A New fossil phyllotine (Rodentia, Sigmodontinae) from the late Pliocene in the Andes of northern Argentina

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A NEW FOSSIL PHYLLOTINE (RODENTIA, SIGMODONTINAE) FROM THE LATE PLIOCENE IN THE ANDES OF NORTHERN ARGENTINA

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ABSTRACT—†*Pardinamys humahuaquensis*, a new genus and species of Phyllotini (Rodentia, Cricetidae), is described on the basis of 111 cranial, mandibular, and dental remains belonging to at least 29 individuals. The fossils were recovered from a microvertebrate assemblage found in late Pliocene deposits (between 3 and 2.5 Ma ago) from the Uquía Formation, central Jujuy Province, northwestern Argentina. †*Pardinamys* is morphologically intermediate between the extant genera *Eligmodontia* and *Calomys* and can be differentiated from these taxa by the combination of several traits, including short masseteric crest, with upper and lower ramus similarly developed; coronoid process well developed; anteromedian flexus in M1 only present in very young individuals, without any trace of anteromedian style; M1 and M2 with developed second minor fold; large M2 and M3; and metaflexus, paracone, and metacone of M3 well developed. The morphologic characteristics of the new genus and the other sigmodontines found in the Uquian assemblage (at least three extinct genera) suggest an important radiation before the establishment of the modern communities in the central Andean region and indicate the need for a reevaluation of the divergence-age estimates for the group. The recovered taxa indicate the presence of open environments during depositional times, within arid or semiarid conditions, unlike previous reconstructions for this geologic unit. The finding reveals the need for improving the fossil record of sigmodontines in the central Andean region and its importance to understanding the radiation of this group in a more inclusive South American context.

INTRODUCTION

Our knowledge of the extinct South American cricetid rodents (Cricetidae, Sigmodontinae) has increased significantly in recent years, with the discovery of seven new genera and 12 new species (Steppan, 1996; Pardiñas, 1997, 2008; Steppan and Pardiñas, 1998; Carleton and Olson, 1999; Ortiz et al., 2000; Quintana, 2002; Zijlstra et al., 2010; see also Pardiñas et al., 2002). With the exception of *Noronhomys* (Carleton and Olson, 1999) and *Agathaeromys* (Zijlstra et al., 2010), all these extinct genera are Pliocene and Pleistocene in age and from Argentina, mainly from the central area (Pardiñas, 1997, 2008; Steppan and Pardiñas, 1998; Pardiñas et al., 2002). These central-Argentine genera include *Panchomys* (Pardiñas, 1997), *Olympicomys* and *Ichthyurodon* (Steppan and Pardiñas, 1998), and *Carletonomys* (Pardiñas, 2008). Notably, four of the seven fossil genera were assigned to the tribe Phyllotini, one of the more diverse extant groups within this subfamily. For northwestern Argentina, the knowledge of extinct sigmodontines is more fragmentary; only one extinct genus is known, *Tafimys*, from middle-late Pleistocene deposits in Tucumán and Catamarca provinces (Ortiz et al., 2000, 2011a, 2011b).

Recently, a rich microvertebrate fossil assemblage was recovered from deposits of the Uquía Formation, Quebrada de Humahuaca, Jujuy Province (middle Pliocene–early Pleistocene), including numerous craniodental remains of a medium-sized phyllotine. Detailed comparisons indicate that the remains belong to an undescribed genus morphologically similar to the extant genera *Calomys* and *Eligmodontia*, showing an intermediate and possibly transitional morphology between these two genera. Here we describe this new taxon, compare it with several genera in the Phyllotini, discuss its paleobiogeographic significance in the context of this tribe in the central Andean region, and evaluate its paleoenvironmental significance.

MATERIALS AND METHODS

Specimens were collected by P. Ortiz and collaborators and are housed in the fossil vertebrate collection of the Instituto Miguel Lillo (PVL), San Miguel de Tucumán, Argentina. The remains come from a bone accumulation generated by the feeding activity of owls that includes several small mammal species, such as marsupials and rodents, as well as remains of small birds, lizards, and frogs. The material was obtained through dry and wet sieving with a mesh of 0.1 mm according to the methodology of McKenna et al. (1994).

For description of the general morphology of Phyllotini, we follow Steppan (1995). Occlusal molar topography and terminology follow Reig (1977) and, secondarily, Hershkovitz (1962). Measurements in millimeters were obtained with digital calipers and a micrometer eyepiece on a binocular microscope. Cranial and mandibular measurements include upper diastema length, incisive foramina length, zygomatic plate breadth, maxillary

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toothrow length, mandibular length, mandibular depth below m1, mandibular toothrow length, lower diastema length, upper incisor width and depth, lower incisor width and depth, and maximum length and width of first, second, and third upper and lower molars. Notations for upper and lower molars are M1, M2, M3, and m1, m2, m3, respectively. The new genus was compared with specimens housed in museum collections (Appendix 1) as well as descriptions from the published literature.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family CRICETIDAE Fischer, 1817
Subfamily SIGMODONTINAE Wagner, 1843
Tribe PHYLLOTINI Vorontzov, 1959
†*PARDINAMYS*, gen. nov.

Type Species—†*Pardinamys humahuaquensis.*
Included Species—Only the type species.
Diagnosis—As for type and only species.
Description—See below.
Distribution—Only recorded in central Jujuy Province, Argentina, late Pliocene (Marplatan age).
Etymology—The generic name honors Dr. Ulyses Francisco José Pardiñas (Centro Nacional Patagónico, Chubut, Argentina), colleague and friend, for his relevant contributions to our knowledge of fossil and recent sigmodontine rodents in South America. Starting at an early age for a modern paleontologist, Ulyses has contributed to the description of five fossil genera and four living species of sigmodontines, producing more than 150 scientific papers on diverse topics about these mammals.

†*PARDINAMYS HUMAHUAQUENSIS*, gen. et sp. nov.
(Figs. 2A, D; 3A, C; 4A, B, E, F)

Holotype—PVL 6316, left premaxilla and maxilla with incisor, M1–2, and zygomatic plate, collected by Pablo E. Ortiz and Daniel A. García López (Fig. 1A, D).

Paratypes—PVL 6266, incomplete right mandible with incisor and m1–2; PVL 6275, incomplete right mandible with incisor and m1–3; PVL 6277, incomplete right mandible with incisor and m1–3; PVL 6280, incomplete left mandible with incisor and m1–3; PVL 6281, incomplete left mandible with m1–3; PVL 6283, incomplete left mandible with m1–3 (Fig. 2C); PVL 6292, incomplete right mandible with m1–3; PVL 6295, incomplete right mandible with incisor and m1–3; incomplete right mandible with m1–3; PVL 6298, incomplete left mandible with incisor and m1 (Fig. 2A); PVL 6299, incomplete left mandible with m1–3; PVL 6311, incomplete left maxilla with M1–2; PVL 6313, incomplete right maxilla with M1–3 and zygomatic plate; PVL 6320, right maxilla with M1–3 and zygomatic plate; PVL 6322, right maxilla with M1–3 and zygomatic plate; PVL 6323, left maxilla with M1–2 and zygomatic plate; PVL 6328, incomplete right maxilla with M1–2 and zygomatic plate; PVL 6380, incomplete left mandible with m1–3; PVL 6381, incomplete left mandible with incisor and m1–3; PVL 6382, right maxilla with M1–3 and zygomatic plate; PVL 6383, incomplete right maxilla with M1–2.

