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DEFINITION AND DIAGNOSIS OF A NEW TRIBE OF SIGMODONTINE RODENTS (CRICETIDAE: SIGMODONTINAE), AND A REVISED CLASSIFICATION OF THE SUBFAMILY

DEFINICION Y DIAGNOSIS DE UNA NUEVA TRIBU DE ROEDORES SIGMODONTINOS (CRICETIDAE: SIGMODONTINAE), Y UNA CLASIFICACION REVISADA DE LA SUBFAMILIA

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ABSTRACT

A new tribe of sigmodontine rodents is formally defined and diagnosed. The tribe contains the extant genera *Abrothrix* (including *Chroeomys*), *Chelemys*, *Geoxus*, *Pearsonomys*, and *Notiomys*, a group of taxa distributed in the central and southern Andes and lowlands both east and west of the cordillera. The new tribe presents a unique combination of characters including nasals and premaxilla usually projected anterior to the incisors, moderately trumpeted; zygomatic plate with upper free border reduced or obsolete; and third upper molar reduced and sub-cylindrical in out-line with an internal ring-like enamel fossette. Molecular phylogenetic analyses indicate that *Abrothrix* is sister to a clade containing the remaining genera of the new tribe.

KEYWORDS: *Abrothrix*, *Chelemys*, *Chroeomys*, *Geoxus*, *Pearsonomys*, *Notiomys*, South America, classification.

With approximately 84 extant genera, cricetids of the subfamily Sigmodontinae (Reig 1980) are one of the most diverse and complex groups of New World mammals. Notably, new sigmodontine taxa are still being erected on the basis of both newly discovered species (e.g., Pardiñas *et al*. 2005) and from revisionary museum work (e.g., Weksler *et al*. 2006). Distributed predominantly in South America, sigmodontines also reach Central and North America, and one extant genus is endemic to the Galapagos Islands (D'Elía 2003a).

Sigmodontine genera have been arranged into different groups, most of which have been given the formal rank of tribes (e.g., Hershkovitz 1966; Reig 1980). In the last 15 years phylogenetic analyses using either or both morphological and molecular data have been used to delimit these groups (e.g., Braun 1993; Smith & Patton 1993, 1999; Steppan 1995; D'Elía 2003b; Pacheco 2003; Weksler, 2003; D'Elía *et al*. 2003, 2005, 2006a, 2006b), causing several instances of major reconsiderations on their limits and contents. One of the most surprising results of DNA sequences phylogenies was a clade of taxa (*Abrothrix*, *Chelemys*, *Chroeomys*, *Geoxus*, *Notiomys*, and *Pearsonomys*), distributed primarily in the South and Central Andes and traditionally considered to be typical akodontine rodents (and in some cases

even considered subgenera of *Akodon* [e.g., Reig 1987]), which do not form part of the akodont radiation (Smith & Patton 1999; D'Elía 2003b; see also the allozyme based studies of Spotorno *et al*. 1990 and Barrantes *et al*. 1993). Smith & Patton (1999:106-107) recommended ranking this group of genera as a tribe, suggesting that an adequate name for it would be Abrotrichini. Although these authors enumerated chromosomal, protein, and parasite features that may be used to diagnose the group, they made no formal definition or diagnosis (e.g., Musser & Carleton, 2005: 1087). Here we provide such a definition and diagnosis. We base our revised classification on the results and conclusions of Carleton (1980), Reig (1980, 1987), Smith & Patton (1993, 1999), Steppan (1995), Engel *et al*. (1998), D'Elía (2003b), Weksler (2003, 2006), Jansa & Weksler (2004), Percequillo *et al*. (2004), Steppan *et al*. (2004), D'Elía *et al*. (2003, 2005, 2006a, 2006b), Musser & Carleton (2005), and Weksler *et al*. (2006) and our assessment of qualitative characters. We recognize a new tribe of Sigmodontinae (family Cricetidae) that we describe as follows.

Abrotrichini, new tribe
Fig. 1

Type genus.—*Abrothrix* Waterhouse, 1837.

Contents.—*Abrothrix* Waterhouse, 1837 (including *Chroeomys* Thomas, 1916; *Habrothrix* Wagner, 1843), *Chelemys* Thomas, 1903, *Geoxus* Thomas, 1919, *Notiomys* Thomas, 1890, and *Pearsonomys* Patterson, 1992.

Definition.—The clade composed of the last common ancestor of *Abrothrix*, *Chelemys*, *Geoxus*, *Notiomys*, and *Pearsonomys* and all of its descendants.

