Sección Especial

EL ÚLTIMO NATURALISTA TIPÓLOGO:

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Artículo

A BRIEF CRITICAL REVIEW OF SIGMODONTINE RODENT ORIGINS, WITH EMPHASIS ON PALEONTOLOGICAL DATA

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ABSTRACT. Most of the contemporary debate about the origin and early diversification of sigmodontine rodents, the most diverse living subfamily of cricetids, is based on the analysis of molecular evidence. In order to promote interest and highlight the importance of fossil evidence, we conducted a critical review of the paleontological record for this group of rodents. Thus, the Mio-Pliocene genera that have been associated directly or indirectly with the origin of the Sigmodontinae are reviewed. Although *Honeymys* (Oklahoma and Nebraska, USA, Clarendonian, late Miocene) has been tentatively associated with the origin of the Sigmodontinae, the oldest reliable records for the subfamily in North America are around 5 Ma, if *Prosigmodon* is considered a sigmodontine (a hypothesis not free of controversy). For South America, poorly-known and fragmentary evidence suggests a first occurrence of sigmodontines towards the late Huayquerian (latest Miocene), although the oldest assemblage with some diversity is from the Montehermosan (early Pliocene). For both North and South America, the most relevant findings, their refined chronological locations, as well as a detail of the main taxonomic problems associated with each one, are discussed. All this information is integrated, in a final section, with that derived from molecular phylogenies. As a guide for future phylogenetic studies based on molecular evidence, several fossils are suggested for calibrations.

RESUMEN. Una breve revisión crítica del origen de los roedores sigmodontinos, con énfasis en datos paleontológicos. La mayor parte del debate contemporáneo sobre el origen y diversificación temprana de los roedores sigmodontinos, la subfamilia viviente más diversa de los cricétidos, se basa en el análisis de evidencia molecular. Con el objetivo de promover el interés y destacar la importancia de la evidencia fósil, aquí se hace un repaso crítico del registro paleontológico para este grupo de roedores. En este contexto, se pasa revista a los géneros mio-pliocenos que han sido asociados en forma directa o indirecta con el origen de los sigmodontinos. Aunque *Honeymys* (Oklahoma y Nebraska, EE. UU., Clarendoniano, Mioceno tardío) ha sido tentativamente vinculado al origen de Sigmodontinae, los registros confiables más antiguos para la subfamilia en América del Norte se ubican hacia los 5 Ma, si es que se toma como sigmodontino a *Prosigmodon* (una hipótesis no libre de controversia). Para América del Sur, evidencia fragmentaria y pobremente conocida sugiere una primera ocurrencia de sigmodontinos hacia el Huayqueriense tardío (Mioceno más tardío), aunque el más

antiguo ensamble con alguna diversidad es del Montehermosense (Plioceno temprano). Tanto para América del Norte como para América del Sur, se comentan los hallazgos más relevantes, sus ubicaciones cronológicas depuradas, y se discuten aspectos de los principales problemas taxonómicos asociados a cada registro. Toda esta información se integra, en una sección final, con aquella derivada de filogenias moleculares. Como guía para futuros estudios filogenéticos basados en evidencia molecular, se sugieren varios fósiles para efectuar calibraciones.

Palabras clave: Cricetidae, Mioceno, Neotominae, Plioceno, Sigmodontinae.

Key words: Cricetidae, Miocene, Neotominae, Pliocene, Sigmodontinae.

INTRODUCTION

Despite their enormous diversity in South America, the origin of sigmodontine rodents remains a mystery primarily because of two influences: 1) the absence of unequivocal sigmodontines from the fossil record prior to the latest Miocene or early Pliocene; and 2) the difficulty in distinguishing between the dentitions of early sigmodontines and those of other non-arvicolines cricetid subfamilies. Pardiñas et al. (2003) and Barbière et al. (2016b) reviewed hypotheses of sigmodontine origins, generating significant questions regarding previous conclusions by North American paleontologists that some North American Miocene cricetids were sigmodontines and ancestral to South American tribes. Martin et al. (2020) recently questionably allocated a Clarendonian (late Miocene) cricetid, *Honeymys mariae*, from Oklahoma and Nebraska, USA, to the Sigmodontinae, and also reviewed various hypotheses of sigmodontine origins.

In the absence of a deep historical fossil record in South America, a number of phylogenetic hypotheses of sigmodontine origins have been generated based on molecular and genetic data derived from solely modern species (e.g., Parada et al. 2013; Leite et al. 2014; Salazar-Bravo et al. 2016). In contrast to the known sigmodontine fossil record that does not predate about 5 Ma, these studies often propose earlier South American Miocene origins for extant sigmodontine tribes (e.g., Steppan & Schenk 2017; Upham et al. 2019; Gonçalves et al. 2020). In this essay, we will summarize the fossil record for Miocene and Pliocene cricetids in North America and South America and compare these results to previous scenarios of sigmodontine origins.

MATERIALS AND METHODS

Our review of sigmodontine origins is derived from our study of original material, cast, or published research. Fortunately, most recent publications on fossil and modern cricetids include high quality photographs of their dentitions, which facilitate comparison with fossil material, composed primarily of isolated molars, occasionally embedded in partial dentaries and maxillae. CTscans of some taxa later discussed have been downloaded from MorphoSource (morphosource.org). Dental terminology follows Reig's (1977) topographical system with minor additions according to more recent proposals (Barbière et al. 2016b; Martin et al. 2020; Ronez et al. 2020b; **Fig.** 1). A new measurement comparing alternation of the primary cusp pairs, paracone/protocone (pa/pr) and metacone/hypocone (me/hyp), on cricetid first upper molars (M1) was introduced by Martin et al. (2020) and protocols for measuring the angle of alternation (AA) of cusps were described in the latter publication. In general, neotomines never display opposite cusps on M1 (AAs on both M1 cusp pairs average >15°) while the vast majority of sigmodontines display opposite cusps on this tooth (average AAs on both M1 cusp pairs <15°). Upper and lower molars are abbreviated by upper and lower case letters (M, m) and are numbered consecutively. Enamel rings with hollow centers are termed "atolls," equal to the "fossettes," "islands," or "pits" of other authors. Additional descriptive terms, such as relative hypsodonty, lophodonty, simplification, etc., follow the definitions in Hershkovitz (1962), Martin & Zakrzewski (2019), Martin et al. (2020) and Ronez et al. (2020b).

There are a variety of cricetid classifications, and information on this topic is dynamic as new tribes of South American sigmodontine cricetids continue to be described based on a combination of morphological and molecular characters (e.g., Pardiñas et al. 2015, 2021; Salazar-Bravo et al. 2016). The one we currently favor is presented in Appendix 1. A classification of North American non-arvicolines cricetids is given in Appendix 2. As discussion below will affirm, the authors of this review are not in agreement on all North American cricetid taxonomic assignments.

The terms Clarendonian, Hemphillian, and Blancan are North America Land Mammal Ages (NALMAs). Chronology of these NALMAs follows Lindsay et

al. (2002), Tedford et al. (2004), Flynn et al. (2005), Lindsay (2008:fig. 27.3), and Martin et al. (2008): Clarendonian (12.6-9.0 Ma), Hemphillian (9.0-4.9 Ma), Blancan (4.9-2.0 Ma). Regarding geochronological units employed here to refer South American studies, the summary presented by Prevosti & Forasiepi (2018) was adopted. Recently obtained absolute ages for Buenos Aires province Pliocene deposits are also employed (Prevosti et al. 2021). Other abbreviations: Colección Paleontología de Vertebrados Lillo, Instituto Miguel Lillo, Tucumán, Argentina (PVL); Museo Municipal de Ciencias Naturales "Carlos Darwin" de Punta Alta, Buenos Aires, Argentina (MD-FM); Departamento Científico Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo de La Plata, La Plata, Argentina (MLP); Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Santa Rosa, Argentina (GHUNLPam); Fort Hayes Sternberg Museum of Natural History, Kansas, USA (FHSM); Instituto de Geología, Ciudad Universitaria, México (IGCU); Instituto de Geología, Universidad Autónoma de México, México (IGM); Museo de Paleontología del Centro de Geociencias, Juriquilla, México (MPGJ); Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata "Lorenzo Scaglia", Mar del Plata, Argentina (MMP); Museum of Northern Arizona, Department of Geology, Flagstaff, USA (MNA); Natural History Museum of Los Angeles County, Los Angeles, USA (LACM); Smithsonian Institution, National Museum of Natural History, Washington D. C., USA (USNM); Oklahoma Museum of Natural History, Oklahoma, USA (OMNH); University of California Museum of Paleontology, Berkeley, USA (UCMP); University of Florida, Florida State Museum of Natural History, Gainesville, USA (UF); University of Texas, Texas Memorial Museum, Austin, USA (TMM).

RESULTS AND DISCUSSION

The fossil record

In the two following sections, the ancient fossil record associated with sigmodontines and sigmodontine-like muroids is summarized, geographically arranged by continent. Emphasis was primarily given to Miocene and early Pliocene taxa. For each continent were constructed timelines of non-arvicolines cricetids from North America and South America (**Figs**. 2 and 3) as well as maps depicting the geographic locations of significant paleontological localities yielding cricetids (**Fig**. 4).

North America records

If we begin with the premise that all New World cricetids evolved from Old World immigrants, then, assuming adequate sampling, sigmodontine ancestors must be found among Neogene North American fossil taxa. Early hypotheses suggesting origin of sigmodontines by waif-dispersal from Africa to South America (Slaughter & Ubelaker 1984; Hershkovitz 1994) are currently considered highly unlikely (Baskin 1978; Pardiñas et al. 2003). None of the earliest North American cricetids, such as *Eumys*, *Geringia*, *Leidymys*, *Paciculus* and *Scottimus* (variously referred to the cricetid subfamilies Cricetodontinae or Eucricetodontinae; Lindsay 2008; for alternative taxonomical judgments see Lazzari et al. 2008, 2015; Gomes Rodriguez et al. 2010; Maridet & Ni 2013) express dental (e.g., incisor ornamentations, true murid on m1; Lindsay 2008; Wahlert 2009) or cranial (e.g., sagittal crest; Lindsay 2008; Korth 2011a) characters consistent with the origin of New World cricetids, and they will not be considered further here.

The earliest cricetid rodents in North America that could include ancestors for sigmodontines have been referred to Miocene *Copemys* and *Peromyscus* (Clark et al. 1964; Shotwell 1967), but none of those allocated to *Peromyscus* belong to that genus (Korth 2011b; Martin & Zakrzewski 2019). Most of these Miocene cricetids were recovered from western North America, with a few from farther east (e.g., Clark et al. 1964; Shotwell 1967; Wilson 1968; Lindsay 1972; Jacobs & Lindsay 1981; Lindsay & Jacobs 1985; Baskin 1986; Czaplewski 1987; Carranza-Castañeda & Walton 1992; Korth 1998; Kelly & Whistler 2014).