Hypodigm—The holotype, the paratypes, and a number of cranial-dental remains and isolated molars and incisors. Includes 29 right maxillae, 23 left maxillae, 27 right mandibles, 28 left mandibles, and more than 60 isolated molars and incisors, belonging to at least 29 individuals: PVL 6267, incomplete right mandible with m1–3; PVL 6268, incomplete right mandible with m1; PVL 6269, incomplete right mandible with m1–2; PVL 6270, incomplete right mandible with m1–3; PVL 6271, incomplete right mandible with m1–2; PVL 6272, incomplete right mandible with m1–3; PVL 6273, incomplete right mandible with m1–3; PVL 6274, incomplete right mandible with m1–3; PVL 6276, incomplete left mandible with m1–2; PVL 6278, incomplete right mandible with m1–3; PVL 6279, incomplete left mandible with
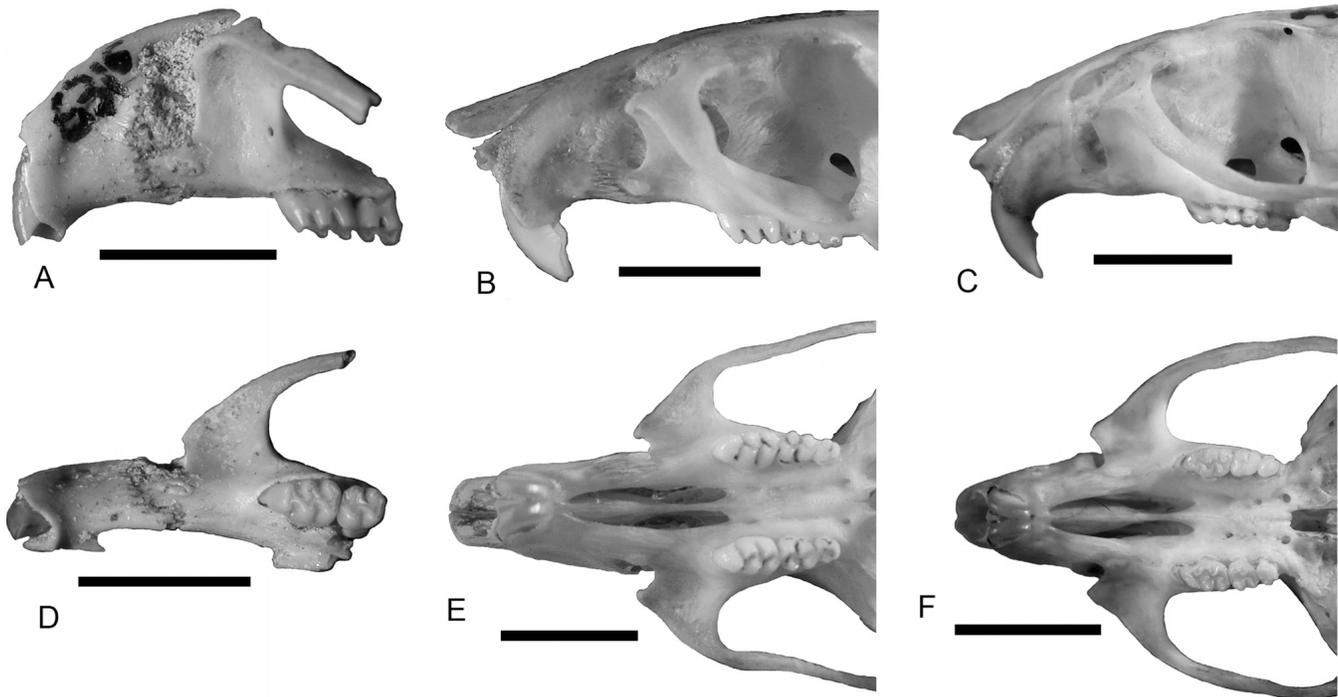

FIGURE 1. Lateral and palatal views of rostral region of †*Pardinamys* compared with representatives of *Eligmodontia* and *Calomys*. **A** and **D**, †*Pardinamys humahuaquensis*, PVL 6316, holotype; **B** and **E**, *Eligmodontia typus*, CML 4432; **C** and **F**, *Calomys musculinus*, CML 7222. All scale bars equal 5 mm.

FIGURE 2. Lateral view of left mandibles of †*Pardinamys* compared with representatives of *Eligmodontia* and *Calomys*. **A**, †*Pardinamys humahuaquensis*, PVL 6298, paratype; **B**, *Eligmodontia typus*, CML 4432; **C**, †*Pardinamys humahuaquensis*, PVL 6283, paratype; **D**, *Calomys musculinus*, CML 7222. All scale bars equal 5 mm.

m1; PVL 6282, incomplete left mandible with m1–2; PVL 6284, incomplete left mandible with m1–2; PVL 6285, incomplete left mandible with m1–2; PVL 6286, incomplete left mandible with m1; PVL 6287, incomplete left mandible with m1–3; PVL 6288, incomplete right mandible with m1–2; PVL 6289, incomplete left mandible with m1–2; PVL 6290, incomplete right mandible with m1–2; PVL 6291, incomplete right mandible with m1–3; PVL 6293, incomplete right mandible with m1; PVL 6294, incomplete right mandible with m1–2; PVL 6295, incomplete right mandible with m1–3; PVL 6296, incomplete left mandible with m1–2; PVL 6297, incomplete left mandible; PVL 6300, incomplete right mandible with m1; PVL 6301, incomplete left mandible with m1; PVL 6302, incomplete right mandible with m1; PVL 6303, incomplete right mandible with m1–2; PVL 6304, incomplete left mandible with m1–2; PVL 6305, incomplete left mandible with m1; PVL 6306, incomplete left mandible with m1–3; PVL 6307, incomplete right mandible with m1–3; PVL 6308, incomplete right mandible with m1; PVL 6309, incomplete right mandible with m1–2; PVL 6310, incomplete left mandible with m1; PVL 6312, incomplete left maxilla with M1–3; PVL 6314, incomplete left maxilla with M1–3; PVL 6315, incomplete right maxilla with M1–2; PVL 6317, incomplete left maxilla with M1–3; PVL 6318, incomplete right maxilla with M1–3; PVL 6319, incomplete right maxilla with M1–3; PVL 6321, incomplete right maxilla with M1; PVL 6324, incomplete left maxilla with M1–3; PVL 6325, left maxilla with M1–2 and zygomatic plate; PVL 6326, incomplete right maxilla with M1–3; PVL 6327, incomplete right maxilla with M1–3; PVL 6329, incomplete left maxilla with M1–3; PVL 6330, incomplete left maxilla with M1–2; PVL 6331, incomplete right maxilla with M1–2; PVL 6332, incomplete left maxilla with M1; PVL 6333, incomplete left maxilla with M1–3; PVL 6334, incomplete left maxilla with M1–3; PVL 6335, incomplete right maxilla with M1–2; PVL 6336, incomplete left maxilla with M1–2; PVL 6337, incomplete right maxilla with M1–2; PVL 6338, incomplete right maxilla with M1–2; PVL 6339, incomplete right maxilla with M1–3; PVL 6340, incomplete right maxilla with M1–3; PVL 6341, incomplete left maxilla with M1–2; PVL 6342, incomplete right maxilla with M1; PVL 6343, incomplete right maxilla with M1 and zygomatic plate; PVL 6344, incomplete left maxilla with M1; PVL 6345, incomplete left maxilla with M1; PVL 6346, incomplete right maxilla with M2–3; PVL 6347, incomplete right maxilla with M1; PVL 6348, incomplete right maxilla with M1; PVL 6349, incomplete right maxilla with M1; PVL 6350, incomplete right maxilla with M1; PVL 6351, left zygomatic plate; PVL 6362, incomplete right maxilla with M1–3; PVL 6378, incomplete left mandible with incisor and m1–3; PVL 6379, incomplete right maxilla with M1–3; PVL 6479, right mandible with incisor and m1–2; PVL 6480, left mandible with incisor and m1–3; PVL 6481, left mandible with m1–2; PVL 6482, left mandible with m1–2; PVL 6483, right mandible with m1–2; PVL 6484, left maxilla with M1–2; PVL 6485, left maxilla with M1–2; PVL 6487, left premaxilla with incisor; PVL 6488, left maxilla with M1–3; PVL 6489, right maxilla with M1–2; PVL 6492, left mandible with m1; PVL 6493, left maxilla with M1–2; PVL 6494, right mandible with m1; PVL 6495, right maxilla with M1–2; PVL 6496, left maxilla with M1–2; PVL 6497, left maxilla with M1.

Type Locality and Stratigraphy—The fossils come from San Roque (26°14′32″S and 65°21′55″W; 2940 m elevation), at 4.4 km SSW of Humahuaca town, Humahuaca Department, Jujuy Province, Argentina (Fig. 3). The remains were excavated from levels assigned to the middle Unit of the Uquía Formation (late Pliocene) (sensu Castellanos, 1950; see also Reguero et al., 2007), which are composed of reddish clays or muds interbedded with reddish fine sand. The Uquía Formation crops out in the Quebrada de Humahuaca in Jujuy Province, and it is composed mainly of siltstones, claystones, silty claystones, and sandstones interbedded with tuff and conglomerate beds. The sequence is related to fluvial environments, and the unit where the fossils were found is gently folded and faulted, overlain by Pleistocene conglomerates and Quaternary alluvium. Lithology, paleontology,

FIGURE 3. Map of Humahuaca area showing the geographic location of San Roque, Jujuy Province, Argentina.

TABLE 1. Cranial and dental measurements for *Pardinamys humahuaquensis*, new genus and species (Phyllotini, late Pliocene, Argentina).

