

KEY TO THE GENERA OF THE TRIBE ORYZOMYINI (RODENTIA: CRICETIDAE: SIGMODONTINAE)

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ABSTRACT: Due to recent phylogenetic and revisionary taxonomic work, the systematics of the Tribe Oryzomyini, the largest group of sigmodontine rodents, underwent profound changes. We present here an artificial key for the genera of this group of rodents, enabling researchers to identify oryzomyines using external, cranial and dental characteristics. We also present the most up-to-date diversity assessment of the tribe, in which we recognize 33 extant and extinct genera (plus three undescribed genus-group taxa) and 130 valid species

RESUMO: Chave para os gêneros da tribo Oryzomyini (Rodentia: Cricetidae: Sigmodontinae). Devido a esforços recentes em filogenia e revisão taxonômica, a sistemática da Tribo Oryzomyini, o grupo mais diversificado dentre os sigmodontíneos, passou por profundas mudanças. Neste trabalho, nós apresentamos uma chave artificial para os gêneros deste grupo de roedores, que permitirá a pesquisadores identificarem oryzomyíneos através de características de morfologia externa, craniana e dentária. Nós também apresentamos o panorama mais recente da diversidade da tribo, na qual reconhecemos 33 gêneros (além de três táxons do grupo do gênero ainda não descritos) e 130 espécies.

Key words. Sigmodontinae. Diversity. Identification. North, Central and South America

Palavras-chave. Sigmodontinae. Diversidade. Identificação. América do Norte, Central e do Sul.

INTRODUCTION

The oryzomyines form the most diverse tribe of sigmodontine rodents: members of the tribe are distributed in the Neotropical and Nearctic (southeastern section) regions from Tierra del Fuego to the Southern and Eastern United States, in the Galapagos Archipelago, and Trinidad and Tobago; extinct forms of the tribe are also found in several Caribbean islands, including Jamaica, Martinique, Curacao, Nevis, and Barbuda, among others (Turvey et al., 2010). Oryzomyines are found in almost

all major biomes in South America, including forests, savannas, swamps, scrublands, and semi-arid environments; in many of these habitats they are among the most speciose and abundant small mammals (Voss and Emmons, 1996; Eisenberg, 1999). Most oryzomyines are predominantly cursorial, but some species display marked arboreal (e.g., *Oecomys*) or semiaquatic (e.g., *Nectomys*, *Holochilus*, and *Lundomys*) specializations. Oryzomyines serve as primary or secondary hosts to a wide range of disease-carrying organisms, including hantavirus, arenavirus, digeneans (*Schistosoma*), and

trypanosomids (Mello, 1979; Rodrigues and Ferraz Filho, 1984; Picot, 1992; Bharadwaj et al., 1997; Fulhorst et al., 1997; Ribeiro et al., 1998; Calderon et al., 1999; Powers et al., 1999; D'Andrea et al., 2000).

The composition of the tribe has been stable since the early 1990's, and has been corroborated by phylogenetic analyses of morphological and nuclear sequences (Voss and Carleton, 1993; Steppan, 1995; Weksler, 2003, 2006), but not mitochondrial data (Smith and Patton, 1999; Bonvicino and Moreira, 2001; but see Percequillo et al. 2011 for combined nuclear and mitochondrial analysis supporting oryzomyine monophyly). For historical shifts in Oryzomyini taxonomy, see Hershkovitz (1944, 1955, 1962), Gardner and Patton (1976), Reig (1984, 1986), Carleton and Musser (1989), Voss (1991), Voss and Carleton (1993), and Weksler (2006).

Systematic work on the tribe has been active in recent years, and work in progress indicates that current taxonomy is not stable yet (Voss et al., 2002; Weksler et al., 2006; Percequillo et al., 2011). Considering these changes in the generic diversity and the lack of one reliable comprehensive source for their identification (D'Elía and Pardiñas, 2007), our aim here is to provide a dichotomous key for the extant taxa of genus-group level to allow the correct identification of these groups.

