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Systematics and evolutionary significance of the small Abrocomidae from the early Miocene of southern South America

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ABSTRACT

Octodontoidea is the most species-rich clade among hystricomorph rodents, and has a fossil record going back to at least the late Oligocene. Affinities of fossils previous to the late Miocene differentiation of the extant families Abrocomidae, Echimyidae and Octodontidae are controversial, essentially because these fossils may share few apomorphies with modern species. In fact, pre-late Miocene representatives of Abrocomidae had not been recognised until very recently. Here we revise the early Miocene genus *Acarechimys*, originally assigned to Echimyidae, and alternatively to stem Octodontoidea or to Octodontidae. A systematic and parsimony-based phylogenetic analysis of the species traditionally included in *Acarechimys* showed that this genus is part of stem Abrocomidae. These results are primarily supported by morphology of the mandible and lower molars. *Acarechimys* is here restricted to three species, *A. minutus*, *A. pulchellus* and *Acarechimys pascuali* sp. nov., while another species, *A. constans*, is here transferred to a new abrocomid genus. The remaining species were nested within Octodontidae. According to these results, Abrocomidae might have been as diverse as its sister clade Octodontidae-Echimyidae during the late Oligocene–early Miocene. Extinction of this diversity would have resulted in marked loss of evolutionary history, with extant abrocomids being currently restricted to late-diverged euhypsodont representatives.

ARTICLE HISTORY

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Rodentia; Octodontoidea;
early Miocene; South
America; phylogeny

Introduction

Octodontoidea is the most diverse clade of hystricomorph rodents (Woods & Kilpatrick 2005). In the recent South American fauna, it includes the families Abrocomidae (chinchilla rats and arboreal chinchilla rats), Echimyidae (spiny rats, tree rats, bamboo rats, coypus) and Octodontidae (including Ctenomyiinae; degus, rock rats, viscacha rats, coruros, tuco-tucos) (Patton et al. 2015). Its fossil record is rich at least since the late Oligocene (Patterson & Wood 1982; Arnal & Vucetich 2015; Verzi et al. 2016). The phylogeny of the extant species of this strongly diversified clade is becoming increasingly better understood through molecular approaches (e.g. Honeycutt et al. 2003; Galewski et al. 2005; Parada et al. 2011; Upham & Patterson 2012, 2015; Fabre et al. 2013). In contrast, the phylogenetic position of fossils, especially of the ancient, pre-late Miocene ones is controversial (e.g. Verzi et al. 2014; Arnal & Vucetich 2015; Verzi et al. 2016). Major issues lie in recognising the relationships between these early representatives and specialised modern Abrocomidae and Octodontidae that exhibit profound morphological modifications as part of their adaptation to open environments of southern South America (Verzi et al. 2015).

The genus *Acarechimys* Patterson is one of those pre-late Miocene octodontoid lineages whose taxonomic history has been unstable. This genus includes unusually small caviomorphs,

which have been alternatively interpreted as Erethizontidae ('Cercolabidae' Ameghino 1889; Simpson 1945), Echimyidae linked to the origin of modern eumysopines (Wood 1955; Pascual 1967; Patterson & Wood 1982), stem Octodontidae (Verzi et al. 2014, 2016) or stem Octodontoidea (Arnal & Vucetich 2015). Beyond the taxonomical issue, the fact that core phylogenetic relationships of these and other early octodontoid lineages remain unsettled obscures our understanding of the evolutionary history of the group (Verzi et al. 2014). Even outside a strictly palaeobiological context, this has obvious consequences for analyses of evolutionary rates and divergence times of the extant clades (Phillips 2016).

This work presents a revision of the systematics, phylogeny and evolutionary significance of the small octodontoids assigned to *Acarechimys*; a new genus is proposed, which includes Patagonian series originally described by Ameghino and new materials recently exhumed from the Santacrucian of north-western Argentina. Although the traits analysed here are essentially those used in previous studies (Verzi et al. 2014, 2016), we revise and adjust our previous proposal of dental homologies, and continue to explore new osteological traits. In this sense, efforts to search for key phylogenetic indicators are necessary given that fossils may share few apomorphies with modern representatives of their own lineages (see Briggs & Fortey 2005).

Materials and methods

Species traditionally assigned to *Acarechimys* were included in a phylogenetic analysis together with other 17 genera representing the three families of Octodontoidea, i.e. Abrocomidae, Echimyidae and Octodontidae. Trees were rooted on the cavioid *Dasyprocta*. The matrix consisted of 25 taxa by 32 craniomandibular and dental characters (Supplementary Material 1). All characters were considered equally weighted and multistate characters were coded as non-additive. The software TNT 1.1 (Goloboff et al. 2008a, 2008b) was used to find the most parsimonious trees and evaluate the level of support for branches. The analysis was based on 1000 random stepwise-addition replicates and tree bisection reconnection (TBR) branch swapping (saving 100 trees per replicate) and an extra round of TBR on the optimal trees (Bertelli & Giannini 2005). Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (Coddington & Scharff 1994). Branch support was calculated using absolute and relative Bremer support indices (Bremer 1994). The materials analysed for each genus correspond to those listed in Verzi et al. (2016, Online Resource 2); those specimens analysed here for the first time and not mentioned in the text are listed in Supplementary Material 2.

Institutional abbreviations

IMCN, Colección Mastozoología, Instituto y Museo de la Universidad de San Juan, San Juan, Argentina; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMH, Museo Municipal de Ciencias Naturales de Monte Hermoso, Monte Hermoso, Buenos Aires, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MPM-PV, Museo Regional Provincial Padre Manuel Jesús Molina, Río Gallegos, Argentina; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; PVSJ, Colección Paleontología, Instituto y Museo de la Universidad de San Juan, San Juan, Argentina; USP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brasil.

Systematic paleontology

Order RODENTIA Bowdich 1821
Suborder HYSTRICOMORPHA Brandt 1855
Infraorder HYSTRICOGNATHI Tullberg 1899
Superfamily OCTODONTOIDEA Waterhouse 1839
Family Abrocomidae Miller and Gidley 1918

Ameghinomys gen. nov.

Figures 1, 4(A) and 6(A)

Type species. *Stichomys constans* Ameghino 1887.

Included species. Only the type species.

Distribution. *Ameghinomys* has been recorded in upper early Miocene deposits of southern and north-western Argentina.

Diagnosis. Small octodontoids, slightly larger than *Acarechimys*. Palate with palatine foramina occupying posterior portion of two deep fossae; anterior portion of palatal bridge, ascending. Lateral crest of mandible curved and strongly descending; notch for tendon of masseter medialis muscle, pars

infraorbitalis, ascending on the origin of the masseteric crest. Lower incisor subtriangular in section, with enamelled surface wider than in *Acarechimys*; markedly medial in juveniles, forming a strong inflection dorsal to alveolar sheath. Deciduous molars (DP4/Dp4) retained throughout life. Mure of M1–M2 shorter (bottom of mesoflexus narrower) than in *Caviocricetus* and *Neophanomys*. Lingual tip of protocone area (posterior outgrowth of the protocone) of M1–M2 oriented more posteriorly than in *Caviocricetus*, *Acaremys* and *Neophanomys*. Dp4 with metaconid area posteriorly extended. Metalophulid II of molars more reduced than in *Acarechimys*; interrupted, leaving a single central fossettid in the anterior lobe of Dp4; lingual tip of this lophid incorporated into the extreme of metalophulid I in m1–2. Lingual tip of metalophulid I and hypolophid of m1–m2 broadened in the adult; mesolophid absent in m1–m2, or present as an infrequent, ontogenetically early relict.

Derivation of name. Dedicated to Florentino and Carlos Ameghino for their contribution to the knowledge of South American fossil mammals.

Ameghinomys constans nov. comb.

