

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3537, 29 pp., 1 figure, 3 tables
October 19, 2006

Ten New Genera of Oryzomyine Rodents (Cricetidae: Sigmodontinae)

MARCELO WEKSLER,¹ ALEXANDRE REIS PERCEQUILLO,²
AND ROBERT S. VOSS³

ABSTRACT

In order to achieve a monophyletic classification of oryzomyine rodents, 10 new genera are described for species or species groups previously referred to the polyphyletic genus *Oryzomys*. The following names are proposed: *Aegialomys*, n.gen. (for the “*xanthaeolus* group” of authors); *Cerradomys*, n.gen. (for the “*subflavus* group”); *Eremoryzomys*, n.gen. (for *polius*); *Euryoryzomys*, n.gen. (for the “*nitidus* group”); *Hylaeamys*, n.gen. (for the “*megacephalus* group”); *Mindomys*, n.gen. (for *hammondi*); *Nephelomys*, n.gen. (for the “*albigularis* group”); *Oreoryzomys*, n.gen. (for *balneator*); *Sooretamys*, n.gen. (for *angouya*); and *Transandinomys*, n.gen. (for *bolivaris* and *talamancae*). All of the new genera thus constituted are morphologically diagnosable and have distinct ecogeographic distributions. Pending revisionary work that is currently in progress by other researchers, six species belonging to the “*alfaroi* group” (herein construed as including *alfaroi*, *chapmani*, *melanotis*, *rhabdops*, *rostratus*, and *saturator*) are provisionally referred to *Handleyomys*. As a result of these changes, the genus *Oryzomys* is restricted to the “*palustris* group” of authors, and the tribe Oryzomyini now comprises 28 genera.

INTRODUCTION

A striking characteristic of muroid rodent classification at the middle of the last century was the large number of species assigned to

a few geographically widespread and morphologically undiagnosable genera. Although *Rattus* (sensu lato) is perhaps the most notorious example (Musser, 1981; Musser and Newcomb, 1983; Musser and Holden,

¹ Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History. Present address: Institute of Arctic Biology and University of Alaska Museum, University of Alaska Fairbanks, Fairbanks, AK 99775 (mwexler@amnh.org).

² Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Caixa Postal 5133, 58051-970 João Pessoa, Paraíba, Brazil (arpercequillo@dse.ufpb.br).

³ Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History (voss@amnh.org).

1991), several New World genera have also served as convenient receptacles for superficially similar but phylogenetically heterogeneous species. In Neotropical mammalogy, this was the traditional role of such elastic taxa as *Akodon*, *Oryzomys*, and *Thomasomys*. Thanks to revisionary research in the last several decades (reviewed by Musser and Carleton, 1993, 2005), each of these genera is now recognized in a much more restricted sense than formerly, but many nomenclatural problems remain. The purpose of this report is to complete the transition from traditional usage to a phylogenetic classification of the species hitherto referred to *Oryzomys*.

As treated in influential mid-20th-century checklists (e.g., Tate, 1932; Gyldenstolpe, 1932; Ellerman, 1941; Hall and Kelson, 1959; Cabrera, 1961), the genus *Oryzomys* contained anywhere from 60 to 120 nominal taxa in five to seven subgenera that collectively ranged from Patagonia to New Jersey. The artificiality of this usage was subsequently emphasized by karyotypic and morphological researchers (e.g., Gardner and Patton, 1976; Carleton and Musser, 1989) who raised all of the subgenera recognized by midcentury authors to generic rank. The species that are still referred to *Oryzomys*, however, do not comprise a monophyletic group (fig. 1), and it is intolerable that this situation should persist.

In order to achieve a monophyletic classification, we now name 10 new genera for species currently classified as *Oryzomys*. Pending the description of other new genera (by M.D. Carleton and G.G. Musser, personal commun.), we provisionally transfer members of the “*alfaroi* group” (herein understood to include *alfaroi*, *chapmani*, *melanotis*, *rhabdops*, *rostratus*, and *saturatior*) to *Handleyomys*, a suboptimal but phylogenetically defensible nomenclatural option previously discussed by Weksler (2006). Table 1 lists all of the oryzomyine genera that we recognize as valid, including those described as new herein.

NEW GENERA

Most of the clades for which we provide new generic names have been recognized in one form or another for many years, usually as informally designated species “groups” or

“complexes” (e.g., by Goldman, 1918; Tate, 1932; Ellerman, 1941; Gardner and Patton, 1976; Weksler, 1996; Musser et al., 1998; Percequillo, 1998, 2003; Sánchez et al., 2001). In the accounts that follow, we designate a type species for each new genus, list the valid species (and synonyms) referred to it, describe its geographic distribution, provide morphological diagnoses and comparisons, and briefly comment on the criteria we used to determine the assignment of species not represented in published analyses of character data. Throughout these accounts, morphological characters are described using terminology defined and illustrated by Voss (1988, 1993), Carleton and Musser (1989), Voss and Carleton (1993), Musser et al. (1998), Voss et al. (2002), and Weksler (2006).