Dimension	N	Mean	SD	Range
			Measurements	
Length of upper diastema	1	6.08	—	—
Length of incisive foramina	1	5.22	—	—
Width of zygomatic plate	8	2.63	0.213	2.33–3.02
Length of maxillary toothrow	24	4.42	0.180	4.01–4.77
Length of M1	35	1.82	0.116	1.56–2.02
Width of M1	35	1.34	0.083	1.15–1.46
Length of M2	31	1.28	0.070	1.12–1.40
Width of M2	31	1.20	0.085	1.04–1.35
Length of M3	18	1.01	0.089	0.85–1.18
Width of M3	18	0.95	0.074	0.80–1.06
Width of upper incisor	1	0.65	—	—
Depth of upper incisor	2	1.60	—	1.5–1.7
Length of mandible	7	14.51	0.806	13.78–15.62
Depth of mandible below m1	30	3.38	0.191	3.00–3.79
Length of mandibular toothrow	30	4.48	0.127	4.26–4.73
Length of m1	38	1.93	0.080	1.80–2.11
Width of m1	39	1.25	0.054	1.14–1.36
Length of m2	29	1.36	0.089	1.22–1.58
Width of m2	29	1.24	0.052	1.12–1.34
Length of m3	17	1.04	0.101	0.86–1.21
Width of m3	16	0.96	0.056	0.81–1.05
Width of lower incisor	20	0.61	0.072	0.47–0.71
Depth of lower incisor	10	1.01	0.090	0.9–1.19
Length of lower diastema	19	3.22	0.316	2.8–3.75

magnetostratigraphy, and geochronology of the Uquía Formation were described by Reguero et al. (2007). Although the bearing deposit at the type locality does not show obvious stratigraphic relationships with respect to dated levels from nearby locations, we propose a correlation between the deposit that yielded the †*Pardinamys* remains and the middle unit in Esquina Blanca, where the stratotype of the Uquía Formation crops out (Marshall et al., 1982; Reguero et al., 2007). This stratigraphic correlation was possible because of the presence of indicative guide levels, including tuffaceous beds, reddish-brown claystones, and the short distances between these outcrops. These correlations allowed us to estimate an age between 3 and 2.5 Ma for †*Pardinamys*.

Diagnosis—A member of the tribe Phyllotini of small to medium size (average maxillary toothrow length = 4.42 mm; average mandibular length = 14.51 mm), similar to the extant *Eligmodontia moreni*, characterized by long incisive foramina (5.22 mm); masseteric crest short, not reaching the mandibular margin; upper and lower ramus of masseteric crest similarly developed, converging at the level of protoconid of m1; coronoid process well developed, reaching or surpassing the height of the condyloid process; anteromedian flexus in M1 only present in very young individuals, without any trace of anteromedian style (sensu Hershkovitz, 1962) or mesostyle; M1 and M2 of young individuals with well-developed second minor fold (sensu Hershkovitz, 1962); M2 and M3 large with respect to M1 in relation to other phyllotines; metaflexus of M3 well developed and in subcentral position, almost closed by the paracone and metacone confluence; and paracone and metacone of M3 well developed.

Measurements—See Table 1.

Etymology—Refers to the geographic occurrence of the fossils. Humahuaca (a word in Quechua language, spoken currently in the central Andes) refers to the omaguaca people, a group of brave tribes found by Spanish conquerors in the 16th century, when they arrived in northwestern Argentina. Moreover, the Quebrada de Humahuaca is an UNESCO (United Nations Educational, Scientific and Cultural Organization) World Heritage Site since 2003.

Description—The rostrum is relatively short. The zygomatic plate is similar to that of *Eligmodontia*, relatively broad, with its anterior border straight or slightly convex and vertically oriented. Some specimens show a very small spine at the anterodorsal angle. The insertion area of the anterior deep masseter muscle is well defined. Most specimens have the incisive foramina extending posteriorly to the protocone of M1, but in some individuals this foramen reaches the level of protoflexus (Fig. 1A, D).

The mandible (Fig. 2A, C) of †*Pardinamys humahuaquensis* is similar in general morphology and robustness to that of *Eligmodontia moreni*. The height of the horizontal ramus, at the level of m1, is greater than that of the diastema. From the anterior wall of m1, the diastema descends obliquely and then rises again to a point below the alveolar plane. The symphysis is short and high; its anterior point is slightly below the alveolar row plane, and a small protrusion at its posterior end forms a projection at the lower edge of the mandible. The mental foramen is medium sized and slightly visible in lateral view in some individuals but not in others. The masseteric crest has two ridges of similar development. The upper ridge is visible at the level of m2, and the lower ridge starts at the level of m1–2 contact; the two join at the level of the protoconid of m1 to produce a broader ridge with rounded edges that forms a slight knob. The upper ridge rises gently until it contacts the base of the coronoid process. The crest ends anteriorly at the level of the anterior border of m1 and at the height of or slightly above the mental foramen, not reaching the dorsal edge of mandible. The capsular projection is well developed, although barely distinguishable in young specimens, and is located below the anterior region of the sigmoid notch. The coronoid process is well developed; its apex exceeds the maximum height of the mandibular condyle, and the sigmoid notch is wide. The condyle is relatively long and somewhat oblique. The angular process is broad and slightly shorter than the condyle and contributes to defining a symmetrical and semicircular angular notch.
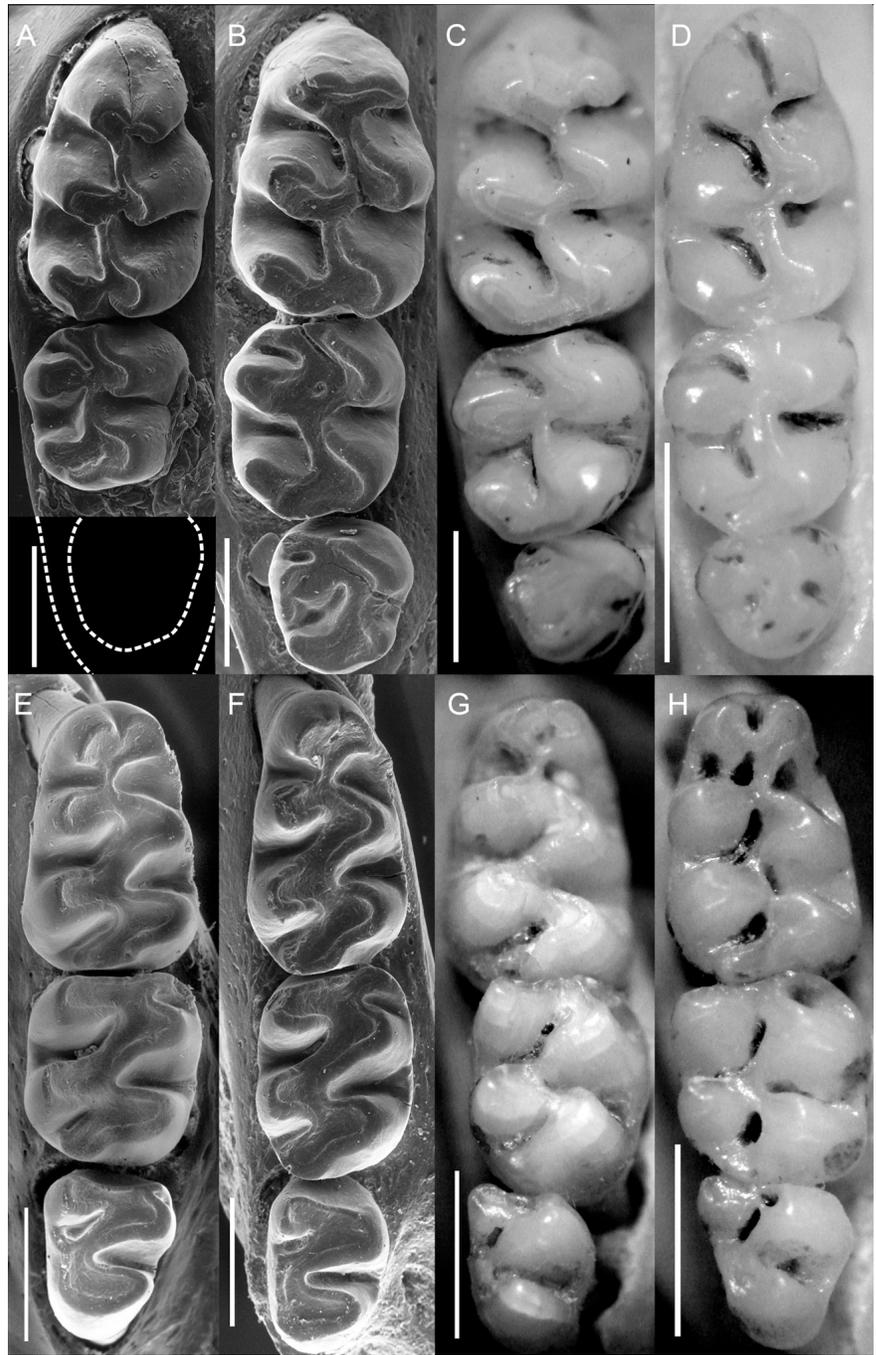
FIGURE 4. Occlusal view of molar series of †*Pardinamys* compared with representatives of *Eligmodontia* and *Calomys*. **A**, right M1–2 of †*Pardinamys humahuaquensis*, PVL 6383, paratype; **B**, upper right molar series of †*Pardinamys humahuaquensis*, PVL 6382, paratype; **C**, upper right molar series of *Eligmodontia puerulus*, CEI 23-2; **D**, upper left molar series of *Calomys laucha*, CML 8554 (mirror image to facilitate comparison); **E**, lower right molar series of †*Pardinamys humahuaquensis*, PVL 6292, paratype; **F**, lower left molar series of †*Pardinamys humahuaquensis*, PVL 6299, paratype (mirror image to facilitate comparison); **G**, lower right molar series of *Eligmodontia puerulus*, CEI 23-2; **H**, lower right molar series of *Calomys laucha*, CML 8554; all scale bars equal 1 mm.

