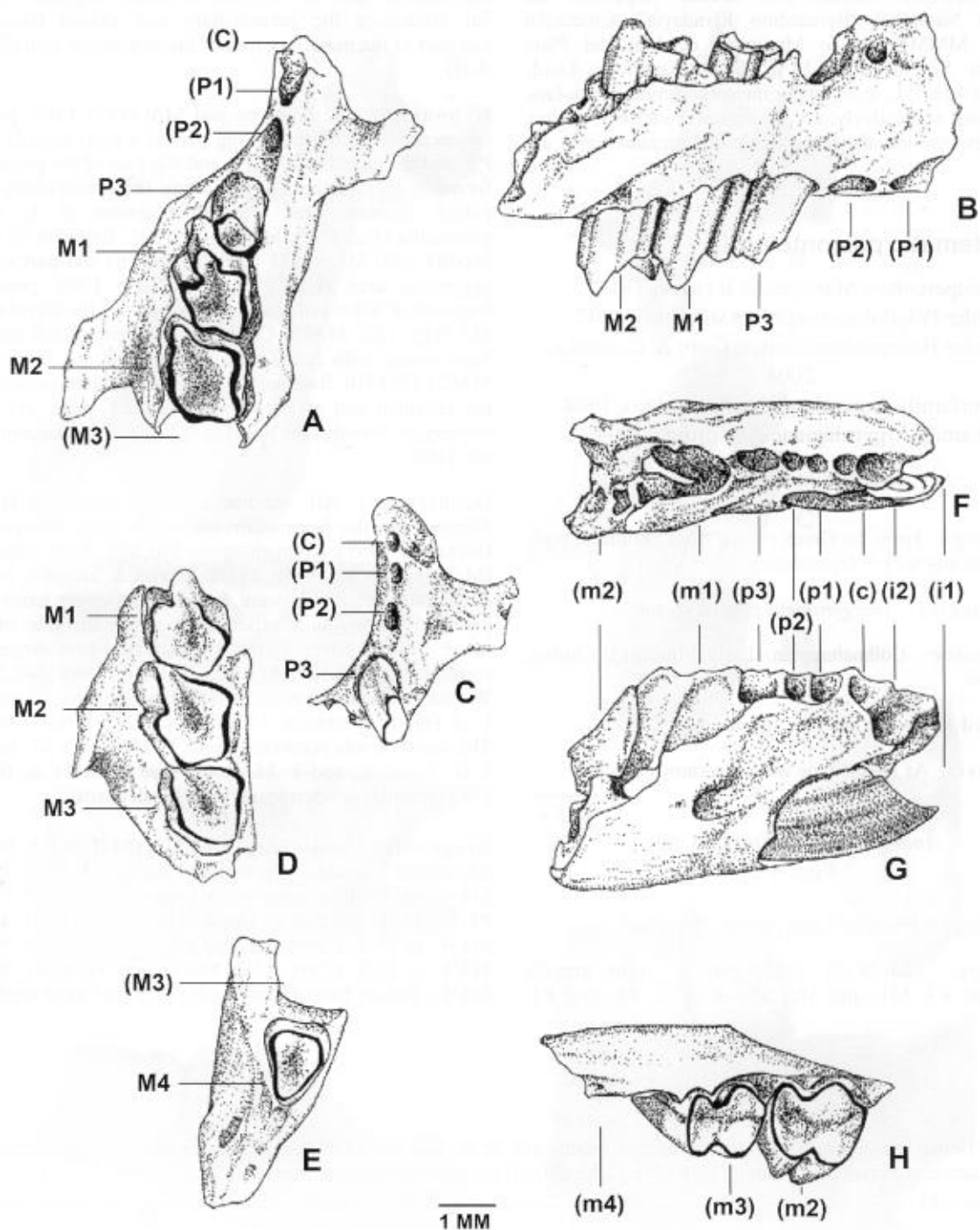
1980; REIG 1981). A second source of arguments is whether this family was part of the Paucituberculatan radiation (caenolestids and allies) or not. These and other aspects of argyrolagid diversity and affinities are the subject of ongoing discussions (SIMPSON 1970a; HOFFSTETTER & VILLARROEL 1974; MARSHALL 1980, 1982, 1987; WOLFF 1984; CARLINI & PASCUAL 1985; PASCUAL & CARLINI 1987; MARSHALL et al. 1990; SÁNCHEZ-VILLAGRA & KAY 1997; FLYNN & WYSS 1999; SÁNCHEZ-VILLAGRA et al. 2000; WYSS et al. 1994; SÁNCHEZ-VILLAGRA 2001; GOIN 2003; GOIN & CANDELA 2004).