Stichomys constans Ameghino 1887.

Acarechimys constans Patterson in Pascual 1967.

Lectotype. MLP 15-391, right mandibular fragment with Dp4–m3 and intra-alveolar incisor of a juvenile specimen with erupting m3.

Hypodigm. The holotype and MLP 15-391c (sintype of *Stichomys constans*), left mandibular fragment with Dp4–m1 and part of incisor; MLP 15-410b (sintype of *Acaremys minutus*), palatal fragment with both M1–M3; MACN A 247 (sintype of *Stichomys constans*), left mandibular fragment with m1–m2 and part of the intra-alveolar incisor; MACN A 247 (248?) (sintype of *Stichomys constans*) right mandibular fragment with Dp4–m2 and intra-alveolar incisor; MACN A 4060, left mandibular fragment with incisor and Dp4–m3; MACN A 4075, right mandibular fragment with incisor and Dp4–m1; PVSJ 1047, right mandibular fragment with m1–3 and intra-alveolar incisor; PVSJ 1083 right mandibular fragment with m1–m2 and intra-alveolar incisor

Locality and Horizon. Santa Cruz Formation, Santacrucean age (upper early Miocene), Santa Cruz province, southern Argentina; the lectotype, MLP 15-391c and MACN A 247 (both mandibles) come from the coastal cliffs of River Santa Cruz (Ameghino 1887; Fernicola et al. 2014 and literature cited therein); MACN A 4060 and MACN A 4075 come from Monte Observación. PVSJ 1047 and PVSJ 1083 come from 'Las Hornillas bearing level' of the Chinchas Formation, at Las Hornillas area, San Juan province, north-western Argentina, Santacrucean age (upper early Miocene; see López et al. 2011).

Diagnosis. As for the genus.

Remarks. Ameghino (1887) provided measurements for the lower molars and mandible; those dental measurements are in agreement with those of MLP 15-391, which is the only specimen among those originally labelled as *Stichomys constans* (as lectotype by Patterson in schedis and Pascual 1967, p. 274) with a complete molariform series. Its morphology and size are consistent with the two mandibles originally labelled as MACN A 247 and illustrated in Ameghino (1889, plate VI, figures 6 and 7–7c). We could not find the specimens MLP 15-39, MLP 15-57, MLP 15-200 and MLP

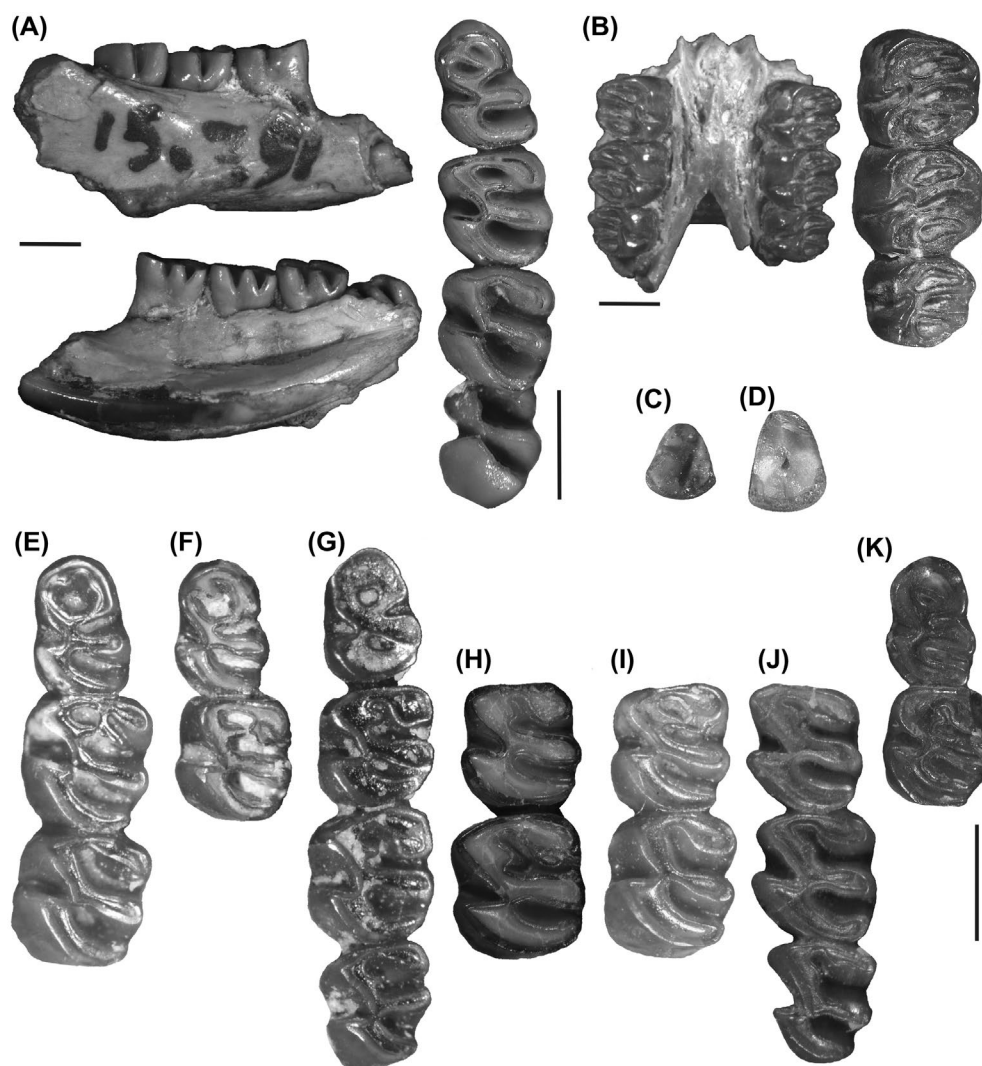


Figure 1. *Ameghinomys constans* nov. comb. (A) Lateral and medial view of right mandible and occlusal morphology of Dp4–m3 (inverted) of MLP 15-391 (lectotype); (B) ventral view of palatal fragment and occlusal morphology of left M1–M3 of MLP 15-410b; (C) cross section of right lower incisor of MLP 15-391; (D) cross section of left lower incisor of MLP 15-391c. Occlusal morphology of left molars: (E) Dp4–m2 of MACN A 247 (248?); (F) Dp4–m1 of MACN A 4075; (G) Dp4–m3 of MACN A 4060; (H), m1–m2 of PVSJ 1083; (I) m1–m2 of MACN A 247; (J) m1–m3 of PVSJ 1047 and (K) Dp4–m1 of 15-391c. Right inverted in E, F, H and J. Scale: 2 mm.

15-346. The specimens MLP 15-391a and MLP 15-391b, originally recognised as part of the *S. constans* series (Patterson in Pascual 1967), are here assigned to a new species of *Acarechimys* (see below). The palate MLP 15-410b was assigned by Ameghino (1887, 1889) to *Acaremys minutus*; however, this material is proportionally larger than the mandibles of *A. minutus*. Its size is consistent with that of *A. constans*, and its molar morphology matches that of the lower molars of the latter species by its short mure/ectolophid. Remarkably, although Ameghino (1887, 1889) does not mention cranial fragments of *S. constans*, he illustrates (Ameghino 1889; plate VI, figures 8 and 8a) a palatal fragment that is completely consistent in size, and at least partially consistent in morphology, with that of MLP 15-410b (both DP4–M2 series, instead of M1–M3, are figured). Taking into account that this type of palatal remain is infrequent among the fossils of small octodontoids of that age, this figure could represent a partially mistaken illustration of MLP 15-410b, especially considering that by that time, Ameghino no longer had access to the material (see Fernicola 2011).

