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A critical appraisal to *Wiedomys marplatensis*, with a note on *Cholomys pearsoni*, two enigmatic fossil cricetids (Rodentia, Sigmodontinae)

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Abstract: The generic placement and tribal affiliation of *Wiedomys marplatensis* is revised based on the study of its holotype and single known remain from San Andrés Formation (Lower Pleistocene; Buenos Aires Province, Argentina). The anatomical traits selected as indicators of belonging to *Wiedomys* are interpreted here as general similarities. *W. marplatensis* is removed from *Wiedomys* and considered it as a junior synonym of *Cholomys pearsoni*. The affiliation of the latter to Wiedomyini is discussed and the alternative hypothesis to allocate *Cholomys* in Oryzomyini is advanced. Although further research and more fossils are necessary to solve this issue, the placement of *Cholomys* as Sigmodontinae incertae sedis and the avoidance to use it as a point of calibration in molecular phylogenies are suggested.

Keywords: Argentina; Cricetidae; retromolar fossa; Wiedomyini.

Among the few extinct cricetids named from Quaternary deposits of Argentina *Wiedomys marplatensis* Quintana, 2002 is an obscure form. This taxon was based on a fragmentary lower jaw with the second and third molars in situ unhearted from the San Andrés Formation (Lower Pleistocene) exposed in southeastern Buenos Aires Province, Argentina. The original description provided by Quintana (2002) was mostly devoted to the comparison of the fossil material against an additional extinct form, *Cholomys pearsoni* Reig, 1980 previously named by Reig (1980) from Pliocene strata in the same general area. Therefore, the allocation of *marplatensis* into *Wiedomys* genus was, in fact, not justified. The latter was transitively assumed from the general similarity detected between this genus and *Cholomys*, a hypothesis early suggested which constitutes the seed of the tribe Wiedomyini (Reig 1980). Taking into account that Quintana (2002:271-272) did not provide the measurements of the holotype of *W. marplatensis*, as well as the clear statement of its type locality and also figured the material with a schematic draw (Quintana 2002:fig. 8A), our consideration of this form as obscure sigmodontine seems not be capricious.

We studied the holotype of *W. marplatensis* housed in the paleontological collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina; acronym MACN) by confronting it with other sigmodontines. We also examined the MACN 19727, a right lower jaw referred by Quintana (2002) to *C. pearsoni* that guided him in his comparisons against *W. marplatensis*. In order to obtain a true impression of *Cholomys* we assessed the holotype of *C. pearsoni*, a right lower jaw housed in the Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata "Lorenzo Scaglia" (Mar del Plata, Buenos

Aires, Argentina; acronym MMP M). All these fossils were compared with several recent sigmodontines; the Appendix 1 contains a list of those material examined. The terminology employed in this note follows Reig (1977) and the general concepts of Hershkovitz (1962).

The holotype and unique known material of *W. marplatensis* (Fig. 1) is a tiny fragment of left dentary (MACN 19697) lacking almost all parts except the m2 and m3 and the adjacent labial portion of bone; the fossil was firmly mounted in a pin probably by the collector in order to facilitate its handle. The field label, written on a small fragment of newspaper, indicates “11-1-90, Santa Isabel;” therefore the material was collected by C. Quintana in January 11, 1990, when he was in charge of the paleontological collection of the MMP. Playa Santa Isabel (ca. 38.19°S, 57.67°W) is a coastal locality placed very near Chapadmalal, General Pueyrredón county, Buenos Aires province and is here restricted as the type locality of *W. marplatensis*.