Diagnosis.—A tribe of the subfamily Sigmodontinae (*sensu* Reig 1980) grouping mice of small to medium size (from approximately 20 g in *Notiomys edwardsii* to 75 g in *Chelemys macronyx*) distinguishable by the following combination of characters: pelage long and soft; tail typically short and well haired; feet large and strongly built, with naked palms; claws equally robust on fore- and hind-feet (Gyldenstolpe 1932; Osgood 1943); skull with long muzzle and rounded braincase, without frontal or lambdoid crests; interorbital region amphora-shaped; nasals and premaxillae slightly projected anterior to the incisors to somewhat trumpeted; nasals longer than frontals; zygomatic plate typically narrow, with the upper free border reduced or absent; infraorbital foramen wide; frontal sinuses moderately developed; palate long; anterior border of mesopterygoid fossa square shaped; mandibular ramus generally gracile and elongated, except in *Chelemys* (Gyldenstolpe 1932; Osgood 1943; Reig 1987); upper incisors broad and ungrooved; teeth brachyodont to mesodont; upper and lower molars with labial and lingual cusps arranged in opposite or slightly alternate pairs; first upper/lower molars with reduced, fan-shaped, procingulum and shallow or absent anteroflexus(id); first upper molars with a very shallow to obsolete anteromedian flexus; para- and metaflexus strongly oriented backward to transversely oriented; paracone globose and oriented forward, mesoloph(id) poorly to moderately developed, usually fused to the paracone; third upper molars reduced and sub-cylindrical in outline, except in *Chelemys*, with an internal ring-like enamel fossette (Gyldenstolpe 1932; Reig 1987; D'Elía *et al*. 2006a). Axial skeleton includes 13 ribs, 13 thoracic vertebrae, 6 lumbar vertebrae, and 18-29 caudal vertebrae (Steppan 1995). Stomach unilocular-hemiglandular (Carleton 1973; D'Elía *et al*. 2006a).

Etymology.—Waterhouse (1837: 21, footnote) coined *Abrothrix*, the type genus of the new tribe, from the Greek words "abros" (soft or delicate) and "thrix" (hair), which capture a key trait of these rodents that he had noted ("fur long and soft"). The tribal name is constructed by dropping the case ending from the genitive singular form of *Abrothrix* (ICZN, Article 29.3), or abro-trichos, to create the stem abrotrich. Thus, the family-group name becomes abrotrich + ini = Abrotrichini, not Abrothricini.

Known distribution.—Argentina (Pliocene-Recent), Bolivia (Recent), Chile (Pleistocene-Recent), Ecuador (Recent), Peru (Recent). Species of this tribe are known from the altiplano in west-central Peru and western mountain ranges in Argentina and Bolivia to southernmost Argentina and Chile, including several austral off-shore islands and the Patagonian steppes to the Atlantic Coast (Osgood 1943; Patterson *et al*. 1984; Teta *et al*. 2006; Fig. 2).