The mandible PVSJ 1083 was first described by López et al. (2011) as *Octodontoidea* indet., Gen. et sp. indet. 2; PVSJ 1047

has not been previously cited. Thus, this is the first mention of *Ameghinomys constans* outside of Patagonia, and it supports the Santacrucian age proposed by López et al. (2011) for the bearing levels (Las Hornillas bearing level) of the Chinchas Formation in San Juan province, north-western Argentina.

Genus *Acarechimys* Patterson in Pascual 1967

Acaremys Ameghino 1887 (*partim*).

Stichomys Ameghino 1891 (*partim*).

Protacaremys Ameghino 1902 (*partim*).

Acarechimys Patterson in Kraglievich 1965 (*nomen nudum*).

Acarechimys Patterson in Pascual 1967.

Acarechimys Patterson in Patterson & Wood 1982.

Type species. *Acaremys minutus* Ameghino 1887.

Included species. the type species, *Acarechimys pulchellus* (Ameghino 1902), and *Acarechimys pascuali* sp. nov.

Distribution. *Acarechimys* has been recorded in early Miocene deposits of Patagonia, southern Argentina (Ameghino 1887, 1889, 1891, 1902; Kramarz 2004; Vucetich et al. 2010). A new

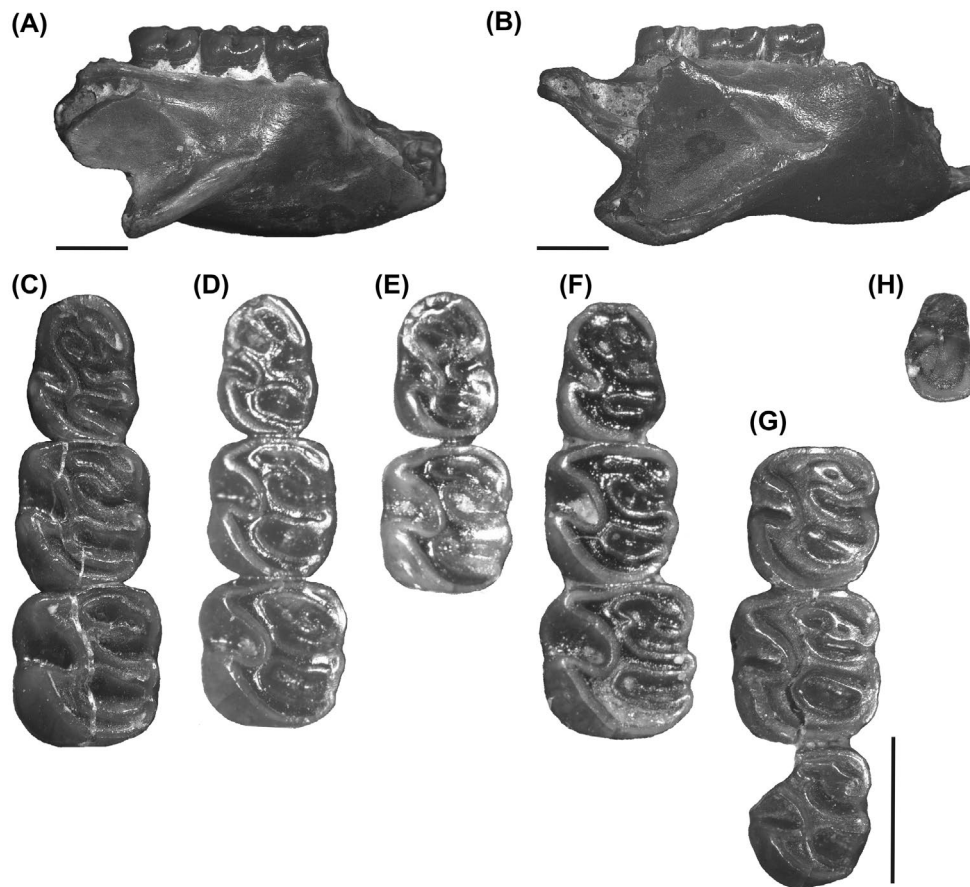


Figure 2. *Acarechimys pascuali* sp. nov. (A) right mandible of MLP 15-391a (holotype); (B) right mandible of MLP 15-391b. Occlusal morphology of left molars: (C) Dp4–m2 of MLP 15-391a (holotype); (D) Dp4–m2 of MACN A 4064; (E) Dp4–m1 of MACN A 4074; (F) Dp4–m2 of MACN A 4117; (G) m1–m3 of MLP 15-391b and (H) cross section of right lower incisor of MLP 15-391a. Right inverted in C, F and G. Scale: 2 mm.

species has been found in the early–middle Miocene of the Cura-Mallín Formation, in south-central Chile (Flynn et al. 2008).

Emended diagnosis. Small Octodontoidea, smaller than *Protacaremys* and similar to or smaller than *Ameghinomys*. Anterior margin of base of the coronoid apophysis, lateral and ventral with respect to alveolar edge of molars. Lateral crest of mandible not following the direction of the anterior margin of coronoid apophysis, more vertical than the latter. Notch for tendon of masseter medialis muscle, pars infraorbitalis, ascending on the origin of the masseteric crest. Lower incisor slender and high, suboval in cross section, with the lingual corner of the enamelled surface at right angle, and the labial one curved. DP4/Dp4 retained throughout life. Mure of M1–M2 shorter (bottom of mesoflexus narrower) than in *Caviocricetus* and *Neophanomys*. Lingual extreme of protocone area (posterior outgrowth of the protocone) of M1–M2 oriented more posteriorly than in *Caviocricetus*, *Acaremys* and *Neophanomys*. Dp4–m2 with metaconid area posteriorly extended. Dp4 with metalophulid II oriented posterolingually and mesolophid as a short spur joined to extreme of metalophulid II–extreme of metaconid area; fossettid between metalophulid II and mesolophid (in the adult) shorter than in *Protacaremys*. The m1–m2 tetra- to trilophodont; metalophulid II weaker than the remaining lophids, more reduced

in m2 than in m1; in m1, this lophid turns posterolingually. Mesolophid absent.

Remarks. The genus *Acarechimys* was first mentioned by Kraglievich (1965, p. 258, attributed to Patterson) for the species *Acaremys minutus*, but with no justification. Subsequently, it was compared and illustrated by Pascual (1967) on the basis of Patterson's unpublished notes, and later, formally erected by Patterson (in Patterson & Wood 1982, p. 529). Patterson (in Pascual 1967 and Patterson & Wood 1982) included in this genus the species *Acaremys minutus* Ameghino 1887 (established as type species in Patterson & Wood 1982), *Stichomys gracilis* Ameghino 1891 (as synonym of *A. minutus*), *Acaremys minutissimus* Ameghino 1887; *Stichomys diminutus* Ameghino 1891; *Sciamys tenuissimus* Ameghino 1894 (the last two as synonyms of *A. minutissimus*), and provisionally *Stichomys constans* Ameghino 1887. We exclude the following taxa from the genus: *Acaremys minutissimus* (including *Stichomys diminutus* and *Sciamys tenuissimus*), the syntype of *Acaremys minutus* MACN A 237 (in schedis) and related materials (as Gen. et sp. nov. in Supplementary Material 2), and MPM-PV 4193 and 4223 (as *Acarechimys minutus* in Verzi et al. 2016). The mandibular and dental morphology of these species suggest that they belong to the family Octodontidae; for the same reason, we exclude *Acarechimys leucotheae* Vucetich, Dozo, Arnal and Pérez 2015,