COMMON ATTRIBUTES

The taxa named below share many attributes that it would be pointless to repeat in each diagnosis. For example, insofar as known (postcranial skeletons have not been examined from all taxa), they resemble other members of the cricetid subfamily Sigmodontinae by having a double articulation of the first rib, lacking an entepicondylar foramen of the humerus, and lacking an entoglossal process of the basihyal. Similarly, the material we examined indicates that they consistently resemble other members of the tribe Oryzomyini in lacking a posterior suspensory process of the squamosal, having 12 ribs, having unilocular-hemiglandular stomachs, and lacking a gall bladder.

Some characters that vary within Oryzomyini are likewise uninformative in the context of these comparisons and need not be repeated below. Like most oryzomyines (with exceptions as noted), all of the taxa described herein have soft fur (*Neacomys* and *Scolomys* have spiny fur); the manual claws are small and unkeeled (*Lundomys* has long, ventrally keeled manual claws); the hind feet lack well-developed natatory fringes and interdigital webs (well-developed natatory fringes and/or webbing are present in *Amphinectomys*, *Holochilus*, *Lundomys*, *Nectomys*, *Oryzomys palustris*, and *Pseudoryzomys*); the mammary complement consists of eight teats in inguinal,

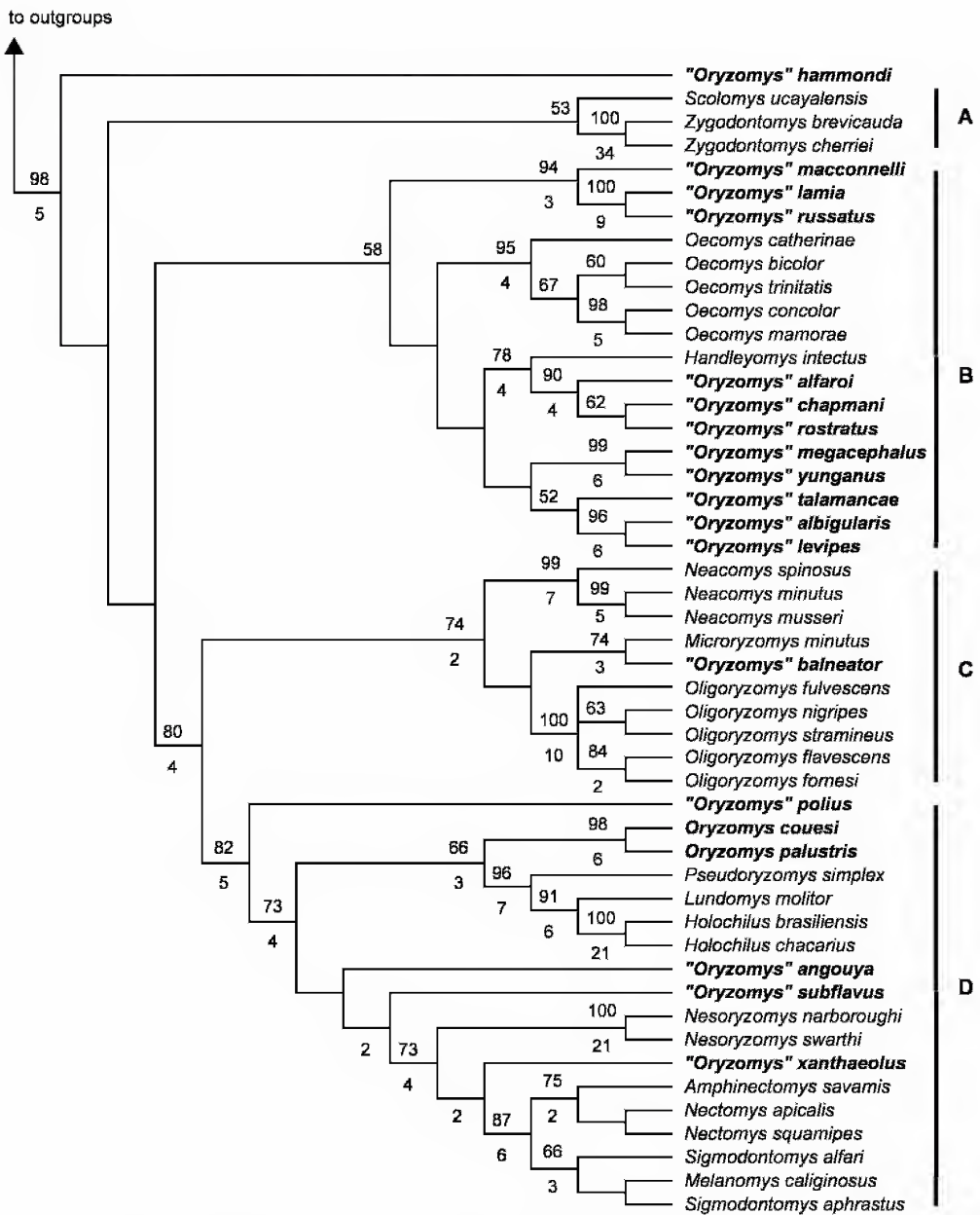


Fig. 1. Phylogenetic relationships of oryzomyines based on a heuristic parsimony analysis of sequence data from the Interphotoreceptor Retinoid Binding Protein (IRBP, 1266 bp from exon 1) and 99 morphological characters (after Weksler, 2006: fig. 37). Numbers above and below branches represent jackknife support (>50%) and decay indices (>1), respectively. Vertical bars on the right-hand side of the figure indicate taxon membership in clades A–D. See Weksler (2006: 14–17) for methodological details.

abdominal, postaxial, and pectoral pairs (*Handleyomys* and *Scolomys* have six mammae because they lack pectoral teats); the sparsely haired tail is covered with more or