MATERIAL AND METHODS

The generic organization of the key follows Weksler et al. (2006), with the addition of taxa described thereafter. The position of the following taxa should be regarded as provisory: *Microakodontomys* is considered here as a valid and distinct genus (despite the previous Hershkovitzian footnote taxonomic decision of Weksler et al., 2006), based on preliminary molecular data (R. Paresque, pers. comm.; J. Hanson, pers. comm.) and on the distinctive morphology, including carotid circulation (pattern 3 of Voss, 1988), presence of alisphenoid strut, developed jugal, and very large orbicular apophysis of malleus (MZUSP specimens from Brasília, Brazil, collected by A. P. Carmignotto: APC 799, 813, 848, 856). The ex-"*Oryzomys alfaroi*" group was previously included in *Handleyomys* (Weksler et al., 2006), but at least one new genus should be erected to contain the *alfaroi-chapmani-melanotis* clade (*alfaroi* and

chapmani groups in the present key; Weksler, 2006; Weksler et al., 2006). *Sigmodontomys*, presently including *S. aphrastus* and *S. alfari*, is not monophyletic (Weksler, 2006; McCain et al., 2007) and a new genus is being described for *S. aphrastus* (*aphrastus* group in the following key; Pine et al., submitted). Thus, despite the lack of formal generic names for these groups, they are included here as separate entries on the key. As a key is only an artificial tool for taxa identification, we are confident that no taxonomic imprudence is being committed here. On the contrary, for practical purposes, our procedure aims to avoid misidentifications.

The collections and specimens examined to elaborate this key were listed elsewhere (Percequillo, 1998, 2003; Weksler, 2006; Weksler et al., 2006; Percequillo et al., 2008, 2011). The nomenclature of anatomic features and figures depicting them can be found in Carleton (1973, 1980), Reig (1977), Voss and Linzey (1981), Voss (1988, 1991, 1993), Carleton and Musser (1989), Weksler (2006). We employed preferentially external traits, in order to make the key useful for field researchers; however, some generic taxa can only be confidently identified with cranial characters. Therefore, the present key combines both external and cranial features to allow the recognition of generic forms.

RESULTS

Diagnosis of Tribe Oryzomyini

The tribe can be diagnosed by seven putative synapomorphies (Voss and Carleton, 1993; Steppan, 1995; Weksler, 2006; Weksler et al., 2006): presence of long palate with prominent posterolateral pits, absence of alisphenoid strut, absence of posterior suspensory process of the squamosal attached to tegmen tympani, absence of gall bladder, 12 thoracic vertebrae, absence of hemal arches on first caudal vertebrae, and fewer than 36 caudal vertebrae; the last two synapomorphies are reversed in several oryzomyine taxa. Members of the tribe can also be recognized by the soft fur (except in *Neacomys* and *Scolomys*, which have spiny fur), small, unkeeled manual claws (except in *Lundomys*, with long, ventrally keeled manual claws); mammary complement of eight teats in inguinal, abdominal, postaxial, and pectoral pairs (except in *Handleyomys* and *Scolomys*, which have six mammae because they lack pectoral teats); sparsely haired tail covered with more or

less conspicuous epidermal scales and lacking a terminal tuft of long hairs (the well-haired tail of *Nesoryzomys* does not appear scaly, and *Drymoreomys* and some species of *Oecomys* have prominently tufted tails); zygomatic plate without anterodorsal spinous process (except in *Pseudoryzomys*, *Lundomys*, and *Holochilus*, which exhibit a spinous process); nasal bones with rounded or squared posterior margins (except in *Nectomys*, *Scolomys*, and *Sigmodontomys*, which have acutely angled posterior nasal margins); smooth posterior wall of the orbit (except in *Holochilus*, which have a well-developed postorbital ridge); bony palate between the molar rows smooth or weakly sculpted (except in *Holochilus* and *Lundomys*, which have a well-developed median keel flanked by deep lateral gutters); alisphenoid canal with a large anterior opening (the anterior opening of the alisphenoid canal is absent or very small in *Scolomys*); upper incisors with smoothly rounded enamel bands (the upper incisor enamel is distinctly faceted in *Holochilus*); low-crowned or terraced molars (except in *Holochilus*, which has high-crowned, planar molars); labial flexi enclosed by a cingulum

(the labial flexi are unenclosed in *Holochilus* and *Lundomys*); parallel maxillary tooththrows (*Holochilus* and *Lundomys* have anteriorly convergent tooththrows); median mure connected to the protocone on M1 (except in *Holochilus*, which have the median mure connected to the paracone); unilocular-hemiglandular stomach; male accessory reproductive gland complements that include one pair each of bulbourethral, dorsal prostate, anterior prostate, vesicular, and ampullary glands, and two pairs of ventral prostate glands (except *Nesoryzomys*).