When at hand the first aspect that calls the attention from the holotype of *W. marplatensis* is its enlarged retromolar fossa (Fig. 1). Although the ascendant ramus is broken at its base, the remainder portion labially delimits a subrectangular area of bone adjacent to the posterior face of the m2 and the entire m3. The floor of this fossa is mostly flat and lacks any perforation. The second striking aspect of the *W. marplatensis* is the robust and planate conditions of its molars (Fig. 2). A more cautionary inspection of the occlusal surface indicates that the m2 has the lingual corner slightly above the remainder portion of the molar suggesting a previous bilevel condition; the m3 is totally flat (Fig. 1). Both retromolar development and molar robusticity and planate condition are partially age-dependent traits amplified in older animals. In fact, the degree of wear of the molar occlusal surfaces in *W. marplatensis* indicates that it represents a full adult individual, a hypothesis reinforced by the thickness of the enamel. The wear effects on the molar design are evident in the m3 where the enamel wall of the main cups are "fused" with cingula. This is particularly evident in the outer margin of the hypoconid and in the anteriormost point of the entoconid (Fig. 2).

The first hypothesis to be tested is if *W. marplatensis* can be allocated in *Wiedomys*, which comprises also two living species, *W. cerradensis* Gonçalves, Almeida, et Bonvicino, 2005 and *W. pyrrhorhinos* Wied-Neuwied, 1821, both distributed in arid lands of northeastern Brazil (Bonvicino 2015). Extant *Wiedomys* are very similar in molar morphology (Gonçalves et al. 2005). *W. marplatensis* shares with living *Wiedomys* the general morphology of the retromolar fossa and of the molar occlusal pattern. However, the fossil form displays several differences including (1) coronal surface mostly planate (*W. marplatensis*) versus crested (living *Wiedomys*); (2) length of m3 subequal to m2 (*W. marplatensis*) versus length of m3 shorter to m2 (living *Wiedomys*); and (3) mesolophids absent (*W. marplatensis*) versus typically present (living *Wiedomys*). Particularly striking is the general proportion of the m3 showed by *W. marplatensis* with respect to the living *Wiedomys*, mainly *W. pyrrhorhinos*. While the former has a m3 with an anteroposteriorly compressed posterior lobe, the latter is characterized by larger m3 where the mesoflexid constitute an broadened valley in order to contain a tiny mesolophid (Fig. 2; Supplemental Figure 1). These differences in proportions are also evident regarding the m2 of these taxa and also involve the orientation of the hypoflexid, more transverse in *W. marplatensis* than in living *Wiedomys*. All these contrasting features are enough to discard the allocation of *marplatensis* in *Wiedomys*.

It is clear that *W. marplatensis* represents a morphologically unusual cricetid in the context of those recorded from the Argentinean fossil record, mostly composed by hypsodont or mesodont forms (e.g., *Akodon*, †*Panchomys*, *Reithrodon*; see Pardiñas et al. 2002). However, it shares with †*C. pearsoni* this condition. *C. pearsoni* is a small fossil cricetid described on a single right lower jaw (MMP M-869; Supplemental Figure 2) recovered from the beds of the Vorohué Formation near Chapadmalal (Reig 1972, 1980). *Cholomys* was allied to *Wiedomys* to cement the concept of the tribe Wiedomyini, a clade recently enlarged with the addition of *Phaenomys* and *Wilfredomys* according to genetic and morphological evidence (Pardiñas et al. 2014, Machado et al. 2015). Quintana (2002) performed a comparison between *W. marplatensis* and *C. pearsoni*, involving, to accomplish this goal, the MACN 19727 (see above). We studied the latter and concluded that it does not belong to *C. pearsoni*. Among other trenchant differential traits, this material is characterized by a low and elongated mandible with a narrow incisor, small retromolar fossa, brachyodont simplified molars with m3 particularly shortened, and procingulum of the m1 lacking an internal ring (see Quintana 2002:fig. 8B; Supplemental Figure 3). By the contrary, *C. pearsoni*, judged from its holotype, is a small sigmodontine with a high and short mandible with an outstanding broad incisor, enlarged retromolar fossa, brachyodont molars with a large m3 and a m1 with complex procingulum. Quintana (2002:273) remarked putative differences between *W. marplatensis* and *C. pearsoni*, including the absence of ectostylid in the m3 and the small retromolar fossa of the latter. However, these traits were retrieved from a material which is, in fact, not a *Cholomys* and more probably a sigmodontine like *Calomys* or †*Chukimys*. When *W. marplatensis* and the holotype of *C. pearsoni* are compared, similarities are evident (Fig.