The genus *Copemys* Wood, 1936, is often considered basal to several cricetid radiations that lead to extant non-arvicoline American cricetid subfamilies (Baskin 1978, 1986; Jacobs & Lindsay 1984; Lindsay & Czaplewski 2011). Recent study of the type species of *Copemys*, *C. loxodon*, and additional species that had previously been allocated to the genus, demonstrates the genus is in need of review and underlines those species with strong morphological departure from *C. loxodon* (Ronez et al. 2020b). Both *Copemys mariae* (Baskin & Korth 1996) and *Copemys esmeraldensis* (Clark et al. 1964) were referred to the recently described genus *Honeymys* (Dalquest et al. 1996; Martin et al. 2020; Kelly et al. 2020). In addition, Kelly et al. (2020) demonstrated that *Copemys dentalis* likely belongs to a genus other than *Copemys*. Consequently, until a detailed examination of all *Copemys* species is completed, we view remaining *Copemys* species either as the general expression of an early Miocene radiation likely including ancestors for many extant New World cricetids, or representing brief evolutionary experiments without descendants. In addition to the taxonomic ambiguity of *Copemys* species, we cannot at this point determine when the various species dispersed from Asia. In the Old World many taxa with morphological similarity to *C. loxodon*, such as for example *Democricetodon* or *Spanocricetodon* (Falbush 1967; Theocharopoulos
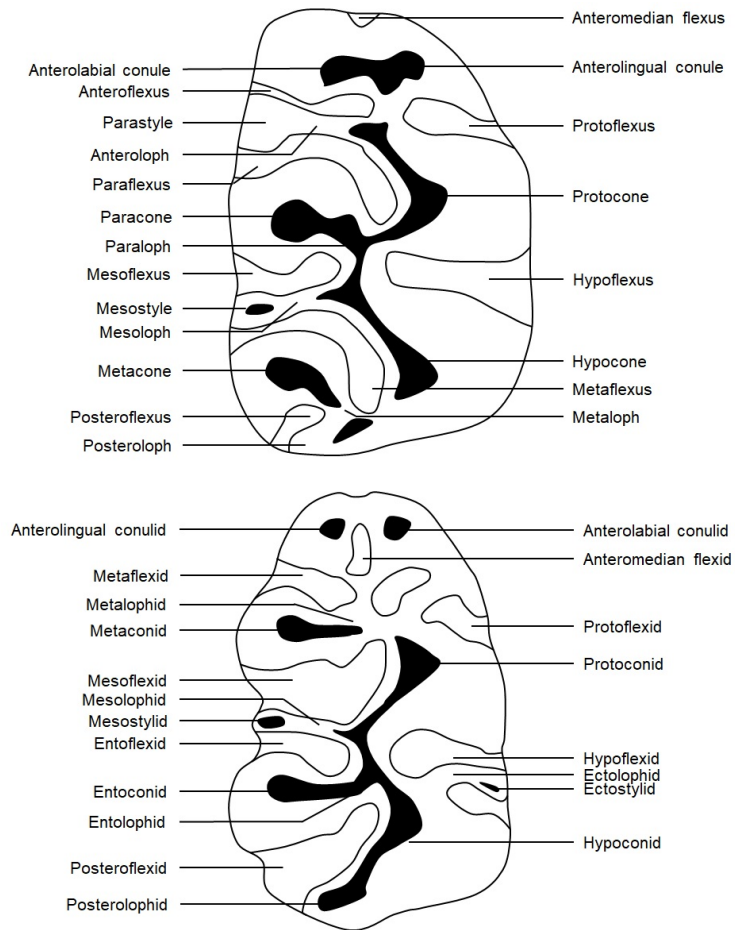
Fig. 1. Traditional dental nomenclature used in this work illustrated with the right M1 and m1 of *Honeymys mariae* (after Reig 1977, with modifications by Barbière et al. 2019b, Martin et al. 2020 and Ronez et al. 2020b).
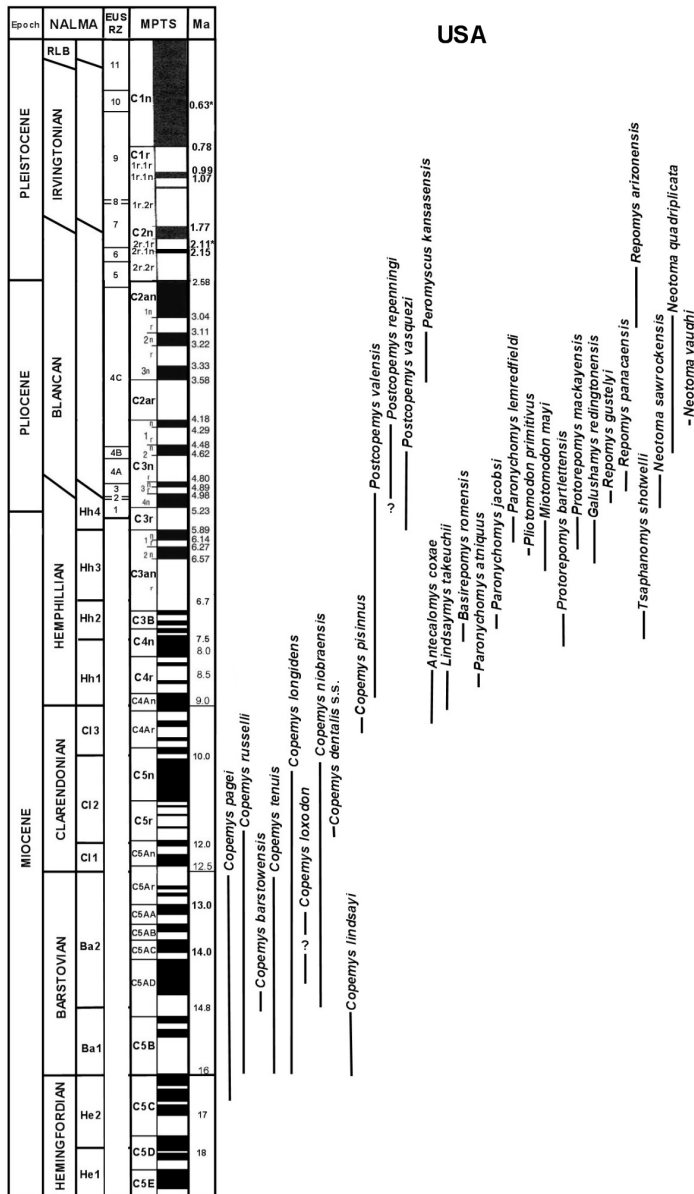
Fig. 2. (Part 1). Temporal distributions of ancient North American cricetids. Eastern United States Rodent Zones (EUS RZ) for the latest Miocene (Hh4) through the Pleistocene (RLB) after Martin & Zakrzewski (2019). Additional abbreviations are: Ma, megannum (one million years in the radioisotopic time scale); MPTS, Magnetic Polarity Time Scale; NALMA, North American Land Mammal age; RLB, Rancho la Brean NALMA.).

Fig. 2. (Part 2). Temporal distributions of ancient North American cricetids. Eastern United States Rodent Zones (EUS RZ) for the latest Miocene (Hh4) through the Pleistocene (RLB) after Martin & Zakrzewski (2019). Additional abbreviations are: Ma, megannum (one million years in the radioisotopic time scale); MPTS, Magnetic Polarity Time Scale; NALMA, North American Land Mammal age; RLB, Rancho la Brean NALMA.
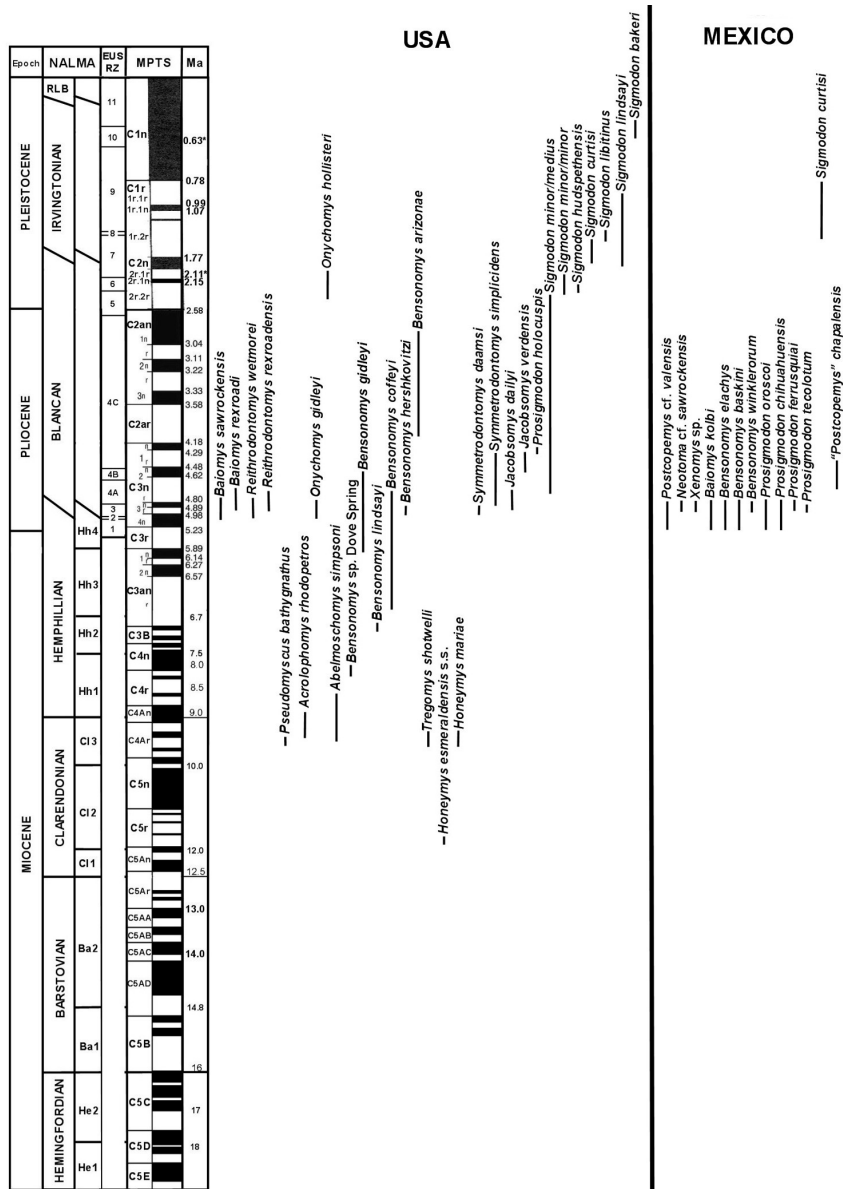
2000; Maridet et al. 2011), are extensively recorded at the same time.

In addition to *Copemys*, we encounter a serie of Miocene cricetids with simpler dentitions, such as *Acrolophomys* Kelly and Whistler, 2014, *Tregomys* Wilson, 1968, *Lindsaymys* Kelly and

Whistler, 2014, *Protorepomys* Martin and Zakrzewski, 2019, and *Tsaphanomys* Martin and Zakrzewski, 2019. Although some of these taxa have previously been regarded as sigmodontines (Lindsay 2008; Kelly & Whistler 2014), recent analyses suggest they are more likely neotomines (Martin & Zakrzewski 2019;
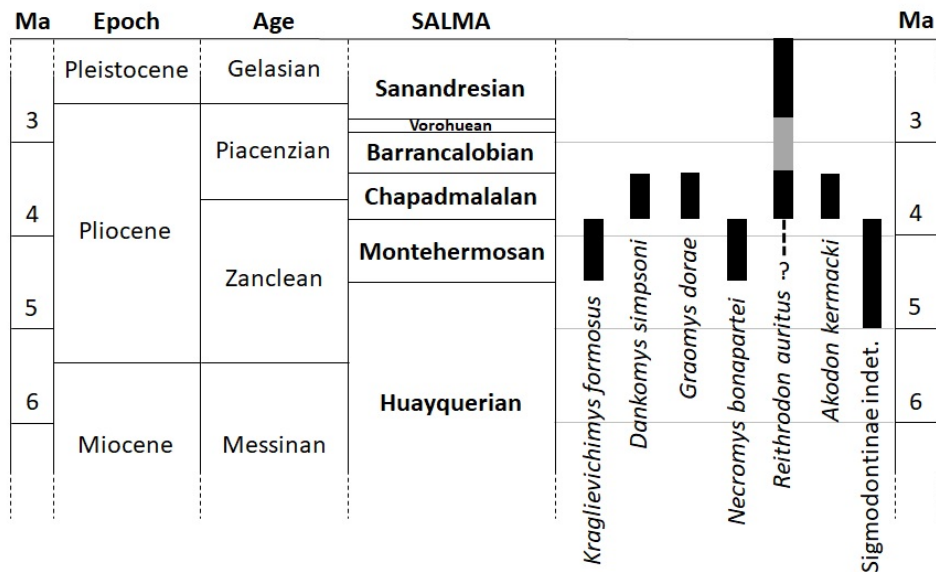
Fig. 3. Temporal distributions of ancient South American sigmodontine cricetids. Basic chronology adapted from Prevosti & Forasiepi (2018) with minor modifications.