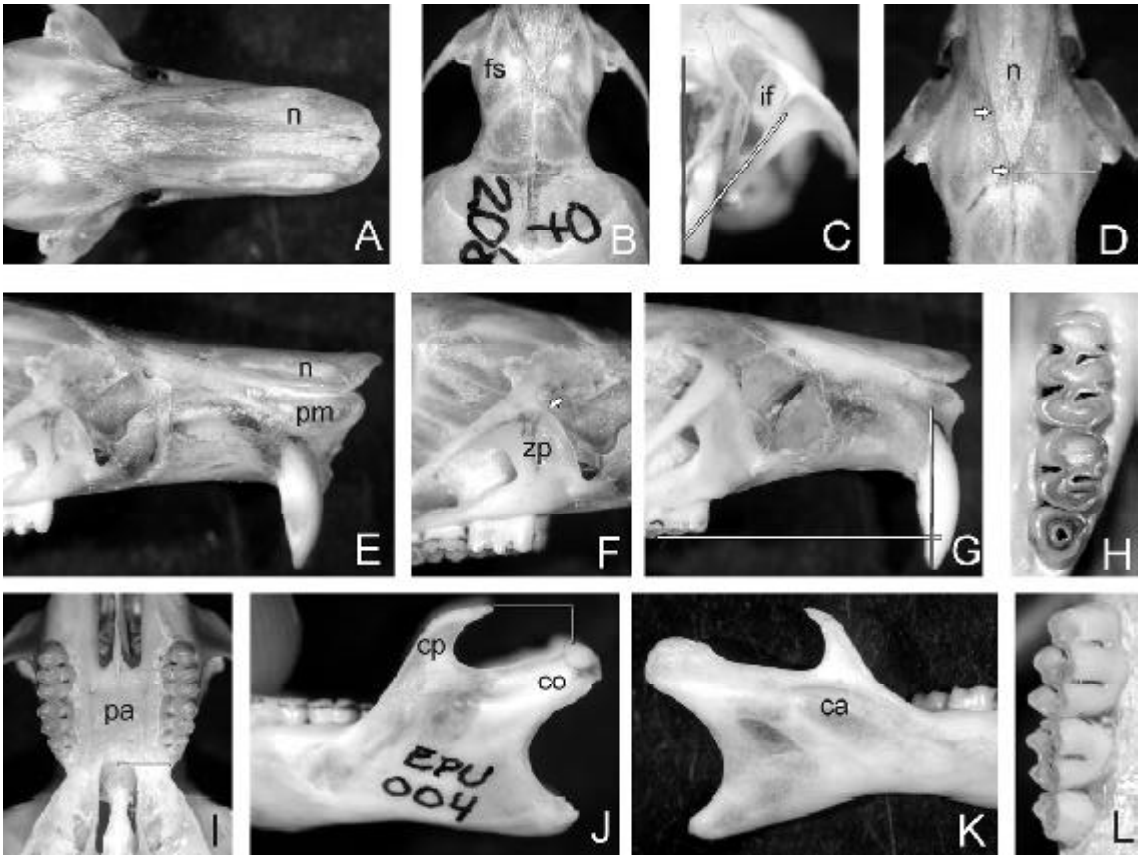

FIGURE 1. View of different Abrotrichini morphological traits. A) Enlarged pointed rostrum (*A. sanborni*). B) Amphoral interorbital region with well developed frontal sinuses (*A. sanborni*). C). Orientation of the zygomatic plate and large infraorbital foramen (*N. edwardsii*). D) Nasals distinctly pointed at their posterior end (*A. longipilis*). E) Nasals and premaxillae projected anterior to the incisors (*A. sanborni*). F) Narrow zygomatic plate with reduced [arrow] upper free border (*A. andinus*). G) Upper incisors robust and orthodont (*C. macronyx*). H) Typical abrotrichine upper molar occlusal pattern with procingulum fan-shape, reduced mesolophs, and internal ring-like enamel fossette in M3 (*A. sanborni*). I) Long palate (*A. jelskii*). J) Robust and high coronoid process (*C. macronyx*). K) Enlarged mandible with inconspicuous capsular projection (*A. lanosus*). L) Bilevel coronal topography (*A. longipilis*). Abbreviations: ca = capsular projection, co = condyle, cp = coronoid process, fs = frontal sinus, if = infraorbital foramen, n = nasal/s, pa = palate, pm = premaxillary, zp = zygomatic plate.

FIGURA 1. Vistas de distintas características morfológicas de Abrotrichini. A) Rostro alargado y acuminado (*A. sanborni*). B) Región interorbitaria en forma de ánfora con senos frontales bien desarrollados (*A. sanborni*). C). Orientación de la placa zigomática y gran desarrollo del foramen infraorbitario (*N. edwardsii*). D) Nasales largos y acuminados en su extremo posterior (*A. longipilis*). E) Nasales y premaxilares proyectados anteriormente a los incisivos (*A. sanborni*). F) Placa zigomática estrecha con borde libre reducido (flecha) (*A. andinus*). G) Incisivos superiores robustos y ortodontes (*C. macronyx*). H) Típica morfología oclusal de los molares superiores desplegada por los abrotrichinos, con un procíngulo con forma de abanico, mesolofos reducidos y una foseta interna de esmalte en forma de anillo en el M3 (*A. sanborni*). I) Paladar largo (*A. jelskii*). J) Proceso coronal robusto y alto (*C. macronyx*). K) Mandíbula alargada con una proyección capsular inconspicua (*A. lanosus*). L) Topografía coronal en dos niveles (*A. longipilis*). Abreviaturas: ca = proyección capsular, co = cóndilo, cp = proceso coronoides, fs = seno frontal, if = foramen infraorbitario, n = nasal/es, pa = paladar, pm = premaxilar, zp = placa zigomática.