2). Both taxa share an enlarged retromolar fossa, brachyodont small teeth with thick enamel and lacking mesolophids, well defined posterolophids directed backwards, and penetrating hypoflexids in the m3. It is not hard to understand the occlusal morphology of the *W. marplatensis* as a more advanced stage of wear of those molars of *C. pearsoni*; the large and produced backwards posterior root of the m3 in *W. marplatensis* points in the same direction (Figure 1). The more plausible hypothesis is that *W. marplatensis* Quintana, 2002 is a junior synonym of *C. pearsoni* Reig, 1980. Accepting this proposal the biochron of †*C. pearsoni* runs between Vorohuean and Sanandresian Stages, roughly Late Pliocene-Lower Pleistocene (~ 3 to 2 MA) according to the traditional chronological charts. As a counterpart, the biochron of *Wiedomys* must be restricted to Late Pleistocene-Holocene deposits in Bahia, Brazil (Oliveira and Lessa 1999).

Concluding that *W. marplatensis* is a synonym of *C. pearsoni* resolves partially the obscure condition of this taxon; now the target is to discuss the affinities of †*C. pearsoni*. The hypothesis advanced by Reig (1980) is that this taxon constitutes an extinct Wiedomyini. Quintana (2002) tacitly supported this idea when he allied *marplatensis* to *Wiedomys*, because *Wiedomys* was the unique living Wiedomyini at the time when Reig (1980) erected the tribe. The morphological traits that we discussed in order to extirpate *marplatensis* from *Wiedomys* can be used to separate this latter genus from *Cholomys*. In fact, both taxa share general similarities such as an enlarged retromolar fossa and brachyodont simplified molars. By the contrary, differences are several including, among others, the amazing structure of the incisor of *Cholomys* and the absence of any trace of mesolophids on their molars (Figs. 2 and 3; Supplemental Figure 2).

We have now the opportunity to discuss deeply some traits mentioned several times along this contribution. The retromolar fossa is an anatomical feature basically unstudied in Sigmodontinae. To our best understanding was mostly Pacheco (2003:85-86) who made observations on this trait highlighting a deep, broad and foraminated retromolar fossa in the genera *Abrawayaomys* and *Rhagomys*. Coincidently, for the latter this condition was described and figured by Luna and Patterson (2003:fig. 8). However, an extensive survey on the morphology of this structure for sigmodontines is still missing, although Weksler (2006:115) did not detect variation in Oryzomyini and Teta (2013:37) apparently referred it as "repisa ósea por detrás del m3" when surveyed Abrotrichini. Our direct inspection of several genera and tribes suggests a moderate morphological diversity in the size, foramination, and form of the retromolar fossa. Clearly *Abrawayaomys* (cf. Pardiñas et al. 2009:fig. 6j) and *Rhagomys* exemplify the condition when the retromolar fossa is developed as a patent basin mainly caudal to the molar series. Contrastingly, in most of the other sigmodontines, the retromolar area is not expressed as a fossa, but instead as a flat or partially depressed region with or without perforations. The geometry of this area follows two main rough types, one subtriangular in outline and basically adjacent to the m3 and another condition resembling a broadened "groove" and also involving the m2. Apparently neither the size nor the development of the incisor are involved to produce these types of retromolar region. For example, the Euneomyini *Neotomys ebriosus* Thomas, 1894, a medium in size sigmodontine with a specialized and very robust incisor has a triangular and poorly developed retromolar fossa. By the contrary the Phyllotini *Calomys callidus* Thomas, 1916, a small sigmodontine with a slender incisor displays the rectangular enlarged type. As a widespread characteristic, age variation is important and older individuals have the retromolar region enlarged contrary to young animals. *Cholomys* -including the type of *W. marplatensis*- has an enlarged "groove" retromolar fossa, a condition shared with *Wiedomys* and *Wilfredomys* (both Wiedomyini) but also by many other sigmodontines such as *Calomys*, *Pseudoryzomys*, *Loxodontomys*, etc. In †*C. pearsoni* the retromolar fossa is anteriorly narrowed probably due to the subadult condition of this individual and shows two important perforations and a recessed sector caudal to the m3. It highly resembles the condition observed in several species of *Calomys*. By the contrary Wiedomyini –including also *Phaenomys*- have a more rectangular and "grooved" retromolar area.