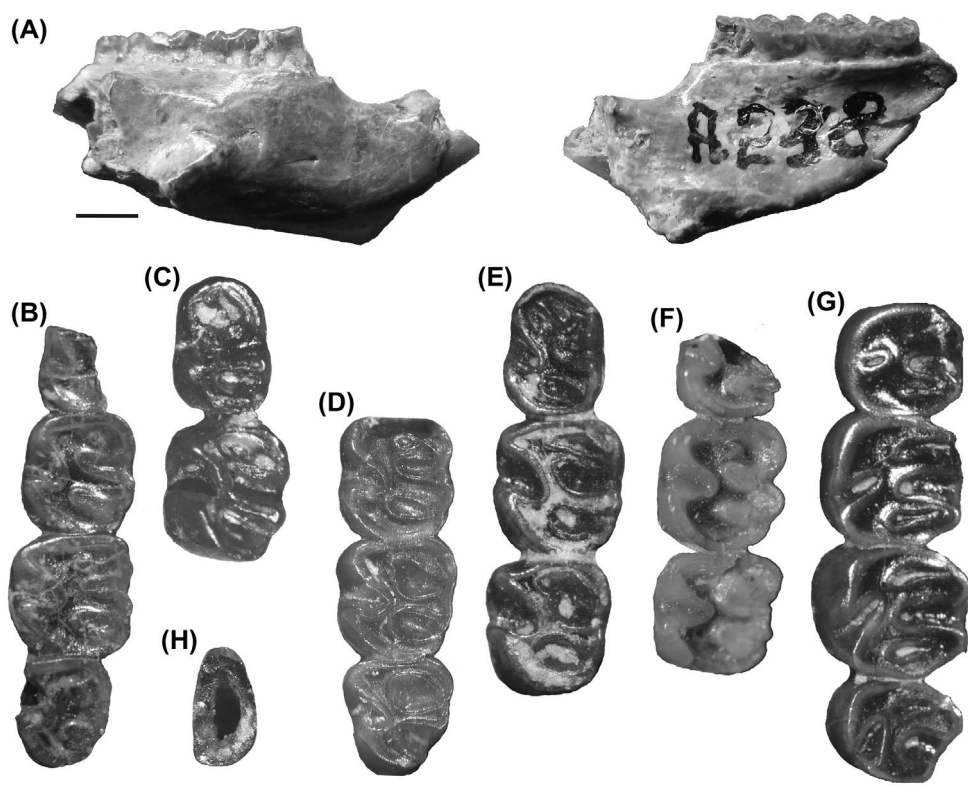


Figure 3. *Acarechimys minutus*. (A) lateral and medial view of right mandible of MACN A 238 (lectotype). Occlusal morphology of left molars: (B) Dp4–m3 of MACN A 238 (lectotype); (C) Dp4–m1 of MACN A 4058; (D) m1–m3 of MLP 15-410a; (E) Dp4–m2 of MACN A 4263 (holotype of *Stichomys gracilis*); (F) Dp4–m2 of MACN A 4065(*); (G) DP4–M3 of MACN A 4070 and (H) cross section of left lower incisor of MLP 15-410a. Right inverted in B and C. Scale: 2 mm. (*) Provisionally included.

the materials assigned to *Acarechimys* from the middle Miocene of Cañadón del Tordillo, Argentina (Vucetich et al. 1993, figure 10), La Venta, Colombia (Walton 1997, figure 24.2.C), and the specimens UATF-V-000952 and UATF-V-001039 from Quebrada Honda, Bolivia (Croft et al. 2011, figure 8b, c).

Acarechimys pascuali sp. nov.

Figures 2, 4(B) and (C), 6(D)

Stichomys constans Ameghino 1887 (*partim*).

Acarechimys constans Patterson in Pascual 1967 (*partim*).

Holotype. MLP 15-391a (sintype of *Stichomys constans*; Patterson in Pascual 1967), right mandibular fragment with Dp4–m2 and intra-alveolar portion of the incisor.

Hypodigm. The holotype and MLP 15-391b (sintype of *Stichomys constans*), right mandibular fragment with m1–m3 and intra-alveolar incisor; MACN A 4062, left mandibular fragment with Dp4–m3 and intra-alveolar incisor; MACN A 4064, left mandibular fragment with incisor and Dp4–m2; MACN A 4074, left mandibular fragment with Dp4–m1 and intra-alveolar incisor; MACN A 4117 (as *Sciamys principalis* in schedis), right mandibular fragment with incisor and Dp4–m2.

Locality and Horizon. Santa Cruz Formation, Santacrucian age (upper early Miocene), Santa Cruz province, southern Argentina. The holotype and 15-391b come from the coastal cliffs of River Santa Cruz (Ameghino 1887; Fernicola et al. 2014 and literature therein). The remaining materials come from Monte Observación.

Emended diagnosis. m2 slightly longer than m1, and nearly 10% longer than the m2 of *Acarechimys minutus*; metalopholid II of m1 more markedly turned posterolingually than in *A. minutus*.

Derivation of name. Dedicated to Rosendo Pascual, for his contribution to the consolidation of vertebrate palaeontology in Argentina.

Remarks. The holotype and specimen 15-391b are part of a sample originally labelled as *Stichomys constans*, and they were quite probably considered as part of the variation of this species by Ameghino in his original description (sintypes of *Stichomys constans*; Patterson in Pascual 1967). However, neither of the two mandibles illustrated in Ameghino (1889) belong to this sample, but rather fit the original sense of *S. constans* as interpreted here (see above). The following materials catalogued as *A. pulchellus* (in schedis) probably represent part of the variation of a *A. pascuali* lineage – MACN A 4061, right mandibular fragment with Dp4–m3 and intra-alveolar portion of incisor; MACN A 4067, left mandibular fragment with Dp4–m3 and intra-alveolar portion of incisor; and MACN A 4068, right mandibular fragment with Dp4–m2 and intra-alveolar portion of incisor. All these materials come from Monte Observación. Unlike the materials of *A. pascuali* s.s., in these specimens m1 and m2 are subequal in length. A temporal variation towards increased overall size, and size of m2 relative to m1, has been observed in the primitive *Cercomys* lineage of the late Miocene of central Argentina. The occurrence of a similar pattern within a presumably undivided

lineage formed by *A. minutus*, *A. pascuali* and intermediate morphologies, remains to be contrasted with new materials associated with more detailed stratigraphic information. In any case, these specimens were not here included as part of the variation of *A. pascuali* in the phylogenetic analyses.

***Acarechimys minutus* (Ameghino 1887)**

Figure 3

Acaremys minutus Ameghino 1887.

Stichomys gracilis Ameghino 1891.

Acarechimys minutus Patterson in Pascual 1967.

Acarechimys minutus Patterson in Patterson & Wood 1982.

Lectotype. MACN A 238, right mandibular fragment with posterior portion of Dp4, m1–m3 (m3 partially damaged) and intra-alveolar incisor.

Referred material. MLP 15-410a (sintype of *Acaremys minutus*; considered as lectotype of this species by Patterson in Pascual 1967, p. 274), left mandibular fragment with m1–m3 (the m1 damaged) and intra-alveolar incisor; MACN A 4058, right mandibular fragment with Dp4–m1; MACN A 4070, left maxillary fragment with root of zygomatic arch and DP4–M3; MACN A 4263, left mandibular fragment with Dp4–m2 and intra-alveolar incisor (holotype of *Stichomys gracilis*); MACN A 4264, left mandibular fragment with Dp4 and intra-alveolar incisor.

Locality and Horizon. Santa Cruz Formation, Santacrucian age (upper early Miocene), Santa Cruz Province, southern Argentina. The holotype and MLP 15-410a come from the coastal cliffs of River Santa Cruz (Ameghino 1887; Fernicola et al. 2014 and literature therein); MACN A 4058 comes from Monte Observación; MACN A 4070, MACN A 4263 and MACN A 4264 come from the River Shehuen (or Chaliá).

Emended diagnosis. Slightly smaller than *A. pascuali*. Lateral crest of mandible little evident; m1 and m2 subequal in length; metalophulid II of m1 only slightly turned posterolingually, more transverse than in *A. pascuali*.