Here we report a new genus and species of Argyrolagidae, recognized on the basis of several cranial, mandibular, and dental specimens recovered from strata of Early Miocene age of Central Patagonia. The description of these new remains, the main goal of this study, adds to the evidence of the morphological diversity and affinities of these remarkable marsupials.



**Fig. 1.** *Anargyrolagus primus* gen. et sp. nov., scanning electron photographs. **A:** MACN-ch-1305 (holotype), fragment of right maxilla with alveoli of C1-P2 and P3-M2 cheek teeth, occlusal view. **B:** MACN-ch-1306, fragment of right maxilla with alveoli of C1-P2 and the P3 cheek tooth, occlusal view. **C:** MACN-ch-1307, fragment of right maxilla with M1-M3 cheek teeth, occlusal view. **D:** MACN-ch-1308, fragment of left maxilla with M4 cheek tooth, occlusal view. **E, F:** MACN-ch-1310, fragment of right mandibular ramus with the alveoli of i2-m2 and the i1 tooth, in occlusal (E) and labial (F) views. **G, H:** MACN-ch-1309, fragment of left mandibular ramus with partial alveolus of m4, and the m2-m3 cheek teeth, in occlusal (G) and labial (H) views. Scale = 1 mm.





**Fig. 2.** *Anagyrolagus primus* gen et sp. nov., **A, B:** MACN-ch-1305 (holotype), fragment of right maxilla with alveoli of C1-P2 and P3-M2 cheek teeth, in occlusal (**A**) and (**B**) labial views. **C:** MACN-ch-1306, fragment of right maxilla with alveoli of C1-P2 and the P3 cheek tooth, occlusal view. **D:** MACN-ch-1307, fragment of right maxilla with M1-M3, occlusal view. **E:** MACN-ch-1308, fragment of left maxilla with M4, occlusal view. **F, G:** MACN-ch-1310, fragment of right mandibular ramus with the alveoli of i2-m2 and the i1 tooth, in (**F**) occlusal and (**G**) labial views. **H:** MACN-ch-1309, fragment of left mandibular ramus with partial alveolus of m4, and the m2-m3 cheek teeth. Parenthesis refer to alveoli for the respective teeth. Scale = 1 mm.

euhypsodont (*sensu* MONES 1979, 1982), except the C/c1 and P/p1-2, known only by their alveoli, which are conical in shape, indicating teeth with closed roots. Dentary is proportionally higher than that of *Proargyrolagus*. M2 with the ectoflexus deeper than in species of *Argyrolagus* and *Microtragulus*; in occlusal view, m2-3 are more isodiametric than in *Argyrolagus* and *Microtragulus*.

**Description:** In overall shape and proportions, the preserved cranial and mandibular remains of *Anargyrolagus primus* resemble those of *Argyrolagus scagliai*, from the Late Pliocene of the Pampean region. The most conspicuous differences between *Anargyrolagus* and *Argyrolagus* concern the dentition, described in the following paragraphs. The preserved incisors, as well as P/p3 and M/m1-4 are euhypsodont; judging from the alveoli the remaining teeth, the C/c1 and P/p1-2 were brachyodont or protohypsodont.

The upper incisors and their alveoli are still unknown. Along the anterior, alveolar portion of the maxilla occur three small alveoli which, in life, most probably beared single-rooted teeth; these we homologize to the C1, P1, and P2 of the metatherian dental formula. The first alveolus (C1), the smallest, leans anteriorly, apparently indicating that the canine was slightly procumbent (MACN-Ch 1305 and 1306). The other two alveoli increase progressively in size and become more nearly vertical. These alveoli are followed by five teeth, arranged in a closely appressed series. The first of the series, P3, is suboval in cross-section, whereas M1-4 are quadrangular, and all very similar.