Phylogenetic relationships.—Phylogenetic relationships among abrotrichine genera have been studied by Smith & Patton (1999), D'Elía (2003b), and D'Elía *et al*. (2006a) based on both mitochondrial and nuclear DNA sequences. Data are available for all currently recognized genera, although not for all species. These studies delineate a basal dichotomy separating *Abrothrix* from a clade composed by the remaining abrotrichines. The distinction of both clades is marked, with both strongly supported and corroborated by patterns of morphological variation. Within the latter clade, the three predominantly fossorial abrotrichine genera (*Geoxus*, *Notiomys*, and *Pearsonomys*) form a clade to which *Chelemys* is sister. Relationships among species of *Abrothrix* have not been thoroughly explored as some species have not been included in any phylogenetic analysis (we are aware of on-going studies that include *A. illuteus*, *A. lanosus*, *A. markhami*, and *A. sanborni*). Available phylogenetic studies, together with some unpublished phylogenetic analyses, indicate that current generic classification of abrotrichines may require adjustment since some genera as currently delimited are not monophyletic (D'Elía, Pardiñas, and Lessa unpublished data; see also D'Elía *et al*. 2006a).

Remarks.—Based on information summarized by Reig (1987) for several abrotrichine taxa (*Abrothrix* spp., *Chelemys macronyx*, *Geoxus valdivianus*) and data provided by Liascovich *et al.* (1989) for *A. illuteus*, and Spotorno *et al.* (1990) for additional species of *Abrothrix*, Smith & Patton (1999) suggested that a diploid number of 2n = 52 could be a synapomorphy for the abrotrichine group. While no study has tested that hypothesis, new data indicates that the 2n = 52 is not a diagnostic character of the tribe. *Pearsonomys annectens* has a 2n = 56 (D'Elía *et al*. 2006a), unpublished results of M. Gallardo indicate that some abrotrichine taxa also depart from a 2n = 52, and a population of *Abrothrix olivaceus* with a 2n = 44 was recently documented by Rodríguez & Theiler (2007). The karyotype of *Notiomys edwardsii* and some other forms remain unknown. Further studies are needed to assess abrotrichine chromosomal evolution. What is important here is to acknowledge that a 2n = 52 is not a diagnostic feature of Abrotrichini, new tribe.

The pelage of the abrotrichinos is generally slate gray or brownish, although there are some blackish (*A. sanborni*, *Chelemys*, *Geoxus*) and brightly colored (*A. jelskii*) forms. Species of *Abrothrix* have elongated phalli with a much reduced or no distal baculum; the genera *Chelemys*, *Geoxus*, *Notiomys* and *Pearsonomys* have a tridigitate distal baculum; the phalli of *Pearsonomys* and *Geoxus* have a prominent dorsal hood that extends beyond the terminal crater (Hooper & Musser 1964; Spotorno 1986; D'Elía *et al*. 2006a). *Abrothrix longipilis*, *A. jelskii*, *A. olivaceus*, and *Geoxus valdivianus* have two pairs of preputial glands (Voss & Linzey 1981). The number of preputial glands in other genera is unknown.

Since Patton & Smith (1999) first identified the abrotrichine clade, the names Abrotrichini, Abrothrichini, and their informal derivatives (including the Spanish abrotrichinos and abrotriquinos) have repeatedly appeared in the literature (e.g., D'Elía 2003; Weksler 2003; Jansa & Weksler 2004; Geise *et al*. 2004; Ojeda *et al.* 2005; Palma *et al*. 2005; Jayat *et al*. 2006). However, none of these usages can be considered as the formal designation of the tribe since no diagnosis was provided, nor did any such appearance explicitly identify the creation of a new taxon (ICZN, 1999: Articles 13 and 16). Similarly, the usage of Abrotrichini by Smith and Patton (1999: 106) cannot be considered a formal designation of the tribe because their statement - "An appropriate name for the new tribe *would be* Abrotrichini …" [emphasis ours]- clearly indicates only a conditional proposal, and as such, it is not available (ICZN, 1999: Articles 15.1, which corresponds to Article 15 of the edition of the Code in usage when the paper was published). Musser & Carleton (2005: 1087) also considered the earlier usages of Abrotrichini to be unavailable and recommended that a "full and proper diagnosis" was needed.

The informal term "Andean clade" has also been used to refer to the abrotrichine group. We note that even though several abrotrichines have exclusively Andean distributions (e.g., *A. jelskii*), several others are distributed in the lowlands west and east of the Andes (e.g., *A. olivaceus*), while still others are not found in the Andes at all (e.g., *P. annectens*).

FIGURE 2. Geographic distribution of Abrotrichini, new tribe.

FIGURA 2. Distribución geográfica de Abrotrichini, nueva tribu.