Generic contents of Tribe Oryzomyini

The tribe presently comprehends 36 extant and recently extinct taxa of the genus-group (including three undescribed genera) and approximately 130 taxa of the species group (including one species to be described); the updated taxonomic arrangement is provided on **Table 1**. Although we present in this table the recently extinct oryzomyine taxa (†*Agathaeromys*, †*Carletonomys*, †*Megalomys*, †*Noronhomys*, †*Pennatomys*), for practical purposes we include on the key only extant groups.

Table 1
List of genera and species currently assigned to Tribe Oryzomyini

Genus	Species
<i>Aegialomys</i> Weksler, Percequillo and Voss, 2006	<i>galapagoensis</i> Waterhouse, 1839 <i>xanthaesus</i> Thomas, 1894
† <i>Agathaeromys</i> Zijlstra, Madern, and van den Hoek Ostende, 2010	<i>donovani</i> Zijlstra, Madern, and van den Hoek Ostende, 2010 <i>praeuniversitatis</i> Zijlstra, Madern, and van den Hoek Ostende, 2010
<i>Amphinectomys</i> Malygin, Aniskin, Isaev and Milishnikov, 1994	<i>savamis</i> Malygin, Aniskin, Isaev and Milishnikov, 1994
† <i>Carletonomys</i> Pardiñas, 2008	<i>cailoi</i> Pardiñas, 2008
<i>Cerradomys</i> Weksler, Percequillo and Voss, 2006 ^a	<i>langguthi</i> Percequillo, Hingst-Zaher and Bonvicino, 2008 <i>maracajuensis</i> Langguth and Bonvicino, 2002 <i>marinhus</i> Bonvicino, 2003 <i>scotti</i> Langguth and Bonvicino, 2002 <i>subflavus</i> Wagner, 1842 <i>vivoi</i> Percequillo, Hingst-Zaher and Bonvicino, 2008
<i>Drymoreomys</i> Percequillo, Weksler and Costa, 2011	<i>albimaculatus</i> Percequillo, Weksler and Costa, 2011

(Table 1 cont.)

<i>Eremoryzomys</i> Weksler, Percequillo and Voss, 2006	<i>polius</i> Osgood, 1913
<i>Euryoryzomys</i> Weksler, Percequillo and Voss, 2006 ^b	<i>emmonsae</i> Musser, Carleton, Gardner and Brothers, 1998 <i>lamia</i> Thomas, 1901 <i>legatus</i> Thomas, 1925 <i>macconnelli</i> Thomas, 1910 <i>nitidus</i> Thomas, 1884 <i>russatus</i> Wagner, 1848
<i>Handleymys</i> Voss et al., 2002 ^c	<i>fuscatus</i> Allen, 1914 <i>intectus</i> Thomas, 1921
<i>Holochilus</i> Brandt, 1835 ^d	<i>brasiliensis</i> Desmarest, 1819 <i>chacarius</i> Thomas, 1906 † <i>primigenius</i> Steppan, 1996 <i>sciureus</i> Wagner, 1842
<i>Hylaeamys</i> Weksler, Percequillo and Voss, 2006 ^e	<i>acritus</i> Emmons and Patton, 2005 <i>megacephalus</i> Fischer, 1814 <i>oniscus</i> Thomas, 1904 <i>perenensis</i> Allen, 1901 <i>seuanezi</i> Weksler, Geise, and Cerqueira, 1999 ^f <i>tatei</i> Musser, Carleton, Gardner and Brothers, 1998 <i>yunganus</i> Thomas, 1902
<i>Lundomys</i> Voss and Carleton, 1993	<i>molitor</i> Winge, 1887
† <i>Megalomys</i> Trouessart, 1891	<i>audreyae</i> Hopwood, 1926 <i>curazensis</i> Hooijer, 1959 <i>desmarestii</i> Fischer, 1829 <i>luciae</i> Major, 1901
<i>Melanomys</i> Thomas, 1902 ^g	<i>caliginosus</i> Tomes, 1860 <i>robustulus</i> Thomas, 1914 <i>zunigae</i> Sanborn, 1949
<i>Microakodontomys</i> Hershkovitz, 1993	<i>transitorius</i> Hershkovitz, 1993
<i>Microryzomys</i> Thomas, 1917	<i>altissimus</i> Osgood, 1933 <i>minutus</i> Tomes, 1860
<i>Mindomys</i> Weksler, Percequillo and Voss, 2006	<i>hammondi</i> Thomas, 1913
<i>Neacomys</i> Thomas, 1900	<i>dubosti</i> Voss, Lunde and Simmons, 2001 <i>guianae</i> Thomas, 1905 <i>minutus</i> Patton, Silva and Malcolm, 2000 <i>mussieri</i> Patton, Silva and Malcolm, 2000 <i>paracou</i> Voss, Lunde and Simmons, 2001 <i>pictus</i> Goldman, 1912 <i>spinosus</i> Thomas, 1882
<i>Nectomys</i> Peters, 1861 ^h	<i>apicalis</i> Peters, 1861 <i>magdalenae</i> Thomas, 1897 <i>palmipes</i> Allen and Chapman, 1893 <i>rattus</i> Pelzeln, 1883 <i>squamipes</i> Brants, 1827