Martin et al. 2020). Unlike *Copemys*, these taxa generally lack accessory structures such as lophules/lophulids and styles/stylids. *Acrolophomys* has been proposed as an early relative of *Onychomys* (Kelly & Whistler 2014) and *Protorepomys* and *Tsaphanomys* have been referred to the Neotomini (Martin & Zakrzewski 2019). Whether these latter taxa are descended from the Miocene *Copemys* complex or represent separate dispersals from Asia remains unknown.

In the North American Miocene and Pliocene record, species of seven genera display opposite cusps on M1 and therefore demonstrate the minimum qualification for potential relationship to the Sigmodontinae: *Honeymys* Martin et al., 2020, *Tregomys* Wilson, 1968, *Jacobsomys* Czaplewski, 1987, *Symmetrodontomys* Hibbard, 1941, *Prosigmodon* Jacobs and Lindsay, 1981, *Sigmodon* Say and Ord, 1825, and *Postcopemys chapalensis* Rincón et al., 2016 (**Figs**. 5 and 6). The North American cricetid time-line shows the earliest of these, *Honeymys esmeraldensis*, appears about 11.7 Ma (Kelly et al. 2020). Some of these forms were hypothesized as sigmodontines at the time of their descriptions (e.g., *Prosigmodon*, Jacobs & Lindsay 1981; *Jacobsomys*, Czaplewski 1987). *Honeymys* and *Jacobsomys* have the most complex dentitions (Czaplewski 1987; Martin et al. 2020), prima facie similar to those of several extant sigmodontine tribes (e.g., Oryzomyini, Thomasomyini), with an anteroloph and mesoloph on M1 and mesolophid on m1. An extension from the base of the paracone may represent a posterior paralophule (see Martin et al. 2020) in *Honeymys*, and this structure connects with the mesoloph in *Jacobsomys dailyi*, as it does for instance in oryzomyines. In *Jacobsomys verdensis* (see Czaplewski 1987) and *Symmetrodontomys simplicidens* (see Martin et al. 2002b) a posterior extension of the paracone may represent the mesoloph fused with the paracone, obscuring the posterior paralophule. This condition is commonly encountered for example in akodontines but also in several other sigmodontine tribes. The First Appearance Datum (FAD) for this sigmodontine-like occlusal morphology is about 5.0 Ma (**Fig**. 2; Lindsay 2008), at the boundary of the Hemphillian and Blancan NALMAs (between 4.7 and 4.8 Ma following Kowallis et al. 2017).

Tregomys is somewhat of an anomaly (**Fig**. 5B), perhaps proving that opposite cusps on M1 do not assure identification as a sigmodontine, in the same manner as alternate cusps are occasionally found in South American sigmodontines. The molars of *Tregomys* are diminutive and simple, lacking accessory structures. There is a single, small, centrally located conulid on m1, an underived condition for cricetids not seen in extant sigmodontines with the exception of *Rhagomys*. Nevertheless, the M1

Fig. 4. Maps showing geographic locations of significant cricetid yielding localities in North America (A) and South America (B). A: 1. Rancho El Ocote, Guanajuato, MX; 2. Yepómera, Chihuahua, MX; 3. Concha, Chihuahua, MX; 4. Redington, Arizona, US; 5. San Pedro Valley localities, Arizona, US; 6. Verde Fm, Arizona, US; 7. Anza-Borrego Desert localities, California, US; 8. Dove Spring Fm, California, US; 9. Bartlett Mountain localities, Oregon, US; 10. McKay Reservoir, Oregon, US; 11. Jacona, New Mexico, US; 12. Sand Raw, Nebraska, US; 13. Norden Bridge, Nebraska, US; 14. Wakeeney, Kansas, US; 15. Meade Basin localities, Kansas, US; 16. Whisenhunt, Oklahoma, US; 17. Coffee Ranch, Texas, US; 18. Blanco, Texas, US; 19. Pipe Creek Sinkhole, Indiana, US; 20. Haile localities, Florida, US; 21. Inglis localities, Florida, US; 22. Coleman 2A, Florida, US; 23. Leisey Shell Pit, Florida, US; 24. Gray Fossil Site, Tennessee, US; 25. Coal Valley Fm, Nevada, US; 26. Barstow Fm, California, US; 27. Fish Lake Valley, Nevada, US. 28, Torreja Fm, Florida, US; 29, El Golfo, Sonora, MX;30, Maxum, California, US;31, Horn Toad Hills, California, US; 32, Tecolotlán, San José Fm, Jalisco, MX ; 33, Chapala Fm, Jalisco, MX; 34. Love Bone Bed, Florida, US. B: 1. Entre Ríos, Catamarca, AR; 2. La Calera, Córdoba, AR; 3. Caleufú, La Pampa, AR; 4. El Guanaco, La Pampa, AR; 5. Cascada Grande and Cascada de la Ruta, Quequén Salado river, Buenos Aires, AR; 6. Farola de Monte Hermoso, Buenos Aires, AR; 7. Mar del Plata-Miramar, Buenos Aires, AR; 8. Norte Casa Chiguaje, Falcón, VE.
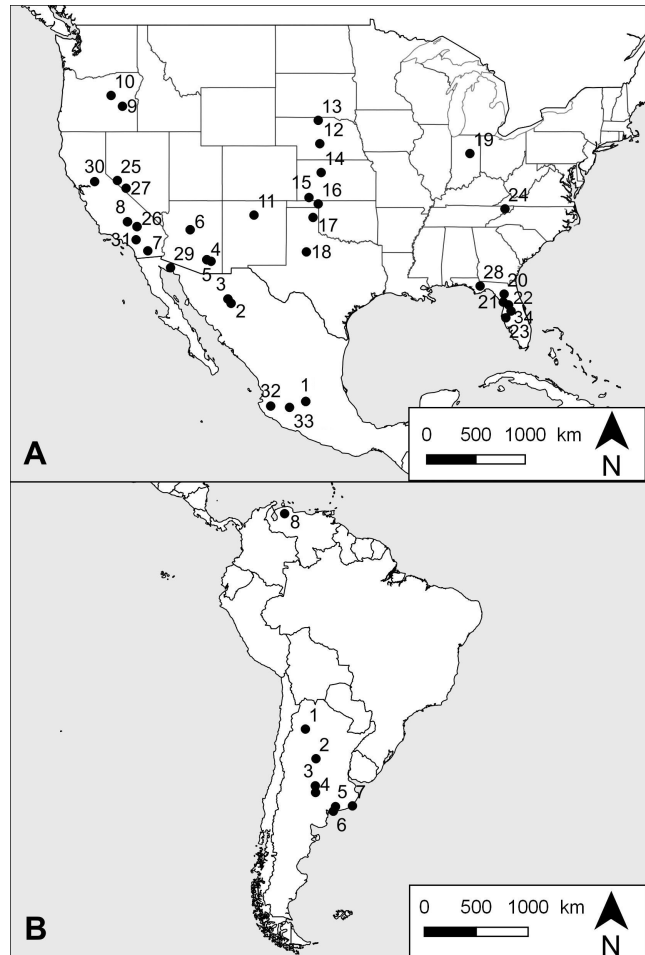
expresses opposite cusps. Unless *Tregomys* is an early branch of the sigmodontines, the opposite M1 cusp morphology may represent an example of convergence. An additional character seen in *Tregomys* is the opposition of the m1 protoconid and metaconid cusps (Wilson 1968; Kelly et al. 2020). No extant sigmodontines display the *Tregomys* suite of characters. The dental anatomy of *Jacobsomys*, *Symmetrodontomys* and *Tregomys* shows that dental features we normally associate with sigmodontines appeared in these North America taxa.

A number of extinct late Pliocene through middle Pleistocene cricetid species have been named and allocated to the Sigmodontini. In chronological order (**Figs**. 4 and 6), these can be identified as 1) a group of small-sized Hemphillian (latest Miocene) species from Mexico referred to the genus *Prosigmodon* (*P. oroscoi* Jacobs and Lindsay, 1981; *P. chihuahuensis* Lindsay and Jacobs, 1985 - both species also being present in early Blancan deposits; *P. ferrusquiai* Carranza-Castañeda and Walton, 1992); 2) the diminutive Hemphillian through late Blancan *Sigmodon minor* Gidley, 1922; 3) a couple of large early Blancan *Prosigmodon* from the Verde Fm. of Arizona and Meade Basin of Kansas (*Prosigmodon holocuspis* Czaplewski, 1987) and from the latest Hemphillian of Jalisco, Mexico (*Prosigmodon tecolotum* Pacheco-Castro et al., 2019); 4) a set of late Blancan through Irvingtonian large cricetids with dentition similar to those of extant cotton rats (*Sigmodon hudspethensis* Strain, 1966, *Sigmodon lindsayi* Martin and Prince, 1989, *Sigmodon curtisi* Gidley, 1922); and 5) Pleistocene extinct and modern cotton rats (e.g., *Sigmodon bakeri* Martin, 1974, *Sigmodon libitinus* Martin, 1979, *Sigmodon hispidus* Say and Ord, 1825). Barbière et al. (2016b) questioned both the assignment of *P. holocuspis* to *Sigmodon* and the allocation of *Prosigmodon* to the Sigmodontini. However, all of the mentioned species were tentatively included in the Sigmodontinae by Martin et al. (2020), although without an explicit support. These divergent opinions reflect different interpretations of dental features, which cannot be considered further here. We understand that fossil records are important in order to calibrate molecular phylogenies, but identifying the exact origin of a particular taxon is a difficult endeavor, and often more fuzzy than clear. Until phylogenetic analyses are completed, we cannot even securely allocate all the above taxa to the Sigmodontini, let alone decide which is the earliest *Sigmodon*. The authors of this study differ in their opinions, with two of us (RAM, TSK) currently convinced that *Prosigmodon*

species are Sigmodontini and ancestral to *Sigmodon* (Appendix 2), and the remaining authors arguing that *P. oroscoi*, type species of *Prosigmodon*, represents a Neotominae. But the problem goes even further, because conclusions can be determined by how one evaluates evolutionary change in the fossil record. For example, Martin (1996) synonymized six species and two genera of North American muskrats into a single species lineage, *Ondatra zibethicus*, composed of a series of temporal populations termed lineage segments or chronomorphs, spanning almost 4 Ma. Phyletic speciation was explicitly rejected. So, following this logic, it is conceivable, but not demonstrated, that the recognized extinct species of *Prosigmodon* and *Sigmodon* represent only a few lineages within which considerable dental change occurred, including size as well as shape. In this scenario, where does one draw the line between *Prosigmodon* and *Sigmodon*? All we can say now is that the earliest *Prosigmodon* (*P. oroscoi*, *P. chihuahuensis*) were recovered from sediments deposited about 5.0 Ma in Hemphillian-Early Blancan deposits around Yepómera (Chihuahua, Mexico), and the earliest species originally named as *Sigmodon* (*S. hudspethensis*) from outcrops in western Texas tentatively dated to about 2.3 Ma. Both ages estimates were derived from biostratigraphic data. Two mentions of *Prosigmodon* sp. in Early Hemphillian deposits have been proposed by Repenning & May (1986) and Whistler et al. (2009). The latter occurrence has been reevaluated by Kelly & Whistler (2014:43) who stated that this material had to be referred to other taxa. The record of Repenning & May (1986) has been discussed in Lindsay (2008:472) who concluded that "the illustration of cf. *Oryzomys* does not distinguish it from *Prosigmodon*, nor does the brief description." Nevertheless, the "cf. *Oryzomys*" of Repenning & May (1986:fig. 1) is not similar to any other known *Prosigmodon* species.