less conspicuous epidermal scales and lacks a terminal tuft of long hairs (the well-haired tail of *Nesoryzomys* does not appear scaly, and some species of *Oecomys* have prominently

TABLE 1
Contents of the Tribe Oryzomyini

Genus	Type species	Valid species ^a
<i>Aegialomys</i> (new)	<i>xanthaeolus</i> Thomas, 1894	2 ^b
<i>Amphinectomys</i> Malygin et al., 1994	<i>savamis</i> Malygin et al., 1994	1
<i>Cerradomys</i> (new)	<i>subflavus</i> Wagner, 1842	4 ^b
<i>Eremoryzomys</i> (new)	<i>polius</i> Osgood, 1913	1 ^b
<i>Euryoryzomys</i> (new)	<i>macconnelli</i> Thomas, 1910	6 ^b
<i>Handleyomys</i> Voss et al., 2002	<i>intectus</i> Thomas, 1921	8 ^c
<i>Holochilus</i> Brandt, 1835	<i>sciureus</i> Wagner, 1842	3
<i>Hylaeamys</i> (new)	<i>megacephalus</i> Fischer, 1814	7 ^b
<i>Lundomys</i> Voss and Carleton, 1993	<i>molitor</i> Winge, 1887	1
<i>Megalomys</i> Trouessart, 1881	<i>pilorides</i> Desmarest, 1826	2
<i>Melanomys</i> Thomas, 1902	<i>phaeopus</i> Thomas, 1894	3
<i>Microroryzomys</i> Thomas, 1917	<i>minutus</i> Tomes, 1860	2
<i>Mindomys</i> (new)	<i>hammondi</i> Thomas, 1913	1
<i>Neacomys</i> Thomas, 1900	<i>spinosus</i> Thomas, 1882	8
<i>Nectomys</i> Peters, 1861	<i>squamipes</i> Brants, 1827	5
<i>Nephelomys</i> (new)	<i>albigularis</i> Tomes, 1860	13 ^b
<i>Nesoryzomys</i> Heller, 1904	<i>narboroughi</i> Heller, 1904	4
<i>Noronhomys</i> Carleton and Olson, 1999	<i>vespucii</i> Carleton and Olson, 1999	1
<i>Oecomys</i> Thomas, 1906	<i>benevolens</i> Thomas, 1901	15
<i>Oligoryzomys</i> Bangs, 1900 ^d	<i>navus</i> Bangs, 1900	18 ^d
<i>Oreoryzomys</i> (new)	<i>balneator</i> Thomas, 1900	1 ^b
<i>Oryzomys</i> Baird, 1858	<i>palustris</i> Harlan, 1837	5 ^c
<i>Pseudoryzomys</i> Hershkovitz, 1962	<i>wavrini</i> Thomas, 1921	1
<i>Scolomys</i> Anthony, 1924	<i>melanops</i> Anthony, 1924	2
<i>Sigmodontomys</i> J.A. Allen, 1897	<i>alfari</i> J.A. Allen, 1897	2
<i>Sooretamys</i> (new)	<i>angouya</i> Fischer, 1814	1 ^b
<i>Transandinomys</i> (new)	<i>talamancae</i> J.A. Allen, 1891	2 ^b
<i>Zygodontomys</i> J.A. Allen, 1897	<i>cherriei</i> J.A. Allen, 1895	2

^aAs recognized by Musser and Carleton (2005) except as noted.

^bAs recognized in this report.