The upper incisors are without grooves in their anterior face and roughly orthodont or opisthodont. The molars (Fig. 4A, B, E, F) are bilevel-crested (or preterraced), with a relatively simplified occlusal design and the main cusps opposite. The M1 has a trilophodont pattern (Fig. 4A, B), with the lophs and flexi oblique in young specimens and a tendency toward a more transverse position in adults. The procingulum is anteroposteriorly compressed and retains traces of an anteromedian flexus in young individuals. The anterior mure is slightly oblique, defined by penetrating protoflexus and paraflexus. Both the paraloph and metaloph are well developed and similarly extended. The inner apices of the mesoflexus and hypoflexus alternate, forming an oblique median mure. In some young individuals, a vestigial posteroflexus and a

well-developed second minor fold (sensu Hershkovitz, 1962) are observed. This molar has four roots, including a small labial medially positioned root. The M2 and M3 are proportionally large in comparison with M1. The M2 of young specimens has a relatively well developed procingulum because of the presence of penetrating protoflexus and paraflexus. Lophs are more transversely oriented than M1. The hypocone is developed similarly to the protocone. In some specimens, evidence indicates a posteroflexus and second minor fold, but less developed than M1. A large lingual root is present in addition to the anterior and posterior roots. In the M3, the four main cusps are well developed. Young individuals retain a well-preserved paraflexus, a penetrating metaflexus, and a well-developed hypoflexus (although less penetrating than

the metaflexus). With wear, a metafossette of subcentral position is generated, which never meets the hypoflexus, whereas all evidence of the paraflexus disappears. This molar has three roots, the posterior larger than the anterior two.

The m1 has a tetralophodont pattern (Fig. 4E, F). The procingulum has a slightly developed anteromedian flexid, present only in relatively unworn teeth. The anterolabial cingulum is well developed but does not extend to the protoconid, always leaving an open protoflexid. The metaflexid is transversely oriented, with its inner apex opposite to that of the protoflexid, forming a short anterior murid slightly displaced toward the lingual side. The posterior murid is oblique. The metalophid and entolophid have a similar development and are slightly oblique. The posterolophid is well developed and oblique. This molar presents two large anterior and posterior roots and a small accessory root at the labial edge. In the m2, the procingulum is small and defines a relatively developed protoflexid. The mesoflexid is penetrating; its apex is oriented slightly forward, forming an oblique median murid with the hypoflexid. The posterolophid is well developed, and a moderate distoflexid (sensu Hershkovitz, 1993) is visible in some young individuals. Very large anterior and posterior roots are present. The m3 is proportionally large relative to m1 and m2 and has a medium-sized mesoflexid, with the transverse area of hypoconid and entoconid well developed. The hypoflexid is very penetrating in the occlusal plane, more than in m1 and m2. This tooth has two roots of equal size.

Variation—Most of the variations observed in †*Pardinamys humahuaquensis* are age dependent, as deduced from tooth wear. The shape of the zygomatic plate shows some variation; its anterior margin varies from straight to slightly convex, and some specimens show a small spinous process at the anterodorsal angle. The lengths of incisive foramina also vary, reaching posteriorly in most specimens to the protocone of M1, but in some individuals is somewhat shorter, reaching the level of protoflexus. Some variation can be observed in mandibular characters, for example, the differences in the anterior/posterior position of the anterior end of the masseteric crest, the position of the mental foramen, and the development of the capsular projection. Most of the individuals present the anterior masseteric crest slightly below the dorsal edge of the mandible, but in a few specimens this knob almost reaches the mandibular margin. The mental foramen is visible in lateral view in most individuals but not in others. The capsular projection varies among individuals from a slight elevation below the sigmoid notch to a distinct capsule projecting out from the mandible. The occlusal surface of molars shows variation according the stages of wear by age. In the M1, lophs and flexi are oblique in young but adopt a more transverse position at more advanced ages. In young specimens, vestigial anteromedian flexus and posteroflexus, and a well-developed second minor fold (sensu Hershkovitz, 1962), can be recognized. The M2 of juveniles retains penetrating protoflexus and paraflexus, as well as evidences of posteroflexus and second minor fold. Young individuals show in the M3 well-developed paraflexus, metaflexus, and hypoflexus. In older individuals, a metafossette is developed and the paraflexus disappears. A slight anteromedian flexid in m1 is present in young specimens. In the m2, some young individuals present a moderate distoflexid (sensu Hershkovitz, 1993).

Comparisons—The following comparisons include the species of Phyllotini that show closer morphologic affinities to the known anatomy of †*Pardinamys* (Table 2). *Eligmodontia* is probably the genus most similar to †*Pardinamys*, but several differences can be found. In lateral view, †*Pardinamys* has a rostrum somewhat shorter than is usual in *Eligmodontia*, but the zygomatic plate is practically indistinguishable (Fig. 1A, B). The incisive foramen is shorter in *Eligmodontia*, generally not surpassing the level of the anterolabial and anterolingual conules of procingulum (Fig. 1E). The mandible in *Eligmodontia* is similar in general morphology and robustness to that of †*Pardinamys,* but the masseteric

crest in *Eligmodontia* has a different development (Fig. 2B). The lower ridge shows a very different course and orientation and is clearly more developed than the dorsal ridge; the two join to form a prominent knob that usually exceeds the dorsal edge of the mandible. Furthermore, in *Eligmodontia* this knob ends clearly above the mental foramen. The coronoid process in this genus is somewhat shorter and more slender than that of †*Pardinamys*, and its apex generally does not exceed the maximum height of the condyle. The condyle in *Eligmodontia* is more elongated than the angular process, and the lunar notch is more asymmetrical (not semicircular) than that of †*Pardinamys* (Fig. 2B). The only specimen of †*Pardinamys* in which the upper incisors were associated with the maxilla appeared slightly more orthodont than *Eligmodontia*. The general morphologies of molars in the two genera are very similar, but some differences are evident. The anteromedian flexus of M1 in *Eligmodontia* is more developed than that of the fossil genus and persists as a slight inflection until old ages (Fig. 4C). The species of *Eligmodontia* lack the second minor fold (sensu Hershkovitz, 1962) clearly observed in M1 and M2 of young individuals of †*Pardinamys* (Fig. 4A, B). In the latter, the M2 and M3 are proportionally larger with respect to M1 than those of *Eligmodontia*. The metaflexus of M3 is less penetrating and developed and is situated well in the posterior half of the molar in *Eligmodontia*, a consequence of the poor development of paracone and metacone. The hypoflexus is clearly less penetrating than in the new genus. The procingulum of m1 in *Eligmodontia* is somewhat more complex than that of †*Pardinamys* and has a more penetrating anteromedian flexid in very young individuals (often forming a small and subcentral enamel island in older specimens) and a clearly distinguishable anterolophid. The m3 is proportionally smaller compared with m1 and m2 in *Eligmodontia*, has a conspicuous concavity between protoconid and metaconid, and has a less-developed posterior transverse section (hypoconid-entoconid) (Fig. 4G).