Rincón et al. (2016) allocated a small sample of molars from the late Pliocene Chapala Fm. of Mexico to the new species *Postcopemys chapalensis*. *Postcopemys* Lindsay and Czaplewski, 2011, was erected to include cricetid species advanced from *Copemys*, predominantly based on the alignment of certain ridges on the upper and lower molars (Lindsay & Czaplewski 2011). However, it is clear from a comparison of specimens allocated to *P. chapalensis* that this species is not closely related to other *Postcopemys*. A review of the genus is beyond the scope of this treatment, but a brief comparison of *P. chapalensis* with the type species of *Postcopemys*, *Postcopemys repenningi* Lindsay and Czaplewski,
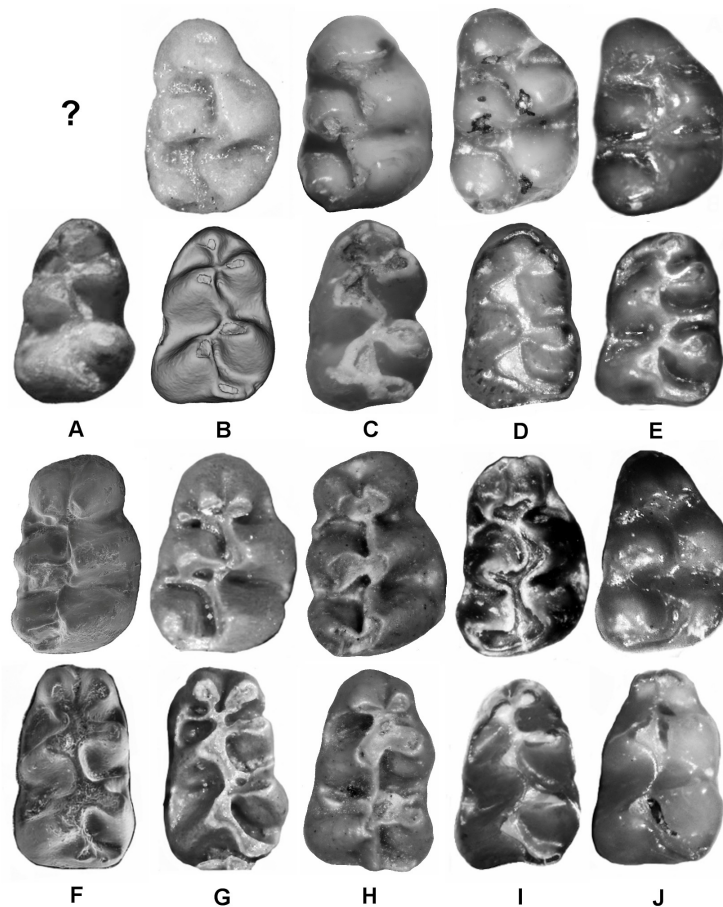
Fig. 5. M1 (above) and m1 (below) of selected North American cricetid taxa. Not to scale, all specimens adjusted to equal size. All occlusal views with anterior up and lingual right. A, *Acrolophomys rhodopetros*: m1, LACM 156372 (holotype, reversed), Dove Spring Fm., from Kelly & Whistler (2014). B, *Tregomys* sp.: M1, cast of OMNH 75054; m1, scan of OMNH 75140, Whisenhunt. C, *Lindsaymys takeuchii*: M1, LACM 126050 (holotype, reversed); m1, LACM 150735 (reversed), Dove Spring Fm., from Kelly & Whistler (2014). D, *Copemys dentalis*: M1, UCMP 310098 (reversed); m1, UCMP 29635 (holotype, reversed), Fish Lake Valley, from Kelly et al. (2020). E, *Copemys loxodon*: M1, UCMP 317469 (reversed); m1, UCMP 317625, Jacona, from Ronez et al. (2020b). F, *Symmetrodontomys simplicidens*: (Meade Basin uncatalogued lab numbers provided) M1, Wiens C-1 (reversed); m1, Wiens C-4 (reversed). G, *Jacobsomys dailyi*: M1, cast of UCMP 320583, Horn Toad Hills; m1, cast of UCMP 387567, Maxum. H, *Jacobsomys verdensis*: M1, cast of MNA V4849 (holotype, reversed); m1, cast of MNA V4849 (holotype), Verde Fm. I, *Bensonomys lindsayi*: (uncatalogued LACM field numbers provided) M1, CVF 14182; m1, CVF 13764 (reversed), Coal Valley Fm. J, *Abelmoschomys simpsoni*: M1, UF 61327; m1, UF 61335 (reversed), Love Bone Bed.

2011 (**Fig**. 6), will suffice to demonstrate a few critical differences, as follows: 1) major cusp pairs on M1 of *P. chapalensis* are opposite rather than alternate, both AAs (angles of alternation) averaging less than 16°, whereas AAs in *P. repenningi* are considerably greater (**Fig**. 6); 2) large, wide, bilobed anteroconid on m1 in *P. chapalensis*, small and single anteroconid in *P. repenningi*; 3) dentine of metaconid and protoconid, entoconid and hypoconid pairs highly confluent after light wear in *P. chapalensis*; these cusp pairs would remain isolated until late wear in *P. repenningi*; 4) isolated posterior enamel atoll on m1 in *P. chapalensis*, likely representing a fused mesolophid and anterolingual entolophulid, absent in *P. repenningi*. As Martin et al. (2020) showed, angles of alternation on both pa/pr and me/hyp M1 pairs, averaging <15° are characteristic of sigmodontines, whereas both pairs in excess of 15°, especially >20-30°, are predominantly found in extant neotomines. Because of some damage to the occlusal surface of the single M1 of *P. chapalensis* we took four AA measurements on each cusp pair. The pa/pr pair ranged from 10.2-22.1, with a mean of 15.6. The me/hyp pair ranged from 0-10.2, with a mean of 6.03. This low combination range is commonly found in extant sigmodontines but never in extant neotomines (Martin et al. 2020: table 1). The above character suite is encountered today almost exclusively in extant oryzomyalian sigmodontines, not in previously named species of *Postcopemys* or extant neotomines. It is too early to be certain of the subfamilial affinity of *P. chapalensis*, but it is certainly not related to *Postcopemys*.

Bensonomys Gazin, 1942 and *Abelmoschomys* Baskin, 1986 have been proposed as early North American sigmodontines, and as Kelly (2007) noted in his review, *Bensonomys* was at times referred to the South American *Eligmodontia* (see Gidley 1922) and *Calomys* (see Baskin 1978). Kelly (2007) also provided a replacement chronology for *Bensonomys* species, spanning the Hemphillian through Blancan NALMAs. Reig (1980) questioned the allocation of *Bensonomys* to *Calomys*, suggesting similarities were due to convergence (see also Pardiñas et al. 2014), and Martin et al. (2002a,b) later removed *Bensonomys* from *Calomys*. A major difference between *Abelmoschomys, Bensonomys* and *Calomys* is that *Bensonomys* and *Abelmoschomys* display M1 cusp alternation more typical of neotomines (Martin et al. 2020).

South America records

Mio-Pliocene cricetids (Sigmodontinae) are restricted to a few Argentinean localities, most of them concentrated in Buenos Aires Province (Pardiñas 1999a; **Fig**. 4B). Outside Argentina, isolated molars of fossil cricetids have been discovered recently in Pliocene sediments (Vergel Member of the San Gregorio Formation) in northwestern Venezuela (Carrillo Briceño et al. 2021).

The oldest published fossil attributed to a cricetid rodent in South America is a fragment of molar extracted from a fossil owl pellet recovered in the Andalhuala Fm. (late Miocene; ca. 7.14 Ma), in deposits exposed near Entre Ríos (Catamarca Province, Argentina; Nasif et al. 2009). The material, unnumbered and without measurements, was briefly described as "… un fragmento de un segundo molar superior diminuto, atribuido a un roedor sigmodontino… La morfología de las dos cúspides y el único flexo preservados señala una superficie oclusal simplificada y relativamente plana que se asemeja a los rasgos observados en el género viviente *Calomys*, por lo que este fragmentario material podría corresponder a un miembro de la Tribu Phyllotini" (Nasif et al. 2009:108). Our interpretation, based on the two published figures (Nasif et al. 2009:fig. 3) and a direct inspection of the specimen is inconclusive. We cannot determine if it represents a molar or a premolar, because it is also difficult to separate the "8-shaped" occlusal pattern from a similar pattern observed in several groups of caviomorph rodents. The crown portion shows an intriguing planed occlusal surface, more in accordance with this condition in caviomorphs than with the usual crested crowns of small sigmodontines. The diminutive size of the molar, ca. 1 mm in length according to the graphic scale provided, suggests a connection with cricetids; although not impossible, a caviomorph below 30 grams of body mass is unlikely. If the material really represents a M2 (**Fig**. 7A), it shows a deep and anteriorly directed hypoflexus, a morphology hard to accommodate with that observed in phyllotines. Our current evaluation of the Andalhuala material is that it is unlikely to represent a sigmodontine.