(Table 1 cont.)

- Nephelomys* Weksler, Percequillo and Voss, 2006ⁱ
- albigularis* Tomes, 1860
 - auriventer* Thomas, 1890
 - caracolus* Thomas, 1914
 - childi* Thomas, 1895
 - devius* Bangs, 1902
 - levipes* Thomas, 1902
 - keaysi* Allen, 1900
 - maculiventer* Allen, 1891
 - meridensis* Thomas, 1894
 - moerex* Thomas, 1914
 - nimbosus* Anthony, 1926
 - pectoralis* Allen, 1912
 - pirrensis* Goldman, 1913
 - one unnamed species
- Nesoryzomys* Heller, 1904
- darwini* Osgood, 1929
 - fernandinae* Hutterer and Hirsch, 1979
 - indefessus* Thomas, 1899
 - swarthy* Orr, 1938
- †*Noronhomys* Carleton and Olson, 1999
- vespucci* Carleton and Olson, 1999
- Oecomys* Thomas, 1906
- auyantepui* Tate, 19939
 - bicolor* Tomes, 1860
 - catherinae* Thomas, 1909
 - cleberi* Locks, 1981
 - concolor* Wagner, 1845
 - flavicans* Thomas, 1894
 - mamorae* Thomas, 1906
 - paricola* Thomas, 1904
 - phaeotis* Thomas, 1901
 - rex* Thomas, 1910
 - roberti* Thomas, 1904
 - rutilus* Anthony, 1921
 - speciosus* Allen and Chapman, 1893
 - superans* Thomas, 1911
 - sydandersoni* Carleton, Emmons and Musser, 2009
 - trinitatis* Allen and Chapman, 1893
- Oligoryzomys* Bangs, 1900ⁱ
- andinus* Osgood, 1914
 - arenalis* Thomas, 1913
 - brendae* Massoia, 1998
 - chacoensis* Myers and Carleton, 1981
 - delicatus* J.A. Allen and Chapman, 1897
 - destructor* Tschudi, 1844
 - flavescens* Waterhouse, 1837
 - fornesi* Massoia, 1973
 - fulvescens* Saussure, 1860
 - griseolus* Osgood, 1912
 - longicaudatus* Bennett, 1832
 - magellanicus* Bennett, 1836
 - microtis* Allen, 1916
 - nigripes* Olfers, 1818
 - stramineus* Bonvicino and Weksler, 1998
 - utiaritensis* Allen, 1916
 - vegetus* Bangs, 1902
 - victus* Thomas, 1898

(*Tabla 1 cont.*)