Calomys is the other most similar genus. The anterior region of the skull in this genus, including the morphology of the zygomatic plate as well as the rostrum and incisive foramina length, is virtually indistinguishable from that of †*Pardinamys* (Fig. 1C, F). In the same way, the mandibular morphology shows many similarities, including the development of the coronoid process, its position respect to the condyle, and the extension of the condyle with respect to the angular process (determining a symmetrical lunar notch) (Fig. 2D). We note, however, some differences related to the masseteric crest. In *Calomys*, it is more developed, as a knob, and extends usually to the edge of the mandible. We find that most of the differences between *Calomys* and the new genus are in the molars. The upper molars in *Calomys* are more slender, narrower, and shorter. The M1 has a very entrant anteromedian flexus with a conspicuous anteromedian style (sensu Hershkovitz, 1962). The M1 and M2 of *Calomys* (except *C. sorellus*) lack any trace of the second minor fold observed in †*Pardinamys*. The M2 and M3 are comparatively shorter with respect to M1 in *Calomys* than in †*Pardinamys*. The M3 shows also a more subcircular shape in *Calomys* (Fig. 4D). The anteromedian flexid of m1 in *Calomys* is clearly more penetrating (sometimes forming an enamel island) and a very small cingulid that could correspond to the metastylid is present. The m2 and m3 are also more slender and narrower in their posterior halves than is the case in †*Pardinamys* (Fig. 4H).

The phyllotine genera *Graomys*, *Andalgalomys*, and *Salinomys* are clearly distinguishable from †*Pardinamys* on morphologic and meristic grounds (Table 2). Species of *Graomys* are large phyllotines, with very distinctive cranial, mandibular, and molar features. The anterior margin of the zygomatic plate is concave, with a conspicuous zygomatic spine in dorsal position, and the incisive foramina are proportionally shorter than those of †*Pardinamys*. In the mandible, the diastema is deeper, and the apex of the coronoid process clearly does not exceed the

TABLE 2. Synthetic comparison of some cranial and dental characters of †*Pardinamys* and related genera.

	†*Pardinamys*	*Eligmodontia*	*Calomys*	*Graomys*	*Andalgalomys*	*Salinomys*
Anterior border of zygomatic plate	Straight. Vertically oriented.	Straight or slightly concave. Vertically oriented.	Straight or slightly concave. Vertically oriented.	Concave, with anterodorsal spine. Vertically oriented.	Concave, with conspicuous anterodorsal spine. Vertically oriented.	Straight or slightly concave. Slanted anteriorly.
Incisive foramina	Long in most specimens, extending to the protocone of M1.	Slightly short, level with the procingulum of M1.	Variable, level with the procingulum or protoflexus of M1.	Slightly short, level with the procingulum of M1.	Short, reach the anterior wall of M1.	Slightly short, level with the procingulum of M1.
Anterior end of masseteric crest	Forms a slight knob. Does not reach the dorsal edge of mandible.	Forms a prominent knob exceeding the dorsal edge of M1.	Well-developed knob. Usually slightly below the edge of mandible.	Well-developed knob. Reaches the dorsal edge of mandible.	Forms a prominent knob, exceeding the dorsal edge of mandible.	Well-developed knob. Just reaches the dorsal edge of mandible.
Coronoid process	Exceeds the maximum height of the condyle.	Subequal or below the condyle.	Exceeds the maximum height of the condyle.	Not exceeding the maximum height of the condyle.	Below the level of the condyle.	Below the level of the condyle.
Angular process	Broad and slightly shorter than the condyle.	Broad and noticeably shorter than the condyle.	At the same level as the condyle.	Narrow, shorter than the condyle.	Narrow, shorter than the condyle.	Broad, slightly shorter than the condyle.
Lunar notch	Symmetrical (semicircular).	Asymmetrical (not semicircular).	Symmetrical (semicircular).	Asymmetrical (not semicircular).	Asymmetrical (not semicircular).	Asymmetrical (not semicircular).
Upper incisors	Orthodont or opisthodont.	Hyperopisthodont.	Opisthodont.	Opisthodont.	Opisthodont.	Orthodont.
Molar hypsodonty	Brachydont.	Brachydont.	Brachydont.	Slightly hypsodont.	Brachydont.	Brachydont.
Upper molars	Bilevel-crested, with relatively simplified occlusal design. Main cusps opposite.	Bilevel-crested, relatively simplified occlusal design. Main cusps alternate.	Crested, more complex occlusal design. Main cusps alternate.	Plane or slightly raised. Main cusps slightly alternate.	Slightly crested. Main cusps opposite.	Slightly crested. Main cusps slightly alternate.
Anteromedian flexus of M1	Vestigial, visible only in young individuals.	Distinguishable, persisting as a slight inflection until old ages.	Prominent.	Absent.	Prominent.	Prominent.
Anteromedian style	Absent.	Absent.	Present on most species and individuals.	Absent.	Usually easily visible.	Usually easily visible.
Second minor fold in M1–2	Well developed.	Absent.	Absent (except *C. sorellus*).	Absent.	Well developed.	Absent.
Size of M3 respect to M1–2	Proportionally large.	Proportionally small.	Proportionally small.	Proportionally large.	Proportionally large.	Proportionally small.
Shape of M3	Elongated Four main cusps well developed.	Subcircular. Paracone and metacone poorly developed.	Subcircular. Paracone and metacone poorly developed.	Slightly elongated. Four main cusps well developed.	Slightly elongated. Four main cusps distinguishable.	Subcircular. Paracone and metacone poorly developed.
Metaflexus M3	Penetrating in young individuals. Never meets the hypoflexus.	Less penetrating. Never meets the hypoflexus.	Less penetrating. Never meets the hypoflexus.	Well penetrating, fused with hypoflexus.	Well penetrating, fused with hypoflexus.	Less penetrating, never fused with hypoflexus.
Anterior murid of m1	Slightly displaced toward the lingual side.	Slightly displaced toward the lingual side.	Displaced toward the labial side.	Approximately in central position.	Approximately in central position.	Clearly displaced toward the lingual side.
Anteromedian flexid of m1	Slightly developed, present only in relatively unworn teeth.	Penetrating in young individuals, forming an enamel island in older specimens.	Penetrating at all ages.	Absent or restricted to a faint remnant of an infolded lake.	Variable, from a shallow notch, rarely a deep groove, to an infolded lake.	Slightly developed, present only in relatively unworn teeth.
Size of m3 respect to m1–2	Proportionally large.	Proportionally small.	Proportionally small.	Proportionally large.	Proportionally small.	Proportionally small.
Mesoflexid of m3	Intermediate.	Poorly developed.	Intermediate.	Intermediate.	Very penetrating, fused with hypoflexid.	Poorly developed.
Hypoconid-entoconid area	Well developed.	Poorly developed.	Poorly developed.	Intermediate.	Well developed.	Poorly developed.

1435

maximum height of the condyle. The upper incisors of *Graomys* are opisthodont. The molars are robust, more hypsodont, planate, and relatively simplified, and their cusps are more triangular and tend toward lamination. In the same way, in *Andalgalomys* the anterior margin of the zygomatic plate concave shows a dorsal spinous process. The incisive foramina are shorter than those of †*Pardinamys*. The mandible has a more developed capsular projection and a posteriorly extended condyle. Furthermore, the coronoid process is notably posteriorly oriented, forming a deep sigmoid notch. The lunar notch is also deeply excavated and clearly asymmetrical. In spite of the presence in *Andalgalomys* of a second minor fold in M1 and M2, several molar traits distinguish it from †*Pardinamys*. The M1 of *Andalgalomys* has, generally, a well-developed anteromedian flexus with an anteromedian style. In the M3, the hypoflexus and metaflexus are very penetrating, separating metacone-hypocone from protocone-paracone. In both †*Pardinamys* and *Salinomys*, the anterior border of the zygomatic plate is straight, but in the latter the plate slants anteriorly. The incisive foramina are somewhat shorter in *Salinomys*. In the mandible of *Salinomys*, the coronoid process is very small, not surpassing the height of the condyle, and the sigmoid notch clearly less excavated. The procingulum of M1 in *Salinomys* is more complex; it has a more developed anteromedian flexus, and anteromedian style, parastyle, and protostyle are present. Moreover, this genus lacks any evidence of a second minor fold in M1 and M2. The M3 of *Salinomys* is proportionally small and more delicate than M1–2, because of the lesser development of hypocone and metacone. The lower molars have a greater tendency toward lamination than do those of †*Pardinamys*; the anterior murid of m1 is distinctively more displaced to the lingual side. In *Salinomys*, the m3 is comparatively smaller with respect to the other lower molars, and the mesoflexid is noticeably less developed. Other phyllotine genera, such as *Tapecomys*, *Phyllotis*, *Auliscomys*, *Loxodontomys*, and *Galenomys*, as well as the extinct genera previously attributed to Phyllotini such as *Tafimys*, *Panchomys*, *Ichthyurodon*, and *Olympicomys*, are all conspicuously divergent in cranial and dental morphology with respect to †*Pardinamys*, so we think that a comparison is unnecessary.