Published as the oldest South American cricetids (Verzi & Montalvo 2008), two fragmentary jaws have been assigned to the Sigmodontinae from deposits interpreted as the Cerro Azul Fm. near Caleufú (La Pampa Province, Argentina; **Fig**. 7B). Contrary to the material from Andalhuala Fm., that of La Pampa can be allocated to the Sigmodontinae without hesitation. According to Barbière (2019), who provided the first detailed taxonomic evaluation of the Caleufú specimens, they belong to *Necromys bonapartei* (Reig, 1978), a species originally described from the Monte Hermoso Fm. in southwestern Buenos Aires
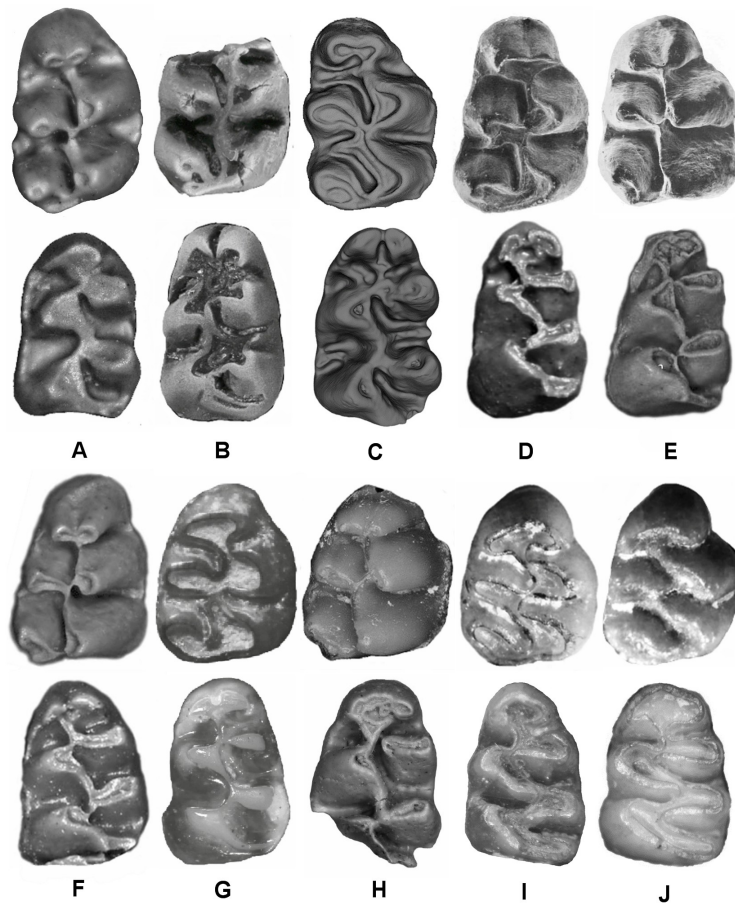
Fig. 6. M1 (above) and m1 (below) of selected North American cricetid taxa. Not to scale, all specimens adjusted to equal size. All occlusal views with anterior up and lingual right. A, *Postcopemys repenningi*: M1, cast of UCMP 87535; m1, cast of UCMP 87901, Maxum. B, *Postcopemys chapalensis*: partial M1, IGM-4851 (reversed); m1, IGM-4850 (holotype), Chapala Fm., from Rincón et al. (2016). C, *Honeymys mariae*: M1, scan of TMM 43645-12871; m1, scan of TMM 43645-12866 (holotype), Whisenhunt. D, *Prosigmodon oroscoi*: M1, IGCU 7244 (reversed), from (Carranza-Castañeda & Walton 1992); m1, cast of IGCU 1245, Rancho el Ocote. E, *Prosigmodon ferrusquiai*: M1, IGCU 7237 (reversed), from (Carranza-Castañeda & Walton 1992); m1, cast of IGCU 7220, Rancho El Ocote. F, *Prosigmodon chihuahuensis*: M1, cast of IGM 5809; m1, cast of IGM 5808, Yepómera. G, *Prosigmodon tecolotum*: M1, MPGJ 1855; m1, MPGJ 3646, Tecolotlán, from Pacheco-Castro et al. (2019). H, *Prosigmodon holocuspis*: M1, FHSM 15457, Meade Basin-Raptor 1C; m1, cast of MNA V4831, Verde Fm. I, *Sigmodon minor*: M1, UF 239721 (reversed), Haile 7G; m1, USNM 10512 (holotype), Curtis Ranch. J, *S. curtisi*: M1, UF 22040, Inglis 1A; m1, USNM 10510 (holotype), Curtis Ranch.
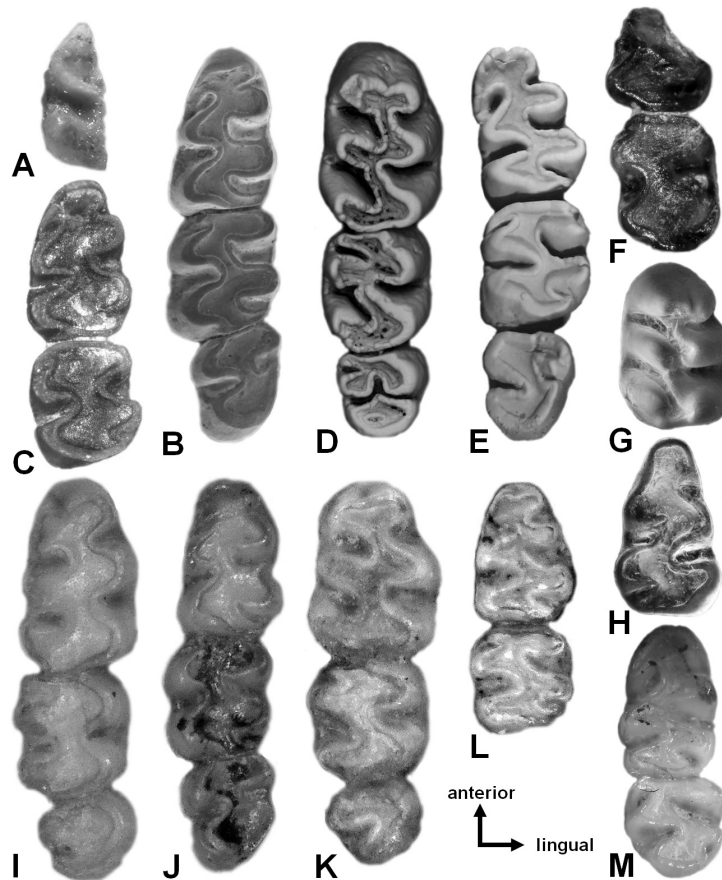
Fig. 7. Ancient South American cricetids: morphological diversity illustrated by dentary and molars (occlusal views) of selected taxa. Not to scale, all specimens adjusted to equal size. A, "Sigmodontinae indet." of Nasif et al. (2009), left M2? Unnumbered, near Entre Ríos, Catamarca, Andalhuala Fm., late Miocene. B, *Necromys bonapartei*, left m1-m3, GHUNLPam 19611, Caleufú, La Pampa, Cerro Azul Fm., Montehermosan. C, *N. bonapartei*, left m1-m2, MD-FM-08-42, Farola de Monte Hermoso, Buenos Aires, Monte Hermoso Fm., Montehermosan. D, *Kraglievichimys formosus*, left M1-M3, MLP 48-XII-16-140, Farola de Monte Hermoso, Buenos Aires, Monte Hermoso Fm., Montehermosan. E, *K. formosus*, right m1-m3, PVL 2397 (holotype, reversed), Farola de Monte Hermoso, Buenos Aires, Monte Hermoso Fm., Montehermosan. F, Sigmodontinae gen. et sp. indet., right partial m1 and m2, unnumbered (reversed), Farola de Monte Hermoso, Buenos Aires, Monte Hermoso Fm., Montehermosan. G, *Kraglievichimys*? left M1, MLP unnumbered, Cascada Grande, Quequén Salado river, Buenos Aires, Irene Fm., Montehermosan. H, Sigmodontinae gen. et sp. indet., right m1, MLP unnumbered (reversed), Cascada de la Ruta, Quequén Salado river, Buenos Aires, Irene Fm., Montehermosan. I, J, *Akodon kermacki*, left M1-M3 and right m1-m3 (reversed), respectively, MMP S-321 (holotype), Punta Lobería, Buenos Aires, Chapadmalal Fm., Chapadmalalan. K, L, *Dankomys simpsoni*, left M1-M3 and right m1-m3 (reversed), respectively, MMP M-1153 (holotype), Playa Chapadmalal, Buenos Aires, Chapadmalal Fm., Chapadmalalan. M, *Graomys dorae*, right m1-m2, MMP M-743 (holotype, reversed), Bajada de las Palomas, Buenos Aires, Chapadmalal Fm., Chapadmalalan.

Province (Reig 1978; see below). The fossil assemblage of Caleufú is composed of 3 200 vertebrate remains, most attributed to avian raptor trophic activities (Verzi et al. 2008:149). Since these birds largely prey on sigmodontines in current times, the fact that just two sigmodontine fossils were recovered in Caleufú suggests very low abundances for these rodents, reflecting a community configuration without modern analogue. Verzi & Montalvo (2008) indicated a late Miocene age, ca. 5.7 to 5.8 Ma, for Caleufú assemblage. However, this chronology was criticized by Prevosti & Pardiñas (2009) who, based on a variety of paleontological evidence, suggested a more likely early Pliocene age (see also Domingo et al. 2020). A third fossil attributed to a sigmodontine from the Cerro Azul Fm. is a fragmentary toothless jaw originally interpreted as a caenolestid marsupial (García-López & Babot 2015:320). We have had no opportunity to study this material (GHUNLPam 5076, a partial right dentary) but from photographs it appears to be a cricetid from a combination of: 1) very small size (the length of the entire molar series is about 3.5 mm); 2) alveolar spaces corresponding to 3 molars (versus the 4-molariform configuration of caviomorphs); and 3) a well-developed retromolar region starting at the level of m2. There is an intriguing, rather large incisor case suggesting a powerful bite. The importance of this badly-preserved material is its potential slightly greater antiquity compared to the Caleufú specimen. This fragmentary hemimandible was collected at El Guanaco (C. Montalvo, com. pers. to UFJP), a locality treated as from the upper part of Cerro Azul Formation (Verzi et al. 2008), and referred to the "late" Huayquerian in the biochronological scheme developed to include these mostly surface assemblages (see Sostillo et al. 2019).

The most famous ancient South American cricetids are those recovered from a short segment of coastal cliffs near Pehuen-có (southern Buenos Aires Province, Argentina), where Pliocene deposits of the Monte Hermoso Fm. (Montehermosan) are exposed (Tonni et al. 1992; Zavala 1993). From this region, classically called Farola de Monte Hermoso (because there is a small lighthouse at the top of the cliff), 13 cricetid fossils have been recovered over a little more than a century, belonging to four sigmodontine genera (Ameghino 1906; Reig 1972, 1978; Pardiñas & Tonni 1998; Pardiñas 2000; Barbière 2019; Barbière et al. 2019a). Ameghino (1906) reported the first cricetid from Monte Hermoso as *Cricetodon*, later assigned to the extant and widespread genus *Reithrodon* (Pardiñas 2000; but see below). Based on the study of Bonaparte (1960), Reig (1972, 1978) then described

the cricetids *Bolomys bonapartei* and *Auliscomys formosus*. The former, later allocated to *Necromys* (Massoia & Pardiñas 1993), was based on a badly preserved anterior mandibular fragment with m1 and m2 (**Fig**. 7C). The original *Auliscomys formosus* material and more recently collected specimens were used to describe the genus *Kraglievichimys* (Barbière et al. 2019a; **Fig**. 7D,E). The remaining specimen from Monte Hermoso Fm. can be allocated to an enigmatic brachydont form with complex molars (UFJP, unpublished data; **Fig**. 7F). Montehermosan deposits have been traditionally treated as early Pliocene in age ca. 5.3 to 4.5 Ma (Tomassini et al. 2013), although in absence of absolute dates this chronological hypothesis is weak (Pardiñas et al. 2017a). Unpublished results based on impactites collected at Montehermosan levels in Cascada Grande (Quequén Salado river, Buenos Aires), suggest a probably age of 4.3 Ma for the Monte Hermoso Fm. (Prevosti et al. 2021). With a diversity of four taxa, the Montehermosan cricetid assemblage reflects a marked increase in taxonomic richness over Caleufú. With confidence, at least three tribes are represented. One is the Reithrodontini, including the oldest record for an extant sigmodontine, *Reithrodon* (but see below). Another is the Phyllotini, since *Kraglievichimys* is morphologically close to *Auliscomys* and its allocation within this tribe seems well supported (Barbière et al. 2019a). Finally, the undescribed brachydont sigmodontine previously mentioned is neither a reithrodontine nor a phyllotine and, therefore, it probably represents a third tribe (the material shows a large lower incisor with an extremely broad band of enamel, a condition not recorded in any other known sigmodontine).

