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ORIGINAL PAPER

New Middle Miocene Caviomorph Rodents from Quebrada Honda, Bolivia

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Abstract The rodents of the middle Miocene fauna of Quebrada Honda Bolivia are described. The most abundant rodent is the chinchillid *Prolagostomus* sp. More precise identification of this species will require revision of early to middle Miocene lagostomines, taking into account variation in modern populations. The next most common rodents are the tiny octodontoid *Acarechimys*, sp. nov.?, and the caviid *Guiomys unica*. The *Acarechimys* species may be unique to Quebrada Honda, but verification awaits revision of this geographically and temporally widespread genus. *Guiomys unica* is a recently described species otherwise known only from two Patagonian localities, El Petiso and Río Chico. Two rodents are unique to Quebrada Honda. *Mesoprocta hypsodus*, gen. et sp. nov., is a dasyproctid distinguished by its very hypsodont, cement-covered cheek teeth. *Quebradahondomys potosiensis*, gen. et sp. nov., is an adelphomyine echimyid distinguished by the less oblique lophids of its trilophodont cheek teeth, among other features. The rodents of Quebrada Honda are more similar to those of Patagonia than those of northern South America, paralleling patterns seen in other mammal groups from this fauna.

Keywords Endemism · Laventan · Neogene · Neotropics · Provinciality · Rodentia · South America

Introduction

Rodents are conspicuous members of nearly all modern South American terrestrial communities. The vast majority of the species pertain to two groups, each of which underwent an adaptive radiation in South America: cricetids (muroids) and caviomorphs. The former includes far more species, but is a geological newcomer in South America. There is no definitive evidence for cricetids in South America prior to about five million years ago (Pardiñas et al. 2002; Prevosti and Pardiñas 2009). Even if cricetids entered South America several million years earlier than indicated by their fossil record, their remarkable diversification into more than 350 species—well over one third of all South American mammal species (Wilson and Reeder 2005)—took place in a surprisingly short period of time. They apparently dispersed to South America from North America via the Panamanian land bridge along with many other participants of the Great American Biotic Interchange (see Webb 2006 for a recent review).

Caviomorph rodents, in contrast, have been in South America for at least half of the Cenozoic, since at least the early Oligocene (Wyss et al. 1993, 1994; Vucetich et al. 1999, 2010b; Flynn et al. 2003). The fossil record of caviomorphs may extend into the late Eocene (Frailey and Campbell 2004), though this locality has no independent temporal constraints and could be as young as late Oligocene (Shockey et al. 2004). The origin of caviomorphs has long

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been a matter of debate (reviewed by Wood 1985), but several lines of evidence now all favor waif dispersal from Africa during the late Eocene (Houle 1998; Huchon and Douzery 2001; Sallam et al. 2009; Coster et al. 2010; Rowe et al. 2010). Platyrrhine primates likely also reached South America in this manner, at approximately the same time (Kay et al. 2008). Although caviomorphs are today represented by fewer than 250 species (Woods and Kilpatrick 2005), the morphological diversity of the group far exceeds that of cricetids. This distinctiveness is highlighted by rodents such as the capybara (*Hydrochoerus hydrochaeris*), the guinea pig (*Cavia porcellus*), the agouti (*Dasyprocta punctata*), and the chinchilla (*Chinchilla laniger*), which are among the most characteristic South American mammals.

The details of caviomorph diversification—such as the timing of cladogenic events, relationship between morphologic and taxonomic diversity, and biogeographic histories of important clades—remain relatively poorly known despite South America's excellent fossil record. This partly stems from the disproportionately small amount of attention they have received from researchers, at least for some time intervals and some regions of the continent. Filling such gaps in knowledge is essential to understanding the radiation of caviomorph rodents and the development of South American mammal communities as a whole. The present study contributes to this effort by describing the caviomorph rodents of Quebrada Honda, an assemblage from a sparsely sampled temporal interval (the middle Miocene) and area of the continent (the Neotropics).

Materials and Methods

The fossils described in this study derive from Quebrada Honda in southern Bolivia (Fig. 1). Specifically, we focus on: (1) new specimens collected in 2007 by DAC and FA and colleagues (see Acknowledgments), which are housed at the Universidad Autónoma Tomás Frías (Potosí, Bolivia); and (2) previously undescribed specimens from the Florida Museum of Natural History in Gainesville that were collected in 1978 and 1981 by FA and B. MacFadden and colleagues. We provisionally identify other Quebrada Honda specimens that we were unable to study firsthand. This is a much revised and updated version of our preliminary report (Chick et al. 2008) and is based on study of additional specimens and museum collections.

The Quebrada Honda Fauna is temporally well constrained to 13.5–11.8 Ma (MacFadden et al. 1990). It pertains to the Laventan South American Land Mammal "Age" (SALMA)(Madden et al. 1997; Croft 2007) (Figs. 1, 2). For additional details on the stratigraphy of the locality, see MacFadden and Wolff (1981) and MacFadden et al. (1990). Two local faunas have been recognized: the Quebrada Honda Local Fauna, from exposures near the town of the same name, and the Río Rosario Local Fauna, from exposures near the town of Río Rosario, located ca. 6 km to the north of the town of Quebrada Honda. Outcrops in both areas are mapped as the Honda Group (MacFadden et al. 1990) and both local faunas appear to be of approximately the same age. In this work, Quebrada Honda refers to the assemblage as a whole unless noted otherwise.

Terminology Nomenclature of dental occlusal structures discussed in this work is presented in Fig. 3. We follow that used in other recent studies of cavioids (Kramarz 1998; Pérez 2010), chinchilloids (Kramarz 2002), and octodontoids (Vucetich and Ribeiro 2003; Vucetich et al. 2010b), all of which are compatible with recent nomenclatural schemes for hystricognaths as a whole (e.g., Marivaux et al. 2004). Uppercase letters denote upper teeth and lowercase letters denote lower teeth. All rodents described in this study possess one pair of incisors (I/i), one pair of premolars (P4/p4), and three molars (M1-3/m1-3). Deciduous premolars (DP4/dp4) are maintained through adulthood in some octodontoids. The suffix "–id" is used to denote structures of the lower dentition. A flexus/flexid is a valley that remains open along the side of the tooth crown. A fossette/fossettid is a flexus/flexid that has become isolated (i.e., closed off from the side of the tooth crown) due to wear. High- and low-crowned dentitions are referred to as hypsodont and brachydont, respectively. Evergrowing, rootless, and/or open-rooted teeth are hypselodont.

Other Notes Hypsodonty index (HI) follows Williams and Kay (2001) and was calculated by dividing m1 height by the square root of the occlusal area (mesiodistal × buccolingual diameter). Diagnostic characters used to identify each species are included in the systematic paleontology section below. Unless otherwise noted, cheek tooth dental measurements are length (= mesiodistal or anteroposterior diameter) × width (= buccolingual or transverse diameter).

Institutional Abbreviations AMNH, American Museum of Natural History, New York; IGM, Instituto Nacional de Investigaciones en Geociencias, Minería y Química (INGEOMINAS), Colombia; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP, Museo de La Plata, Argentina; MPEF, Museo Paleontológico Edigio Feruglio, Trelew, Argentina; UATF, Universidad Autónoma Tomás Frías, Potosí, Bolivia; UCMP, University of California Museum of Paleontology; UF, Florida Museum of Natural History, Gainesville, Florida; YPM-PU, Princeton University Collection of Yale Peabody Museum, New Haven, Connecticut. Specimens from these museums were studied firsthand. Dental measurements were made to the nearest 0.1 mm using digital calipers. Published sources were used as supplemental resources.

Fig. 1 Map of South America indicating the location of Quebrada Honda and other localities discussed in the text. Argentine Mayoan localities are grouped together. Abbreviations: **C**, Cerdas; **N**, Nazareno

Systematic Paleontology

Class Mammalia Linnaeus, 1758
  Order Rodentia Bowdich, 1821
  Suborder Hystricognathi Tullberg, 1899
  Infraorder Caviomorpha Wood and Patterson, 1955

Comments: Caviomorph rodents are a monophyletic group of New World hystricognaths that share numerous derived craniodental and molecular character states (e.g., Wood and Patterson 1959; Huchon and Douzery 2001; Marivaux et al. 2004; Rowe et al. 2010). More than 60 genera are extant or have gone extinct in historical times, and more than twice this number have been described from fossil deposits; they are currently divided among 12 extant and five extinct families (McKenna and Bell 1997; Vucetich et al. 1999; Woods and Kilpatrick 2005). Phylogenies of extant families based on nuclear and/or mitochondrial genes support recognition of four main clades (superfamilies) within Caviomorpha: Cavioidea (Caviidae, Cuniculidae, and Dasyproctidae), Chinchilloidea (Chinchillidae and Dinomyidae), Erethizontoidea (Erethizontidae only), and Octodontoidea (Abrocomidae, Capromyidae, Ctenomyidae, Echimyidae,

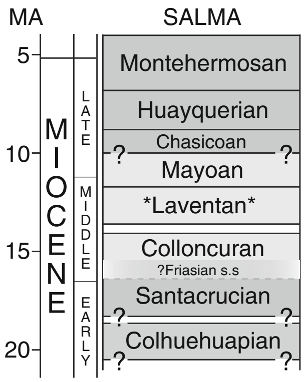


Fig. 2 Miocene South American Land Mammal "Ages" (SALMAs). The age of Quebrada Honda (the Laventan SALMA) is indicated by asterisks. *Light shading* denotes the Friasian sensu lato (see discussion in Croft et al. 2009). Modified from Croft et al. (2009)

Myocastoridae, and Octodontidae) (Huchon and Douzery 2001; Opazo 2005; Sallam et al. 2009; Rowe et al. 2010). As noted above, the caviomorph fossil record begins in the early Oligocene, but they are not found in abundance until later in the Oligocene (Vucetich et al. 1999, 2010b).

Superfamily Cavioidea Fischer de Waldheim, 1817
Family Dasyproctidae Gray, 1825
Mesoprocta hypsodus, gen. et sp. nov.
Figs. 3b, 4, 5a

Holotype: UF 26915, right dentary bearing m1.

Etymology: The genus combines the common suffix for dasyproctids (*−procta*) with reference to its provenance in the middle latitudes of South America (*Meso-*); the species name refers to its teeth (*−odus*), which are higher crowned (*hyps-*) than some other members of the family.

Type Locality: Quebrada Honda Local Fauna, Unit 2 of Section 1 of MacFadden and Wolff (1981).

Age and distribution: Unnamed formation (Honda Group) of Quebrada Honda, southern Bolivia, middle Miocene age, Laventan South American Land Mammal “Age” (SALMA) (present study).

Diagnosis: *Mesoprocta*, like other Miocene and younger dasyproctids, is a relatively large rodent with high-crowned, lophate cheek teeth and thick enamel (Walton 1997) (Figs. 4, 5). It resembles *Neoreomys* Ameghino, 1887 (Fig. 5e–f) but clearly differs in its much greater hypsodonty and possession of cement. It further differs in having less oblique crests (especially the hypolophid), a less pronounced anterofossettid, and a more persistent metaflexid (Kramarz 2006b). It differs from “*Neoreomys*” *huilensis* (Fig. 5b–c) in the characters noted above for *Neoreomys* (= *N. australis*) as well as in its much larger size (40% larger than the holotype based on AP length of m1), its large, triangular i1 (as opposed to small and oval), and probably in its larger p4, as estimated from the portion that is preserved (Fields 1957; Walton 1997). *Mesoprocta* is approximately 30% smaller than poorly characterized *Megastus* Roth, 1898. *Mesoprocta* differs from *Australoprocta* Kramarz, 1998 (Fig. 5d) and the small dinomyid “*Scleromys*” (sensu Walton 1997) in possessing a metaflexid that does not join the hypoflexid. *Mesoprocta* also has a smaller anterofossettid than *Australoprocta* (Kramarz 1998), and its buccal flexids do not extend as far lingually as in “*Scleromys*.” *Mesoprocta* differs from *Alloiomys* Vucetich, 1977 (Fig. 5g) in having lophids that are nearly perpendicular to the long axis of the tooth (as opposed to markedly oblique) and a straighter lingual face. *Mesoprocta* superficially resembles some early Miocene eocardiids (e.g., *Luantus* Ameghino, 1899), but is about 30% larger, has a much more robust mandible, and has a metaflexid that persists after isolation of the mesoflexid (see Kramarz 2006a).