<i>Oreoryzomys</i> Weksler, Percequillo and Voss, 2006	<i>balneator</i> Thomas, 1900
<i>Oryzomys</i> Baird, 1858 ^{k, l}	<i>albiventer</i> Merriam, 1901 <i>†antillarum</i> Thomas, 1898 <i>couesi</i> Alston, 1877 <i>dimidiatus</i> Thomas, 1905 <i>gorgasi</i> Hershkovitz, 1971 <i>nelsoni</i> Merriam, 1898 <i>palustris</i> Harlan, 1837 <i>peninsulae</i> Thomas, 1897
† <i>Pennatomys</i> Turvey, Weksler, Norris and Nokkert, 2010	<i>nivalis</i> Turvey, Weksler, Norris and Nokkert, 2010
<i>Pseudoryzomys</i> Hershkovitz, 1962 ^m	<i>simplex</i> Winge, 1877
<i>Scolomys</i> Anthony, 1924 ⁿ	<i>melanops</i> Anthony, 1924 <i>ucayalensis</i> Pacheco, 1991
<i>Sigmodontomys</i> J.A. Allen, 1897 ^o	<i>alfari</i> Allen, 1897
<i>Sooretamys</i> Weksler, Percequillo and Voss, 2006	<i>angouya</i> Fischer, 1814
<i>Transandinomys</i> Weksler, Percequillo and Voss, 2006 ^p	<i>bolivaris</i> Allen, 1901 <i>talamancae</i> Allen, 1891
<i>Zygodontomys</i> J.A. Allen, 1897 ^q	<i>brevicauda</i> Allen and Chapman, 1893 <i>brunneus</i> Thomas, 1898 <i>cherriei</i> Allen, 1895
<i>alfaroii</i> group (unnamed taxon)	<i>alfaroii</i> Allen, 1891 <i>melanotis</i> Thomas, 1893 <i>rostratus</i> Merriam, 1901 <i>rhabdops</i> Merriam, 1901
<i>chapmani</i> group (unnamed taxon)	<i>chapmani</i> Thomas, 1898 <i>saturatior</i> Merriam, 1901
<i>aphrastus</i> group (unnamed taxon)	<i>aphrastus</i> Harris, 1932

a- Percequillo et al., 2008. b- Weksler, 1996; Musser et al., 1998; Percequillo, 1998. c- Voss et al., 2002; d- Steppan, 1996 e- Musser et al., 1998; Percequillo, 1998; Emmons and Patton, 2005. f- We believe that *laticeps* is a junior synonym of *megacephalus* and that the valid name for the species occurring in the Atlantic Forest in Brazil, from Bahia to Rio de Janeiro, is *H. seuanzei* (Weksler, Geise, and Cerqueira, 1999); additional revisionary work is required to resolve this issue; g- Hanson and Bradley (2008) stated that genus *Melanomys* assembles four species, *M. caliginosus*, *M. chrysomelas* and two other forms; we are convinced that the genus is more diverse than previously known, but as more consistent analysis of morphological variation along with examination of type specimens are still lacking, we will keep the current usage; h- Bonvicino, 1994. i- Percequillo, 2003; j- Weksler and Bonvicino, pers. com.; k- Voss and Weksler, 2009; l- Carleton and Arroyo-Cabral, 2009; m-Voss and Myers, 1991; n- Gómez-Laverde et al., 2004; o-Hanson and Bradley (2008) recovered *Sigmodontomys* and *Melanomys* as not reciprocally monophyletic employing the genus cyt-b, but with weak support; this relationship deserves a comprehensive analysis, as *Melanomys* is clearly one of the most distinctive groups of Oryzomyini (Weksler 2006), possessing several apomorphies related to its vole-like aspect: short tail, lack of counter-shading, dark pelage, and short pinna; p- Musser et al., 1998; q-Voss, 1991; Weksler, 2006; González et al. 2010; the latter stated that genus *Zygodontomys* is more diverse than previously considered, but more consistent analysis should be performed to validate these assumptions.