The Farola de Monte Hermoso sigmodontine assemblage embraces several uncertainties beyond those derived from the scarce material available for study. The fossil referred to *Reithrodon* is part of collections made more than a century ago and lacks stratigraphic provenance (Pardiñas & Tonni 1998; Pardiñas 2000). The genus is recorded again, with moderately abundant material, in Chapadmalalan deposits (see below), but there are no additional records from older beds (either in Monte Hermoso, or in other Lower Pliocene deposits such as those of Quequén Salado river or Quequén Grande river). *Reithrodon* is the best represented sigmodontine in the Pampean paleontological record (Reig 1978; Pardiñas 1995). Consequently, we are not confident that *Reithrodon* is present at Monte Hermoso. The material, a partial right dentary with the entire dentition (Pardinas 2000:fig. 1, incorrectly stated as left hemimandible), has a similar appearance to several

fossils of small vertebrates recovered from Monte Hermoso. However, the sequence exposed in the cliffs of Farola de Monte Hermoso includes several stratigraphic units ranging from Lower Pliocene to Recent (Zavala 1993). The issue is not trivial since if the genus really has its first apparition in the Montehermosan, its known geologic range increases by about 0.5 Ma over the next lowest record. The taxonomy of *Necromys bonapartei* is poorly resolved. Its generic allocation was considered tenuous (Pardiñas 1995). An unpublished revision (Barbière 2019) grouped the materials recovered in Caleufú with two specimens from Farola de Monte Hermoso, in a new genus without resolved tribal affinities. If this hypothesis is correct, the same species of ancient South American cricetid would be recovered from two distant localities (Caleufú and Farola de Monte Hermoso are separated by about 350 km).

Montehermosan cricetids are also recorded in two paleontological localities within the Quequén Salado river basin, Cascada Grande and Cascada de la Ruta (Pardiñas et al. 2017a). Particularly in Cascada Grande, where deposits assigned to the Irene Fm. are exposed in a cliff of about 7 m high, sigmodontine remains are limited to the uppermost levels, above an absolute date of 4.4 Ma (Prevosti et al. 2021). The available material consists of a few isolated teeth, recovered by wet washing and sieving of lenses of coarse sands and fine gravels. At least three taxa are recorded, one probably referable to *Kraglievichimys* (**Figs**. 7G, H). From the same river but a different locality, Cascada Escondida, Beilinson et al. (2017:figs. 8G, 8H) pictured two m1s referred to the Phyllotini. One of the illustrated molars is too worn to confirm this identification, but the other shows a prominent anteromedian fossetid, an unusual trait in living member of this tribe.

Bracketed between approximately 3.8 and 3.3 Ma (Schultz et al. 1998, 2006; Prevosti et al. 2021), deposits of the Chapadmalal Fm. form the basal section of the continuous coastal cliffs exposed from the Atlantic cities Mar del Plata to Miramar (southeastern Buenos Aires Province, Argentina). Paleontologically surveyed for more than a century, with thousands of fossils retrieved, rodents are a major component of the Chapadmalalan assemblage (Cione et al. 2015:23). Cricetids, although a minor component relative to caviomorphs, are represented by four genera and species and three tribes. These forms were studied in successive contributions by Reig (1972; 1978; 1987; Reig & Linares 1969) and remain virtually unrevised. The most common cricetid of Chapadmalal beds is *Akodon* (*Abrothrix*) *kerma-*

cki Reig, 1978, treated as representing the tribe Akodontini (sensu Reig 1987). Teta et al. (2014) reassessed the status of *A. kermacki* and considered it neither an *Abrothrix* nor an abrotrichine, but rather an akodontine, representing an undescribed genus. However, a detailed study of this sigmodontine, fortunately represented by at least 10 specimens in various collections (a rare occurrence among Pliocene sigmodontines), is still pending (**Fig**. 7I, J). Another sigmodontine originally allocated to the Akodontini is *Dankomys simpsoni* Reig, 1978, restricted to the holotype (**Fig**. 7K, L), consisting of fragmentary maxillaries and mandibles belonging to a single individual (Reig 1978). It is important to observe that *D. simpsoni* was considered so different from any previously known sigmodontine to constitute a new genus even during the "lumper" paradigm characterizing cricetid systematics during the second half of the nineteenth century. A second species of *Dankomys*, *D. vorohuensis*, appeared in a posthumous contribution (Reig 1994), was recently considered as neither *Dankomys* nor an akodontine, but a member of the extinct genus *Chukimys* and, therefore, probably representing the tribe Reithrodontini (Barbière et al. 2016a). Although still unpublished, a revision of *D. simpsoni* was conducted by Barbière (2019), who treated the genus as a phyllotine, a tribal allocation more in line with the simplified morphology of the molars and the robust and broad zygomatic plate exhibited by this sigmodontine. Concomitantly, Barbière (2019) added new Chapadmalalan remains to *D. simpsoni* but excluded from the genus a fossil from Córdoba in Central Argentina (Tauber 2000). Phyllotines are also represented in Chapadmalalan beds by another genus and species, *Graomys dorae* Reig, 1978, based on a single mandible (Reig 1978). The morphology of this specimen supports its assignation to *Graomys* (Barbière 2019), a widespread living Chacoan sigmodontine (Martínez & Gardenal 2016). However, the available material is so poor and the occlusal design so simplified that the possibility of a different genus, perhaps extinct, cannot be totally ruled out (**Fig**. 7M). Finally, *Reithrodon* also occurs in the Chapadmalal Fm., represented by several specimens (Reig 1978), including the original material employed to coin *Proreithrodon* Ameghino, 1908 (Rovereto 1914; Hershkovitz 1955; Pardiñas 1999b; Pardiñas & Galliari 2001). Although *Proreithrodon chapalmalense* Ameghino, 1908 was later considered a junior synonym of *Reithrodon auritus* (see Reig 1978; Pardiñas 1999b), the issue deserves further examination given the abundant fossil remains attributed to this taxon.

It is intriguing why cricetids are so poorly represented in the Chapadmalalan assemblage. We largely suspect a taphonomic bias. The basal section of the Chapadmalal Fm., composed of beds exposed at the base of the cliffs in localities near Mar del Plata (such as Playa Los Acantilados, Punta Martínez de Hoz, Barranca de los Lobos, Playa las Palomas, Playa Los Lobos, etc.), represents the area where the bulk of fossil material was extracted (and upon which the Chapadmalalan concept was based; Ameghino 1908). A simple reason for this geographic emphasis is accessibility: cliffs near Mar del Plata are vertical walls reaching 20-25 m high and sampling was mostly limited to where stairs were constructed. The accessible strata are mainly exposed in short segments limited by ocean tides. The sediments are silty to clayey/silty deposits of volcanoclastic composition, largely composed of filled burrow systems deeply modified by pedogenesis (Zárate 1989). A significant portion of the fossils came from inside these burrows. Identity of the burrow engineers has been debated, but the abundance of caviomorph rodents (especially *Actenomys*, *Eumysops* and cavies) and a rodentiform ungulate (*Paedotherium*) suggests one or more of these taxa may have been responsible for burrow construction (Genise 1989). A paleoenvironment with extensive burrow systems in a parkland context developed on massive soils under more mesic conditions seems plausible (Fernández et al. 2000). In this context, fossilization probability favored those animals that died inside burrows, acting as a deterrent to weathering. Currently, fossorial caviomorphs and cricetids may be sympatric (Pearson 1984), but the same situation might not be expected for communities dominated by *Actenomys* (phenotypically more similar to a chinchillid than to an octodontid). Small marsupials are, like cricetids, very scarce in Chapadmalal (Reig 1958), suggesting a similar taphonomic bias. Local younger deposits, such as those of Vorohué and San Andrés Fms., have produced a diverse sample of cricetids. The marked increase in the abundance of remains can be associated with owls acting as taphonomic agents (Pardiñas 1995, 1999a). Overall, sigmodontine scarcity in Pampean Pliocene deposits points more to a lack of appropriate circumstances of accumulation and preservation than to a natural rarity in past communities.

Hypotheses of sigmodontine origins: integrating paleontological and genetic data

The earliest history of Sigmodontinae has been a matter of intense debates in the second half of the past century and has been booming again in the last two decades with of the advent of molecular data. The main concerns mostly deal with the place and time of the origin of the group and its dispersal to South America. The purpose of the following is to compare paleontological and molecular data in order to explore which are the plausible scenarios for these issues. Although previous hypotheses both identified early sigmodontines in North America and proposed that the diversification of sigmodontines occurred there during the Miocene and Pliocene (e.g., Baskin 1978, 1986; Jacobs & Lindsay 1981), a number of more recent studies and evaluations suggest that taxa previously allocated to the Sigmodontinae are more likely either indeterminate ancient cricetids or early neotomines (e.g., Reig 1980, 1984, 1986; Steppan 1995; Pardiñas et al. 2003, 2014; Barbière et al. 2016b; Martin et al. 2020). With the possible exception of the Sigmodontini, there is currently no fossil evidence for a North American ancient radiation of extant sigmodontine tribes.

Origin of Sigmodontinae

Estimates of divergence times as well as the ancestral range reconstruction based on molecular clocks propose a common ancestor of Sigmodontinae and Tylomyinae during the early-middle Miocene (Parada et al. 2013; Schenk et al. 2013; Vilela et al. 2013; Leite et al. 2014) or the late Miocene (Parada et al. 2015) in North America (Mexico) or Central America. These studies also propose that the initial diversification of the crown group (dichotomy between Oryzomyalia and Sigmodontalia sensu Steppan et al. 2004 and Leite et al. 2014, respectively) occurred in the lower-middle Miocene (Vilela et al. 2013) or middle-late Miocene (Parada et al. 2013; Schenk et al. 2013; Leite et al. 2014; Gonçalves et al. 2020).

These scenarios face some issues. Divergence estimates based on molecular clocks require calibration points from the fossil record (**Table** 1). Depending on the selected fossil taxa for calibration (e.g., Parada et al. 2013; Vilela et al. 2013; Leite et al. 2014; Gonçalves et al. 2020), results may differ strongly. The interval for the origin of Sigmodontinae in the above studies ranges from around 9 Ma to 20 Ma. Reconstructions of ancestral areas of distribution are based on the current distribution of sigmodontine taxa, and hence do not consider that part of the evolutionary history that may have occurred outside of the current distribution of the subfamily.

If we overlook methodological issues inherent to the use of molecular data to establish divergence

Table 1

Recommended taxa (chronologically ordered) to be used as confident calibration points in phylogenetic studies based on the most current, well documented radioisotopic, magnetostratigraphic and biostratigraphic evidence. The authors of this study differ in defining the status of some taxa, we provide them with their approximate age and node to be applied: *Jacobsomys verdensis* (4.3 Ma, ?Sigmodontinae[a]), *Sigmodon minor/medius* (4.6 Ma, *Sigmodon*), *Honeymys esmeraldensis* (11.7 Ma, ?Sigmodontinae[b]).

Taxon	Stratigraphic provenance	Approximate age	Node to be applied
†*Sigmodon hudspethensis*[c]	Ft. Hancock and Love Fms	2.5 Ma	*Sigmodon*
†*"Akodon" kermacki*	Chapadmalal Fm., basal levels	3.8 Ma	Akodontini
Graomys dorae	Chapadmalal Fm., basal levels	3.8 Ma	*Graomys*
Reithrodon	Chapadmalal Fm., basal levels	3.8 Ma	*Reithrodon*
†*Kraglievichimys formosus*	Monte Hermoso Fm.	4.3 Ma	Phyllotini
†*Neotoma sawrockensis*[d,e]	Rexroad Fm.	4.57 Ma	*Neotoma*
†*Repomys gusteylyi*	Horned Toad Fm	6.5 Ma	Galushamyina
†*Tsaphanomys shotwelli*	Juniper Creek	7.0 Ma	Neotomina

[a] Following Czaplewski (1987). [b] Martin et al. (2020) proposed *Honeymys* as ?Sigmodontinae. [c] We consider *S. hudspethensis* as the earliest most confident records of *Sigmodon*. [d] Martin & Zakrzewski (2019) indicated the existence of an unconfirmed record of *Neotoma* sp. (6.6 Ma, Coffee Ranch). [e] Martin & Zakrzewski (2019) reviewed *Paraneotoma* and invalidated the genus.

dates, these data do strongly contribute information on sigmodontine systematics, and therefore fundamental to our current understanding of the evolution of the subfamily (e.g., Barbière et al. 2016a; Martin et al. 2020).