Description: The holotype is the anterior portion of a right dentary bearing m1 and the bases of i1 and p4 (Fig. 4). Little mandibular morphology can be discerned due to the state of preservation, though it is evident that the dentary is quite robust (greatest depth is ca. 15 mm near m1) and bears a large symphyseal region (ca. 19×6 mm). The lower incisor is broken and partially obscured by broken bone, but the exposed anterolabial surface is 5.0 mm wide. It is triangular in cross section and has a nearly flat buccal enamel face. The base of the incisor passes lingual to m1 and extends 6.4 mm past its distal surface. It cannot be

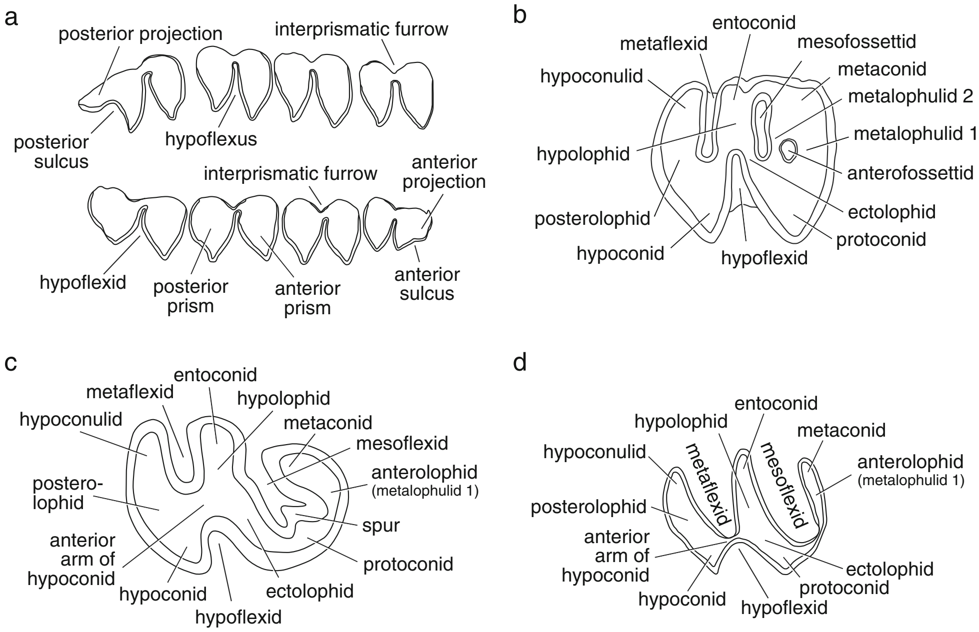


Fig. 3 Terminology used to describe caviomorph premolar and molar occlusal structure. **a** right upper dentition (above, UATF-V-001038) and right lower dentition (below, UATF-V-000971) of *Guiomys unica* (Caviidae); **b** Rm1 of *Mesoprocta hypsodus* (Dasyproctidae; holotype, UF 26915); **c** Rdp4 of *Acarechimys*, sp. nov.? (Octodontoidea; UATF-V-000934); **d** Rm3 of *Quebradahondomys potosiensis* (Echimyidae: Adelphomyinae; holotype, UATF-V-001030). Anterior is to the right in all illustrations. Drawings are not to scale

Fig. 4 *Mesoprocta hypsodus*, gen. et sp. nov., partial right dentary bearing m1 (UF 26915, holotype) in occlusal (*above*) and buccal (*below*) views, anterior to the right. Scale bar equals 5 mm

determined if this is the actual base of the incisor or whether it would have extended further in life.

Only the base of p4 is preserved. In superior view, it is composed of two roots that are just beginning to diverge as they pass into the body of the dentary. The posterior root is triangular in cross section and is much larger than the elliptical anterior root; they measure 5.0×4.7 mm and 3.6×2.8 mm, respectively. The total length of the p4 alveolus is 8.8 mm. The preserved portion of the diastema between p4 and i1 measures 8.3 mm, though this would be greater in a complete specimen.

The m1 is well preserved and its distal face is entirely exposed. The tooth extends 5.5 mm above the alveolar border and 14 mm below it. Its base lies just above the inferior border of the dentary and its roots are not closed. At a minimum, HI=3.6. Based on the exposed portion of the tooth, it appears that its dimensions would have changed little with additional wear. The surface of the tooth is noticeably worn; relief is evident between the enamel and dentin and the occlusal surface is trough-shaped, highest lingually and buccally. It measures 6.1× 4.9 mm at its occlusal surface. Cement fills the lingual half of the hypoflexid and the fossettids and likely would have covered most of the tooth. A thin layer of cement covers the buccal half of the mesial face, and fresh edges are evident in cross section near the base of the tooth, apparently where it was removed during preparation.

The molar is tetralophodont. The buccal conids are thick and are separated by a hypoflexid that extends to near the buccolingual midpoint of the tooth. The flexid is oriented nearly perpendicular to the long axis of the tooth. Two fossettids are present, the anterofossettid and the mesofossettid. The metaflexid is open lingually but would have become isolated with 1.1 mm of additional wear, as judged by the lingual face. The anterofossettid is small and circular and located near the buccolingual midpoint of the tooth. It appears that it would be rapidly lost with additional wear. The mesofossettid and metaflexid are parallel to each other and perpendicular to the long axis of the tooth. Both extend buccally about halfway across the occlusal surface. The entoconid is separated from the metaconid by a small inflection of enamel, possibly a remnant of the lingual opening of the mesoflexid. Enamel is thickest along the mesial face of the hypoflexid and the distal face of the posterolophid; it is thinnest surrounding the anterofossettid, mesofossettid, and metaflexid.

Discussion: Extant members of the Dasyproctidae include more than a dozen species of *Dasyprocta* Illiger, 1811, and *Myoprocta* Thomas, 1903 (mainly the former; Woods and Kilpatrick 2005). These species clearly are closely related to each other, but their relationship to the many extinct species referred to the family is unclear

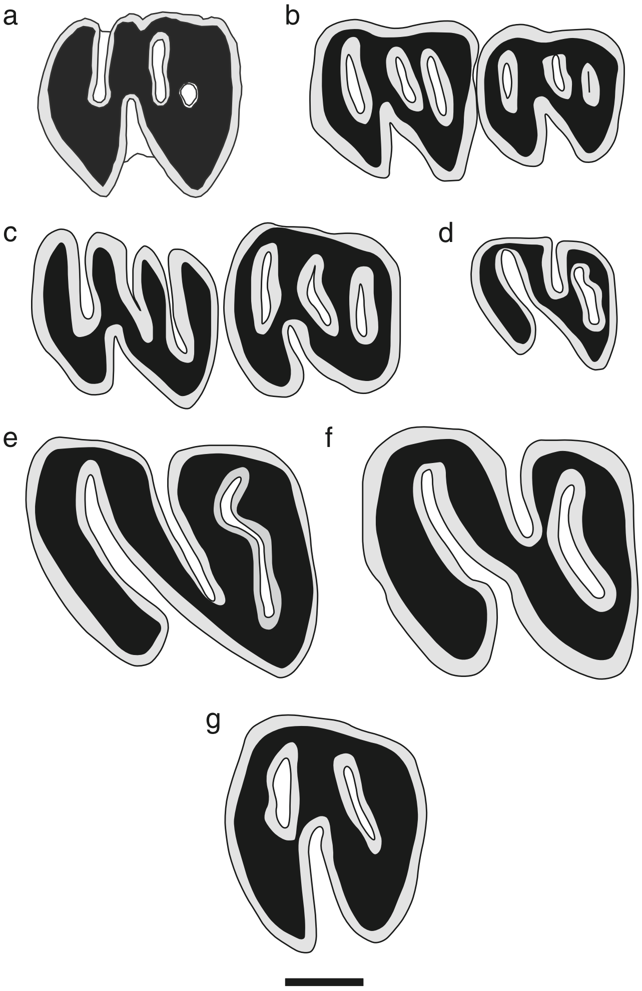


Fig. 5 Comparison of dasyproctid lower molars. **a** m1 of *Mesoprocta hypsodus* (UF 26915, holotype)1; **b** m1-2 of "*Neoreomys*" *huilensis* (IGM 183327) from Walton (1997); **c** m2-3 of "*N.*" *huilensis* (IGM 183683) from Walton (1997); **d** m2 of *Australoprocta fleaglei* (MACN CH 1784) from Kramarz (1998); **e** m1 or m2 of *Neoreomys pinturensis* (MACN Pv SC2211) from Kramarz (2006a, b); **f** m1 or m2 of *N. australis* from Kramarz (2006a, b); **g** m2 of *Alloiomys* sp. (MLP 76-VIII-30-4). Black indicates dentine and gray indicates enamel. Anterior is to the right in all illustrations. Scale bar equals 2 mm

(Walton 1997; Vucetich and Verzi 2002). A phylogenetic analysis of these species likely would help clarify the situation, especially considering that good cranial material exists for some species in addition to dentitions (e.g., *N. australis*, "*N.*" *huilensis*, and *Alloiomys pattersoni*).

In an unpublished PhD thesis, Frailey (1981:61–62) tentatively referred UF 26712 (a poorly preserved partial right dentary bearing p4-m3) to *Neoreomys*. We have been unable to study this specimen firsthand. Based on the limited information provided by Frailey (1981), we cannot assess whether this specimen pertains to *Mesoprocta hypsodus*. We presently consider it as Dasyproctidae gen. et sp. indet.

Family Caviidae Fischer de Waldheim, 1817

Diagnostic characters: Caviids have simple, hypselodont cheek teeth with triangular lobes and deep sulci. Enamel is reduced or absent on the lingual surfaces of lower cheek teeth and on the buccal sides of upper cheek teeth, at least in adults. In most cheek teeth, a narrow isthmus obliquely connects the lobes. Caviids differ conspicuously from "eocardiids" such as *Eocardia* and *Luantus* in their lack of fossettes/fossettids in all ontogenetic stages, as well as in the morphology of the external face of the mandible (Pérez 2010; Pérez et al. 2010; Pérez and Vucetich 2011).

Discussion: The family Caviidae traditionally has included two subfamilies, Dolichotinae and Caviinae. Recent molecular studies have indicated that capybaras (Hydrochoeridae) should be included as a third subfamily (Rowe and Honeycutt 2002; Rowe et al. 2010). Both of these arrangements are based on modern representatives (Woods and Kilpatrick 2005), and many extinct taxa do not unequivocally fit into this tripartite scheme. Hydrochoerids (hydrochoerines) and their close relatives are easily distinguished from other caviids by the additional well-developed flexuses and flexids on their cheek teeth (e.g., Vucetich et al. 2005; Deschamps et al. 2007). The validity, contents, and distinguishing characters of the two other subgroups are less clear (Quintana 1996, 1998; Ubilla et al. 1999; Ubilla and Rinderknecht 2003; Pérez 2010). The situation is further complicated by the many extinct species known only from dental remains and/or small samples that preclude adequate assessment of population variation.

Guiomys Pérez, 2010

Type species: *Guiomys unica* Pérez, 2010.

Included species: The type only.

Age and distribution: Unnamed formation of El Petiso locality, Chubut, Argentina, middle? Miocene age, Laventan? SALMA (Pérez 2010); Collón Curá Formation, Río Negro, Argentina, middle Miocene age, Colloncuran SALMA (Pérez 2010); unnamed formation (Honda Group) of Quebrada Honda, southern Bolivia, middle Miocene age, Laventan SALMA (present study).