^cIn addition to the taxa referred to *Handleyomys* by Voss et al. (2002), we provisionally allocate the following species to this genus pending the description of new genera to contain them (M.D. Carleton and G.G. Musser, personal commun.): *alfaroi* J.A. Allen, 1891; *chapmani* Thomas, 1898; *melanotis* Thomas, 1893; *rhabdops* Merriam, 1901; *rostratus* Merriam, 1901; and *saturatior* Merriam, 1901. See Musser and Carleton (2005) for synonyms.

^dIncluding *Microakodontomys* Hershkovitz, 1993, based on a single anomalous specimen of *Oligoryzomys* lacking mesoloph(id)s.

^eAs restricted herein, *Oryzomys* consists of the "palustris group" as defined and diagnosed by Sánchez et al. (2001). We recognize the following species as valid: *antillarum* Thomas, 1898; *couesi* Alston, 1877; *dimidiatus* Thomas, 1905; *gorgasi* Hershkovitz, 1971; and *palustris* Harlan, 1837. See Musser and Carleton (2005) for synonyms and Morgan (1993) for comments on the status of *O. antillarum* (not recognized as valid by Musser and Carleton, 2005). The subfossil material that McFarlane and Debrot (2001) described as *O. curasoae* is likewise referable to *Oryzomys* sensu stricto, but this name may be a junior synonym of *O. gorgasi*.

tufted tails); the zygomatic plate lacks an anterodorsal spinous process (a spinous process is present in *Pseudoryzomys*, *Lundomys*, and *Holochilus*); the nasal bones have rounded or squared posterior margins (*Nectomys*, *Scolomys*, and *Sigmodontomys* have acutely angled posterior nasal margins); the posterior wall of the orbit is smooth (*Holochilus* has

a well-developed postorbital ridge); the bony palate between the molar rows is smooth or weakly sculpted (the palates of *Holochilus* and *Lundomys* have a well-developed median keel flanked by deep lateral gutters); the alisphenoid canal has a large anterior opening (the anterior opening of the alisphenoid canal is absent or very small in *Scolomys*); the upper

incisors have smoothly rounded enamel bands (the upper incisor enamel is distinctly faceted in *Holochilus*); the molars are low-crowned and bunodont or terraced (*Holochilus* has high-crowned, planar molars); the labial flexi are enclosed by a cingulum (the labial flexi are unenclosed in *Holochilus* and *Lundomys*); the maxillary toothrows are parallel (*Holochilus* and *Lundomys* have anteriorly convergent toothrows); mesolophs are present on all upper molars (*Holochilus*, *Lundomys*, *Pseudoryzomys*, *Scolomys*, and *Zygodontomys* lack mesolophs on one or more upper teeth); the median mure is connected to the protocone on M1 (the median mure is connected to the paracone in *Holochilus*); the paracone of M2 lacks an accessory loph (an accessory loph is present in *Oecomys*); and a posteroflexid is present on m3 (posteroflexids are absent on m3 in *Holochilus*, *Lundomys*, *Pseudoryzomys*, and *Zygodontomys*). Likewise, all dissected oryzomyines (except *Nesoryzomys*) have 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.

In effect, the species that still remain in *Oryzomys* are those that lack the conspicuously divergent morphological traits of oryzomyines hitherto referred to other genera. However, the taxa named below differ in other characters that provide an unambiguous basis for the following diagnoses and comparisons.

Aegialomys, new genus

TYPE SPECIES: *Oryzomys xantheolus* Thomas, 1894.

CONTENTS: *galapagoensis* Waterhouse, 1839 (including *bauri* J.A. Allen, 1892) and *xantheolus* Thomas, 1894 (including *baroni* J.A. Allen, 1897, and *ica* Osgood, 1944).

DISTRIBUTION: In the lowland dry forests of western Ecuador (including the Galapagos Islands) and western Peru, but also at higher elevations (to about 2500 m) in the upper Marañón valley of northern Peru.

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage coarsely grizzled yellowish- or grayish-brown; ventral pelage abruptly paler (superficially whitish or pale yellow), but ventral hairs always gray-based. Pinnae small, not reaching

eye when laid forward. Mystacial and superciliary vibrissae not extending posteriorly beyond pinnæ when laid back. Hind foot with conspicuous tufts of unguis hairs at bases of claws on dI–dV; plantar surface densely covered with distinct squamae distal to thenar pad; hypothenar pad present and large; claw of dI extending beyond middle of phalange 1 (almost to first interphalangeal joint) of dII; claw of dV extending just beyond first interphalangeal joint of dIV. Tail about as long as head and body in *A. galapagoensis* but distinctly longer than head and body in *A. xantheolus*; weakly to distinctly bicolored (dark above, pale below).