PHYLOGENETIC RELATIONSHIPS

Morphologic Affinities

From their cranial-dental anatomy, †*Pardinamys* can be easily associated with the small-sized genera of the tribe Phyllotini. The morphology of the new genus seems generalized in the context of the tribe, without outstanding features, and distinguishable from the other genera only by a combination of characters.

The morphology of the zygomatic plate and the posterior extent of incisive foramina in †*Pardinamys* follow the same pattern as do those of most phyllotine genera. Similarly, the mandible shows a generalized morphology, without distinctive features (e.g., no particularly elongated or reduced process or crests). The mandible of †*Pardinamys* clearly resembles that of *Calomys*, with the relatively robust coronoid process higher than the condyle. In this feature, and in the particular development of the masseteric crest, †*Pardinamys* displays the most conspicuous mandibular differences from *Eligmodontia*, *Andalgalomys*, *Salinomys*, and *Graomys*. In contrast, †*Pardinamys* displays a dental pattern markedly different from that of *Calomys* and the previously mentioned genera, excepting *Eligmodontia*. Thus, the relatively simplified molar pattern in †*Pardinamys* resembles more closely that of *Eligmodontia*, presenting the same degree of lophodonty and hypsodonty. †*Pardinamys* also shows a second minor fold in M1 and M2, a character only present in *Andalgalomys*, *Calomys sorellus*, and the enigmatic *Punomys* among sigmodontines.

Although the morphology of the new genus seems transitional between the generalized phyllotine condition (represented by *Calomys*) and the relatively specialized morphology in *Eligmodontia*, the unique combination of traits displayed by †*Pardinamys* deserves generic recognition. Another possible classificatory scheme would be to consider this form an extinct species of *Eligmodontia*, but we do not favor inclusion in this last genus because all living species share several characters in mandibular and dental traits that are absent in †*Pardinamys*. In this context, the best choice, according to the taxonomic arrangement of the tribe and the previously referred diagnostic features, is the erection of a new genus. We point out that Reig (1986) suggested that *Eligmodontia* evolved from a *Calomys*-like ancestor in the Puna region, which could be represented by †*Pardinamys* or a †*Pardinamys*-like form.

The Phyllotini are the best-known sigmodontine tribe from the paleontological record; 5 of the 10 extinct sigmodontine genera are attributed to the Phyllotini (but see caveats below). With the addition of †*Pardinamys*, this tribe reaches a generic paleodiversity approaching that of the nine living genera. Unfortunately, the still unstable phylogeny of this group, mainly the changing position of *Eligmodontia*, prevents building a robust hypothesis regarding the relationship of †*Pardinamys* to the remaining phyllotines. In recent molecular analyses based primarily on fast-evolving mitochondrial genes, *Eligmodontia* has fluctuated from (a) being the sister group of a clade formed by *Salinomys* + *Andalgalomys* (Salazar-Bravo et al., 2001), to (b) being basal to the remaining phyllotines (D'Elía, 2003), sister group of *Calomys* (Almeida et al., 2007), to (c) being sister group of *Graomys* with this clade sister to the remaining phyllotines (Haag et al., 2007), to (d) being sister group of *Graomys* and this clade sister to the remaining phyllotines excepting *Calomys* (Steppan et al., 2007), to (e) being sister to the *Phyllotis* + *Salinomys* clade, with this group derived respect to *Graomys* and *Calomys* (Mares et al., 2008). None of these relationships was strongly supported. We suggest that †*Pardinamys* is likely to be either sister to all phyllotines except *Calomys* (the nuclear data are consistent in showing *Calomys* as sister to all living phyllotines), or sister to *Eligmodontia*, a member of the stem lineage to the sister group to *Eligmodontia*, or a member of the stem lineage leading to *Eligmodontia* plus most other phyllotines (Fig. 5). Until the morphologic synapomorphies of phyllotine clades can be reassessed in light of developing molecular phylogenies, precisely placing the new genus phylogenetically remains difficult. At the same time, this uncertainty about the true phylogenetic relationships in phyllotines forces us to be cautious when a biogeographic scenario is invoked and when divergence-time estimates are used to explain the radiation of the tribe.

Paleobiogeographic Significance

The fossil record of sigmodontines has been mostly restricted to lowlands of central Argentina, constraining the formulation of fossil-based hypotheses about the historical biogeography of sigmodontines. Reig (1984, 1986) suggested, on the basis of extant diversity and distributional patterns, that the main centers of differentiation for Akodontini and Phyllotini occurred in the Andean Puna (roughly between 13°S and 27°S), from which they dispersed toward lowland areas of eastern and south-central South America. Phyllotines constitute the main group of cricetid rodents with distribution along the Altiplano of the central Andean region. The origin and evolution of this group has been studied by several authors (e.g., Hershkovitz, 1962; Reig, 1984, 1986; Braun, 1993; Steppan, 1995; Spotorno et al., 2001) on the basis of morphologic, biogeographic, and genetic data. Supported by the predominantly central Andean distribution of most of their genera and species, Reig (1986) hypothesized that the area of original differentiation of phyllotines was the Andes of southern Peru, southwestern Bolivia, northern Chile, and northwestern Argentina. This area matches the present
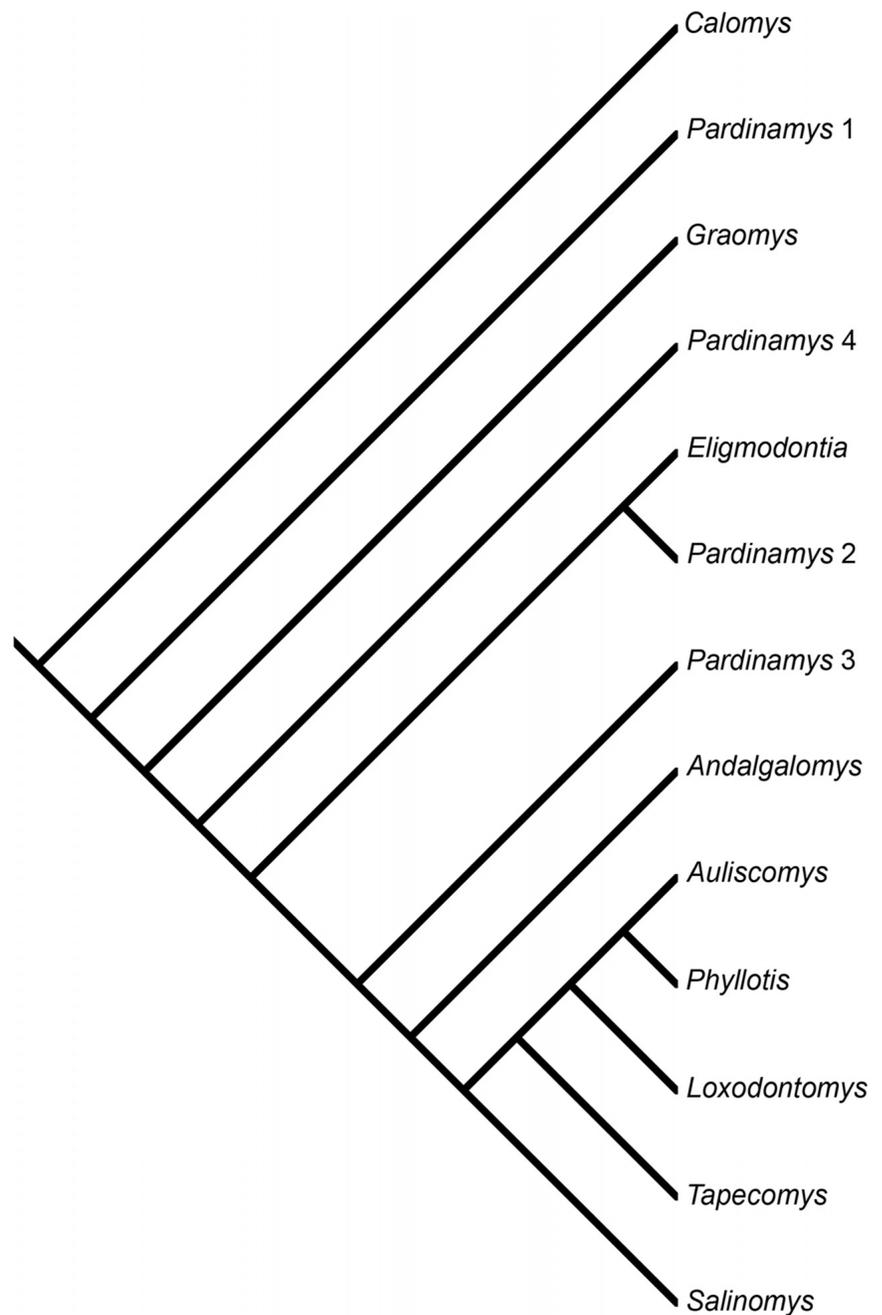
FIGURE 5. Four alternative phylogenetic placements of †*Pardinamys* in the context of the Tribe Phyllotini. 1, sister to all phyllotines except *Calomys*; 2, sister to *Eligmodontia*; 3, a member of the stem lineage to the sister group to *Eligmodontia*; and 4, a member of the stem lineage leading to *Eligmodontia* plus most other phyllotines.