Diagnostic characters: *Guiomys* is a small caviid (toothrow length similar to *Orthomyctera rigens* Ameghino, 1889) that is distinguished by its autapomorphic mandibular morphology. On the external face of the mandible, the shelf for the insertion of the masseter medialis pars infraorbitalis (mmpi) is distinct from and anterior to both the horizontal crest and the masseteric crest. The shelf for the insertion of the mmpi is horizontal relative to the inferior border of the mandible, whereas the horizontal crest lies an angle of ca. 30°, paralleling the superior border of the horizontal ramus. The p4 bears a distinct, wide buccal anterior sulcus between the anterior prism and its anterior projection, but the shapes and sizes of these three structures apparently vary among individuals. The teeth of *Guiomys* lack transverse dentine crests, which characterize later-diverging members of the family (Pérez and Vucetich 2011).

Guiomys unica Pérez, 2010
Figs. 6a, c-d, 7

Holotype: MPEF-PV 3504, partial right dentary bearing p4–m3.

Referred specimens: UATF-V-000962, UATF-V-000971, UATF-V-000973, UATF-V-000981, UATF-V-001008, UATF-V-001017, UATF-V-001038, UF 26914, UF 66003, UF 236852, UF 236853, UF 236854, UF 236858, UF 236859, UF 236860 (Appendix 1).

Provisionally referred specimens: UF 26717, UF 26718, UF 26719, UF 26720 (see below).

Localities: Quebrada Honda Local Fauna, Units 2 and 4, and Río Rosario Local Fauna, levels equivalent to Units 2 and 4 of Quebrada Honda of MacFadden and Wolff (1981), as well as unspecified lower levels.

Diagnostic characters: As for genus.

Description: The dentition and mandibular crests of *G. unica* are described in detail by Pérez (2010). We therefore focus our description on new information provided by the more complete material from Quebrada Honda.

Fig. 6 Specimens of *Guiomys unica* from Quebrada Honda and other caviids. **a** partial cranium of *G. unica* (UF 236852) in right lateral (*above*) and palatal (*below*) views; **b** holotype cranium of *Orthomyctera andina* (MACN 8350) in right lateral (*above*) and palatal (*below*) views; **c** partial cranium of *G. unica* (UF 236853) in right lateral (*above*) and palatal (*below*) views; **d** partial mandible of *G. unica* (UF 236854) in left lateral (*above, reversed*) and occlusal (*below*) views; **e** holotype of *Orthomyctera rigens* (MACN A 1661–62), cranium in palatal view (*left*), left dentary in lateral view (*above right*, *reversed*), and close-up view of left maxillary dentition in occlusal view (*below right*). Anterior is to the right in all photos. Scale bar equals 1 cm

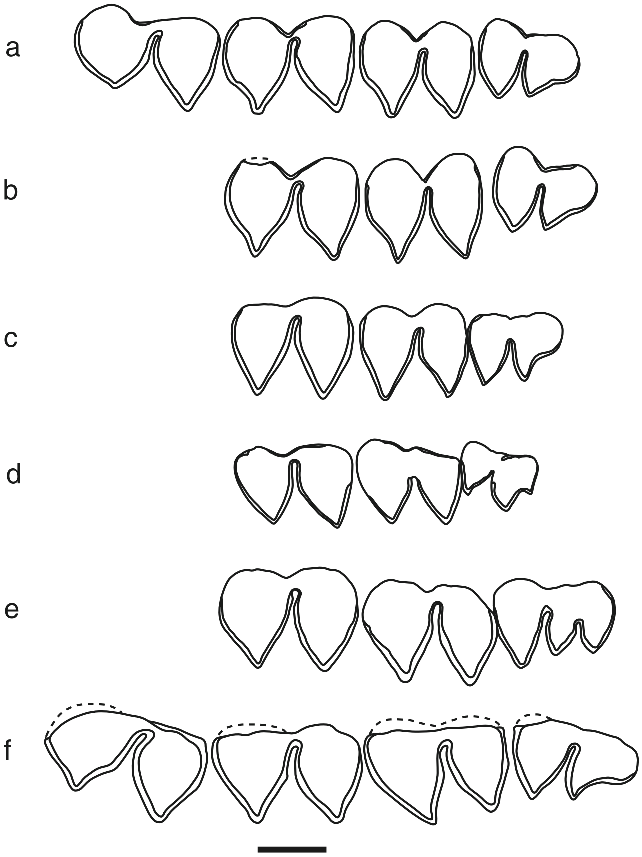


Fig. 7 Right lower dentitions of *Guiomys unica* from Quebrada Honda. **a** UATF-V-000971, right p4-m3; **b** UATF-V-001017, left p4-m2 (*reversed*); **c** UF 26914, left p4-m2 (*reversed*); **d** UF 236858, right p4-m2; **e** UF 66003, right p4-m2; **f** UF 236854, right p4-m3. Anterior is to the right in all illustrations, and specimens are aligned at the m2 hypoflexid. Scale bar equals 2 mm

UF 236852 is a nearly complete cranium in moderately good condition (Fig. 6a). Much of the overall morphology of the cranium is evident, but many details are not preserved. All teeth except RP4 are present (though only part of the base of LP4 remains) and about half are not fully situated in their alveoli. The soft tissue anchoring the teeth apparently decomposed prior to burial of the specimen, permitting some teeth to partially slide out of their alveoli. This suggests that the specimen was exposed for an intermediate period of time prior to fossilization: long enough to permit soft tissue decomposition but not long enough to degrade the bone or dentition. Most of the skull roof is missing (nasals, frontals, parietals), exposing a natural endocast of the nasal passages, cranial cavity, and other spaces. The small portion of the roof that is present is fractured into small pieces, suggesting that the skull roof was lost when the fossilized specimen was exposed through erosion. Greatest skull length is 86.2 mm. The skull is relatively narrow, measuring 28.6 mm across the para-occipital processes, ca. 48 mm across the zygomatic arches (only the right is preserved), and ca. 18 mm at the premaxillary-maxillary suture (part of the right premaxilla is missing). The zygomatic arch is straight in dorsal view, and is directed slightly toward the midline anteriorly.

In lateral view, the skull has a slightly curved profile, and the large auditory bullae lie below the level of the tooth row. Among extant caviids, the profile of UF 236852 most resembles *Kerodon rupestris* Weid, 1826 (Quintana 1998).

The incisive foramina are long and narrow in palatal view (ca. 14×3.5 mm), unlike any extant caviine but similar to the condition in *Dolichotis* Desmarest, 1820 (Campos et al. 2001). The dispositions of the upper tooth rows are not evident in UF 236852, but can clearly be seen to be straight and anteriorly convergent in another partial cranium, UF 236853 (Fig. 6c). The palate of this specimen is 11.0 mm wide at the posterior lobe of M3 and only 2.6 mm wide at the anterior lobe of P4. Toothrow lengths for these and other specimens are provided in Appendix 1. UF 236853 also preserves the posterior border of the palate in *G. unica* (i.e., the anterior border of the mesopterygoid fossa; see Carleton and Musser 1989:fig. 16). It sits opposite the anterior or posterior lobe of M3 and is broadly rounded with a slight midline tubercle. The area also is preserved in UF 236860, UATF-V-001038 and, to a lesser extent, in UATF-V-000962. This is more similar to the condition present in most modern caviines (except *K. rupestris*) than it is to that of *Dolichotis* and other dolichotines. In *K. rupestris* and dolichotines, the mesopterygoid fossa extends farther anteriorly and is more triangular, coming to a point anteriorly.

The left upper incisor of UF 236852 measures 4.3× 2.6 mm in section near its tip (anteroposterior × mesiodistal diameter). This is the only specimen in which the upper incisors are preserved. The upper cheek teeth of Quebrada Honda specimens of *G. unica* generally resemble those from El Petiso. The morphology of P4 cannot be discerned clearly in UF 236852, but it is present on both sides in UF 236853 and UF 236859. In all specimens, P4-M2 each consists of two subequal prisms separated by a hypoflexus that is broad lingually and narrow buccally. Cement fills the buccalmost portion of the hypoflexus. Enamel is present along the lingual faces of the teeth. It is completely absent on the buccal faces of some specimens (UF 236852, UATF-V-000962, UATF-V-001038) and restricted to the shallow interprismatic sulci in others (UF 236852, UF 236859). This may represent ontogenetic variation.

The greatest variation in cheek tooth morphology is evident in M3, which is preserved in several specimens. The M3 of UF 236852 resembles MPEF-PV 3534 and 3535 (Pérez 2010:figs. 2, 6) in having a straight-sided posterior (distal) projection that is lingually separated from the posterior prism by a sulcus that forms an angle of 90°. (The posterior projection is considered a distinct prism by some authors, in which case this posterior sulcus separates the second and third prisms; Ubilla and Rinderknecht 2003.) In other Quebrada Honda specimens (UATF-V-001038, UF 236853; Fig. 3a), the posterior sulcus is rounded and more similar to that of *Orthomyctera* Ameghino, 1889 (Ubilla and Rinderknecht 2003:fig. 4). Based on variation in extant caviids (Contreras 1964) and the relatively limited data presently available for *Orthomyctera* and other extinct taxa, we provisionally interpret this as intraspecific variation (see also discussion below).

The mandibular morphology of *G. unica* is best preserved in UF 236854, which includes most of both horizontal rami (Fig. 6d). On both sides, the diagnostic morphology of *G. unica* is evident. The insertion of the mmpi is a shelf that protrudes laterally from each side of the mandible and is broadest from below the posterior prism of m2 to the hypoflexid of m1. The horizontal crest is superior to this shelf. Its anterior end lies below a point between m2 and m3 and its posterior end extends well posterior to the distal border of m3.

The most variable tooth of the lower dentition is p4. In most Quebrada Honda specimens (Fig. 7a–d, f), it resembles specimens from El Petiso in having a shallow anterior sulcus on its buccal face that separates the anterior prism from a rounded anterior projection. In UF 66003 (Fig. 7e), however, this sulcus is quite deep and parallels the hypoflexid, creating two subequal divisions of the anterior prism. This morphology is more similar to the condition in *Prodolichotis pridiana* Fields, 1957, than other *G. unica*. In the absence of unambiguous evidence to the contrary, we interpret this as intraspecific variation rather than as indicative of a second species.

The molars resemble those of *G. unica* from El Petiso, though some variation is present. For example, in UATF-V-000971, the m3 interprismatic furrow is broad and posteriorly directed, unlike in most other specimens from Quebrada Honda (Fig. 7a). This is a characteristic feature of *Microcardiodon williensis* Pérez and Vucetich, 2011, and *Eocardia robusta* Vucetich, 1984 (Pérez and Vucetich 2011), but is not evident in the other molars of this specimen, suggesting it represents an example of dental variation within *G. unica*. Such variation is expected in m3, which tends to be quite variable in caviids, even within a single species (M. Pérez, pers. comm., April 2011). The first and second molars are subequal in size, whereas m3 is slightly larger. A similar pattern is evident in the only specimen of *G. unica* from El Petiso that preserves all lower molars (Pérez 2010:table 2). This apparently differs from the condition in *M. williensis*, in which the molars increase in size posteriorly (distally), though no single specimen from El Petiso that completely preserves all three molars (Pérez and Vucetich 2011:table 2).

Discussion: UF 236854 clearly illustrates the autapomorphic structure of the external face of the mandible characteristic of *G. unica*. Less complete dentaries from Quebrada Honda appear to have a similar morphology. The dentitions of Quebrada Honda specimens generally resemble *G. unica* from El Petiso (with a few exceptions noted above), and dimensions of individual teeth mainly fall within the range of specimens from El Petiso (Pérez 2010: table 2). Together, these provide clear evidence that *G. unica* is present at Quebrada Honda. It is possible that larger samples or more complete specimens from Quebrada Honda and El Petiso could demonstrate that the two populations represent distinct species or that more than one species is present at Quebrada Honda. Nevertheless, we think it is prudent at the present time to interpret differences among Quebrada Honda specimens as intraspecific rather than interspecific variation.