Currently (Carleton & Musser 2005 with the present modification), nine tribes are recognized within Sigmodontinae; these are: Abrotrichini new tribe, Akodontini, Ichthyomyini, Oryzomyini, Phyllotini, Reithrodontini, Sigmodontini, **Thomasomyini, and Wiedomyini. In addition, several genera (e.g.,** *Abrawayaomys*, *Phaenomys*, *Wilfredomys*) are considered as Sigmodontinae *incertae sedis* (Smith & Patton 1999; D'Elía 2003; Jorge Salazar-Bravo, personal communi-cation). We are aware of four additional genera that are to be proposed in the near future, two in the Akodontini and two in Oryzomyini. We close this contribution by offering the following revised classification of the extant Sigmodontinae.

Sigmodontinae Wagner, 1843
- *Abrawayaomys* Souza Cunha & Cruz, 1979
- *Andinomys* Thomas, 1902
- *Chinchillula* Thomas, 1898
- *Delomys* Thomas, 1917
- *Euneomys* Coues, 1874
- *Irenomys* Thomas, 1919
- *Juliomys* González, 2000
- *Neotomys* Thomas, 1894
- *Phaenomys* Thomas, 1917
- *Punomys* Osgood, 1943
- *Wilfredomys* Avila-Pires, 1960

Abrotrichini, new tribe
- *Abrothrix* Waterhouse, 1837
- *Chelemys* Thomas, 1903
- *Geoxus* Thomas, 1919
- *Notiomys* Thomas, 1890
- *Pearsonomys* Patterson, 1992

Akodontini Vorontsov, 1959
- *Akodon* Meyen, 1833
- *Bibimys* Massoia, 1979
- *Blarinomys* Thomas, 1896
- *Brucepattersonius* Hershkovitz, 1998
- *Deltamys* Thomas, 1917
- *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

Ichthyomyini Vorontsov, 1959
- *Anotomys* Thomas, 1906
- *Chibchanomys* Voss, 1988
- *Ichthyomys* Thomas, 1893
- *Neusticomys* Anthony, 1921
- *Rheomys* Thomas, 1906

Oryzomyini Vorontsov, 1959
- *Aegialomys* Weksler, Percequillo, & Voss, 2006
- *Amphinectomys* Malygin, 1994
- *Cerradomys* Weksler, Percequillo, & Voss, 2006
- *Eremoryzomys* Weksler, Percequillo, & Voss, 2006
- *Euryoryzomys* Weksler, Percequillo, & Voss, 2006
- *Handleyomys* Voss, Gómez-Laverde, & Pacheco, 2002
- *Holochilus* Brandt, 1835
- *Hylaeamys* Weksler, Percequillo, & Voss, 2006
- *Lundomys* Voss & Carleton, 1993
- *Melanomys* Thomas, 1902
- *Microryzomys* Thomas, 1917
- *Mindomys* Weksler, Percequillo, & Voss, 2006
- *Neacomys* Thomas, 1900
- *Nectomys* Peters, 1861
- *Nephelomys* Weksler, Percequillo, & Voss, 2006
- *Nesoryzomys* Heller, 1904
- *Oecomys* Thomas, 1906
- *Oligoryzomys* Bangs, 1900
- *Oreoryzomys* Weksler, Percequillo, & Voss, 2006
- *Oryzomys* Baird, 1857

Pseudoryzomys Hershkovitz, 1962
Scolomys Anthony, 1924
Sigmodontomys J. A. Allen, 1897
Sooretamys Weksler, Percequillo, & Voss, 2006
Transandinomys Weksler, Percequillo, & Voss, 2006
Zygodontomys J. A. Allen, 1897
Phyllotini Vorontsov, 1959
Andalgalomys Williams & Mares, 1978
Auliscomys Osgood, 1915
Calomys Waterhouse, 1837
Eligmodontia F. Cuvier, 1837
Galenomys Thomas, 1916
Graomys Thomas, 1916
Loxodontomys Osgood, 1947
Phyllotis Waterhouse, 1837
Salinomys Braun & Mares, 1995
Tapecomys Anderson & Yates, 2000
Reithrodontini Vorontsov, 1959
Reithrodon Waterhouse, 1837
Sigmodontini Wagner, 1843
Sigmodon Say & Ord, 1825
Thomasomyini Steadman & Ray, 1982
Aepeomys Thomas, 1898
Chilomys Thomas, 1897
Rhagomys Thomas, 1917
Rhipidomys Tschudi, 1845
Thomasomys Coues, 1884
Wiedomyini Reig, 1980
Wiedomys Hershkovitz, 1959

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