Lower simplified molars, and particularly those simplified with respect to the upper ones, is a recurrent feature in sigmodontines. A variety of examples can be listed across different genera and tribes. A striking case is when the mesoloph is present in upper molars and their counterpart, the mesolophid, absent (or very small) in lower ones. Hershkovitz (1993) dealt with this case when he described *Microakodontomys* (an Oryzomyini); in fact he detected examples of *Oligoryzomys* lacking mesolophids (Hershkovitz 1993:fig. 3, note that in that figure the lower molar series of A and B are transposed). According to this author "the evolutionary process of molar crown simplification… commence with the lower molars, the second usually earliest" (Hershkovitz 1993:10). *Calassomys*, a Cerrado endemic phyllotine, also represents an example where lower molars are mesolophid-free but upper molars display this structure, although poorly-developed (Pardiñas et al. 2014). *Wiedomys* constitutes a well example of this condition. While the upper molars are characterized by well-developed mesolophs, the equivalent structure in the lower molars is much less expressed. However, mesolophids are not absent in *Wiedomys* as was stated by Reig (1980:266) when he constructed the diagnosis of Wiedomyini. Actually, mesolophids in *Wiedomys* are filiform crests of enamel which link the median mure to the base of the metaconid. A clear indication of their existence is, for example in the m3, the projection of the entoconid in its anterolingual corner. *Wilfredomys*, another living Wiedomyini added long after Reig's definition of the tribe, also shows very narrow mesolophids (Figures 1 and 2, Supplemental Figure 1), which are more patent in *Phaenomys* (cf. Pardiñas et al. 2014:fig. 5). Therefore, living Wiedomyini typically have mesolophids although with variable expression according to wear condition.

In this context, the absence of any trace of mesolophids in the molars of *Cholomys* could be an indication that its allocation in this tribe is inappropriate. Furthermore, the marked difference between the hypsodont condition displayed by living Wiedomyini regarding *Cholomys* add another justification to our proposal. The main cups in the former are "mounted" in a molar "shelf" forming the type tubercular hypsodonty (Hershkovitz 1962:89); this condition is patent in subadult animals (Supplemental Figure 1). By the contrary, main cups in the holotype of †*C. pearsoni* (Figures 2 and 3) follow the type described as coronal hypsodonty (Hershkovitz 1962:88). More indeed, several m1 differences unrelated *Cholomys* to living Wiedomyini (Figure 3), including (1) procingulum well-developed with anteromedian fossetid centrally located (*Cholomys*) vs. procingulum compressed with a small and lingually displaced anteromedian fossetid (living Wiedomyini); (2) anterosinusid (sensu Freudenthal et al. 1994) "single" (*Cholomys*) vs. "complex" (living Wiedomyini); (3) transverse entoconid (*Cholomys*) vs. oblique entoconid (living Wiedomyini).