One issue that cannot be answered presently is how the mandibular morphology of *G. unica* compares to that of *Orthomyctera* Ameghino, 1889, another early caviid. *Orthomyctera* is a rather poorly characterized genus despite its broad geographic range. It has been reported from late Miocene to early Pliocene faunas (Chasicoan to Montehermosan SALMAs) from Bolivia to central Argentina (Rovereto 1914; Bondesio et al. 1980a; Marshall and Patterson 1981; Hoffstetter 1986; Marshall and Sempere 1991; Herbst et al. 2000; Tauber 2005; Verzi et al. 2008). Five species have been referred to the genus: *O. rigens* Ameghino, 1889; *O. vaga* Ameghino, 1889; *O. chapalmalense* Ameghino, 1889; *O. lacunosa* Ameghino, 1889; *O. andina* Rovereto, 1914; and *O. brocherense* Castellanos, 1956. Of these, *O. chapalmalense* probably pertains to *Dolichotis* (Kraglievich 1930a; Ubilla and Rinderknecht 2003) and *O. lacunosa* probably pertains to *Prodolichotis* Kraglievich, 1932 (Kraglievich 1932). *Orthomyctera vaga* is based on a fragmentary maxilla bearing M3 and has been disregarded by most authors (e.g., Quintana 1998; Ubilla and Rinderknecht 2003), though Kraglievich (1932) referred a cranium to this species. The distinctiveness of *O. brocherense* also is dubious. Only two species are based on adequate type material: *O. rigens* (the type species) and *O. andina*.

The holotype of *O. rigens*, MACN A 1661–62, includes a poorly preserved cranium bearing LP4-M3 and parts of RP4-M2, and a partial left dentary bearing i and m1 (Fig. 6e). It appears to differ from *G. unica* primarily in having more pronounced interprismatic furrows in the upper dentition. The M3 morphology differs from that of El Petiso *G. unica* in having a broad, rounded posterior sulcus lingually separating the posterior prism from its posterior projection. Based on specimens of *G. unica* from Quebrada Honda, however, this may represent intraspecific variation. It would be useful to test this hypothesis with a larger sample of *O. rigens*. The shape and position of the mesopterygoid fossa in *O. rigens* resembles that of specimens of *G. unica* from Quebrada

Honda. Size also is comparable; toothrow length of MACN A 1661–62 is ca. 16 cm, within the range of Quebrada Honda *G. unica*. The partial dentary of the holotype of *O. rigens* unfortunately does not permit the morphology of the external face of the mandible to be assessed. Transverse dentine crests appear to be present on the molars, which would distinguish this species from *G. unica* and earlier-diverging caviids.

The holotype of *O. andina*, MACN 8350, is a fairly well-preserved cranium (Fig. 6b). It is noticeably smaller overall than both *O. rigens* and specimens referred to *G. unica* from Quebrada Honda. Total skull length of MACN 8350 is ca. 60 mm, compared to 86.2 mm for UF 236852. The unfused cranial sutures of MACN 8350 suggest that the specimen is from a young individual, and this might partly account for its smaller size. However, the dentition is fully erupted. The shape of the skull in lateral view does not closely resemble that of UF 236852. The postorbital portion is proportionally smaller (anteroposteriorly) and more rounded, similar to the condition in *Dolichotis*. As is the case for *O. rigens*, the morphology of the external face of the mandible in *O. andina* is not known. The dentition appears to preserve transverse dentine crests, a feature lacking in *G. unica*.

Pérez (2010; see also Pérez and Vucetich 2011) performed an extensive phylogenetic analysis of caviids (34 taxa, 83 characters) but only included *O. chapalmalense* among species of *Orthomyctera*. As noted above, this species likely pertains to *Dolichotis* (Kraglievich 1930a; Ubilla and Rinderknecht 2003). Thus, the degree to which the mandibular morphology of *G. unica* differs from species referred to *Orthomyctera* presently is not known, because this character cannot be assessed in the holotypes of *O. rigens* and *O. andina*. Such comparisons must await recovery of more complete mandibular material of *Orthomyctera*. Larger sample sizes of relevant species also would be useful for assessing intraspecific dental variation more accurately.

Frailey (1981:66–74) referred three UF Quebrada Honda specimens to *Schistomys*, sp. nov. (UF 26718, 26719, 26720), and one to *Eocardia* cf. *montana* Ameghino, 1887 (UF 26717). Frailey (1981) did not directly compare these specimens to caviids, and although we have been unable to study these specimens firsthand, there is no evidence for referral of them to the Eocardiidae; fossettes/fossettids apparently are absent, and there is little variation in morphology among the teeth (Pérez 2010; Pérez and Vucetich 2011). Dental measurements provided for these specimens fall within the range of variation of *G. unica* from Quebrada Honda, except for some measurements of UF 26717. Length of p4-m3 of this specimen is given as 20.7 mm, but m3 appears to be incompletely preserved (measured at 6.4 mm). Because measurements of other teeth of this specimen fall within the range of *G. unica*, it appears that the length of m3 (and the toothrow) is an overestimate. All four of these specimens appear to pertain to *G. unica*.

Superfamily Octodontoidea Simpson, 1945
Acarechimys Patterson, 1965 (in Kraglievich 1965)

Type species: *Acarechimys minutus* (Ameghino, 1887).

Included species: the type, *A. constans* (Ameghino, 1887), *A. minutissimus* (Ameghino, 1887), *A. pulchellus* (Ameghino, 1902).

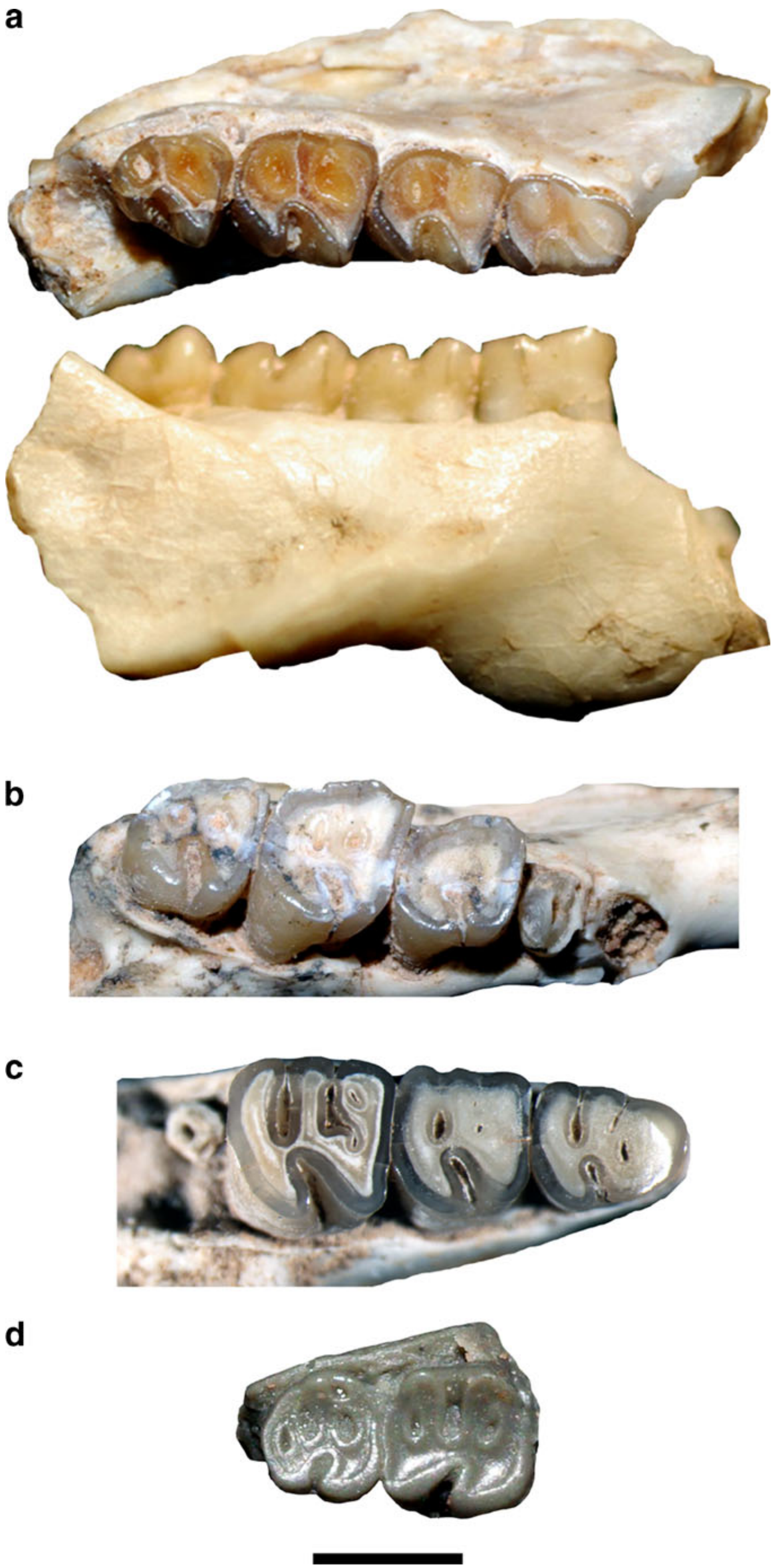
Age and distribution: Sarmiento Formation, Chubut, Argentina, early Miocene age, Colhuehuapian and Santacrucian? SALMAs (Kramarz et al. 2010; Vucetich et al. 2010a); Chichinales Formation, Río Negro, Argentina, early Miocene age, Colhuehuapian SALMA (Kramarz et al. 2004); Chucal Formation, Region XV, Chile, late early Miocene age, Santacrucian SALMA (Croft et al. 2007); middle and upper sequences of Pinturas Formation, Santa Cruz, Argentina, late early Miocene age, Santacrucian? SALMA (Kramarz 2004; Kramarz and Bellosi 2005); unnamed formation of Pampa Castillo, Region XI, Chile, early Miocene age, Santacrucian SALMA (Flynn et al. 2002b); Santa Cruz Formation, Santa Cruz, Argentina, late early Miocene age, Santacrucian SALMA (Ameghino 1887, 1889; Scott 1905); Cura-Mallín Formation, Region VIII, Chile, late early to middle Miocene age (Flynn et al. 2008); Collón Curá Formation, Neuquén, Argentina, early middle Miocene age, Colloncuran SALMA (Vucetich et al. 1993); Honda Group, Colombia, middle Miocene age, Laventan SALMA (Walton 1997); unnamed formation (Honda Group) of Quebrada Honda, southern Bolivia, middle Miocene age, Laventan SALMA (present study); conglomerates of Fitzcarrald Arch, eastern Peru, middle Miocene age, Laventan SALMA (Antoine et al. 2007; Negri et al. 2010); questionably present in Madre de Dios and other formations, eastern Peru, late Miocene age (Campbell et al. 2006).

Diagnostic characters: *Acarechimys* includes very small, brachydont rodents that retain DP4/dp4 (Patterson and Wood 1982; Vucetich et al. 2010a). The lower molars have three main transverse crests and upper molars have four such crests. The labial flexi and lingual flexids are shallow and form fossettes or fossettids after relatively little wear. As is true of octodontids, the mesofossettid forms after the metafossettid.