If we consider *Copemys* or its relatives as a potential ancestor for Sigmodontinae and *Honeymys* as the earliest expression of the sigmodontine stem-group, then their occurrence in the Miocene of USA (Kelly et al. 2020; Martin et al. 2020; Ronez et al. 2020b) is somewhat in agreement with molecular-based estimates that propose a Miocene time of origin. This evidence would further imply that at least an early part of sigmodontine history occurred north of Mexico. This is likely because we do not know of another ancestral clade and distributional source for sigmodontines except Miocene cricetids that dispersed to North America across Beringia (Falbush 1967; Jacobs & Lindsay 1984; Theocharopoulos 2000; Maridet et al. 2011). However, with the possible exception of *Prosigmodon* and *Sigmodon*, the absence of fossil sigmodontine taxa assignable to modern tribes in the late Miocene and Pliocene of North America seems to clearly indicate that the radiation of these tribes, and their dispersal to South America, took place farther south.

The oldest undisputed sigmodontines were found in southern South America (*K. formosus*, *N. bonapartei*) and seem well integrated in the modern radiation of the subfamily with a molar pattern that fits well into the simplest forms of modern sigmodontine morphospace. These records are no older than about ca. 5 Ma (see above), suggesting that evolution and geographic dispersal from an ancestor with more complex molars probably occurred earlier (Reig 1978), but the site of origin and specific time of dispersal is not known. The virtual absence of Miocene and early Pliocene South American sigmodontines with complex molars and the absence of cricetids clearly assignable to the Oryzomyalia in the United States prior to the Pleistocene certainly suggests that the adaptive radiation of modern sigmodontine tribes (with the possible exception of the Sigmodontini), as noted above, took place in a region between Mexico and northern South America.

Invasion of South America

As the geographic origin of the Sigmodontinae seems to be outside South America (see above), a remaining issue deals with the timing and source of the sigmodontine radiation into South America. With the data at hand, resolving this issue is difficult due to a scarcity of fossils, but some scenarios might be discussed.

It is now well established that sigmodontines entered South America prior to the completion of the Panamanian Isthmus estimated at 3 Ma (Vilela et al. 2013), during one of the various episodes of the Great American Biotic Interchange (Morgan 2005; Woodburne et al. 2006; Woodburne 2010; Bacon et al. 2015). It has been suggested that the group invaded South America in the northwest through the Central

American Seaway (Parada et al. 2013; Vilela et al. 2013; Leite et al. 2014; see also D'Elía 2000 ; Pardiñas et al. 2003), which may have been temporarily closed by an earlier formation of the Panama Isthmus, as some geological studies propose (Kirby & McFadden 2005; Montes et al. 2015). Nevertheless, in La Venta, a highly fossiliferous Miocene locality in Colombia with sediments of the Honda Group spanning from 13.5 to 11.5 Ma, many mammal groups have been identified (small mammals such as chiropteran, marsupials and caviomorphs), but no cricetids have been recorded (Kay et al. 1997 and references therein). Following the hypothesis of a northwest invasion of South America, it is noteworthy that in a locality near the potential entry point where a micromammal fauna abounds (Benites-Palomino et al. 2020:fig. 1), cricetids are not recorded. This absence supports the proposal that the cricetid dispersal into South America occurred after the La Venta fauna.

Another possibility to consider is an entry to South America through a place other than the northwestern corner of the continent, perhaps farther east in the current areas of Venezuela, Guyana or Suriname via maritime dispersal, through the Caribbean Sea and the islands of the Antilles. Under this hypothesis, sigmodontines could have entered these areas anytime during the Miocene or Pliocene before, during or after the deposition of La Venta and diversified there and further south. The presence of the Pebas system, a long complex of lakes, rivers and swamps with possible maritime incursions that developed between 23 Ma and 10-8 Ma in the western part of Amazonia (Lundberg et al. 1998; Wesselingh et al. 2001; Wesselingh 2006; Hoorn et al. 2010; Wilkinson et al. 2010; Bloom & Lovejoy 2011; Cooke et al. 2011; Benites-Palomino et al. 2020), may have prevented the dispersion of the group to the west of the continent, in particular to the La Venta area, acting as an important geographic barrier (Wesselingh 2006; Jaramillo et al. 2011, 2017; Boonstra et al. 2015). This hypothesis is supported only by the evidence of modern oryzomyines in this region (except in Cuba, Haití and República Dominicana), plus a few tantalizing records of extinct oryzomyalians with both simple and complex dentitions that supposedly date to the Pliocene and Pleistocene (Zijlstra et al. 2010; Zijlstra 2012).

Ancestral area reconstructions studies based on data from extant sigmodontines (Parada et al. 2013; Leite et al. 2014) cannot distinguish between an initial diversification of the crown group of Sigmodontinae (split between Sigmodontalia and Oryzomyalia) in Central America and a later in-

vasion of South America, or on the contrary, an initial diversification in South America with further dispersals northwards to Central and North America.

Following the hypothesis of a unique invasion from the north, this implies that a member of the sigmodontine stem group entered South America and both Oryzomyalia and Sigmodontalia diversified in situ. Although ancestral range reconstructions support an origin of Oryzomyalia in South America, this is not the case for Sigmodontalia which would have its origin in Central America (Parada et al. 2013; Leite et al. 2014). However, the taxonomic sampling for Sigmodontalia in these studies was quite poor and molecular-based phylogenetic analyses retrieved the Sigmodontini *Sigmodon alstoni* and *Sigmodon peruanus*, two species distributed in Peru and Northern South America, as basal (Peppers et al. 2002; Henson & Bradley 2009; Lessman et al. 2011; Steppan & Schenk 2017; Pardiñas et al. 2017b; Upham et al. 2019). Zijlstra et al. (2014) described *Cordimus*, an extinct ?late Pliocene to Holocene taxon from islands off the north coast of South America. They estimated that *Cordimus* invaded these islands by maritime dispersal from a lineage in South America and proposed that it could be a member of the stem-group of sigmodontines. This hypothesis is not supported by phylogenetic analyses and more studies are necessary to determine the affinities of *Cordimus* (Zijlstra et al. 2014; Salazar-Bravo et al. 2016). However, as noted above, if *Cordimus* is part of a lineage from which the Sigmodontalia and Oryzomyalia diverged, then an invasion of at least the Caribbean prior to this basal dichotomy is likely.

A hypothesis of multiple invasions to South America comprises different scenarios. An initial hypothesis would consider that Oryzomyalia and Sigmodontalia originated outside South America and then dispersed and radiated after arriving on the continent. Another possibility consists of multiple invasions by ancestral sigmodontines. Either way, only one ancestral lineage gave rise to Sigmodontalia and Oryzomyalia in South America. Or, multiple ancestral species dispersed from the north into South America, each giving rise to modern South American sigmodontine tribes. Perhaps some ancestral forms later dispersed North from South America giving rise to sigmodontalians and oryzomyalians in Central and North America, including an endemic genus (*Rheomys*). The problem is that the fossil record is so meager that all of these ideas, and other ingenious hypotheses, cannot be rejected.

During the last decades, many hypotheses have been advanced on the origin of Sigmodontinae

and their dispersal to South America. Because of a paucity of fossil specimens, the storyline has been based mainly on molecular studies; the paleontological record has only been considered for calibration purpose (Barbière et al. 2016b; **Table** 1). In order to clarify our understanding of the origin of the Sigmodontinae, it seems that further efforts must be made through additional detailed morphological and phylogenetic analyses of known fossil material (Barbière 2019; Kelly et al. 2020; Martin et al. 2020; Ronez et al. 2020b).

CONCLUSIONS

One of the great biological puzzles remaining to be solved is the time and place of origin of sigmodontine rodents and their dispersal history into South America. Available evidence suggests sigmodontines evolved from among a set of Miocene North American cricetid immigrants from Asia, including *Copemys* and related taxa. *Copemys* is in revision and likely includes a number of genera, one of which, *Honeymys*, might represent the earliest sigmodontine. The latter is useful as working hypothesis but needs to be supported with more ample evidence, especially from other anatomical systems (e.g., dentary, zygomatic plate). A critical character complex separating ancestral cricetids and neotomines from sigmodontines is the presence of relatively opposite, rather than alternate, cusps on upper molars. This difference has been preliminary quantified (Martin et al. 2020), and at least currently in order to be considered as a possible sigmodontine, a fossil taxon must at least display opposite cusps. On this basis, many fossil North American taxa previously considered as sigmodontines cannot surely be allocated to the Sigmodontinae and some are likely ancient neotomines. However, other dental traits should be studied. Among the several lines of evidence, in order to enrich the complex scenario to understand ancient American cricetids, the evolutionary trends involving procingulum development (from one to two conules/lids) as well as the probably linked tendency to increase M1/m1 length and to reduce M3/m3 length deserve attention.

The earliest known record of *Honeymys* is *H. esmeraldensis*, recovered from a site in Nevada just above a tuff dated at 11.7 Ma (Kelly et al. 2020). With the exception of *Honeymys mariae* from late Miocene localities in Oklahoma and Nebraska (ca. 10-9 Ma), fossil cricetids with potential ties to the Sigmodontinae do not appear again in the North American record until after about 5 Ma, in the early Pliocene, represented by *Jacobsomys*,

Postcopemys chapalensis, *Prosigmodon*, *Sigmodon*, and *Symmetrodontomys*. Although dentitions of these taxa display some characters in common with extant sigmodontines, none except *Sigmodon* are clearly referable to extant tribes. Thus we conclude that with the possible exception of the Sigmodontini (if *Prosigmodon* is there allocated), extant sigmodontine tribes did not occur in North American prior to the Pliocene.

The oldest rodents from South America clearly assignable to the Sigmodontinae were recovered from the Cerro Azul and Monte Hermoso formations in Argentina. Neither are associated with radiometric dates, and they are currently considered to be latest Miocene or early Pliocene in age. The Montehermosan species, such as *Kraglievichimys formosus*, display simple molars, without accessory structures such as styles/stylids and lophs/lophids, similar to those of some extant phyllotines. It is possible that the currently indeterminate species from Monte Hermoso noted in **Fig**. 3 has more complex molars, but this has yet to be determined. The earliest oryzomyalian sigmodontine with relatively complex molars is represented by a species referred originally to *Akodon kermacki* from the Chapadmalal Fm. in Argentina, dated between 3.8 and 3.3 Ma. If, as has been postulated (Martin et al. 2020), ancestral sigmodontines had complex molars, the relationships of Montehermosan sigmodontines to each other and to modern tribes remains equivocal.

Divergence times for the Oryzomyalia and Sigmodontalia are estimated by molecular studies between 20 and 9 Ma (e.g., Parada et al. 2013; Schenk et al. 2013; Vilela et al. 2013; Leite et al. 2014; Gonçalves et al. 2020). Paleontologically, sigmodontines may have first appeared in North America between 12 and 10 Ma. According to these maximum estimates and the available paleontological evidence, if the molecular dates were correct, this would imply an interval of about 10 million years in which ancestral sigmodontines existed but left no fossil record. Radiations into modern tribes, with the possible exception of the Sigmodontini, are not documented in the fossil record, and neither the timing nor the route of dispersal of sigmodontine tribes to South America is represented by paleontological evidence. The absence of unequivocal oryzomyalians from Pliocene North American sites, indicate that the radiation of modern sigmodontine tribes took place geographically between Mexico and northern South America, but their precise diversification times remain unknown.

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APPENDIX 1

Classification of extant and extinct (†) South American sigmodontine genera including those Caribbean assigned to the subfamily (compiled from several sources; tribes authorships after Cazzaniga et al. 2019).