Skull with stout rostrum flanked by deep zygomatic notches; interorbital region anteriorly convergent with strongly beaded supra-orbital margins; braincase oblong, usually with well-developed temporal crests; lambdoidal and nuchal crests often well developed in older adults. Posterior margin of zygomatic plate dorsal to M1 alveolus in some examined specimens, anterior to M1 alveolus in others. Jugal present but small (the maxillary and squamosal zygomatic processes broadly overlapping in lateral view but not in contact). Nasals extending posteriorly behind lacrimals in *A. galapagoensis* but shorter (extending to but usually not behind lacrimals) in *A. xantheolus*; lacrimals usually with longer maxillary than frontal sutures. Fronto-squamosal suture usually colinear with frontoparietal suture. Parietals with broad lateral expansions. Incisive foramina long, typically extending posteriorly to or between M1 alveoli; almost parallel-sided (in *A. galapagoensis*) or widest at midlength and tapering symmetrically anteriorly and posteriorly (in *A. xantheolus*). Posterolateral palatal pits large, complex, and recessed in deep fossae; mesopterygoid fossa penetrating anteriorly between maxillae in *A. galapagoensis* but often not in *A. xantheolus*; bony roof of mesopterygoid fossa perforated by very large sphenopalatine vacuities. Alisphenoid strut absent (buccinator-masticatory foramen and accessory foramen ovale confluent). Stapedial foramen and posterior opening of alisphenoid canal small; squamosal-alisphenoid groove and sphenofrontal foramen absent; secondary anastomosis of internal carotid crosses dorsal surface of

pterygoid plate (= carotid circulatory pattern 3 of Voss, 1988). Postglenoid foramen large and rounded; subsquamosal fenestra small but distinct in most forms, but vestigial or absent in an unnamed species from coastal Ecuador. Periotic exposed posteromedially between ectotympanic and basioccipital, but usually not extending anteriorly to carotid canal; mastoid unfenestrated or with a small but distinct posterodorsal fenestra (in specimens from coastal Ecuador). Capsular process of lower incisor alveolus well developed in most fully adult specimens; superior and inferior masseteric ridges conjoined anteriorly as single crest below m1.

Labial and lingual flexi of M1 and M2 not interpenetrating. First upper molar (M1) anterocone divided into anterolabial and anterolingual conules by distinct anteromedian flexus in some forms (e.g., *A. galapagoensis* and an undescribed species from coastal Ecuador), undivided in others (e.g., *A. xantheolus*, which, however, has a small internal fossette that seems to represent a vestigial anteromedian flexus); anteroloph well developed and fused with anterostyle on labial cingulum, separated from anterocone by persistent anteroflexus in some species (e.g., *A. xantheolus*) but fused with anterocone (anteroflexus reduced or absent) in others; proto-style absent; paracone usually connected by enamel bridge to posterior moiety of protocone. Second upper molar (M2) protoflexus present; mesoflexus present as single internal fossette. Third upper molar (M3) with posteroloph and diminutive hypoflexus (the latter tending to disappear with moderate to heavy wear). Accessory labial root of M1 often present.

First lower molar (m1) anteroconid usually without an anteromedian flexid; anterolabial cingulum present on all lower molars; anterolophid present on m1 but absent on m2 and m3; ectolophid absent on m1 and m2; mesolophid distinct on unworn m1 but reduced on m2; m2 hypoflexid short. Accessory lingual and labial roots of m1 present; m2 and m3 each with two small anterior roots and one large posterior root.

Fifth lumbar (17th thoracolumbar) vertebra with well-developed anapophysis. Hemal arch between second and third caudal verte-

brae with posterior spinous process. Supratrochlear foramen of humerus present.

Stomach without extension of glandular epithelium into corpus. One pair of preputial glands present. Distal bacular cartilage of glans penis small and trifid (with a short and slender central digit); nonspinous tissue on rim of terminal crater does not conceal bacular mounds; dorsal papilla spineless; urethral processes without subapical lobules.

COMPARISONS: *Aegialomys* was represented by "*Oryzomys*" *xantheolus*⁴ in the phylogenetic analyses of Weksler (2003, 2006), who consistently recovered it as a member of clade D. Within clade D, "*O.*" *xantheolus* usually appeared as the sister taxon of a group composed of *Amphinectomys*, *Melanomys*, *Nectomys*, and *Sigmodontomys* (as in fig. 1). Phenetically, however, *Aegialomys* more closely resembles *Oryzomys* sensu stricto (the "*palustris* group" of authors), *Cerradomys* (the "*subflavus* group"), and *Eremoryzomys* (the "*polius* group"). Comparisons with *Oryzomys* sensu stricto and *Cerradomys* are provided here, and comparisons with *Eremoryzomys* are included in the account for that genus (below). Table 2 summarizes key morphological comparisons among all of the new taxa belonging to clade D.