Remarks. Ameghino (1887) erected the species *Acaremys minutus* on the basis of materials collected by Carlos Ameghino from the coastal cliffs of River Santa Cruz in his 1887 field work, and deposited in MLP. Later, Ameghino (1889) provided more details for this species, as he had promised in 1887; he states that the species is represented by mandibles and one fragmentary palate with both M1–M3 series. The measurements are the same that were published in 1887, although with some additional ones. The measurements of the lower molars and mandible do not coincide with those of the material labelled as *Acaremys minutus* MLP 15-410a (sintype of *Acaremys minutus*; lectotype according to Patterson in Pascual 1967); instead, they are consistent with those of MACN A 238. In addition, the mandible illustrated by Ameghino (1889, plate IV, figures 22a–c) corresponds to MACN A 238. We think that Ameghino already had this specimen at the time of the original description, and that it was only later deposited in MACN (see Fernicola 2011). MACN A 238 is similar in size and morphology to the mandible MLP 15-410a, sintype of this species, and to the holotype of *Stichomys gracilis* MACN A 4263.

In addition to MACN A 238, the specimen MACN A 237 is the other material labelled as type of *Acaremys minutus* (in schedis) or accepted as part of its hypodigm (Arnal et al. 2014, Appendix 4). However, on the basis of its mandibular and dental

morphology, MACN A 237 is an octodontid corresponding to an unpublished genus and species similar to *Acaremys minutissimus* although somewhat larger (as Gen. et sp. nov in Supplementary Material 2).

The palate MLP 15-410b is undoubtedly the one described by Ameghino (1887, 1889) as part of the *A. minutus* series. However, it is larger than the mandibles of this species, and on the basis of both its measurements and its morphology is assigned here to *Ameghinomys constans* (see above). According to this, in our view the series assigned by different authors to *Acarechimys minutus* have been a composite of materials actually belonging to this species, and also to *Ameghinomys constans* and to an undescribed Octodontidae genus (see Arnal et al. 2014, Appendix 4; Verzi et al. 2016, Online Resource 2).

MACN A 4065, a left mandibular fragment with part of the Dp4 and m1–m2 of a senile specimen could belong to *A. minutus*. The specimen MACN PV SC 2158 from the Pinturan (upper early Miocene; see Kramarz 2004), represented by an anterior fragment of a right mandible with incisor and Dp4, is morphologically close to *A. minutus*, but smaller than the latter. As Kramarz (2004), we accept it as belonging to the genus *Acarechimys* but without assigning it to any of its known species.

***Acarechimys pulchellus* (Ameghino 1902)**

Protacaremys pulchellus Ameghino 1902.

Acarechimys pulchellus Vucetich et al. 2010.

Holotype. MACN A 52-128, left mandibular fragment with Dp4–m3 and intra-alveolar incisor (Vucetich et al. 2010, figures 14.2 J, K).

Referred material. Only the holotype.

Locality and Horizon. Gran Barranca, Colhuehuapian age (early Miocene), Chubut province, southern Argentina.

Emended diagnosis. Similar in size to *A. pascuali*; m1 and m2 subequal in length, with anterior surface more convex and the metaconid area more extended posteriorly than in *A. minutus* and *A. pascuali*.

Remarks. *Protacaremys pulchellus* Ameghino (1902) was transferred to the genus *Acarechimys* by Vucetich et al. (2010, figures 14.2 J, K). This is the oldest species of the genus. Remarkably, no additional material has been found after its original description, despite constant efforts in the search of small materials in Colhuehuapian fossil beds of Gran Barranca and Gaiman, in Chubut Province (Madden et al. 2010).

Dental and mandibular morphology

Lower molars

A revision of the lower molar morphology of Octodontoidea, with a new interpretation for the homologies of crests, has recently been proposed (Verzi et al. 2016). In this proposal, it is assumed firstly that, at least in octodontoids, the recognition of homologies requires interpreting changes in the relationships between crests and cusps (or the areas presumably occupied by the latter) or even more frequently, just between crests. Secondly, that the morphology of lophate Dp4, more stable than that of m1 and m2 (the latter showing more frequent reduction and fusion of crests at both ontogenetic and evolutionary scales), may be used to understand that of permanent molars (Verzi et al. 2016).

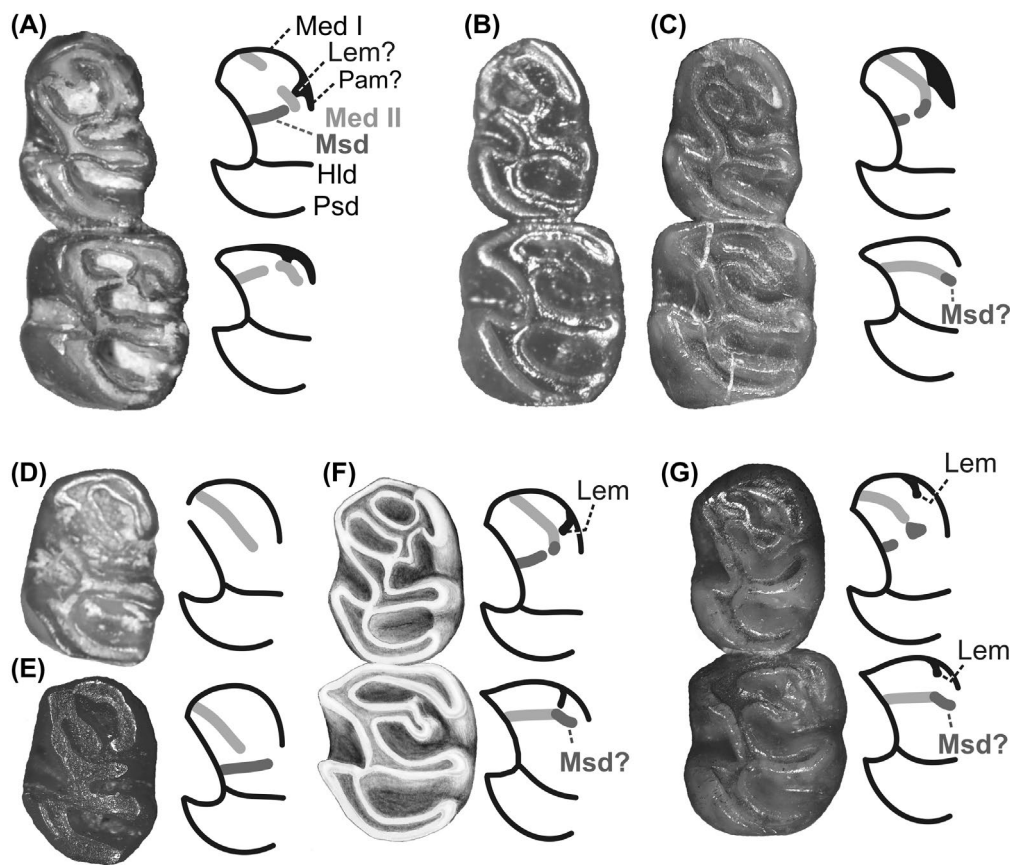


Figure 4. Occlusal morphology of left Dp4–m1 (A, B, C, F, G), and left Dp4 (D, E), with corresponding schematic illustrations of molar homologies. (A) *Ameghinomys constans* nov. comb. MACN A 4075; (B) *Acarechimys pascuali* sp. nov. MACN A 4064; (C) *Acarechimys pascuali* sp. nov. MLP 15-391a (holotype); (D) *Acarechimys* MACN PV SC 2158; (E) *Protacaremys* MPEF-PV S/N°; (F) *Protacaremys avunculus* MACN A 52–126 (holotype; based on Vucetich et al. 2010, figure 14.2G); (G) *Plesiacarechimys koenigswaldi* MLP 91-X-1-42; (right inverted in A, C, D, E, F and G). Abbreviations: Hld, hypolophid; Lem, lingual extension of the metaconid; Med I, metalophulid I; Med II, metalophulid II; Msd, mesolophid; Pam, posterior arm of the metaconid; Psd, posterolophid. Not to scale.