Acarechimys, sp. nov.?
Figs. 3c, 8, 9

Referred Specimens: UATF-V-000935, UATF-V-000896, UATF-V-000897, UATF-V-000934, UATF-V-000940, UATF-

Fig. 8 Dentitions of *Acarechimys*, sp. nov.? from Quebrada Honda. **a** UATF-V-000935, partial right dentary bearing dp4-m3 in occlusal (*above*) and buccal (*below*) views. **b** UATF-V-000952, partial right dentary bearing m1-3 (and roots of dp4) in occlusal view. **c** UATF-V-001039, partial right dentary bearing dp4-m2 in occlusal view. **d** AMNH 107911 (= UF 26713), partial right maxilla bearing M2-3. Anterior is to the right in all photos. Scale bar equals 2 mm



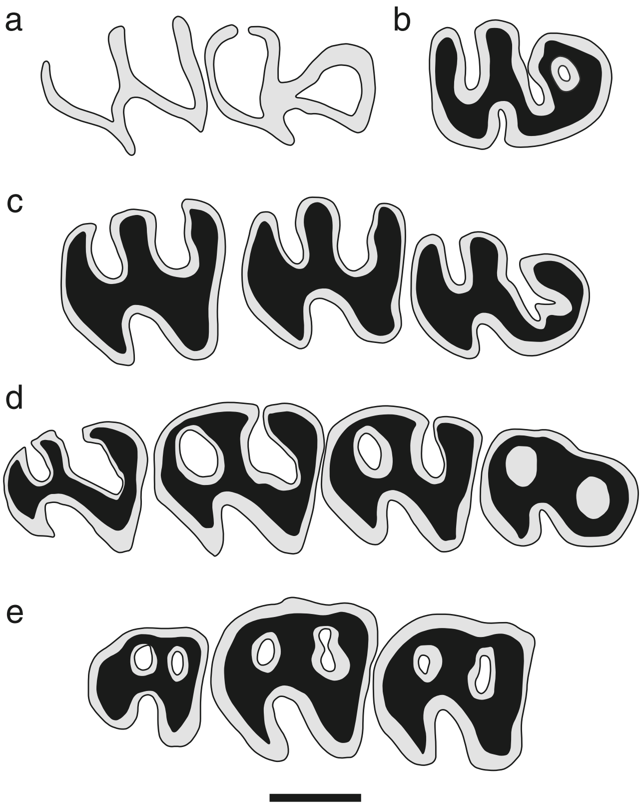


Fig. 9 Lower dentitions of *Acarechimys*, sp. nov.? **a** UATF-V-000960, Rdp4-m1; **b** Ldp4 of UATF-V-000974 (*reversed*); **c** UATF-V-000934, Rdp4-m2; **d** UATF-V-000935, Rdp4-m3; **e** UATF-V-000950 Lm1-m3 (*reversed*). *Black* indicates dentine and *gray* indicates enamel. Anterior is to the right in all illustrations. Scale bar equals 1 mm

V-000950, UATF-V-000952, UATF-V-000958, UATF-V-000960, UATF-V-000974, UATF-V-000983, UATF-V-001039, AMNH 107907 (= UF 26695), AMNH 107908 (= UF 26696), AMNH 107909 (= UF 26697), AMNH 107910 (= UF 26698 or 26699), AMNH 107912 (= UF 26698 or 26699) (Appendix 2).

Localities: Units 2, 3, and 6 of MacFadden and Wolff (1981), Quebrada Honda Local Fauna; Río Rosario Local Fauna, unspecified lower levels equivalent to Units 2–4 of Quebrada Honda Local Fauna.

Description: The most complete specimen, UATF-V-000935, is a moderately worn partial right dentary bearing dp4-m3 and the base of i1 (Figs. 8a, 9d). A small scar for the insertion of the masseter medialis pars infraorbitalis is located just anterior to the masseteric crest, a feature that is characteristic of octodontids and kin (Verzi et al. 1994; Verzi 1999, 2002).

The total length of the toothrow is 7.1 mm. Based on measurements by Scott (1905), this is larger than *A. minutissimus* (5.0 mm) and within the lower part of the range of *A. minutus* (7.0–8.0 mm). However, based on the data of Walton (1990:fig. 8), m1s of Quebrada Honda *Acarechimys* are much larger (in length and breadth) than those of both *A. minutissimus* and *A. minutus*, presumably closer to *A. constans* and *A. pulchellus* (Kramarz 2004, Vucetich et al. 2010a). Ameghino notes a toothrow length of 9.0 mm for *A. constans* (Ameghino 1889) and 8.0 mm for *A. pulchellus* (Ameghino 1902). UATF-V-000935 is the only Quebrada Honda specimen that preserves dp4-m3, but many other specimens preserve three of the four cheek teeth. All are at least as large as UATF-V-000935. Estimated toothrow lengths for these specimens based on UATF-V-000935 average 7.5 mm and range up to 8.3 mm (Appendix 2). This overlaps the range of both *A. minutus* and *A. pulchellus*.

The largest tooth in the dental series is m2, which tends to be broader than all other teeth and longer than all others except dp4. The smallest tooth is m3, which is 70–90% the anteroposterior length of m2. In overall form, dp4 is rectangular, m1 and m2 are quadrangular, and m3 is triangular.

All cheek teeth of UATF-V-000935 are trilophodont. The hypoflexid is the deepest flexid (i.e., the last to form a fossettid). It is open externally in all teeth and extends across ca. 40% of the buccolingual diameter of each tooth. It is directed distolingually toward the metaflexid/metafossettid, but is separated from it by the anterior arm of the hypoconid. The metaflexid has become isolated as a metafossettid in all teeth of UATF-V-000935 except m3. The mesoflexid, in contrast, is open lingually in all teeth except dp4. The mesoflexid is slightly larger than the metaflexid, as is the corresponding fossettid in teeth in which it has become isolated. It is much larger than the metaflexid in m3, but in moderately worn specimens (e.g., UATF-V-000950; Fig. 9e), the resulting fossettids are subequal in size. The greater persistence of the mesofossettid is evident in the most heavily worn specimen, UATF-V-000983. The metafossettid is absent in this specimen, but both the mesofossettid and hypofossettid are present. The latter is larger and has thicker enamel. The depth of these structures evidently varies among individuals. In m1 of UATF-V-000952 (Fig. 8b), both the meso- and metafossettid are absent, but a hypoflexid has not yet formed a hypofossettid.

Variation also is evident in dp4, as is typical for basal octodontoids (Kramarz 2004). In UATF-V-000934 (Figs. 3c, 9c), dp4 has an expanded metaconid and a small spur on the anterolophid (= metalophulid 1) in the region of the protoconid. The spur is directed distolingually, resulting in a mesoflexid that bifurcates buccally. The ectolophid is slightly expanded near its juncture with the hypolophid. The posterolophid joins the hypo- and ectolophid via the anterior arm of the hypoconid, which is flanked by subequal meta- and hypoflexids. In UATF-V-000960 (Fig. 9a), a specimen exhibiting very little wear, a trigonid fossettid (anterofossettid) is present between the metalophulid 1 and another lophid. Unlike a typical metalophulid 2, this lophid does not extend transversely across the tooth from the metaconid, however, but rather distolabially toward the anterior arm of the hypoconid. The resulting anterofossettid is quite large and the metaflexid is directed more distally than in other specimens. UATF-V-000974 is not well preserved, but it shows yet another variation (Fig. 9b). Both an anterofossettid and mesoflexid are present. The mesial and distal sides of the mesoflexid approach each other near its buccolingual midpoint, nearly creating a distinct fossettid. With additional wear, it is possible that this specimen would have had an anterofossettid, a mesofossettid, and a mesoflexid. In UTAF-V-000935 (Figs. 8, 9d), most of the structure of dp4 has been worn away. Only the bases of the anterofossettid and metafossettid are present.

UATF-V-001039, a partial right dentary bearing dp4-m2, is noteworthy among Quebrada Honda specimens in being the only one with a more complex molar morphology, best seen in m2 (Fig. 8c). Unlike other Quebrada Honda specimens, the m2 of UATF-V-001039 bears a small, anterolingually directed spur on the ectolophid and a small mesolophid (metalophulid 2) that connects the posterior (distal) edge of the metaconid to the midpoint of the anterolophid (metalophulid 1), resulting in a lingually positioned anterofossettid. The overall occlusal pattern is more similar to that of a dp4 than a typical m2, though its size and relative proportions are comparable to m2s of other specimens (other than being slightly wider). The morphology of m1 is much less clear due to greater wear, but the presence of two tiny trigonid fossettids rather than a single mesofossettid suggests that the unworn morphology was similar to that of m2.

UF 26713, a moderately worn partial right maxillary dentition preserving M2-3, may pertain to the same species of *Acarechimys*. This specimen was referred to Acaremyinae (= Acaremyidae) indet. by Frailey (1981). A cast in AMNH collections (AMNH 107911) of a Quebrada Honda specimen that was collected in 1978 matches the description of this specimen as well as its stratigraphic provenance and therefore likely represents UF 26713 (Fig. 8d). M2 is slightly broader anteriorly (mesially) than posteriorly and bears four transverse lophs. Two flexuses are present, the mesoflexus and the hypoflexus. The former is perpendicular to the long axis of the tooth whereas the latter runs anterolingually from the buccal face. They are separated by the anterior arm of the hypoconid, which is as broad as the four main lophs. Two small, oval fossettes are present, one between the anteroloph and protoloph (parafossette) and the other between the metaloph and posteroloph (metafossette). Their long axis are parallel to the mesoflexus, and both are narrower anteroposteriorly than the mesoflexus. The M3 is slightly smaller than M2 and also is tetralophodont. A hypoflexus is present, but the mesoflexus has become isolated as a mesofossette. It and the parafossette are subequal in size and both are larger than the metafossette. A fifth fossette, slightly smaller than the metafossette, is present just lingual to the parafossette and may represent a separately isolated portion of the paraflexus. The tip of the paracone lies just posterior to this accessory fossette.

Discussion: Five Quebrada Honda specimens (four dentaries and one maxilla) are listed in the UF collections database as pertaining to Echimyidae (UF 26695–26699). The study of Frailey (1981) made no mention of them, and we have not been able to study them firsthand. However, these appear to be represented by five casts in AMNH collections: AMNH 107907, 107908, 107909, 107910, and 107912. The accompanying labels read “Santacrucian, Quebrada Honda, Tarija Prov., Bolivia, Frailey party, 1978,” but no field numbers or UF collections numbers are associated with the specimens. The stratigraphic data for each of these specimens precisely matches that for the five echimyid specimens in the UF collections database. They closely (but not precisely) match the brief descriptions provided in the UF database; one specimen listed as a maxilla actually is a dentary, and one preserves dp4-m1 rather than dp4-m2. These discrepancies probably are due to initial misinterpretations of the teeth represented. We therefore interpret these casts as representing UF 26695–26699. They match UATF specimens of *Acarechimys* in size and morphology and clearly represent the same species.

Species and specimens of *Acarechimys* are clearly in need of revision. The three Santacrucian species (*A. minutus*, *A. minutissimus*, *A. constans*) are distinguished primarily by size (Vucetich et al. 1993), but whether such differences are valid for large samples sizes has not been demonstrated. *Acarechimys pulchellus* was recently transferred from *Protacaremys* to *Acarechimys*, but no characters distinguishing this species from others in the genus were provided (Vucetich et al. 2010a). As noted by Vucetich et al. (2010a), no specimens referred to *Acarechimys* from localities other than Santa Cruz have been referred to a particular species, although resemblances have been noted in some instances (e.g., *Acarechimys* cf. *A. minutus* from Pampa Castillo and *Acarechimys* cf. *A. minutissimus* from La Venta). Moderate metric and morphological variation certainly is present among specimens referred to *Acarechimys*, but no published study other than the present one has described variation among a reasonably large sample from a single locality. In the absence of other such studies, the identity of the Quebrada Honda species cannot be determined with certainty. Its relatively large size, proportionately small m3, and absence of metalophulid 2 (mesolophid) and other accessory lophids in m1-3 of most individuals, among other characters, suggest that it may be distinct from early Miocene species of *Acarechimys*.

Family Echimyidae Gray, 1825
Subfamily Adelphomyinae Patterson and Pascual, 1968

Diagnostic characters: Adelphomyines exhibit a tendency towards hypsodonty (Kramarz 2001) and m2 is often the largest tooth in the molar series (*Prostichomys*, *Stichomys*). Members of this subfamily possess trilophodont or tetralophodont molars with oblique lophids that tend to form plates. Adelphomyines such as *Adelphomys*, *Stichomys*, *Spaniomys*, and *Maruchito* also possess shortened lower incisors that do not extend posteriorly past m2 (Vucetich et al. 1993). It apparently represents a monophyletic group (Vucetich et al. 2010a).