The combination brachyodont simplified teeth plus enlarged retromolar fossa plus strong subrectangular incisor plus very small size, i.e., the mosaic that characterizes *Cholomys*, is unique among sigmodontines. However, this bauplan resembles to members of two living tribes, Oryzomyini and Phyllotini. Convergences between a few genera of both clades are classic issues in sigmodontine systematics. An emblematic example is *Pseudoryzomys* (see Hershkovitz 1962, Braun 1993, Voss and Myers 1991). But it is to note that the simplification in Oryzomyini is related to the development of laminarity (sensu Hershkovitz 1962) such as in *Holochilus* or *Pseudorizomys*. *Cholomys* does not exhibit such laminarity in its occlusal pattern. The hypothesis of *Cholomys* as a specialized Phyllotini or a simplified Oryzomyini is not only coherent on morphological grounds but also makes sense biogeographically. Wiedomyini are sigmodontines restricted to southeastern Brazil and northern Uruguay mostly associated to forested humid or dry environments;

Oryzomyini and Phyllotini are widespread in mesic, temperate or cold open areas (Patton et al. 2015). In addition, nothing acts as an obstacle to suppose the occurrence of a Wiedomyini in southern Buenos Aires province during Pliocene-Pleistocene. However, the evidence accumulated during more than three decades (i.e., after Reig 1980) regarding fossil cricetids in Central Argentina points to limited shifts of tribes and the correctness of current distributions as a mirror of past biogeography (Barbiere et al. 2016).

In brief, we propose here that *Wiedomys marplatensis* is a junior synonym of *Cholomys pearsoni*. We also preliminary questioned the allocation of *Cholomys* in Wiedomyini. We suggest that this issue requires further exploration and better fossils; in the meantime, we suggest to avoid the use of *Cholomys* as a calibration point for the tribe and the allocation of this genus as a Sigmodontinae incertae sedis. We are aware of growing necessity of fossils to set molecular clocks in sigmodontines. However, we think that the unsupported use of problematic or poorly-known fossils, such as *Prosigmodon* (cf. Leite et al. 2014:table S2; actually, a Neotominae) or “aff. *Abrothrix*” (cf. Parada et al. 2015:3; currently, an Akodontini), produce more noise than answers in the complex universe of sigmodontine evolution.

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Appendix 1. Specimens studied in this contribution belong to the following collections: Colección de Mamíferos del Centro Nacional Patagónico (CNP; Chubut, Argentina); Colección de Material de Egagrópilas y Afines "Elio Massoia," Centro Nacional Patagónico (CNP-E; Chubut, Argentina); Colección Nacional de Paleontología Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN; Buenos Aires, Argentina); Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata "Lorenzo Scaglia" (MMP-M; Mar del Plata, Buenos Aires, Argentina); Museu Nacional (MN; Rio de Janeiro, Brasil).

Cholomys pearsoni.- MMP M-869 (holotype), incomplete right lower jaw; Baliza San Andrés, Buenos Aires, Argentina, Vorohué Formation.

Wiedomys marplatensis.- MACN 19697 (holotype), incomplete left lower jaw; Playa Santa Isabel, Buenos Aires, Argentina, San Andrés Formation.

Wiedomys pyrrhorhinos.- CNP 3643, CNP 4728, Sítio Marimbondo, Caruaru, Pernambuco, Brasil; MN 68601, Riacho da Ressaca, Piripá, Bahia, Brasil; MN 71607, MN 71608, Parque Nacional da Chapada Diamantina, Salinas, Morro do Chapéu, Bahia, Brasil; MN 73419, Berilo, Minas Gerais, Brasil; MN 73520, Usina Hidroelétrica Irapé, Berilo, Minas Gerais, Brasil.

Wilfredomys oenax.- CNP 2378, CNP 2379, Cerro Colorado, Soriano, Uruguay.

Table 1.- Coronal measurements (in mm) of *Wiedomys marplatensis*, *Wiedomys pyrrhorhinos*, and *Cholomys pearsoni*.