Aegialomys differs from *Oryzomys* in numerous traits, among which the most noteworthy are its large, distinct hypothenar pad on the hind foot (the hypothenar pad is absent or vestigial in *Oryzomys*); conspicuous tufts of long ungual hairs at the bases of the claws on pedal digits II–V (the ungual hairs are sparse and short in *Oryzomys*); M1 anteromedian flexus present or vestigial (the anteromedian flexus is unambiguously absent in *Oryzomys*); M1 paracone usually attached by an enamel bridge to the posterior moiety of the protocone (the attachment is usually to the anterior moiety in *Oryzomys*); M2 mesoflexus forming a single internal fossette (the M2 mesoflexus usually forms two internal fossettes in *Oryzomys*); lack of distinct anterolophids on

⁴ Subsequent study indicates that this terminal taxon was a composite based on material of the unnamed Ecuadorean species mentioned in the preceding diagnosis together with *Aegialomys xantheolus* sensu stricto. Taxonomic differences therefore account for some of the character variation scored as polymorphisms of *A. xantheolus* in Weksler's (2006) analyses.

TABLE 2
Selected Morphological Comparisons Among New Genera from Clade D

	<i>Aegialomys</i>	<i>Cerradomys</i>	<i>Eremoryzomys</i>	<i>Sooretamys</i>
Mystacial vibrissae:	short	short	short	long
Tail:	weakly to distinctly bicolored	weakly to distinctly bicolored	distinctly bicolored	unicolored
Interorbit:	anteriorly convergent with beaded margins	anteriorly convergent with beaded margins	anteriorly convergent with beaded margins	hourglass-shaped with squared margins
Jugal:	small	small	large	small
Incisive foramina:	long	long	very long	long
Mesopterygoid fossa:	extends between maxillae	extends between maxillae	extends to or between molar rows	extends between maxillae
Alisphenoid strut:	absent	present or absent	present	absent
Capsular process:	well developed	well developed	indistinct or absent	well developed
M1 anterocone:	divided	undivided	divided	undivided
M2 internal fossette(s):	one	two	one or two	two
M1 accessory root:	present	present	absent	absent
m1 accessory roots:	labial and lingual	labial and lingual	absent	labial only
Baculum:	trifid	bifid	unknown	trifid

m2 and m3 (anterolophids are usually distinct on unworn m2 and m3 in *Oryzomys*); and mesolophids that tend to disappear as distinct structures with only moderate wear (mesolophids are persistent as distinct structures in *Oryzomys*). In addition, *A. xantheolus* has a well-developed anapophysis on the fifth lumbar vertebra that is absent in *O. couesi* and *O. palustris*; a tridigitate bacular cartilage with a short and slender central digit (the central digit is robust in *O. couesi* and *O. palustris*); a spineless dorsal papilla (the dorsal papilla is provided with spines in *O. couesi* and *O. palustris*); and urethral processes that lack subapical lobules (subapical lobules are present on the urethral processes of *O. couesi* and *O. palustris*).

Although *Aegialomys xantheolus* and *Cerradomys subflavus* differ in numerous morphological characters and were never recovered as sister taxa in Weksler's (2003, 2006) phylogenetic analyses, only a few traits distinguish their respective genera as recognized herein. This difficulty arises from substantial character variation among species within

each genus: for example, as documented in Langguth and Bonvicino's recent (2002) descriptions of new species of *Cerradomys*, and by our remarks about character variation in *Aegialomys* (above). In fact, *Aegialomys* and *Cerradomys* do not appear to differ consistently in any integumental or cranial feature that we have been able to identify. Several dental and genitalic characters, however, suggest that these are distinct taxa that merit formal recognition. Because they are so few, each character merits particular attention.

In *Aegialomys galapagoensis*, the unworn anterocone of M1 is divided into subequal anterolabial and anterolingual conules by an anteromedian flexus, but in *A. xantheolus* (from coastal Peru) the anterocone is undivided and the anteromedian flexus is present only as an internal fossette whose faint connection to a shallow median sulcus in the anterior face of the anterocone is transient and can only be seen on minimally worn teeth (e.g., AMNH 10111, 42398). By contrast, the anterocone of M1 in *Cerradomys* is never divided into labial and lingual conules by an

anteromedian flexus, and the internal fossette of the procingulum that is visible in some unworn dentitions (e.g., AMNH 134566, illustrated by Musser et al., 1998: fig. 144) is clearly derived from the anteroflexus, a labial enamel infolding.

The mesoflexus of M2 is present as a single internal fossette in *Aegialomys*. Although occasional rare variants are to be expected in such traits, this morphology appears to be exhibited consistently by examined specimens of *A. galapagoensis*, *A. xantheolus* (including *baroni*), and the unnamed form from coastal Ecuador. The mesoflexus of *Cerradomys*, however, is usually represented by two internal fossettes, of which one is labial and other is nearer the midline of the tooth (as illustrated for "*Oryzomys*" *subflavus* by Musser et al., 1998: fig. 144).