Quebradahondomys potosiensis, gen. et sp. nov.
Figs. 3d, 10, 11a

Holotype: UATF-V-001030, right dentary bearing m1-m3.

Provisionally referred specimen: UF 26714, left dentary bearing m1-2.

Etymology: The genus name combines reference to the type locality with the common suffix for rodent genera (−*mys*). The specific epithet honors Potosí, Bolivia, the location of the Universidad Autónoma Tomás Frías, a critical supporter of our investigations in Bolivia.

Type locality: Quebrada Honda Local Fauna, Unit 2 of MacFadden and Wolff (1981).

Age and distribution: Unnamed formation (Honda Group) of Quebrada Honda, southern Bolivia, middle Miocene age, Laventan SALMA (present study).

Diagnosis: *Quebradahondomys* differs from *Spaniomys* Ameghino, 1877, in having trilophodont molars (tetralophodont in *Spaniomys*). It differs from *Maruchito* Vucetich et al., 1993, in its straighter, less undulating lophids, shallower and medially-directed hypoflexids, and narrower buccal lophids. *Quebradahondomys* differs from *Stichomys* Ameghino, 1887, *Prostichomys* Kramarz, 2001, *Xylechimys* Patterson and Pascual, 1968, and *Deseadomys* Wood and Patterson, 1959, in its lack of an anterofossettid and its more transverse lophids. It further differs from *Stichomys* in having a hypoflexid that is less penetrating and proportionally wider lingually, and in m3 being the largest tooth in the molar series (it is the smallest in *Stichomys*). *Quebrada-*

Fig. 10 Right dentary of *Quebradahondomys potosiensis*, gen. et sp. nov. (holotype, UATF-V-001030) in occlusal (*above*) and lateral (*below*) views, anterior to the right. Scale bar equals 2 mm

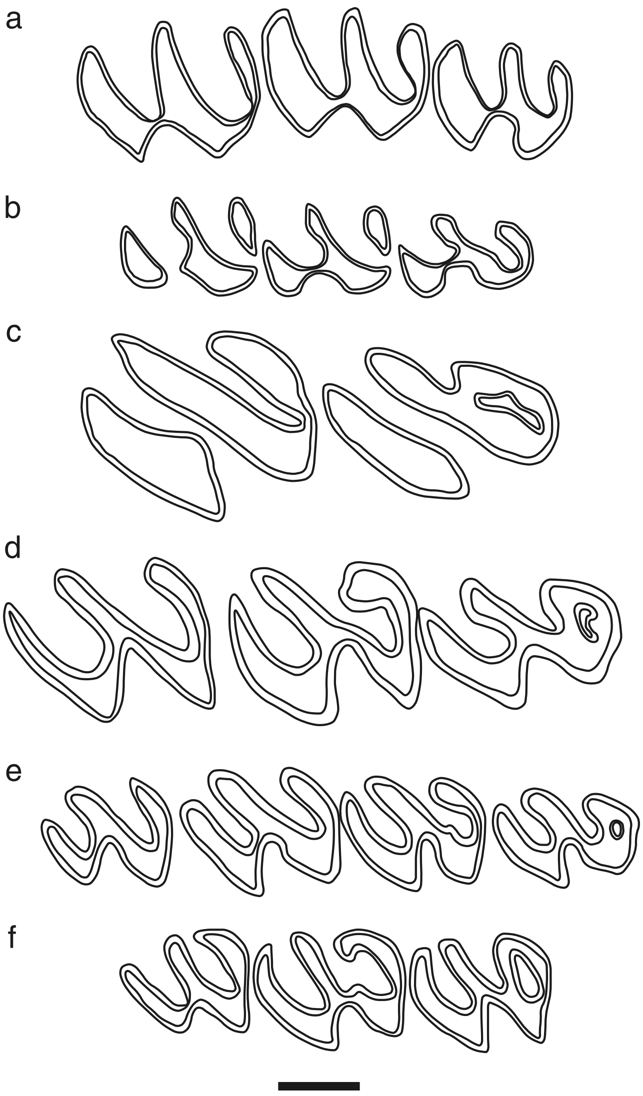


Fig. 11 Lower dentition of adelphomyines. **a** *Quebradahondomys potosiensis*, gen. et sp. nov. (holotype, UATF-V-001030) Rm1-m3; **b** *Ricardomys longidens* (IGM 183847) Ldp4-m2 (*reversed*) from Walton (1997); **c** *Paradelphomys fissus* (MLP 125) Ldp4-m1 (*reversed*) from Patterson and Pascual (1968); **d** *Adelphomys candidus* (YPM-PU 15090) L dp4-m2 (*reversed*); **e** *Stichomys* sp. Rdp4-m3 from Kramarz (2001); **f** *Prostichomys bowni* (MACN SC 3856) Ldp4-m2 (reversed) from Kramarz (2001). Anterior is to the right in all illustrations. Scale bar equals 2 mm

hondomys resembles *Adelphomys* Ameghino, 1887, in having the hypoflexid and metaflexid separated only by a very narrow isthmus, but in *Quebradahondomys* the hypoflexid is shallower, the lophids are more transverse, and the posterolophid is anteroposteriorly thicker. *Quebradahondomys* lacks the confluence of the hypoflexid and mesoflexid present in *Paradelphomys* Patterson and Pascual, 1968. The molars of *Ricardomys* Walton, 1990, are smaller, proportionately narrower, and have less penetrating hypoflexids than *Quebradahondomys* (Fig. 11).

Description: The holotype is a right dentary bearing m1-m3 and the base of the incisor. Its depth is 6 mm below the first molar. The base of the incisor measures ca. 1.7× 1.3 mm in section at its mesial end, and the distal end does not extend posterior to m2. The teeth are hypsodont. The crowns extend ca. 2 mm above the alveolar border. The molars are formed by a series of thin laminae with uniform, thin enamel. They increase in anteroposterior diameter from m1 to m3. Total molar row length is 9.2 mm. The individual molars measure 2.4×2.1 mm (m1), 3.0×2.5 mm (m2), and 3.2×2.6 mm (m3). The premolar alveolus is 3.8 mm long. All molars are generally similar in form. Each is composed of three lophids that are relatively less oblique to the long axis of the dentary than in most other adelphomyines. The hypoconid and protoconid are large, and the ectolophid and posterolophid are correspondingly thick (anteroposteriorly). They are separated by a moderately deep hypoflexid that extends less than halfway across the tooth. It is proportionately deepest in m1 and forms an acute angle. It approximates a right angle in m2-3. The hypoflexid is separated from the metaflexid by a very narrow isthmus connecting the hypoconid to the hypolophid. The hypolophid is markedly narrower anteroposteriorly than the posterolophid in m1, slightly narrower in m2, and roughly equal in m3. The anterolophid (metalophulids 1 and 2) bears no evidence of an anterofossettid. Its lingual portion (metaconid) is expanded in m1-2 and only slightly expanded in m3. Similarly, the connection to the protoconid is thickest in m1, intermediate in m2, and very narrow in m3. These primarily appear to be due to differences in wear among the molars. The mesoflexid and metaflexid are approximately equal in their buccolingual extend.

Discussion: Frailey (1981:44–47) tentatively identified UF 26714 (a partial left dentary bearing m1-2) as a new species of *Spaniomys*. We have been unable to study this specimen firsthand, but based on the figures and measurements in Frailey (1981), it closely matches UATF-V-001030 in both size (m1=2.7×2.1 mm, m2=3.1×2.7 mm) and morphology. It very likely pertains to *Quebradahondomys potosiensis*.

Superfamily Chinchilloidea Bennett, 1833
Family Chinchillidae Bennett, 1833
Subfamily Lagostominae Wiegmann, 1832

Diagnostic characters: Chinchillids have very characteristic hypsodont to hypselodont cheek teeth composed of parallel laminae with reduced enamel between them. The teeth of lagostomines are composed of only two laminae, whereas those of chinchillines often have three laminae (\Flynn et al. 2002a). Fossettids are present in the teeth of basal chinchillids from the Oligocene (e.g., Vucetich 1989) but are lacking in the adult teeth of later species.

Genus *Prolagostomus* Ameghino, 1887

Type species: *Prolagostomus pusillus*, Ameghino, 1887.

Included species: The type; *Prolagostomus divisus* Ameghino, 1887; *Prolagostomus profluens* Ameghino, 1887; *Prolagostomus imperialis* Ameghino, 1887; *Prolagostomus amplus* Ameghino, 1889; *Prolagostomus obliquidens* Scott, 1905; *Prolagostomus rosendoi* Vucetich, 1984.

Age and distribution: See Discussion.

Diagnostic characters: *Prolagostomus* resembles *Pliolagostomus* Ameghino, 1887, in having bilobed cheek teeth with oblique laminae. However, *Pliolagostomus* possesses molar laminae with relatively straight anterior and posterior margins, whereas those of *Prolagostomus* are more rounded (Vucetich 1984). Also, the M3 of *Pliolagostomus* has a smaller, more triangular third prism that is more lingually oriented than that of *Prolagostomus*.

Discussion: Prolagostomus is widespread throughout middle and high latitude faunas from at least the late early Miocene to the early late Miocene. The earliest occurrence of the genus is in the Pinturas Formation of southern Argentina (Santacrucian SALMA, though older than the Santa Cruz Formation; Kramarz 2002). The latest occurrence is the Arroyo Chasicó Formation of east-central Argentina (Chasicoan SALMA; Bondesio et al. 1980a). The range of *Prolagostomus* extends as far north as Bolivia (Nazareno, Quebrada Honda, possibly Cerdas; Marshall and Sempere 1991; Oiso 1991; Croft 2007; Croft et al. 2009; present study) and as far west as south-central Chile (Flynn et al. 2008) though it apparently is absent from the late early Miocene of northern Chile (Flynn et al. 2002a; Croft et al. 2007). Most of these reports do not include species level identifications, and no study has assessed whether early Miocene and late Miocene species referred to *Prolagostomus* actually pertain to the same genus. The temporal and geographic distribution of the genus therefore should be considered provisional.

Prolagostomus sp.
Fig. 12

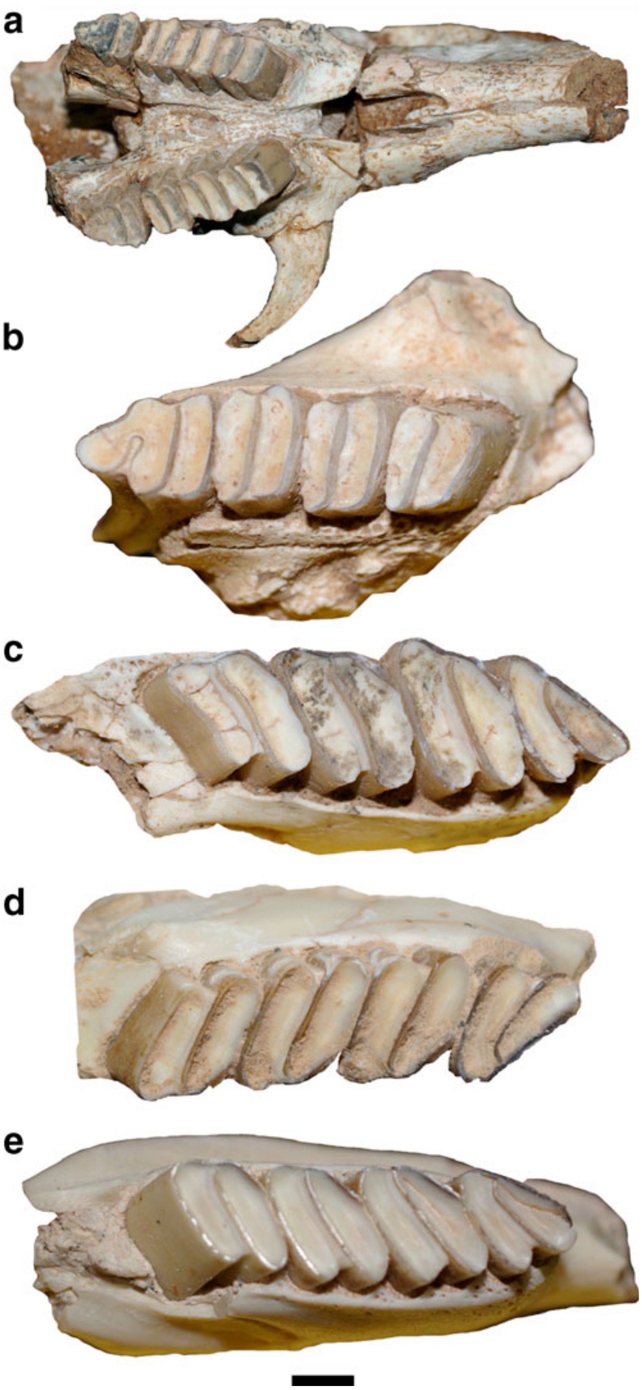


Fig. 12 Representative specimens of *Prolagostomus* sp. in occlusal view **a** UATF-V-000887, rostrum; **b** UATF-V-001025, LP4-M3 (*reversed*); **c** UATF-V-000933, Rp4-m3; **d** UATF-V-000929d, Lp4-m3; **e** UATF-V-001029, Rp4-m3. Anterior is to the right in all photos. Scale bar equals 5 mm (**a**) or 2 mm (**b**–**e**)