We analysed the morphology of the lower molars of *Acarechimys* and *Ameghinomys* following those criteria (Figure 4). In the Dp4 of *Acarechimys*, the metaconid area is extended posterolingually (posterior arm of the metaconid?), to the level at which metalophulid II meets a short mesolophid. The metalophulid II of m1 is slightly turned posterolingually; this lophid is more reduced in m2. There are no vestiges of mesolophid in the m1–m2; however, the morphology of *Protacaremys avunculus*, partly similar, suggests the possibility that a small part of the mesolophid remains fused to the extreme of metalophulid II. In addition, here we reinterpret (vs. Verzi et al. 2016) the pattern of *Plesiacarechimys koenigswaldi* as equivalent to the one described above (Figure 4(G)). A small spur originates from the metaconid area in *Plesiacarechimys*. This is also present in other octodontoids such as *Protacaremys avunculus* (Figure 4(F)), *Acaremys* (*Sciamys principalis*; Figure 5(A)), *Cercomys primitiva* (Figure 5(E)), *Sallamys* (Shockey et al. 2009) and *Llithun* (Vucetich et al. 2015b). This structure was described by Vucetich et al. (2015b) as ‘posterior extension of the metalophulid I’. Because its relationship with the metaconid area seems to be constant, we indicate it as ‘lingual extension of the metaconid’. This extension connects with the metalophulid II or a remnant of it in some deciduous and permanent molars (Figures 4(F) and 5(A)).

The pattern of *Ameghinomys* is partially different from that of *Acarechimys*; in the Dp4, metalophulid II is comparatively less developed than in *Acarechimys*, or even interrupted, while the mesolophid

is relatively more evident (Figure 4(A)). In any case, the known variation suggests that this pattern is similar to that of *Acarechimys*. In MACN A 4075, the morphology of the second crest of m1 is similar to that of the metalophulid II of Dp4. Additionally, in the unpublished specimen MACN PV SC 125 (right mandibular fragment with Dp4–m1) both Dp4 and m1 possess a vestigial mesolophid, in the same location and with a degree of development comparable to that observed in some juvenile specimens of *Caviocricetus lucasi* (Verzi et al. 2016, figure 3d–d’). On the basis of this evidence, we assume that the second crest of *Ameghinomys* corresponds to the metalophulid II as in *Acarechimys*.

The morphology of the Dp4 of *Acaremys minutissimus* and Gen. et sp. nov. (Supplementary Material 2; *Acaremys minutus* in schedis) follows the pattern shown by Octodontidae species such as *Acaremys messor*, *Sciamys principalis* and *Cercomys primitiva* (Figure 5). The mesolophid is a well developed crest that ascends anterolingually to contact the metaconid area, so that the latter does not extend posteriorly. Metalophulid II forms a posterolingually oriented spur or crest. In some individuals, such as MACN A 237 (Figure 5(F)), the mesolophid is interrupted and the resulting morphology is superficially similar to that of *Acarechimys* MACN PV SC 2158 (Figure 4(D)).

Concerning the m1–m2, the degree of crest reduction obscures the interpretation of their homologies; beyond this, according to the pattern of the Dp4, the vestiges of a second

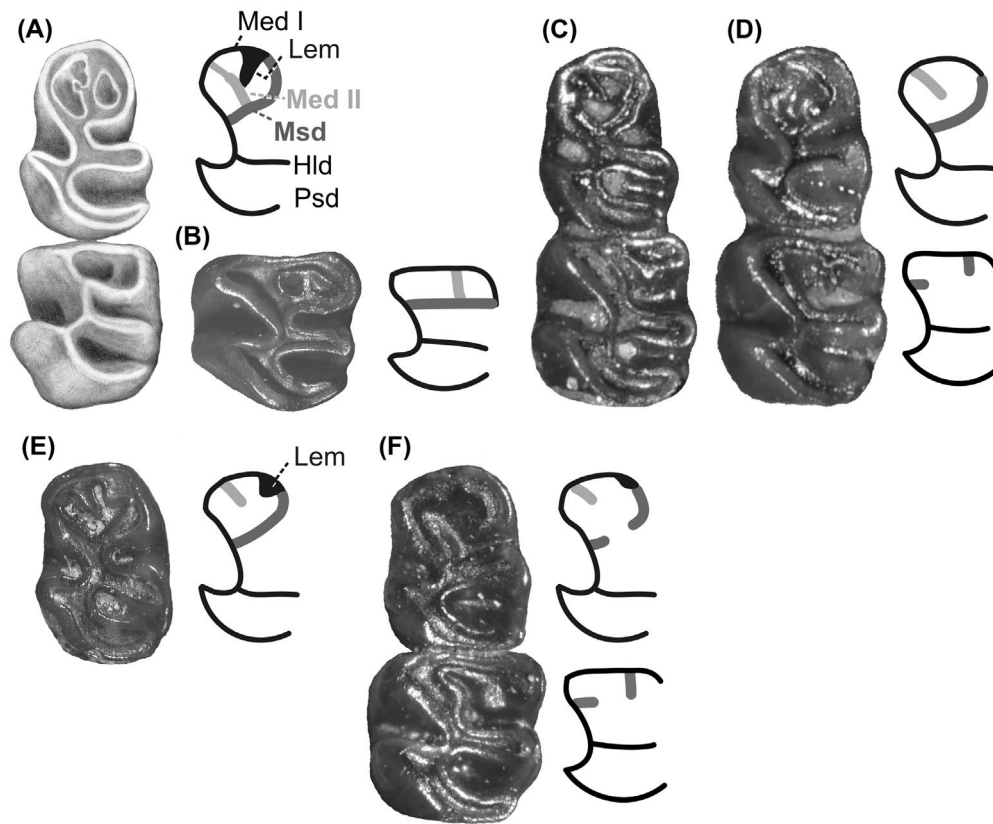


Figure 5. Occlusal morphology of left Dp4–m1 (A, C, D, F), left m1 (B) and left Dp4 (E) with corresponding schematic illustrations of molar homologies. (A) *Acaremys* (*Sciamys principalis*) MACN PV SC 2394 (based on Arnal & Pérez 2013, figure 2B); (B) *Acaremys* (*Sciamys principalis*) MLP 15-349; (C) *Acaremys minutissimus* MACN A 4076; (D) *Acaremys minutissimus* MACN A 4091; (E) *Cercomys primitiva* MMH CH 84-4-104 and (F) Gen. et sp. nov. MACN A 237 (sintype of *Acaremys minutus*). Abbreviations: Hld, hypolophid; Lem, lingual extension of the metaconid; Med I, metalophulid I; Med II, metalophulid II; Msd, mesolophid; Psd, posterolophid. Not to scale.

crest that appear variably as one or two spurs originating from the protoconid area and from metalophulid I, respectively, correspond in high probability to the mesolophid.

Masseteric morphology of the mandible

The masseteric morphology of the mandible of *Acarechimys*, *Ameghinomys* and other octodontoids shows variation regarding the lateral crest and the notch for the tendon of masseter medialis muscle, pars infraorbitalis (and associated fibres; Woods & Howland 1979), which has not been previously analysed; this morphological variation provides potentially valuable information to interpret systematic and phylogenetic affinities (Figure 6).