Judging from the size of their alveoli, P1 and P2 were small and had conical roots; they are separated from each other and from P3 by small gaps. The P1 alveolus is nearly vertical, whereas this of P2 is canted somewhat posteriorly. The P3, notably larger than the two anterior premolars, is smaller than the molars; it is simple, somewhat recumbent, and its distal extralveolar half closely approaches the "parastylar" extension of M1; in outline, it is subelliptical to subtriangular, and surrounded by an enamel layer. The size progress of P3-M4 is: P3 < M1 < M2 > M3 > M4; with M4 markedly smaller than the other molars.

As in the Mio-Pleistocene species of *Argyrolagus*, M1 is distinctively shaped, having a well-differentiated anterobuccal lobe (parastylar lobe), and showing a deep ectoflexus. M1-3 are prismatic, quadrangular, somewhat rhomboidal in cross section, with almost vertical faces. The posterior face of the molars progressively decrease in width towards the M4, where it is nearly absent, giving this tooth a subtriangular cross section. All cheek-teeth develop interstitial wear facets from contact with anteriorly and posteriorly adjacent teeth. M1 possesses a narrow and low facet with the P3, and a taller and wider one with M2. Both M2 and M3 show two contact points, one anterolabial and the other posterolingual, the latter relatively higher. M4 has an anterolabial contact point with M3. All molars are completely surrounded by a relatively thick enamel layer, which becomes notably thinner on the anterolabial and posterolingual corners. These thinner areas correspond to the extremes of the major diagonal of the outline in cross section. There is a discontinuous, thin coating of cementum,

especially well-developed on the lingual and labial faces. The molars show a large, smoothly excavated occlusal surface, where it is possible to distinguish an anterolabial to posterolingual oriented wear groove, bordered by prominent enamel crests on its anterolingual and posterolabial angles. The enamel layer is interrupted only at those points where it is thinner.

All lower cheek-teeth are bilobed in occlusal view. The only preserved lower are part of i1 and the complete m2-3; the morphology of the other dental elements can only be inferred from their alveoli. The lower incisors are procumbent, and are here identified as i1 and i2, following convention; they are followed by five alveoli that we homologize as those of c1, p1-3 and m1; these are followed by two cheek teeth, m2-3, and the m4 alveolus. The i1 is subelliptical in cross section, at least on its intralveolar preserved portion, and is surrounded by enamel which becomes thinner on its mesial face; it is labially convex and deeply implanted within an alveolus extending posteriorly below m1, and ending against the alveolus of m2. Based on its alveolus, i2 was notably smaller and shorter than i1; its oblique orientation suggests that the occlusal apex was appressed against the occlusal tip of i1. The m1-4 are markedly bilobed, with deep vertical grooves on both the lingual and labial faces, extending the entire height of these teeth. This is seen not only in the preserved m2-3, but is also in the alveoli of m1 and m4. The grooves are opposed in such a way that the anterior lobe (the trigonid) is larger than the posterior one (the talonid). The second and third lower molars are completely surrounded by an enamel layer, which becomes thinner on the anterolabial and posterolingual corners. On the whole, the lower cheek-teeth of *Anargyrolagus* differ from those of *Argyrolagus* in that in the former they are subquadrangular in cross section – in *Argyrolagus* they are subtriangular.

### 3. Discussion

At present Argyrolagidae includes: *Microtragulus* AMEGHINO, 1904, *Argyrolagus* AMEGHINO, 1904, *Proargyrolagus*, WOLFF 1984, *Hondalagus* VILLARROEL & MARSHALL, 1988, and *Anargyrolagus* gen. nov. Notwithstanding, the validity of two of these taxa is (*Microtragulus*) and was (*Hondalagus*) doubtful. According to HOFFSTETTER & VILLARROEL (1974: 1949), in the holotype of *Microtragulus bolivianus* (from the Montehermosan of Bolivia) i1 extends posteriorly to a point below m3. This interpretation is doubtful: among Argentine species of *Argyrolagus* the alveolus and incisor never extend beyond the anterior wall of the m2 alveolus (although a bulge in the ramus sometimes extends below m3). This, together with the problems in assigning the holotype of the type species of *Microtragulus* (the type specimen of the type species of *Microtragulus* is based not on