	W. marplatensis MACN 19697 holotype	*W. pyrrhorhinos* (N = 5)*	*C. pearsoni* MMP M-869 Holotype**
m2, length	1.58	1.35 ± 0.18	1.47
m2, width	1.34	1.11 ± 0.05	1.20
m3, length	1.56	1.22 ± 0.13	1.49
m3, width	1.18	0.94 ± 0.09	1.12

* Including measurements from MN 73419, 71608, 73520, 71607 and 68601;

** Measurements after Reig (1980:table II).

Figure legends

Figure 1. Holotype of *Wiedomys marplatensis* (MACN 19697; incomplete left lower jaw; Playa Santa Isabel, Buenos Aires, Argentina, San Andrés Formation). A. Lingual view; B. Dorsal view; C. Caudal view. Acronyms: m2 = second molar; m3 = third molar; pr = posterior root; rf = retromolar fossa.

Figure 2. Comparison among the m2-3 in occlusal view of *Wiedomys marplatensis* (A = holotype, MACN 19697) and those of individuals of *Wiedomys pyrrhorhinos* (B = juvenile, CNP 3643; B = full adult, CNP 3718), and *Wilfredomys oenax* (D = adult, CNP 2379), two living members of the tribe Wiedomyini.

Figure 3. Comparison among the m1 in occlusal view of *Cholomys pearsoni* (A and B = holotype, MACN 19697) and those of individuals of *Wiedomys pyrrhorhinos* (B = juvenile, CNP 3643; B = full adult, CNP 3718), and *Wilfredomys oenax* (D = adult, CNP 2379), two living members of the tribe Wiedomyini. The arrows highligt the differential orientation of the entoconid between *Cholomys* and the living Wiedomyini. Acronyms: ali = anterolingual conulid; alb = anterolabial conulid; ci = cingulum; af = anteromedian flexid; as = anterosinusid; m = mesolophid.

Supplemental Figure 1. Comparison between m2-m3 of *Wiedomys marplatensis* (A; holotype MACN 19697) and those of several specimens of *Wiedomys pyrrhorhinos* (B = MN 68601, C = MN 73520, D = MN 71608, E = MN 73419, F = MN 71607) illustrating variations due to differential wear on the occlusal molar surface.

Supplemental Figure 2. Holotype of *Cholomys pearsoni* (MMP M-869, incomplete right lower jaw; Baliza San Andrés, Buenos Aires, Argentina, Vorohué Formation). A. Labial view; B. Lingual view; C. Incisor, detail; D. Retromolar fossa, detail.

Supplemental Figure 3. Anatomical details of MACN 19727 (San Andrés Formation, Buenos Aires Province), a rigth lower jaw referred by Quintana (2002) to *Cholomys pearsoni* but reasigned here to a Phyllotini genus probably *Calomys* or †*Chukimys*; A. Third lower molar in labial view; note its small size with respect to the m2. B. Retromolar fossa (rf) in dorsal view.