In *Acarechimys* and *Ameghinomys*, the position of the lateral crest on the mandibular body is markedly ventral; it descends more abruptly than the anterior margin of the coronoid apophysis, describing a curve whose trajectory is uncoupled from the direction of the above-mentioned margin (this is more clearly visible in *Acarechimys*) and whose most dorsal anterior extreme corresponds to the anterior portion of the mandibular notch. The notch for the tendon and associated fibres of the masseter medialis muscle (pars infraorbitalis) lies on the origin of the masseteric crest, so that, like the latter, it descends posteroven- trally. With some degree of variation, the same pattern is present in *Caviocricetus*, *Protacaremys*, *Prospaniomys*, *Spaniomys* and *Abrocoma* (Figure 6(A)–(F)). In *Abrocoma*, the mandibular notch is subhorizontal and independent from the masseteric crest.

In *Acaremys minutissimus*, *Acarechimys leucotheae* and Gen. et sp. nov., the lateral crest is higher on the mandibular body, and descends in a straight line towards the posterior portion of the mandibular notch, following the direction of the anterior margin of the coronoid apophysis. The mandibular notch is subhorizontal and is lodged in the mandibular body rather than on the origin of the masseteric crest. With some variations (e.g. differences in the inclination of the lateral crest related to the height of the coronoid apophysis), this pattern occurs in living and extinct echimyids and octodontoids (including ctenomyines; Figure 6(G)–(L)).

The lateral crest is the most dorsal and medial site of insertion for the fibres of the masseter medialis muscle, pars zygomatico-mandibularis anterior (Woods 1972; Woods & Howland 1979; Álvarez & Arnal 2015). In those species in which this crest is lower, a more ventral arrangement of this fibre package would be expected. Further myological analyses, building on the one made by Álvarez and Arnal (2015), remain to be performed.

Phylogenetic relationships

Our analysis resulted in three most parsimonious trees of 43 steps (CI = 0.84, RI = 0.92; Supplementary Material 1), and recovered the three major clades of Octodontoidea (Figure 7): Abrocomidae (node A), Octodontidae (node B) and Echimyidae (node C). Most recovered clades have low support but no character conflict. Abrocomidae is diagnosed by: morphology of

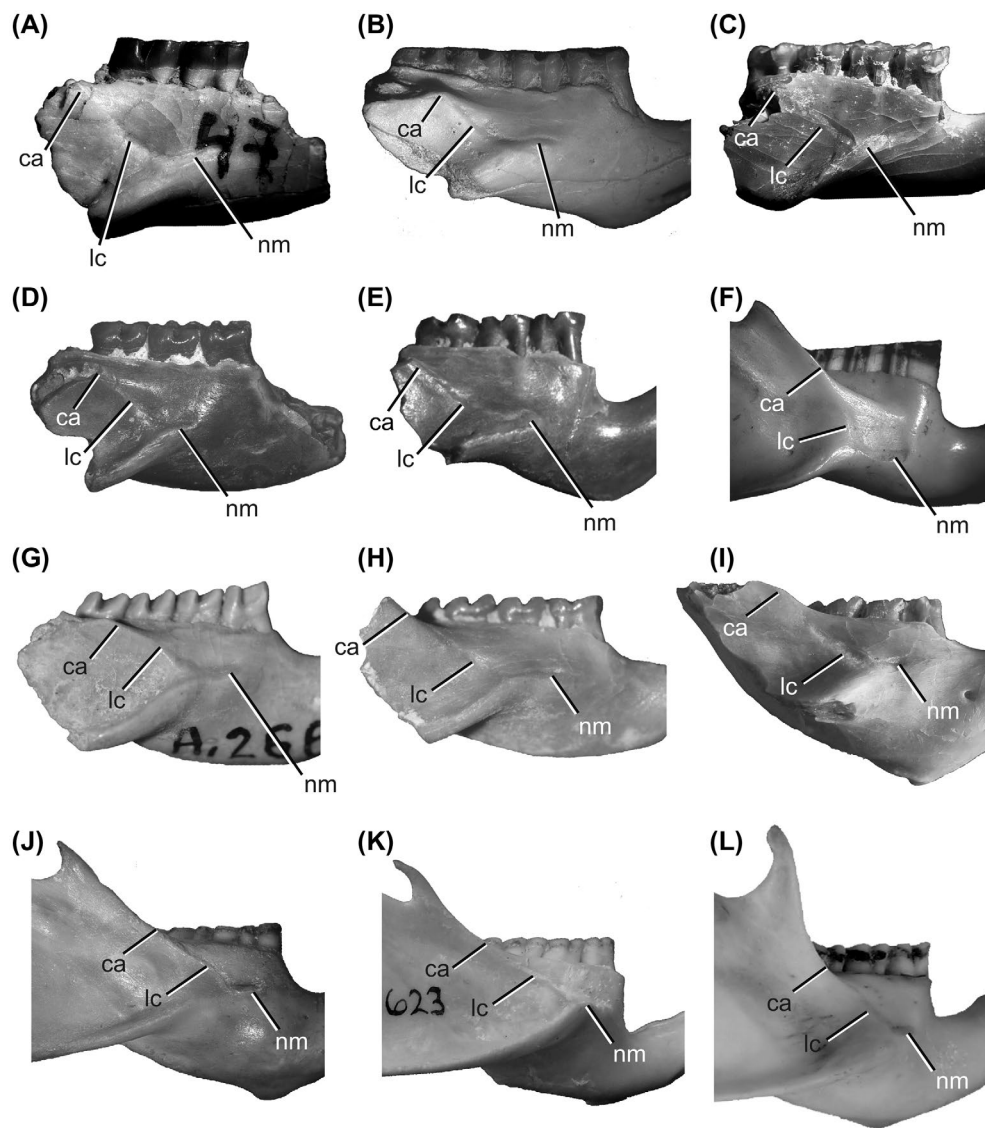


Figure 6. Masseteric morphology in right mandibles of: (A) *Ameghinomys constans* nov. comb. PVSJ 1083; (B) *Prospaniomys priscus*, MMP 945-M; (C) *Caviocricetus lucasi* MPEF PV 5073; (D) *Acarechimys pascuali* sp. nov. MLP 15-391a (holotype); (E) *Spaniomys modestus* MLP 15-37 (sintype); (F) *Abrocoma bennettii* MLP 2273; (G) *Acaremys murinus* MACN A 266 (sintype); (H) *Acaremys minutissimus* MACN A 1896; (I) *Protadelphomys latus* MPEF PV 1413; (J) *Octomys mimax* IMCN 024; (K) *Proechimys brevicauda* MVZ 153623 and (L) *Euryzygomatomys spinosus* USP 26559 (left inverted in B, C, H and I). Abbreviations: ca, anterior margin of the coronoid apophysis; lc, lateral crest; nm, notch for the tendon of m. masseter medialis, pars infraorbitalis. Not to scale.

the lateral crest of the mandible (character state 19-1), and pattern of lophids in m1-2 (character state 29-2). *Acarechimys* and *Ameghinomys* were grouped with stem Abrocomidae. *Ameghinomys* and *Plesiacaarechimys* are sister groups to the clade formed by *Acarechimys* species + *Caviocricetus* + *Prospaniomys* – *Protacaremys* – *Spaniomys* + *Abrocoma*; the latter clade (node D) is supported by the morphology of the base of the coronoid apophysis, whose anterior margin is lateral and ventral with respect to the alveolar edge of the molars (character state 20-1). *Acarechimys* species included in this clade do not form a monophyletic group.

Acaremys minutissimus, *Acarechimys leucotheae* and Gen. et sp. nov. were nested within Octodontidae (Octodontinae, node E) together with *Galileomys*, *Acaremys* (including *Sciameys*), *Neophanomys*, and the extant *Octomys* and *Octodontomys*. These taxa share the morphology of the protocone area (character state 24-1). *A. leucotheae* and *A. minutissimus* were clustered with

Neophanomys by the morphology of the DP4 with an anterior or anterolingual inflection on the anteroloph (character state 22-1), and reduced or absent mesolophule (character state 23-2; polymorphic in *A. minutissimus*).