Referred specimens: UATF-V-000887, UATF-V-000888, UATF-V-000898, UATF-V-000901, UATF-V-000902, UATF-V-000903, UATF-V-000904, UATF-V-000905, UATF-V-000906, UATF-V-000907, UATF-V-000908, UATF-V-000910, UATF-V-000915, UATF-V-000927, UATF-V-000929a, UATF-V-000929b, UATF-V-000929c, UATF-V-000929d, UATF-V-000929e, UATF-V-000929f, UATF-V-000933, UATF-V-000937, UATF-V-000938, UATF-V-000939, UATF-V-000941, UATF-V-000942, UATF-V-000943, UATF-V-000946, UATF-V-000947, UATF-V-000948, UATF-V-000949, UATF-V-000954, UATF-V-000955, UATF-V-000957, UATF-V-000963, UATF-V-000965, UATF-V-000970, UATF-V-000972, UATF-V-000977, UATF-V-000984, UATF-V-000985, UATF-V-001004, UATF-V-001005, UATF-V-001009, UATF-V-001021, UATF-V-001024, UATF-V-001025, UATF-V-001026, UATF-V-001031, UATF-V-001032, UATF-V-

001034, UATF-V-001037, UATF-V-001040, UATF-V-001041, UATF-V-001046, UATF-V-001050, UF 26912, UF 26916, UF 26917, UF 26919, UF 26920, UF 26924, UF 26927, UF 26932, UF 26935, UF 26940, UF 26942, UF 26943, UF 26944, UF 27897, UF 66001, UF 66002, UF 236855, UF 236856, UF 236857, UF 236861.

Provisionally referred specimens: UF 26682, UF 26683, UF 26684, UF 26685, UF 26686, UF 26687, UF 26688, UF 26689, UF 26690, UF 26691, UF 26692, UF 26693, UF 26694, UF 26700, UF 26701, UF 26702, UF 26703, UF 26704, UF 26705, UF 26706, UF 26707, UF 26708, UF 26709, UF 26710, UF 26711 (see below).

Localities: Units 2–4 of Quebrada Honda Local Fauna as well as unspecified lower levels; Río Rosario Local Fauna, levels equivalent to Units 2 and 4 of Quebrada Honda (MacFadden and Wolff 1981).

Discussion: The great quantity of lagostomine material from Quebrada Honda shows much metric and morphologic variation. In the absence of studies of dental variation in modern lagostomine populations (or fossil ones, for that matter), it is not possible at this time to confidently distinguish among ontogenetic, intraspecific, and interspecific variation. Moreover, the species of *Prolagostomus* have not been revised in more than a century. We therefore do not attempt to provide specific identifications at this time. Representative photos are presented in Fig. 12. The material to which we have access is currently under study by a CWRU graduate student whose thesis will integrate a study of modern lagostomine dental variation with description of Quebrada Honda lagostomines.

Frailey (1981) referred 25 Quebrada Honda chinchillid specimens from UF collections to the Santacrucian species *P. divisus*, *P. imperialis*, and *P. profluens*. Illustrations and measurements of these specimens (Frailey 1981:47–61) suggest that these specimens do not differ significantly from those currently under study by our research group.

Community Structure and Paleoecology

The Quebrada Honda rodent community is dominated by lagostomine chinchillids (*Prolagostomus* sp.), which constitute more than two-thirds (69.9%) of identified rodent specimens (Fig. 13). Caviids (*Guiomys unica*) and incertae sedis octodontoids (*Acarechimys* sp. nov.?) are the next most abundant rodents (13.7% and 12.3%, respectively). Dasyproctids and adelphomyine echimyids are uncommon, represented by only two specimens each. The same may be true for cephalomyids, but we have been unable to verify the presence of this group at Quebrada Honda in our recent collections or through study of available UF specimens. The possible occurrence of cephalomyids at Quebrada Honda is based on the referral of two specimens (UF 26715 and UF 26716) to *Cephalomys* by Frailey (1981). The illustrations in Frailey (1981) suggest that these specimens represent a species distinct from those described here. If referral of these specimens to Cephalomyidae is accurate, it extends the temporal range of the family by more than 5 Ma. Celphalomyids otherwise are unknown in faunas younger than Colhuehuapian in age (upper boundary ca. 19 Ma; Flynn and Swisher 1995; Kramarz 2005; Ré et al. 2010).

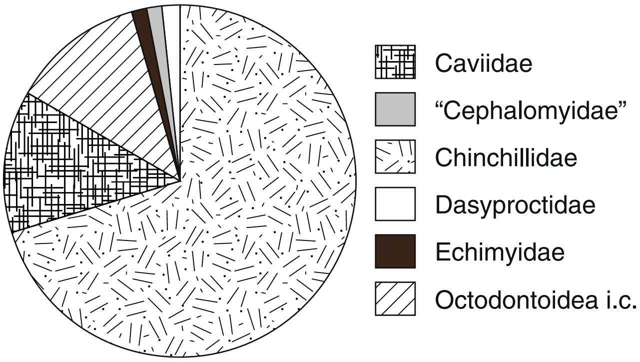


Fig. 13 Number of Identifiable Specimens (**NISP**) of rodents at Quebrada Honda, coded by family. Data are from UATF and UF specimens studied firsthand ($N=112$) as well as others noted in this study ($N=34$)

Chinchillids are the most abundant rodents in both local faunas of Quebrada Honda, though they comprise a slightly smaller percentage of specimens in the Río Rosario Local Fauna (RRLF; 62.5%) than in the Quebrada Honda Local Fauna (QHLF; 72.6%). Caviids are the next most abundant group in the RRLF, accounting for nearly one third of rodent specimens (30.0%), and octodontoids account for the remainder (<8%). None of the rarer species have yet been collected at Río Rosario. In the QHLF, the second and third most abundant groups of rodents are reversed; octodontoids account for just over 14% of specimens whereas caviids account for <8% of specimens. The conspicuous difference in relative abundances of octodontoids and caviids in the two local faunas probably is related to differences in habitat and/or mode of accumulation at the two sites. The rodents collected from the two sites do not differ in any manner that would suggest that they represent temporally distinct populations. All of the rarer species come from the QHLF. This is not surprising given that the QHLF accounts for nearly three times as many rodent specimens as the RRLF, and therefore would be more likely to sample rare species.

The abundances, taxonomic affinities, and presumed dietary adaptations of the rodents of Quebrada Honda indicate that a mixed vegetational structure likely was present in the area in the middle Miocene, probably with a greater proportion of open areas than forested ones. Modern chinchillids are colonial and occur in the Andean highlands of Peru, Bolivia, and Chile (*Chinchilla*, *Lagidium*) as well as the lowlands of Argentina, Bolivia, Paraguay, and Uruguay (*Lagostomus*). They prefer open, arid habitats of various types and are primarily folivorous (Redford and Eisenberg 1992; Jackson et al. 1996). The abundant chinchillids at Quebrada Honda suggest a colonial lifestyle also characterized extinct species and implies that significant open areas were present.

Modern caviids (excluding hydrochoerines) occupy a wide variety of habitats. Some live in open and/or arid habitats whereas others prefer more forested or riparian areas (Redford and Eisenberg 1992; Eisenberg and Redford 1999). They generally do not occur in areas of tropical rainforest (Mares and Ojeda 1982), and their presence at Quebrada Honda argues against a heavily forested habitat. Modern dasyproctids, in contrast, are frugivores characteristic of tropical forests (Emmons and Feer 1997). Their presence at Quebrada Honda implies at least some forested areas were present. The cheek teeth of *Mesoprocta* are much higher crowned than those of modern dasyproctids, however (HI≥3.6 in *Mesoprocta* vs. < 1.6 for modern dasyproctids; Williams and Kay 2001). This suggests that *Mesoprocta* may have had a more abrasive diet than modern forms and perhaps preferred more open habitats. The relative rarity of dasyproctids at Quebrada Honda could reflect a relatively small proportion of forested habitat and/or lower population densities due to a non-social lifestyle.

Echimyids mostly inhabit rainforest habitats, and many species are arboreal or semi-arboreal (Emmons and Feer 1997). The crown group therefore is a reliable indicator of tropical forests. Adelphomyines are an extinct subgroup of echimyids, and their relationships to extant echimyids are unclear (Kramarz 2001). They tend to be more hypsodont that most extant species and may represent a distinct radiation (Kramarz and Bellosi 2005). *Quebradahondomys* therefore probably is not a reliable habitat indicator. Similarly, the closest extant relatives of *Acarechimys* are unknown. Affinities with octodontids have been proposed (Verzi 2002), and this might suggest that *Acarechimys* occupied open habitats. Nevertheless, the brachydont cheek teeth of *Acarechimys* contrast markedly with the hypsodont ones of early octodontids such as *Chasichimys*, indicating that *Acarechimys* may have been dissimilar ecologically. Its broad geographic and temporal range in the fossil record (see below) implies that it may have had broad habitat tolerances.

Faunal Comparisons and Biogeography

The most apparent characteristic of the rodent fauna of Quebrada Honda is the preponderance of chinchillids. Modern chinchillids have been described as "by and large… a temperate zone family that has colonized both montane and lowland habitats" (Redford and Eisenberg 1992:348). As illustrated by Quebrada Honda and other fossil localities, this does not accurately describe the past distribution of the group. Chinchillids have been present in central Chile since the early Oligocene (Flynn et al. 2003; Croft et al. 2008) and in the southern Neotropics and lowland Argentina since at least the late Oligocene (Vucetich 1989). Most of the uplift of the Andes post-dated the Oligocene and early Miocene (Gregory-Wodzicki 2000; Bershaw et al. 2010), indicating that chinchillids ancestrally occupied lowland areas in both temperate and tropical latitudes. It is thus plausible that the common ancestor of chinchillids originally occupied lowland habitats, perhaps even in the tropics, only later expanding to higher elevations and latitudes. Chinchillines may have originated in a more montane habitat (Flynn et al. 2002a), but their fossil record is extremely sparse and nearly all fossil occurrences for the family, including those at Quebrada Honda, pertain to species more closely related to modern *Lagostomus*.

Regardless of the precise area of origin of chinchillids, they apparently have been restricted to the southern Neotropics and more southerly latitudes for most of their history. We are unaware of any Tertiary records of the family north of central Bolivia (i.e., about 16° S, roughly the latitude of Lake Titicaca). Chinchillids are nearly ubiquitous in Miocene fossil localities south of this point, though the fossil record is mainly limited to areas outside of present-day tropical lowlands. Exceptions to the widespread occurrence of chinchillids include a handful of rather poorly characterized Mayoan SALMA faunas of western Argentina from which chinchillids have not yet been reported. These include localities in the Río Mayo Formation (Cerro Guenguel and Arroyo Pedregoso), Laguna Blanca, Río Fénix, and Río Huemules (Kraglievich 1930b; Bondesio et al. 1980b). Interestingly, dinomyids are present in all of these faunas and are absent from at least some other middle Miocene faunas in which chinchillids are present (e.g., Collón Curá, Río Senguerr). Dinomyids have not yet been reported from any Miocene locality in Bolivia or northern Chile, though they commonly occur in lower latitude faunas of Peru (Antoine et al. 2007), Ecuador (Madden et al. 1994), and Colombia (Fields 1957; Walton 1997).