Subfamily Sigmodontinae Wagner, 1843
  Sigmodontinae incertae sedis
    Abrawayaomys Souza Cunha and Cruz, 1979
    Chinchillula Thomas, 1898
    †*Cholomys* Reig, 1980[a]
    †*Cordimus* Zijlstra, McFarlane, van Den Hoek Ostende and Lundberg, 2013[b]
    Delomys Thomas, 1917
  Tribe Abrotrichini D'Elía, Pardiñas, Teta and Patton, 2007
    Abrothrix Waterhouse, 1837
    Chelemys Thomas, 1903
    Geoxus Thomas, 1919
    Notiomys Thomas, 1890
    Paynomys Teta, Cañon, Patterson and Pardiñas, 2017
  Tribe Akodontini Cockerell and Printz in Cockerell et al., 1914
    Akodon Meyen, 1833
    Bibimys Massoia, 1980[c]
    Blarinomys Thomas, 1896
    Brucepattersonius Hershkovitz, 1998
    Castoria Pardiñas, Geise, Ventura and Lessa, 2016

†*Dankomys* Reig, 1978[d]

Deltamys Thomas, 1917

Gyldenstolpia Pardiñas, D'Elía and Teta, 2009

Juscelinomys Moojen, 1965

Kunsia Hershkovitz, 1966

Lenoxus Thomas, 1909

Necromys Ameghino, 1889

Oxymycterus Waterhouse, 1837

Podoxymys Anthony, 1929

Scapteromys Waterhouse, 1837

Thalpomys Thomas, 1916

Thaptomys Thomas, 1916

Tribe Andinomyini Salazar-Bravo, Pardiñas, Zeballos and Teta, 2016

Andinomys Thomas, 1902

Punomys Osgood, 1943

Tribe Euneomyini Pardiñas, Teta, and Salazar-Bravo, 2015

Euneomys Coues, 1874

Irenomys Thomas, 1919

Neotomys Thomas, 1894

Tribe Ichthyomyini Cockerell and Printz in Cockerell et al., 1914

Anotomys Thomas, 1906

Chibchanomys Voss, 1988

Daptomys Anthony, 1929[e]

Ichthyomys Thomas, 1893

Neusticomys Anthony, 1921

Rheomys Thomas, 1906

Tribe Neomicroxini Pardiñas, Curay, Brito and Cañón, 2021[f]

Neomicroxus Alvarado-Serrano and D'Elía, 2013

Tribe Oryzomyini Vorontsov, 1959

Aegialomys Weksler, Percequillo and Voss, 2006

†*Agathaeromys* Zijlstra, Madern and van Den Hoek Ostende, 2010

Amphinectomys Malygin, 1994

†*Antillomys* Brace, Turvey, Weksler, Hoogland and Barnes, 2015

†*Carletonomys* Pardiñas, 2008

Cerradomys Weksler, Percequillo and Voss, 2006

Drymoreomys Percequillo, Weksler and Costa, 2011

†*Dushimys* Zijlstra, 2012

Eremoryzomys Weksler, Percequillo and Voss, 2006

Euryoryzomys Weksler, Percequillo and Voss, 2006

Handleyomys Voss, Gómez-Laverde and Pacheco, 2002

Holochilus Brandt, 1835

Hylaeamys Weksler, Percequillo and Voss, 2006

Lundomys Voss and Carleton, 1993

†*Megalomys* Trouessart, 1881

†*Megaoryzomys* Lenglet and Coppois, 1979[g]

Melanomys Thomas, 1902

Microakodontomys Hershkovitz, 1993

Microryzomys Thomas, 1917

Mindomys Weksler, Percequillo and Voss, 2006

Neacomys Thomas, 1900

Nectomys Peters, 1861

Nephelomys Weksler, Percequillo and Voss, 2006

Nesoryzomys Heller, 1904

†*Noronhomys* Carleton and Olson, 1999

Oecomys Thomas, 1906

Oligoryzomys Bangs, 1900

Oreoryzomys Weksler, Percequillo and Voss, 2006

Oryzomys Baird, 1857

Pattonimus Brito et al., 2020[h]

†*Pennatomys* Turvey, Weksler, Morris and Nokkert, 2010

Pseudoryzomys Hershkovitz, 1962

†*Reigomys* Machado, Leite, Christoff and Giugliano, 2013

Scolomys Anthony, 1924

Sigmodontomys Allen, 1897

Sooretamys Weksler, Percequillo and Voss, 2006

Tanyuromys Pine, Timm and Weksler, 2012

Transandinomys Weksler, Percequillo and Voss, 2006

Zygodontomys Allen, 1897

Tribe Phyllotini Vorontsov, 1959

Andalgalomys Williams and Mares, 1978

Auliscomys Osgood, 1915

Calassomys Pardiñas, Lessa, Teta, Salazar-Bravo and Câmara, 2014

Calomys Waterhouse, 1837

Eligmodontia Cuvier, 1837

Galenomys Thomas, 1916

Graomys Thomas, 1916

†*Ichthyurodon* Steppan and Pardiñas, 1998[i]

†*Kraglievichimys* Barbière, Ortiz and Pardiñas, 2018

Loxodontomys Osgood, 1947

†*Panchomys* Pardiñas, 1997[j]

†*Pardinamys* Ortiz, Jayat and Steppan, 2012

Phyllotis Waterhouse, 1837

Salinomys Braun and Mares, 1995

†*Tafimys* Ortiz, Pardiñas and Steppan, 2000

Tapecomys Anderson and Yates, 2000

Tribe Reithrodontini Cazzaniga, Cañón and Pardiñas, 2019

†*Chukimys* Barbière, Cruz, Ortiz and Pardiñas, 2016

†*Olympicomys* Steppan and Pardiñas, 1998[k]

Reithrodon Waterhouse, 1837

Tribe Sigmodontini Wagner, 1843

Sigmodon Say and Ord, 1825

Tribe Thomasomyini Steadman and Ray, 1982

Aepeomys Thomas, 1898

Chilomys Thomas, 1897

Rhagomys Thomas, 1917

Rhipidomys Tschudi, 1845

Thomasomys Coues, 1884

Tribe Wiedomyini Reig, 1980

Juliomys González, 2000

Phaenomys Thomas, 1917

Wiedomys Hershkovitz, 1959

Wilfredomys Ávila-Pires, 1960

Notes

[a]Originally placed in Wiedomyini (see Reig 1987); incertae sedis status was advanced by Pardiñas & Barbière (2018). [b]Although treated as Sigmodontinae incertae sedis in the original publication, at least the type species, *Cordimus debuisonjei*, seems an Oryzomyini. [c]Traditionally dated as 1978 or 1979, the paper where *Bibimys* was named and described was effectively published in 1980. [d]Considered as Phyllotini in Barbière (2019). [e]Resurrected by Salazar-Bravo and collaborators (unpublished data). [f]A monotypic tribe recently advanced to contain the Andean endemic *Neomicroxus* (Pardiñas et al. 2021). [g]Traditionally treated as Thomasomyini, here is treated as Oryzomyini according to Ronez et al. (2020a). [h]A genus recently described to allocate forest montane oryzomyines in northern Ecuador and southern Colombia (Brito et al. 2020). [i]Considered as Oryzomyini in Barbière (2019). [j]Considered as Reithrodontini in Barbière (2019). [k]Considered as Reithrodontini by Barbière et al. (2021).

APPENDIX 2

Classification of extant and extinct (†) non- arvicoline cricetid genera of North America including the subregion of Central America (compiled from several sources; authorships of Sigmodontinae tribes and Peromyscini follow Cazzaniga et al. 2019).

Family Cricetidae Fischer de Waldheim, 1817
    Cricetidae incertae sedis
        †*Abelmoschomys* Baskin, 1986
        †*Bensonomys* Gazin, 1942[a]
        †*Copemys* Wood, 1936[a]
        †*Pliotomodon* Hoffmeister, 1945
        †*Postcopemys* Lindsay and Czaplewski, 2011[b]
        †*Pseudomyscus* Korth, 1997
        †*Symmetrodontomys* Hibbard, 1941
        †*Tregomys* Wilson, 1968
    Subfamily ?Sigmodontinae Wagner, 1843
        †*Honeymys* Martin et al., 2020[c]
        †*Jacobsomys* Czaplewski, 1987[d]
    Subfamily Sigmodontinae Wagner, 1843
        Tribe Ichthyomyini Cockerell and Printz in Cockerell et al., 1914
            Ichthyomys Thomas, 1893
            Rheomys Thomas, 1906
        Tribe Oryzomyini Vorontsov, 1959
            "*Handleyomys*" Voss, Gómez-Laverde and Pacheco, 2002
            Melanomys Thomas, 1902
            Neacomys Thomas, 1900
            Nephelomys Weksler, Percequillo and Voss, 2006
            Oecomys Thomas, 1906
            Oligoryzomys Bangs, 1900
            Oryzomys Baird, 1857
            Sigmodontomys Allen, 1897
            Tanyuromys Pine, Timm and Weksler, 2012
            Transandinomys Weksler, Percequillo and Voss, 2006
            Zygodontomys Allen, 1897
        Tribe Sigmodontini Wagner, 1843
            †*Prosigmodon* Jacobs and Lindsay, 1981[a]
            Sigmodon Say and Ord, 1825
    Subfamily Neotominae Merriam, 1894
        Neotominae incertae sedis
            †*Acrolophomys* Kelly and Whistler, 2014

            †*Antecalomys* Korth, 1998
            †*Basirepomys* Korth and DeBlieux, 2010
            †*Lindsaymys* Kelly and Whistler, 2014
            †*Paronychomys* Jacobs, 1977
    Tribe Baiomyini Musser and Carleton, 2005
        Baiomys True, 1894
        Scotinomys Thomas, 1913
    Tribe Neotomini Merriam, 1894
        Subtribe Galushamyina Lindsay, 2008[e]
            †*Galushamys* Jacobs, 1977
            †*Miotomodon* Korth, 2011
            Nelsonia Merriam, 1897
            †*Protorepomys* Martin and Zakrzewski, 2019
            †*Repomys* May, 1981
        Subtribe Neotomina Merriam, 1894[e]
            Hodomys Merriam, 1894
            Neotoma Say and Ord, 1825
            †*Tsaphanomys* Martin and Zakrzewski, 2019
            Xenomys Merriam, 1892
    Tribe Ochrotomyini Musser and Carleton, 2005
        Ochrotomys Osgood, 1909
    Tribe Peromyscini Cockerell and Printz, 1914
        Habromys Hooper and Musser, 1964
        Isthmomys Hooper and Musser, 1964[f]
        Megadontomys Merriam, 1898
        Neotomodon Merriam, 1898
        Onychomys Baird, 1857
        Osgoodomys Hooper and Musser, 1964
        Peromyscus Gloger, 1841
        Podomys Chapman, 1889
        Reithrodontomys Giglioli, 1874[f]
    Subfamily Tylomyinae Reig, 1984
        Tribe Nyctomyini Musser and Carleton, 2005
            Nyctomys Saussure, 1860
            Otonyctomys Anthony, 1932
        Tribe Tylomyini Reig, 1984
            Ototylomys Merriam, 1901
            Tylomys Peters, 1866

Notes

[a]These genera likely contains several taxa that may deserve distinct generic recognition.[b]Considered as ancestor of *Peromyscus* by Lindsay & Czaplewski (2011). [c]Considered as such by Martin et al. (2020). [d]Following Czaplewski (1987). [e]Rank and species contents were defined in Martin & Zakrzewski (2019). [f]Both *Isthmomys* and *Reithrodontomys* were considered as a separate tribe, Reithrodontomyini, by Keith (2015).