Discussion

Patterson (in Patterson & Wood 1982) included in the genus *Acarechimys* the species *A. minutus*, *A. minutissimus* and only provisionally *A. constans*; more recently, Vucetich, Kramarz et al. (2010), Vucetich, Dozo et al. (2015b) expanded the concept of *Acarechimys* by including the species *Protacaremys pulchellus* and *Acarechimys leucotheae*, respectively. In accordance with Patterson's stance, here we transfer *Stichomys constans* Ameghino to a new genus. Within the variation of *Acarechimys*, we recognise a new species, *A. pascuali*, whose hypodigm includes materials previously assigned to *Acarechimys constans* (Pascual

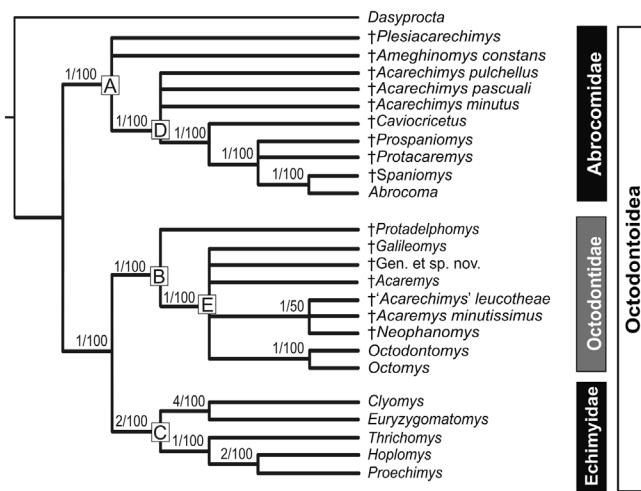


Figure 7. Strict consensus of the three most parsimonious trees resulting from the morphological phylogenetic analysis. Values of absolute/relative Bremer support are indicated above branches. A–E represent nodes mentioned in the text.

1967). Our concept of *Acarechimy minutus* might also be more restricted than previous notions, given that it excludes materials originally labelled as belonging to this species or accepted as part of its hypodigm (see above), which according to our results correspond to Octodontidae.

In the resulting phylogeny, the species assigned here to *Acarechimy* did not form a monophyletic group; nevertheless, we consider this stems from the low number of characters included in the matrix due to the fragmentary record of the genus, and that *Acarechimy* is systematically cohesive if *Acarechimy leucotheae*, *Acaremys minutissimus*, and part of the variation of *Acaremys minutus*, as well as *Ameghinomys constans*, are excluded.

Acarechimy, including *Ameghinomys*, was originally interpreted as an echimyid lineage leading to the origin of the subfamily Eumysopinae (as Heteropsomyinae in Patterson & Wood 1982; figure 6; Pascual 1967; for the systematic content of this subfamily see Patterson & Pascual 1968; Patton & Emmons 2015). Such an interpretation of affinities is not restricted to *Acarechimy*; there has been some consensus in assigning many of the early, pre-late Miocene octodontoids to Echimyidae (see Verzi et al. 2016; Appendix Table 2), partly because the living species of this family have a conservative, lophate molar morphology that is at least superficially similar to that of extinct species of octodontoids with rooted molars. More recent phylogenies have produced disparate results regarding the affinities of *Acarechimy*, alternately recovering this genus as the sister of extinct octodontoids + Dactylomyinae-Echimyinae (Carvalho & Salles 2004), sister group of Octodontidae + Echimyidae (Arnal et al. 2014), forming a polytomy with ‘Acaremyidae’ (Arnal & Vucetich 2015), or as stem Octodontidae (Verzi et al. 2014, 2016). Even beyond the fact that in the above-mentioned works *Acarechimy* is a taxon based on partial, taxonomically composite samples (see above), such inconsistencies occur repeatedly in the interpretation of the phylogenetic affinities of extinct Octodontoidea.

Certain factors appear to be the primary sources that underlie the state of flux of our understanding of the phylogeny connecting extinct and living octodontoids. The predominant use

of dental characters (frequently the best preserved traits) for phylogenetic reconstructions generates much of the controversy, often as a result of different competing primary hypotheses of loph and lophid homologies (cf. Candela & Rasia 2012; Arnal & Vucetich 2015; Verzi et al. 2016). In our view, this may generate major difficulties when interpreting species and lineages in which the molars exhibit marked occlusal simplification. Diverse octodontoid lineages seem to have acquired molars with only three main lophids by way of different transformation patterns that involve non-homologous structures (Verzi et al. 2016, figures 1–3); this appears to have been the reason for *Acarechimy* originally including species whose molar patterns are only superficially similar (see Pascual 1967). On the other hand, the specialised dental morphologies of modern, euhypsodont lineages are often difficult to compare with those of ancient fossils. Thus, the search for phylogenetically informative osteological characters is particularly relevant.

Our results show that *Acarechimy* and *Ameghinomys*, as defined here, share a molar pattern with stem abrocomids (Figure 4; Verzi et al. 2016, figure 3). Permanent molars are interpreted as lacking a mesolophid, this lophid appearing infrequently as a vestige, especially in early ontogeny; this absence of mesolophid coexists with diverse degrees of development of metalophid II, showing that in this group the pattern of lophid reduction is different from that of Octodontidae (including Ctenomyinae) and Echimyidae (Verzi et al. 2016, figures 1–3). In the latter, modifications in the anterior portion of permanent molars affect both the metalophid II and the mesolophid, in that order or nearly simultaneously. In addition, *Ameghinomys*, *Acarechimy* and other stem abrocomids exhibit a mandibular masseteric morphology that appears to be unique, and that should be studied in depth in a wider sample of octodontoids. Due to taphonomic reasons (Andrews 1990) mandibles are more frequent than maxillae in samples of fossil rodents, and therefore mandibular variation may supply valuable information to understand affinities among extinct octodontoids (Verzi 1999).

Until recently, Abrocomidae had been thought to have originated during the late Miocene (Simpson 1945; Wood 1955), based on the first appearances of species with hypsodont molars characteristic of the extant representatives during this lapse (Vucetich et al. 2015a). However, the recognition of a group in the fossil record on the basis of the most evident diagnostic characters of its living representatives should be assumed to be an operational restriction rather than the indication of an actual pattern. Fossils, and especially those preceding the stage of morphological differentiation of their respective lineages, may share few, and even slightly evident apomorphies with modern species (see Briggs & Fortey 2005); efforts to search for such frequently elusive phylogenetic indicators are indispensable to interpret the deep history of lineages. Verzi et al. (2014, 2016) recognised for the first time stem Abrocomidae among the pre-late Miocene rooted-molared octodontoids. Here, we add *Acarechimy*, *Ameghinomys* and *Plesiacarechimy* to the stem group of this family. In addition to having systematic and phylogenetic implications, this interpretation has key evolutionary significance. In fact, according to these results, abrocomids might have been as diverse as their sister clade Octodontidae-Echimyidae during the late Oligocene–early Miocene, and may even have been the most diverse of the three families (compare these results and Verzi et al. 2016; Appendix Table 2). This diversity would have included small-sized species that could

have coexisted with small octodontids during the Pinturan and Santacrucian ages (upper early Miocene; Patterson & Wood 1982; Kramarz 2004). Extinction of this diversity of stem abrocomids would have resulted in marked loss of evolutionary history (sensu Erwin 2008), with extant abrocomids being restricted to late-diverged euhypsodont representatives (Upham & Patterson 2015). An exhaustive analysis of these hypotheses in the context of a broad sample of living and extinct octodontoids is still due.

Supplementary data

Supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/08912963.2016.1168410>.

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