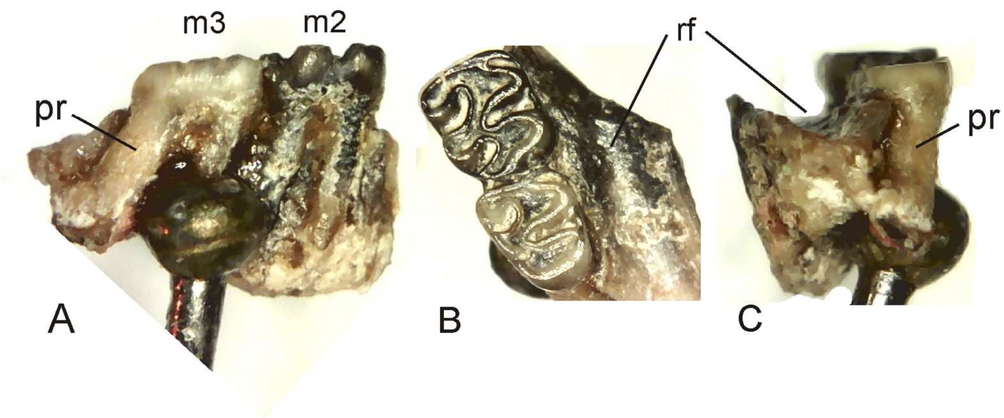

Figure 1

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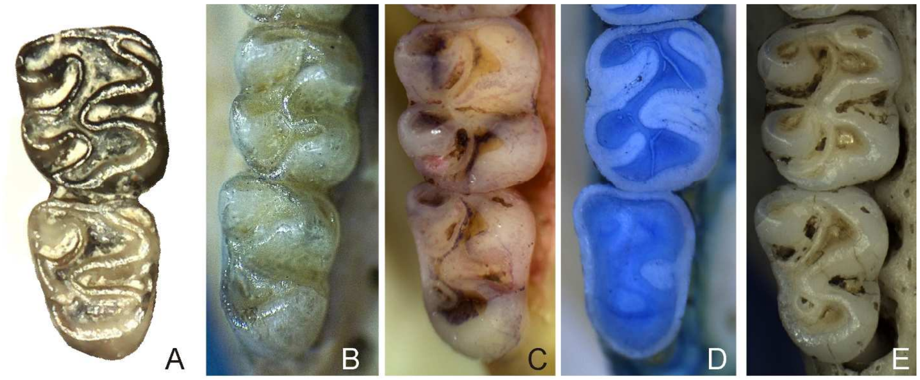

Figure 2

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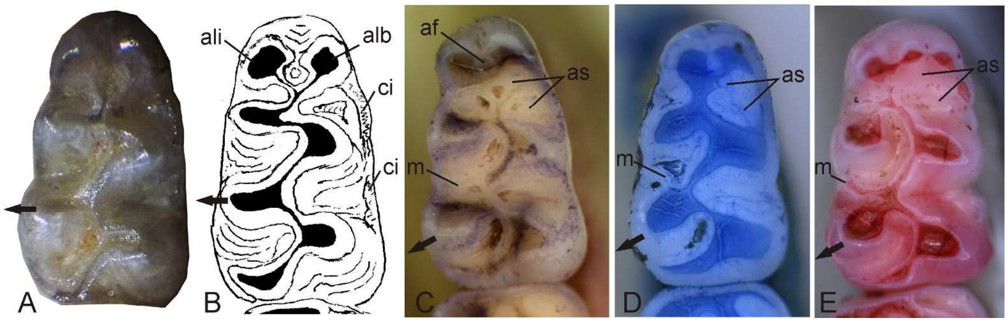

Figure 3

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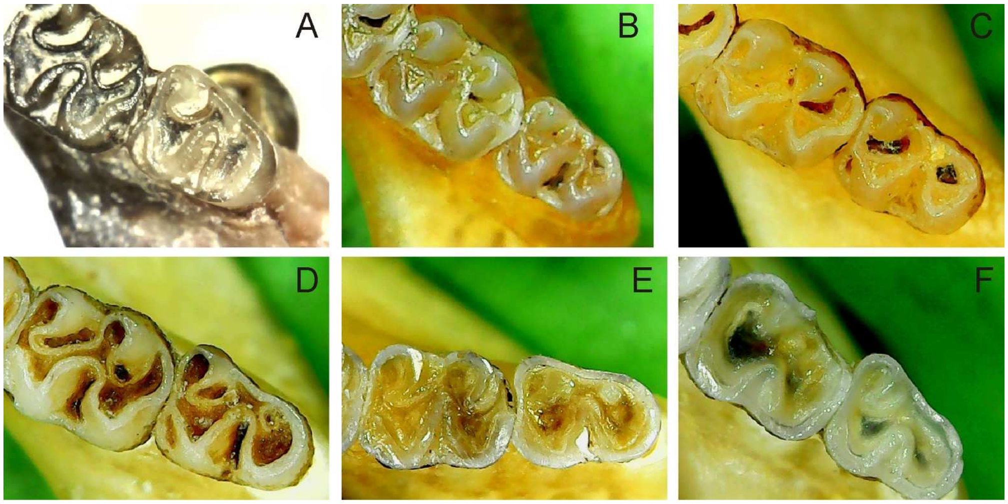