ARTIFICIAL KEY TO ORYZOMYINE GENERA

1. Dorsal and ventral fur with grooved spines..... 2
- 1'. Dorsal and ventral fur without grooved spines 3
2. Six mammae in inguinal, abdominal, and postaxial pairs (**Fig. 1A**) *Scolomys*
- 2'. Eight mammae in inguinal, abdominal, postaxial, and pectoral pairs *Neacomys*
3. Hindfeet with hypotenar pad absent or vestigial (**Fig. 1B**) 4
- 3'. Hindfeet with developed hypotenar pad 11
4. Hindfeet without natatory fringes – continuous combs of stiff hairs along the plantar margins and sometimes between the digits (**Fig. 1C**) 5
- 4'. Hindfeet with natatory fringes 8
5. Dorsal surface of hindfeet covered with dark hairs, feet appear brown 6
- 5'. Dorsal surface of hindfeet sparsely covered with short silvery hairs, feet appear grayish white or pale tan 7
6. Hind feet black or dark brown, with interdigital webs (**Fig. 1D**) *Sigmodontomys*
- 6'. Hind feet without interdigital webs *aphrastus* group
7. Interorbital region weakly beaded even in adults (**Fig. 2A**), mesoloph small on M1, M2, absent in M3 (**Fig. 3C**) *Pseudoryzomys*
- 7'. Interorbital region with strongly developed supraorbital crest in adults (figure 2A), mesoloph present and well developed on M1-M3 *Oryzomys*
8. Nasal with acutely pointed posterior terminus (**Fig. 2B**); molars brachydont, cingula closing labial folds 9
- 8'. Nasal with blunt posterior terminus, molars hypsodont or planar, labial folds open 10
9. Body pelage with strong countershading; upper incisors orthodont *Amphinectomys*
- 9'. Body pelage with weak countershading; upper incisors opisthotont *Nectomys*
10. Alisphenoid strut present (**Fig. 2C**); postorbital ridge present; accessory labial root on M1 present *Holochilus*
- 10'. Alisphenoid strut absent; postorbital ridge absent; accessory labial root on M1 absent *Lundomys*
11. Plantar pads on hindfeet highly developed, large and fleshy, interdigitals 1–4 set close together, often in contact (**Fig. 1B**); mystacial vibrissae long and abundant (**Fig. 1E**) 12
- 11'. Pads smaller, interdigitals 1 and 4 displaced proximally relative to 2 and 3, mystacial vibrissae shorter and more sparse 13
12. Venter without gular patch of self-colored hairs; palate long (**Fig. 3A**); supraorbital margins squared, strongly beaded or with distinct crests (**fig. 2A**) *Oecomys*
- 12'. Venter with gular patch of self-colored hairs; dorsal surface of hindfeet with distinct dark patch; palate short; supraorbital margins lightly beaded *Drymoreomys*
13. Tail much shorter than head and body (ca. 85% of head and body length) 14
- 13'. Tail subequal or longer than head and body 15
14. Dorsal pelage grizzly or light brown *Zygodontomys*
- 14'. Dorsal pelage dark brown *Melanomys*
15. Sphenofrontal foramen absent (**Fig. 2D**) 16
- 15.'. Sphenofrontal foramen present 24
16. Small mice (HBL of adults rarely larger than 110 mm) 17
- 16'. Medium or large rats (HBL of young rarely smaller than 110 mm) 19
17. Anteromedian flexus present (**Fig. 3C**) 18
- 17'. Anteromedian flexus absent *chapmani* group
18. Jugal absent or vestigial; alisphenoid strut absent; stapedial foramen present (pattern 2; Voss, 1988; except in *Oligoryzomys rupestris*); mesoloph and mesolophid frequently present (**Fig. 3C**; absent in a few specimens of *O. fornesi*) *Oligoryzomys*