The middle Miocene fauna of La Venta, Colombia is the only well-characterized fauna in South America that is at least partially equivalent in age to Quebrada Honda (Madden et al. 1997; Croft 2007). A preliminary comparison by Croft (2007) of the fauna of Quebrada Honda with that of La Venta and two faunas from Argentina (Collón Curá, which is slightly older, and Arroyo Chasicó, which is slightly younger) indicated that Quebrada Honda was most similar

Table 1 Rodents of Quebrada Honda as identified by Frailey (1981) and the present study

Family	Frailey (1981)	Present Study
Dasyproctidae	*Neoreomys pachyrhynchus?*	*Mesoprocta hypsodus*, gen. et sp. nov.
Cephalomyidae	*Cephalomys*, sp. nov.	(unavailable for study)
Eocardiidae/Caviidae	*Eocardia* cf. *montana* *Schistomys*, sp. nov.	*Guiomys unica*
Octodontidae (?)	Acaremyinae indet.	*Acarechimys*, sp. nov.?
Echimyidae	*Spaniomys*?, sp. nov.	*Quebradahondomys potosiensis*, gen. et sp. nov.
Chinchillidae	*Prolagostomus imperialis* *Prolagostomus profluens* *Prolagostomus divisus*	*Prolagostomus* sp.

to Collón Curá. The two faunas had at least 23% of genera in common. A minimum of 11.5% of genera were shared with La Venta, despite its more similar age. This pattern indicates that a more significant biogeographic barrier existed north of Bolivia and Chile than south of the region. However, this study relied on provisional rodent identifications for Quebrada Honda as recorded in UF collections. The present study has clarified the identities of Quebrada Honda rodents (Table 1), thus permitting a more accurate analysis of faunal resemblance among the rodents. These comparisons indicate that the rodents exhibit a pattern similar to that of the fauna as a whole. One-third (33%) of Quebrada Honda rodent genera are shared with Collón Curá (*Acarechimys* and *Prolagostomus*) whereas only 1/6 (17%) of genera (*Acarechimys*) are shared with La Venta.

Several other faunas are potentially contemporaneous with Quebrada Honda but have not yet been analyzed in detail: El Petiso (Chubut, Argentina), Fitzcarrald (eastern Peru), and the Girón Basin (Ecuador). Quebrada Honda shares only one genus (*Guiomys*) with El Petiso, but only two genera have been identified thus far (Pérez 2010; Pérez and Vucetich 2011). A full analysis of resemblance must await description of the remaining rodents, which include representatives of Dasyproctidae, Chinchillidae (Lagostominae), Echimyidae, Acaremyidae, and Octodontidae (Villafañe et al. 2008). No genera are shared between Quebrada Honda and Fitzcarrald (Antoine et al. 2007) nor the Girón Basin (Madden et al. 1994), at least based on the present state of knowledge.

Several early to middle Miocene faunas from northern Chile and Bolivia are close to Quebrada Honda both geographically and temporally (Fig. 1). The rodents of the late early Miocene fauna of Chucal, Chile have not yet been described, but preliminary studies indicate that at least one new species of chinchilline chinchillid accounts for the vast majority of recovered specimens (Flynn et al. 2002a; Croft et al. 2004, 2007). Other rodents include the dasyproctid *Neoreomys*, the octodontoid *Acarechimys*, and possibly another octodontoid (Croft et al. 2007). Chucal thus generally parallels Quebrada Honda in ecological diversity; most specimens pertain to medium-sized hypselodont species, and a few pertain to small and brachydont or large and very hypsodont species. *Acarechimys* is the only genus potentially shared between the two faunas. The late early to early middle Miocene fauna of Cerdas, Bolivia includes a single rodent, an indeterminate lagostomine chinchillid (Croft et al. 2009). The locality of Nazareno, Bolivia is temporally unconstrained but may be of middle Miocene age. Two rodents have been identified, *Prolagostomus* sp. and Octodontidae gen. et sp. indet. (Oiso 1991). The former is present at Quebrada Honda. The latter is larger than *Acarechimys*, based on the measurements provided, but is close in size to *Quebradahondomys*. Unfortunately, the occlusal morphology is unclear in the published photographs, and we have been unable to study the specimens firsthand.

Conclusions

The locality of Quebrada Honda has been known for more than three decades (Hoffstetter 1977). A few taxonomic studies were published not long thereafter (Frailey 1987, 1988), but it is only within the past decade or so that most specimens and species have received detailed attention in the scientific literature (e.g., Sánchez-Villagra et al. 2000; Goin et al. 2003; Croft and Anaya 2006; Forasiepi et al. 2006; Croft 2007). Rodents have been conspicuously absent from any of these treatments, though they were described early on in an unpublished dissertation thesis (Frailey 1981). Our identifications of the rodents of Quebrada Honda differ substantially from those of Frailey (1981) (Table 1). Moreover, we see no strong resemblance between the rodents of Quebrada Honda and those of the early Miocene fauna of Santa Cruz, Argentina, as advocated by Frailey (1981). Instead, we observe much greater resemblance with faunas that are closer in space (northern Chile, Bolivia) and/or time (middle Miocene, Colloncuran and Laventan SALMAs). We also find that some species are unique to Quebrada Honda. Few Tertiary intervals in South America are represented by contemporaneous faunas at low, intermediate, and high latitudes. The late middle Miocene appears to be one such interval. Further study of Quebrada Honda, La Venta, and El Petiso therefore will provide a rare opportunity to assess latitudinal provinciality within South America and to better understand the major factors that resulted in the biogeographic patterns seen in South American mammals today.

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Appendix 1

Dental measurements (in mm) for *Guiomys unica* (Caviidae) from Quebrada Honda. Abbreviations: **AP**, anteroposterior length; **LF**, local fauna; **ML**, mediolateral width; **QH**, Quebrada Honda Local Fauna; **RR**, Río Rosario Local Fauna; **TTL**, total toothrow length (only included for specimens preserving three or four cheek teeth). Measurements in parentheses are estimates.

					P4		M1		M2		M3	
Specimen	LF	Element	Side	TTL	AP	ML	AP	ML	AP	ML	AP	ML
UATF-V-000962	RR	Palate	R	–	3.3	2.8	3.3	3.3				
UATF-V-000962	QH	Palate	L	–			3.5	3.3				
UATF-V-000981	RR	Maxilla	R	–	3.1	3.0						
UATF-V-001038	QH	Palate	R	15.8	3.3	3.3	3.4	3.0	3.5	2.8	4.5	3.2
UATF-V-001038	RR	Palate	L	(16.1)	(3.2)	(2.9)	3.5	3.1	3.3	3.1	5.0	2.7
UF 236852	RR	Cranium	R	13.6	–	–	3.6	3.3	3.6	3.2	4.9	3.2
UF 236852	RR	Cranium	L	13.9	–	–	3.9	3.3	–	3.3	5.1	3.1
UF 236853	RR	Cranium	R	(16.0)	4.3	3.5	3.5	3.4	3.7	(3.0)	–	–
UF 236853	RR	Cranium	L	15.9	4.2	3.0	3.8	3.3	3.7	3.3	4.0	3.0
UF 236859	RR	Rostrum	R	–	3.1	–	3.3	3.3				
UF 236859	RR	Rostrum	L	–	3.3	2.8	3.1	3.0				
UF 236860	RR	Palate	R	(15.3)	3.5	3.1	3.1	3.5	3.4	3.3	–	(3.5)
UF 236860	RR	Palate	L	(15.5)	–	–			3.5	3.3	(4.5)	(3.6)

					p4		m1		m2		m3	
Specimen	LF	Element	Side	TTL	AP	ML	AP	ML	AP	ML	AP	ML
UATF-V-000971	RR	Dentary	R	16.1	3.1	2.4	3.5	3.2	4.3	3.2	4.9	2.9
UATF-V-000973	RR	Dentary	R	13.3	(2.0)	2.4	3.4	2.7	3.5	3.0	4.3	2.8
UATF-V-001008	RR	Dentary	R	11.6			3.0	2.8	3.4	2.8	3.9	3.0
UATF-V-001017	RR	Dentary	L	10.9	3.0	2.5	3.5	3.3	4.1	3.2		
UF 26914	QH	Dentary	L	10.1	3.0	2.2	3.4	3.0	3.7	2.8		
UF 66003	RR?	Dentary	R	12.0	3.4	2.9	4.0	3.3	4.0	3.4		
UF 236854	RR	Mandible	R	18.0	3.6	2.7	4.2	3.2	4.7	3.2	4.9	3.2
UF 236854	RR	Mandible	L	17.5	3.6	2.8	4.3	3.2	4.6	3.5	(5.0)	3.3
UF 236858	RR	Dentary	R	9.2	2.3	2.1	3.2	2.9	3.5	2.7		

Appendix 2

Dental measurements (in mm) for *Acarechimys*, sp. nov.? (Octodontoidea) from Quebrada Honda. Abbreviations: **AP**, anteroposterior length; **ETL**, estimated toothrow length (based on UATF-V-000935); **LF**, local fauna; **ML**, mediolateral width; **QH**, Quebrada Honda Local Fauna; **RR**, Río Rosario Local Fauna; **TTL**, total toothrow length. **ETL** and **TTL** are only provided for specimens preserving at least three cheek teeth.

					dp4		m1		m2		m3	
Specimen	LF	Side	TTL	ETL	AP	ML	AP	ML	AP	ML	AP	ML
UATF-V-000896	QH	L	–	–	–	–	–	–	1.8	1.8	1.5	1.6
UATF-V-000897	QH	L	–	–	1.7	1.3	–	–				
UATF-V-000934	QH	R	5.6	7.4	2.0	1.4	2.0	1.8	1.6	2.0		
UATF-V-000935	QH	R	7.1	n/a	1.9	1.4	1.7	1.6	1.8	1.8	1.6	1.6
UATF-V-000940	QH	R	–	–					1.7	1.8	1.6	1.5
UATF-V-000950	QH	L	5.2	7.2	–	1.5	1.8	1.8	1.9	2.0	1.3	1.4
UATF-V-000952	QH	R	5.5	7.7	–	–	1.8	1.8	1.9	1.9	1.5	1.4
UATF-V-000958	QH	R	–	–					1.7	2.0		
UATF-V-000960	QH	R	–	–	1.9	1.5	1.8	1.7				
UATF-V-000974	RR	L	5.5	7.7	1.9	1.5	1.9	1.7	1.7	1.7		
UATF-V-000983	RR	L	5.8	7.6	1.9	1.5	1.8	2.1	2.1	2.1		
UATF-V-001039	RR	R	6.3	8.3	2.1	1.7	2.1	2.0	1.9	2.3		
AMNH 107907 (= UF 26695)	QH	L	5.2	7.2			1.7	2.0	1.9	2.0	1.6	1.7
AMNH 107908 (= UF 26696)	QH	L	5.4	7.1	1.9	1.7	1.7	1.8	1.8	2.0		
AMNH 107909 (= UF 26697)	QH	R	6.0	7.9	2.0	1.6	1.9	1.9	2.1	2.0		
AMNH 107910 (= UF 26698 or 26699)	QH	R	5.8	7.6	1.9	1.5	1.8	1.9	2.1	2.1		
AMNH 107912 (= UF 26698 or 26699)	QH	R	–	–	1.9	1.4	1.9	1.7				

			DP4		M1		M2		M3	
Specimen	LF	Side	AP	ML	AP	ML	AP	ML	AP	ML
AMNH 107911 (= UF 26713)	QH	R					2.1	2.1	1.5	1.8

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