distribution of the Puna ecoregion, a xeric highland and relatively flat area over 3400 m elevation, mostly characterized by open shrub-land environments. Following Reig's hypothesis and on the basis of cytogenetic data, Spotorno et al. (2001) indicated a diversification of the ancestral phyllotine from the Altiplano toward the south and the north, also suggesting this same diversification pattern for several polytypic genera such as *Calomys*, *Eligmodontia*, and *Phyllotis*, but these studies included a number of genera traditionally classified within the phyllotines that were subsequently excluded from the tribe by molecular analyses on the basis of mitochondrial (Smith and Patton, 1999; D'Elía, 2003) and nuclear (D'Elía, 2003; Weksler, 2003; Jansa and Weksler, 2004; Steppan et al., 2007) genes. Currently, molecular support exists for the inclusion of only nine genera within Phyllotini

(*Auliscomys*, *Andalgalomys*, *Calomys*, *Eligmodontia*, *Graomys*, *Loxodontomys*, *Phyllotis*, *Salinomys*, and *Tapecomys*); there are no published data for *Galenomys* and *Chinchillula*. Genera traditionally classified within the phyllotines as *Reithrodon*, *Euneomys*, *Neotomys*, *Andinomys*, and *Irenomys* were removed from the tribe on the basis of nuclear gene data (Jansa and Weksler 2004, Steppan et al., 2004, Schenk et al., unpubl. data). Those biogeographic hypotheses for phyllotines must therefore be interpreted according to the new phylogenetic scenario produced by the molecular evidence and the recently described fossils. Most of the molecular studies agree that *Calomys* is the sister group to the remaining phyllotines (Engel et al., 1998; Smith and Patton, 1999; Haag et al., 2007; Steppan et al., 2007) and that *Eligmodontia* is often grouped with *Andalgalomys*, *Salinomys*,

or *Graomys*, but not *Auliscomys*, *Loxodontomys*, *Phyllotis*, or *Tapecomys* (Salazar-Bravo et al., 2001; Haag et al., 2007; Steppan et al., 2007; Mares et al., 2008; Schenk et al., unpubl. data).

The fossil evidence accumulated up to now for northwestern Argentina seems to support Reig's hypotheses. The assemblage from Uquía Formation, in which we detected at least two additional enigmatic phyllotines besides †*Pardinamys* (Ortiz et al., in press), supports the hypothesis that the central Andes represented an area of high diversity for this tribe during the late Pliocene, with the presence of forms without modern representatives of generic rank. On the other hand, the fossils exhumed by Ortiz and Pardiñas (2001; see also Ortiz et al., 2000) in Tucumán Province constitute evidence about the establishment of a modern sigmodontine community at least from the middle-upper Pleistocene, with the presence of the living *Calomys* and *Phyllotis* and the extinct *Tafimys* among the phyllotines. A late Pliocene diversification may also be evident for lowland areas of central Argentina, in which *Panchomys* (Pardiñas, 1997), *Dankomys* (Reig, 1978; see Pardiñas, 1997, regarding possible assignment to the Phyllotini), *Olympicomys*, *Ichthyurodon* (Steppan and Pardiñas, 1998), *Auliscomys* (Quintana, 2002), and an undescribed form (Bond et al., 1998; Pardiñas et al., 2002) indicate a great generic diversity of Phyllotini for this period (but note that if the 'Reithrodon' group' [Olds and Anderson, 1989; Steppan, 1995] of the extant *Reithrodon*, *Euneomys*, and *Neotomys*, is removed from Phyllotini, then it is likely that several of the extinct genera should be as well, particularly *Tafimys* and *Panchomys*). Pardiñas (1997) proposed two episodes for the establishment of the phyllotines in the Pampean region, the first during the Chapadmalalan stage (lower and middle Pliocene), characterized by medium to large species, and the second during the Ensenadan stage (lower-middle Pleistocene), in which small forms such as *Eligmodontia* or *Calomys* have their first records and become predominant (Pardiñas, 1995, 1997). †*Pardinamys*, the first small phyllotine recorded from pre-Ensenadan times, suggests that these small morphotypes effectively differentiated in extra-Pampean areas, as Pardiñas (1995, 1997) proposed.

Although the Uquian assemblage includes at least five sigmodontine forms that deserve generic rank, no extant genera have been recorded (Ortiz et al., in press). This pattern suggests that most extant phyllotine genera radiated long after the middle and late Miocene, at odds with the hypotheses established by some authors. Salazar-Bravo et al. (2001), for example, have estimated the separation of *Calomys* from the remaining phyllotines at between 11.4 and 13.3 Ma and the most recent common ancestor (MRCA) of this genus at about 8 Ma. If these divergence and radiation times were realistic, we would expect to find representatives of what are today the diverse and broadly distributed genera *Calomys*, *Eligmodontia*, and *Phyllotis* in Uquian sediments, at about 2.5–3 Ma. Estimates more consistent with our fossil evidence are those of Almeida et al. (2007) and Steppan et al. (2007), which have suggested basal splits in *Calomys* around the Miocene–Pliocene boundary at 5 and at 4.5 Ma (mean) respectively, and the nuclear phylogeny of Steppan et al. (2004), which places the divergence of *Calomys* from all other phyllotines at approximately 5 Ma. Moreover, Mares et al. (2008) estimated that the lineage leading to *Eligmodontia* separated from a phyllotine ancestor at about 7–13 Ma, and dated the crown group of this genus at 2.8 Ma. Notwithstanding these more realistic estimates, our data suggest a somewhat later radiation for the extant phyllotine genera.

Paleoenvironmental Conditions

The Humahuaca region, at 2900–3000 m elevation, is today a semiarid area included within the Monte de Sierras y Bolsones ecoregion (sensu Burkart et al., 1999), characterized by a steppe vegetation with scattered columnar cacti or 'cardones'

(*Trichocereus* spp.), low bushes, and small trees of 'churqui' (*Prosopis ferox*) that can reach up to 3 m in height.

Faunistic elements for Uquía Formation, mostly characterized by medium-sized and large mammals such as Gomphotheriidae, Tayassuidae, Camelidae, Cervidae, Equidae, and Hydrochoeridae (Castellanos, 1950, 1953; Rusconi, 1930; Kraglievich, 1934; Walther et al., 1996; Prado et al., 2001), suggest that the environment was warmer and more humid than the present one in the area. More recently, Reguero et al. (2007) cited for this unit a crocodile and the porcupine *Erethizon*, clear evidence for warmer and wetter environmental conditions, but the micromammal species associated with †*Pardinamys humahuaquensis* suggest a different habitat. These taxa, including some rodents allied to the extant genera *Abrothrix*, *Akodon*, *Auliscomys*, and *Microcavia*, seem to reflect a community of semiarid and open habitats at medium or high elevations (Ortiz et al., in press). Extant phyllotines are grazing sigmodontines, mainly denizens of open habitats (Pearson, 1958, Hershkovitz, 1962; Reig, 1986). All the genera morphologically similar to †*Pardinamys* are common in open arid or semiarid habitats. *Eligmodontia*, the genus most similar mophologically to †*Pardinamys*, is widespread in arid areas of western Argentina and the Altiplano of Bolivia and Chile (Mares et al., 2008). *Eligmodontia* typically inhabits areas of open vegetation with high proportions of bare soil, including flatlands of *Larrea*, sandy scrub areas, sandy flats with halophytic plants, and open shrublands (Mares, 1975a, 1975b; Corbalán and Ojeda, 2004, Gonnet and Ojeda, 1998). In addition, *Calomys* is a typical inhabitant of open environments, with many records both in dry shrublands and in more humid grasslands of the Pampean area. Taking into account all the evidence, we can infer the paleoenvironment in which †*Pardinamys humahuaquensis* lived to be a community dominated by xerophytic plants, in a more or less open habitat with some bare sandy or rocky soils. Clearly, these greatly contrasting environmental scenarios can indicate the occurrence of important climatic pulses during the deposition time of the Uquía Formation, with increasingly colder and more variable climatic conditions, related to the late Pliocene global cooling and drying event. This global cooling has been documented in South America in the form of a conspicuous faunal turnover (Tonni et al., 1992; Ortiz Jaureguizar et al., 1995; Verzi and Quintana, 2005). This cooling began ca 3.2 Ma ago as a trend changing from the warmer and more stable climate prevalent before (Kennett, 1995; Schultz et al., 1998). The composition of the micromammal assemblage could be the result of the establishment of a rain-shadow effect caused by the 'Diaguita' diastrophic phase (late Pliocene) of the Andean orogeny. This uplift of the eastern orographic systems of Argentina, including the Puna and eastern Cordillera, resulted in xeric conditions for intermontane valleys such as Quebrada de Humahuaca (Ortiz Jaureguizar and Cladera, 2006), change that would have begun to take place at the time of deposition of the San Roque assemblage.