The male genitalia of *Aegialomys galapagoensis* ("*Oryzomys bauri*") and *A. xantheolus* ("*O. xantheolus*") were described and illustrated by Patton and Hafner (1983). In both species, the distal bacular cartilage is unambiguously trifid, with a slender but distinct central digit. By contrast, the glans penis of *Cerradomys scotti*, *C. subflavus*, and an undescribed congener from northeastern Brazil have a bifid distal bacular cartilage because the middle digit is vestigial or absent.

REMARKS: Although "*Oryzomys*" *galapagoensis* and "*O.*" *xantheolus* have long been recognized as closely related species (e.g., by Thomas, 1894; Gardner and Patton, 1976; Patton and Hafner, 1983), no published phylogenetic analysis of biochemical or morphological data is currently available to support the monophyly of *Aegialomys* as constituted herein. The presence of at least one undescribed species among the material we examined, together with questions that have been raised elsewhere concerning the taxonomic status of *ica* (by Musser and Carleton, 2005: 1156) and our own reservations about *baroni*, suggest that a revision of this group is needed to identify the terminal taxa that should be represented in future phylogenetic analyses.

ETYMOLOGY: From *aegialos* (Greek for the seashore), in reference to the predominantly coastal distribution of these species in western South America.

Cerradomys, new genus

TYPE SPECIES: *Hesperomys subflavus* Wagner, 1842.

CONTENTS: *maracajuensis* Langguth and Bonvincino, 2002; *marinhus* Bonvincino, 2003; *scotti* Langguth and Bonvincino, 2002 (including *andersoni* Brooks et al., 2004); and *subflavus* Wagner, 1842 (including *vulpinus* Lund, 1840; *vulpinoides* Schinz, 1845; and *laticeps* Winge, 1888 [not Lund, 1840]).

DISTRIBUTION: In dry tropical and subtropical forests of the Caatinga, Cerrado, and Chaco from northeastern Brazil to eastern Bolivia.

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage coarsely grizzled, usually some shade of reddish- or yellowish-brown; ventral pelage abruptly paler in some species (superficially whitish or yellowish) or not (the ventral coloration merging gradually with that of the dorsum), but ventral hairs always gray-based. Pinnae small, not extending to eye when laid forward. Mystacial and superciliary vibrissae not extending posteriorly beyond pinnae when laid back. Hind foot with conspicuous tufts of long ungual hairs at bases of claws on dI-dV; plantar surface densely covered with distinct squamae distal to thenar pad; hypothenar pad small but distinct; claw of dI extending beyond middle of phalange 1 but not quite to first interphalangeal joint of dII; claw of dV extending to but not beyond first interphalangeal joint of dIV. Tail longer than combined length of head and body, weakly bicolored in most species but distinctly bicolored in others (e.g., *C. scotti*).

Skull with long, tapering rostrum flanked by deep zygomatic notches; interorbital region anteriorly convergent, with strongly beaded supraorbital margins; braincase oblong, with well-developed temporal crests; lambdoidal and nuchal crests well developed in older adults. Posterior margin of zygomatic plate usually anterior to M1 alveolus. Jugal present but small (maxillary and squamosal zygomatic processes overlapping in lateral view but not in contact). Nasals not extending posteriorly beyond lacrimals; lacrimals usually sutured equally to maxillary and frontal bones (except in *C. maracajuensis*, which has longer maxillary than frontal sutures). Frontosquamosal suture usually colinear with frontoparietal

suture. Parietals with broad lateral expansions. Incisive foramina long, usually extending posteriorly to or between M1 alveoli; usually widest at midlength and tapering symmetrically anteriorly and posteriorly. Posterolateral pits large, complex, and recessed in deep fossae; mesopterygoid fossa penetrating anteriorly between maxillae but usually not between molar rows; bony roof of mesopterygoid completely ossified in some species (e.g., *C. marinhus* and *C. maracajensis*) but perforated by large sphenopalatine vacuities in others (e.g., *C. scotti*). Alisphenoid strut absent (buccinator-masticatory foramen and accessory foramen ovale confluent) in most species, but present (foramina separate) in *C. scotti*. Stapedial foramen and posterior opening of alisphenoid canal vestigial or absent; squamosal-alisphenoid groove and sphenofrontal foramen absent; secondary anastomosis of internal carotid crosses dorsal surface of pterygoid plate (= carotid circulatory pattern 3 of Voss, 1988). Postglenoid foramen large and rounded; small subsquamosal fenestra distinct and patent in most species but absent or vestigial (not patent) in *C. scotti*. Periotic exposed posteromedially between ectotympanic and basioccipital but usually not extending anteriorly to carotid canal; mastoid completely ossified or fenestrated (variation observed within and among species). Capsular process of lower incisor alveolus strongly developed below base of coronoid process; superior and inferior masseteric ridges converge anteriorly as open chevron below m1.