- 18'. Jugal present; alisphenoid strut always present; stapedial foramen absent (pattern 3; Voss, 1988); mesoloph and mesolophid always absent *Microakodontomys*
19. Stapedial foramen present (**Figs. 2D, 3B**) *Hylaeyamys*
- 19'. Stapedial foramen absent or vestigial 20
20. Tail densely furred, scales not visible *Nesoryzomys*
- 20'. Tail sparsely furred giving naked impression, scales visible 21
21. Mystacial vibrissae very long (**Fig. 1E**); interorbital region hour-glass shaped with squared margins (**Fig. 2A**) *Sooretamys*
- 21'. Mystacial vibrissae short; interorbital region anteriorly convergent with beaded margins 22
22. First upper and lower molars without accessory roots; mandible capsular process absent or indistinct (**Fig. 2E**) *Eremoryzomys*
- 22'. First molars with accessory roots; capsular process well developed 23
23. Anterocone of M1 undivided (anteromedian flexus absent; **Fig. 3C**); baculum bifid
..... *Cerradomys*
- 23'. Anterocone of M1 divided by anteromedian flexus; baculum trifid *Aegialomys*
24. Very small mice (HBL<100) with tail much longer than body length 25
- 24'. Medium and large rats (HBL>100) with tail as long as or longer than body length 26
25. Pelage distinctly countershaded; foramen magnum oriented caudally; anteroconid of m1 undivided (anteromedian flexid absent; **Fig. 3D**) *Oreoryzomys*
- 25'. Pelage not countershaded; foramen magnum oriented posteroventrally; anteroconid of m1 divided by anteromedian flexid *Microryzomys*
26. Superciliary vibrissae extending posteriorly beyond pinnae (**Fig. 1E**) 27
- 26'. Superciliary vibrissae not extending posteriorly beyond pinnae 28
27. Zygomatic notch (**Fig. 2B**) indistinct, small zygomatic plate *Mindomys*
- 27'. Zygomatic notch deep, broad zygomatic plate *Transandinomys*
28. Anterocone of M1 divided by anteromedian flexus (**Fig. 3C**) *Nephelomys*
- 28'. Anterocone of M1 undivided, anteromedian flexus absent 29
29. M1 without labial accessory root, m2 with 2 roots *Euryoryzomys*
- 29'. M1 with labial accessory root, m2 with 3 roots 30
30. Six mammae in inguinal, abdominal, and postaxial pairs (**Fig. 1A**); hindfoot with hypotenar pad present; long rostrum; sphenopalatine vacuities long and wide *Handleymys*
- 30'. Eight mammae in inguinal, abdominal, postaxial, and pectoral pairs; hindfoot with hypotenar pad absent; short rostrum; sphenopalatine vacuities absent or small *alfaroii* group

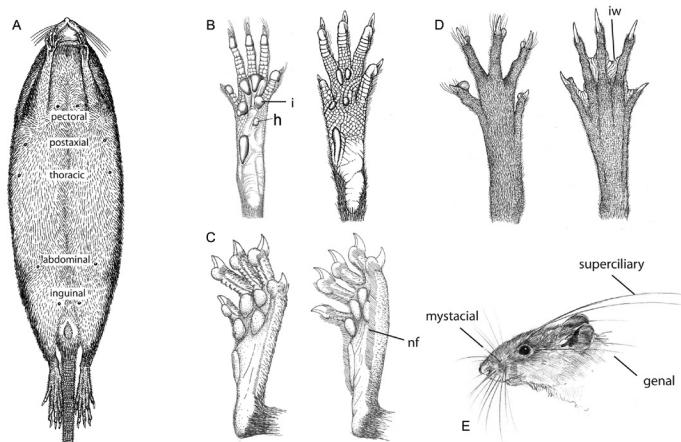


Fig. 1. Integumental characters used in the key for oryzomyine genera. **A.** Anatomical position of mammary pairs in sigmodontine rodents; modified from Voss and Carleton (1993: fig. 8). **B.** Plantar view of left hindfoot, illustrating the presence (left) and absence (right) hypothear pad (**h**), and the anatomical position of the interdigital pads (**i**); modified from Weksler (2006: fig. 9) and Carleton and Musser (1989: fig. 9). **C.** Ventrolateral view of left hindfoot illustrating the absence (left) and presence (right) of natatory fringes (**nf**); modified from Voss (1988: fig. 6). **D.** Dorsal view of hindfoot left illustrating the absence (left) and presence (right) of interdigital webbing (**iw**); modified from Weksler (2006: fig. 10). **E.** Anatomical position of facial vibrissae in sigmodontine rodents; modified from Musser et al. (1998: fig. 53).