dental remains but on an isolated cannon bone; see SIMPSON 1970a), casts some doubts on the validity of this genus. In turn, the diagnostic features originally used to distinguish *Hondalagus altiplanensis* as a new genus and species of Argyrolagidae by VILLARROEL & MARSHALL (1988) are questionable, as the holotype of this species is a left maxillary fragment with M3-4, rather than a right mandibular ramus with m3-4 as thought by these authors (CARLINI and PASCUAL, pers. com. to SÁNCHEZ VILLAGRA et al. 2000). As such, the outlines of the cheekteeth do not differ markedly from the homologous teeth in species of *Argyrolagus*. It was not until SÁNCHEZ VILLAGRA et al.'s (2000) authoritative review of *Hondalagus altiplanensis*, on the basis of new and quite complete cranial remains, that this species was adequately diagnosed.

Of all known argyrolagids, *Anargyrolagus* compares most closely with species of *Argyrolagus* (see Fig. 3), which span through the Upper Miocene up to the uppermost Pliocene of southern South America. It is remarkable that, in spite of the obvious dental differences between these two genera, their general morphologic pattern (at least as revealed from their homologous remains) seems to have been quite stable throughout no less than 16 Ma. That is, they share a quite similar molar cross-section, euhypsodonty, and the same implantation and extension of the hypertrophied lower incisor. On the other side, the information provided by this new genus does not lead to a better understanding of the higher-level relationships of argyrolagids: *Anargyrolagus*' morphology is already too derived.

Even though their extension to *Anargyrolagus* is not guaranteed, hypothesis concerning the paleobiology of *Argyrolagus* (including locomotion, feeding habits and life history) stress similarities between these marsupials and the desert-dwelling rodents of the genus *Dipodomys* (Heteromyidae; MARES 1993). Kangaroo-rats are nocturnal, mainly granivorous, ricochetal animals. They show physiological adaptations related to arid environments. Moreover, the rodent fauna, and specialized marsupials (Patagoniidae), associated to the type and other specimens of *Anargyrolagus* have indicated more eremic environmental conditions than those characterizing Colhuehuapian levels of central Patagonia (i. e., the southern cliff of the Colhue Huapi lake, were most of the Colhuehuapian-aged mammals come from (VUCETICH 1984; PASCUAL & CARLINI 1987). It seems no coincidence that the origins and radiation of argyrolagoids (sensu GOIN & CANDELA 2004; i. e., including the Groeberiidae, Patagoniidae,

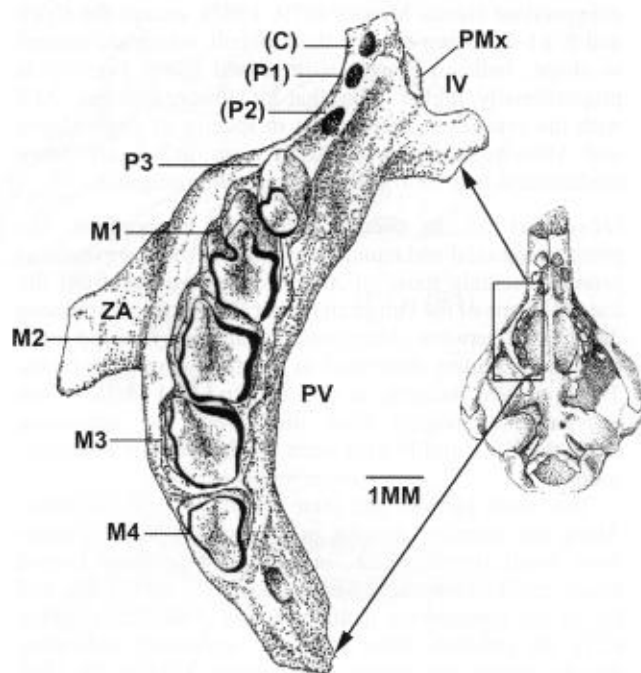


Fig. 3. *Anargyrolagus primus* gen. et sp. nov., reconstructed right maxilla with alveoli of C1-P2 and P3-M4 cheek teeth compared with a palatal view of *Argyrolagus scagliai* (MMMP 785s) modified from SIMPSON 1970a. IV: premaxillary vacuity; PMx: premaxilla; PV: palatal vacuity; ZA: root of the zygomatic arch. Not to scale.

and Argyrolagidae) coincides with the generalized, worldwide biotic turnovers that had already taken place by the Eocene-Oligocene boundary.

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