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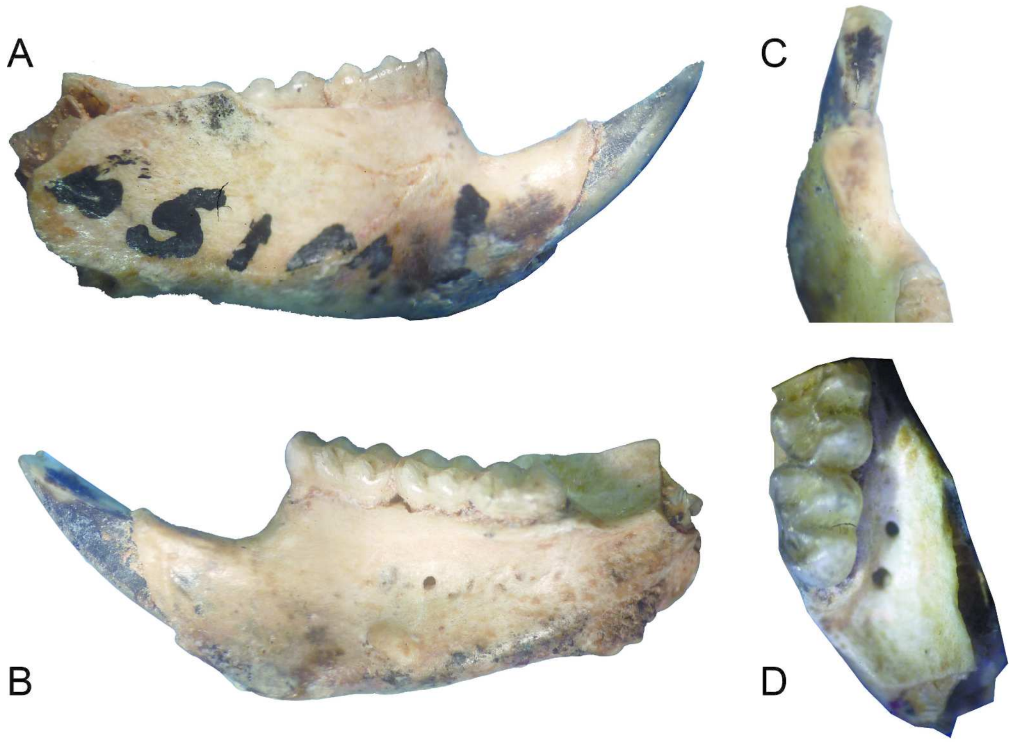

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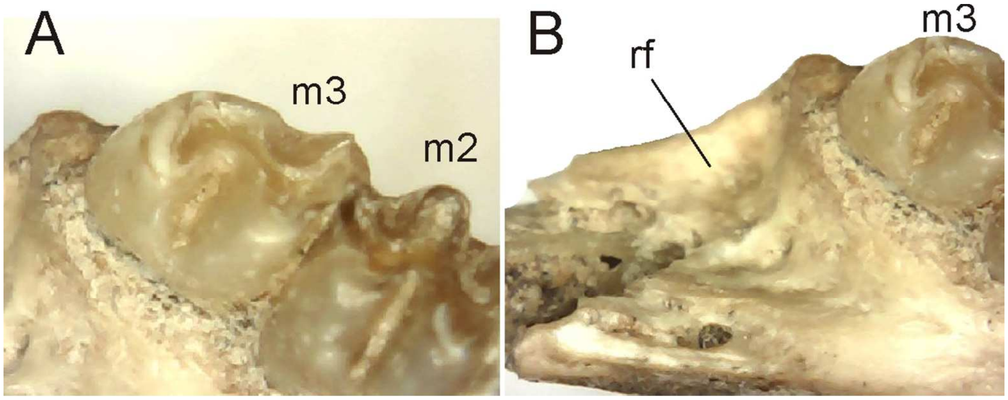

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