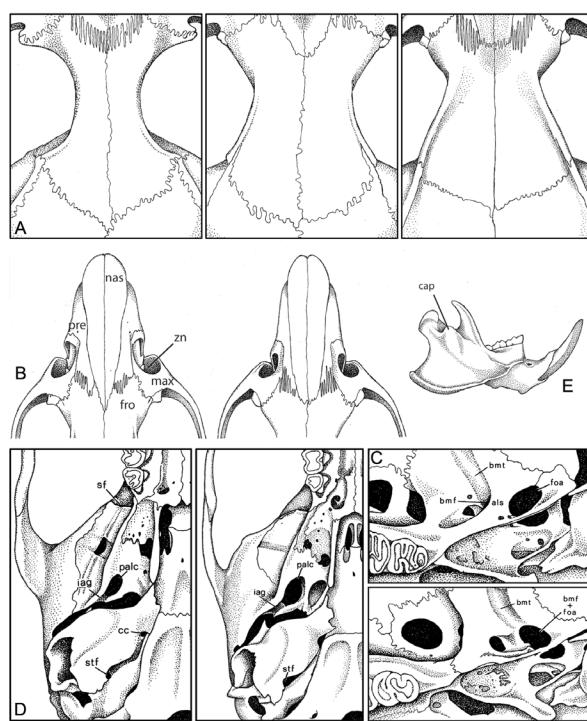


Fig. 2. Cranial characters used in the key for oryzomyine genera. **A.** Dorsal view of interorbital region illustrating the variations in its shape: hourglass (left), weakly beaded and convergent anteriorly (center), and strongly beaded and convergent anteriorly (right); modified from Weksler (2006: Fig. 13). **B.** Dorsal view of rostrum illustrating the shape of the posterior nasal terminus, pointed (left) or blunt (right), and the anatomical position of the zygomatic notch. Abbreviations are **fro**, frontal; **max**, maxillary; **nas**, nasal; **pre**, premaxillary; **zn**, zygomatic notch; modified from Weksler (2006: Fig. 11). **C.** Lateral view of the braincase illustrating the presence (left) and absence (right) of the alisphenoid strut. Abbreviations are **als**, alisphenoid strut; **bmf**, buccinator-masticatory foramen; **foa**, foramen ovale accessorius; modified from Voss and Carleton (1993: Fig. 10). **D.** Ventral view of basicranium illustrating variation of carotid circulatory patterns. Abbreviations are **cc**, carotid canal; **iag**, groove for the infraorbital branch of stapedial artery; **palc**, posterior opening of the alisphenoid canal; **sf**, sphenofrontal foramen; **stf**, stapedial foramen. Modified from Carleton and Musser (1989: Fig. 17). **E.** Lateral view of right mandibles illustrating the anatomical position of the capsular process of the lower incisor alveolus (**cap**); modified from Weksler (2006: Fig. 24).

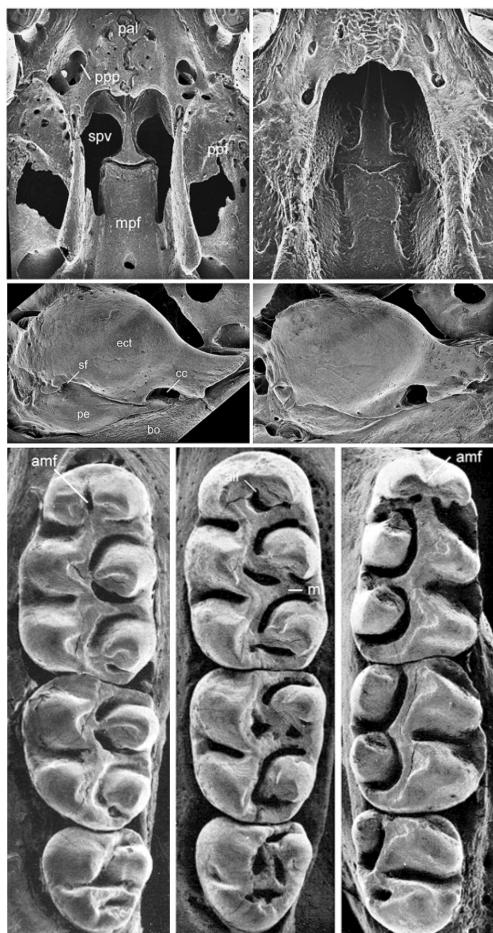


Fig. 3. Cranial and dental characters used in the key for oryzomyine genera. **Above:** Ventral view of the palatal and basicranial region illustrating the variations in the morphology of posterior palate. Abbreviations are **mpf**, mesopterygoid fossa; **pal**, palatine; **ppf**, parapterygoid fossa; **ppp**, postrolateral pit; **spv**, sphenopalatine vacuity. **Middle:** Medial view of auditory bulla illustrating variations in the ectotympanic morphology. Abbreviations are **bo**, basioccipital; **cc**, carotid canal; **ect**, ectotympanic; **pe**, periotic; **sf**, stapedial foramen. **Below:** Anatomical position of the anteromedian flexus (**amf**) and mesoloph (**m**) in the upper molars of oryzomyines. **D**. Anatomical position of the anteromedian flexid (**amf**) in the first lower molar of oryzomyines.

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