CONCLUSIONS

The newly described extinct genus †*Pardinamys* appears to be a sigmodontine in the tribe Phyllotini, most similar to *Eligmodontia*. Our results highlight the importance of the fossil record for sigmodontines in the central Andean region to understanding the evolution of some groups (mainly Phyllotini and Akodontini). The San Roque assemblage is clearly distinctive in its taxonomic composition, indicating that at least one radiation episode took place previous to the establishment of the modern communities. The new genus also indicates that we must be cautious when calibrating molecular clocks to estimate divergence age and that all the estimations currently available must be reevaluated. Finally, our findings provide valuable information for use in evaluating paleobiogeographic scenarios and for a better understanding of

the paleoenvironmental conditions during the late Pliocene in the region.

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APPENDIX 1. Specimens examined.

Institutional Abbreviations—CEI, Colección de Material de Egagrópilas del Instituto Superior de Correlación Geológica, Tucumán, Argentina; **CM**, Carnegie Museum of Natural History, Pittsburgh, U.S.A; **CMI**, Colección Mastozoológica del Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina; **CML**, Colección de Mamíferos del Instituto Miguel Lillo, Tucumán, Argentina; **CNP**, Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Argentina; **CNP-E**, Colección de Material de Egagrópilas y Afines "Elio Massoia" del Centro Nacional Patagónico, Puerto Madryn, Argentina; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MMP-Ma**, Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Argentina; **PVL**, Colección de Paleontología de Vertebrados del Instituto Miguel Lillo, Tucumán, Argentina.

Andalgalomys olrog—Argentina: Catamarca, West Bank Rio Amanao, about 15 km W (by road) Andalgalá (CM 44024, holotype); southern entrance road to the city of Catamarca, along Highway 38, 483 m (CEI 40-2).

Auliscomys sublimis—Argentina: Jujuy, 3 km S Guayrazul (CEI 58-4); Salta, 3 km E La Poma (CEI 41-4, 45-3).

Calomys fecundus—Argentina: Salta, Tartagal, Laguna de las Catas (CML 2341), Los Colorados, 17 km E Santo Domingo (CML 3013), San Martín del Tabacal Sugar Mill (CML 5843); Tucumán, 5 km SW El Siambón, 3100 feet (CML 7104), San Ignacio Dam (CML 7176).

Calomys laucha—Argentina: Entre Ríos, approximately 6 km E Ceibas, on the road to the Ñancay stream (CML 8554); Santiago del Estero, INTA La María experimental station,

1.2 km W of the station entrance, 72 m (CNP 2359); Tucumán, junction of Highway 9 and India Muerta stream, 658 m (CNP 2360).

Calomys lepidus—Argentina: Catamarca, Laguna Blanca, 3243 m (CNP 2361).

Calomys musculinus—Argentina: Catamarca, Estancia Narváez, 5.5 km N Las Chacritas on Highway 1 (CML 7222, 7223); San Luis, 1 km N Paso del Rey, along Arroyo de la Cañada Honda, 4400 feet (CML 3592), 12 km N Varela (by road), 2200 feet (CML 3589); Santiago del Estero, INTA La María experimental station, 1.2 km W of the station entrance, 72 m (CNP 2362), INTA La María experimental station, 2.9 km W of the station entrance, 72 m (CNP 2363).

Eligmodontia bolsonensis—Argentina: Catamarca, establecimiento Río Blanco, 25 km S, 9.3 km W Andalgalá, 680 m (MACN 23322, paratype), Hualfín, Los Baños Termales (CML 881, 869), Hualfín, Agua del Dionisio (CML 872).

Eligmodontia moreni—Argentina: Catamarca, Corral Quemado (MLP 11.XII.35.43), Hualfin, Agua Tapada (MACN 17619); Hualfín, Quebrada Los Médanos (CML 873).

Eligmodontia puerulus—Argentina: Catamarca, Pasto Ventura (CML 8167, 7181); Jujuy, 1 km N Escuela Portillo, on the road between Humahuaca and El Aguilar (CEI 32-2), 12.3 km N, 11.5 km W San Antonio de los Cobres (by road) (CML 8548, 8549).

Eligmodontia sp.—Argentina: La Rioja, 26 km SW Quimilo (CML 7184, 7186, 7188).

Eligmodontia typus—Argentina: Chubut, Península Valdes (CML 1767); Mendoza, 2 mi. E Puesto Gendarmería Cruz de Piedra (CML 4330, 4377, 4393), approximately 4 km NE Uspallata (CML 4432).

Graomys chacoensis—Argentina: Salta, Finca Los Colorados, 17 km E Santo Domingo (CML 5196, 5959); Santiago del Estero, Buena Vista, 15 km NE Villa Ojo de Agua on Highway 13 (CML 3548), Santo Domingo (CML 3551), Pozo Hondo, Finca El Duende (CML 4126).

Graomys domorum—Argentina: Tucumán, Las Tipas, Parque Sierra de San Javier (CML 5987, 5988).

Graomys griseoflavus—Argentina: Salta, 17 km NW Cachi, 10,350 feet (CML 7109); San Juan, Ischigualasto, Agua de la Peña (CML 1295), Castaño Nuevo, 9 km NW Villa Nueva (CML 3490).

Loxodontomys micropus—Argentina: Neuquén, Las Breñas (CNP-E 17).

Phyllotis anitae—Argentina: Tucumán, 10 km by road south of Hualinchay on the trail to Lara (CML 6379, 6380, 6381; CNP 736, 737, 809).

Phyllotis caprinus—Argentina: Jujuy, Maimará (CML 282, 338; MACN 31.34), Maimará, 2300 m (MACN 27120), Sierra de Zenta, 4500 m (MACN 32.52, 31125), La Lagunita, 4500 m (MACN 32.53).

Phyllotis osilae—Argentina: Catamarca, about 2 km SE Huaico Hondo, along Highway 42, 1992 m (MACN 23485), El Rodeo, 1.5 km NE of Highway 4, 1500 m (CML 3448), Río Vallecito, 2900 m (MACN 50-441); Jujuy, Calilegua, San Francisco (CML 478), Cerro Hermoso (MACN 19521, 19540); Cerro San Francisco (CML 379), Chilcayoc (CML 7231), El Duraznillo, Cerro Calilegua, 2600 m (CML 1724,1725); Salta, about 15 km W of Escoipe, on Highway 33, 2680 m (MACN 23498), about 5 km NW of Campo Quijano, km 30 of Highway 51, 1600 m (MACN 23502); Tucumán, Aconquija, 3000 m (MACN 29.260, 29.264), Cerro San Javier, 2000 m (MACN 26-145), El Infiernillo, on Highway 307, km 74, 2562 m (MACN 19069, 19070).

Phyllotis xanthopygus—Argentina: Catamarca, Chumbicha, 1 km NW by road from balneario, 850 m (CML 3451); Jujuy, Abra Pampa (CML 1276, 1277, 1278, 1283), La Ciénaga, Abra Pampa (CML 1280), 10 km W Purmamarca, on Highway 52 (CML 3942), Yavi, 3600 m (CML 2871); San Juan, Estancia El Leoncito, 2 km E of astronomical observatory (CML 3624); Tucumán, on the road to Amaicha, km 98 of Highway 307 (CML 5564).

Salinomys delicatus—Argentina: Catamarca, Pipanaco salt flat, 740 m (CMI 06815); La Rioja, La Antigua salt flat, 45 km NE of Chamical, 467 m (CMI 03795); San Juan, 6 km N km 514 Highway 20 (CML 3556); San Luis, 15 km E Salinas del Bebedero (CML 3171).

†*Tafimys powelli*—Argentina, Tucumán, La Angostura (middle-late Pleistocene; PVL 4825, holotype; PVL 4830, 4841, 4842, 4855, 4920–4922, 5272, 5450, paratypes).

Tapecomys wolffsohni—Argentina: Jujuy, road between San Francisco and Pampichuela, 1200 m (CNP 828, 829); Salta, Santa Victoria Oeste, 2100 m (MACN 17719), Santa Victoria Oeste, 2200 m (MACN 17723).