Labial and lingual flexi of M1 and M2 not interpenetrating. First upper molar (M1) anterocone not divided into labial and lingual conules (anteromedian flexus absent); anteroloph well developed and fused with anterostyle on labial cingulum, usually separated from anterocone by persistent anteroflexus; proto-style usually absent; paracone connected by enamel bridge to middle or to posterior moiety of protocone. Second upper molar (M2) protoflexus present; mesoflexus usually present as two internal fossettes. Third upper molar (M3) with posteroloph; hypoflexus present or absent. Accessory labial root of M1 present.

First lower molar (m1) anteroconid without an anteromedian flexid; anterolabial cingulum

present on all lower molars; anterolophid present on m1 but absent on m2 and m3; ectolophid usually absent on m1 and m2; mesolophid well developed on m1 and m2 in most species, but mesolophid (and mesostylid) reduced or absent in *C. scotti*; m2 hypoflexid short. Accessory lingual and labial roots present on m1; m2 and m3 each with one large anterior root and one large posterior root.

Fifth lumbar (17th thoracolumbar) vertebra with well-developed anapophysis. Hemal arch between second and third caudal vertebrae with posterior spinous process. Supratrochlear foramen of humerus present.

Stomach without extension of glandular epithelium into corpus. Distal bacular cartilage of glans penis bifid (the central digit is vestigial or absent); nonspinous tissue on crater rim does not conceal bacular mounds; dorsal papilla spineless; urethral processes without subapical lobules.

COMPARISONS: *Cerradomys* was represented by "*Oryzomys*" *subflavus* in the phylogenetic analyses of Weksler (2003, 2006), who consistently recovered it as a member of clade D (as in fig. 1). Although its phylogenetic position within clade D was never strongly supported in any analytic permutation based on morphological and/or IRBP sequence characters, *Cerradomys* never appeared as the sister taxon of any other species of *Oryzomys* sensu lato. However, it is phenetically most similar to *Aegialomys* (the "*xanthaeolus* group" of authors), *Oryzomys* sensu stricto (the "*palustris* group"), and *Sooretamys* ("*Oryzomys*" *angouya*). Comparisons with *Oryzomys* are provided here, whereas comparisons with *Aegialomys* and *Sooretamys* are provided in the accounts for those taxa (above and below, respectively).

Cerradomys differs from *Oryzomys* sensu stricto by its distinct hypothenar pad on the hind foot (the hypothenar is absent or vestigial in *Oryzomys*); conspicuous tufts of long ungual hairs at the bases of the claws on pedal digits II–V (the short ungual hairs of *Oryzomys* do not form distinct tufts); lacrimals that are usually sutured equally to the maxillary and frontal bones (the lacrimals are primarily sutured with the maxillaries in *Oryzomys*); shorter palate (the mesopterygoid

fossa does not extend anteriorly between the maxillary bones in *Oryzomys*); absence of an anterolophid on m2 and m3 (the anterolophid is distinct on unworn m2 and m3 in *Oryzomys*); presence of an anapophysis on the fifth lumbar vertebra (absent in *Oryzomys*); bifid distal bacular cartilage (the distal bacular cartilage is trifid in *Oryzomys*); dorsal papilla of glans penis spineless (spinous in *Oryzomys*); and urethral processes without subapical lobules (present in *Oryzomys*).

REMARKS: Compelling evidence for the monophyly of *Cerradomys* is provided by parsimony and maximum likelihood analyses of cytochrome b mtDNA sequences (Bonvicino and Moreira, 2001; Bonvicino, 2003). The highly distinctive anatomy of the glans penis, which lacks a central bacular digit, likewise supports this conclusion. Hopefully, the flurry of recently published descriptions of new species of *Cerradomys* (e.g., by Langguth and Bonvicino, 2002; Bonvicino, 2003; Brooks et al., 2004) will soon be followed by more synthetic and comprehensive studies to convincingly document species identifications and geographic distributions across the entire range of this obviously diverse clade. At least some of the many unstudied specimens representing this genus from Bolivia and Paraguay are likely to belong to taxa recently described from Brazilian material, but others may represent new forms. Unfortunately, no taxonomic study published to date has effectively transcended national boundaries.

ETYMOLOGY: For the Cerrado, a vast mosaic of savannas and dry forests, where many species of this clade are found.

Eremoryzomys, new genus

TYPE SPECIES: *Oryzomys polius* Osgood, 1913.

CONTENTS: *polius* Osgood, 1913.

DISTRIBUTION: Known only from a few localities in the upper Río Marañón valley of northern Peru.

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage coarsely grizzled-grayish (but brownish- or yellowish-gray in some old and possibly soiled specimens); ventral pelage paler (superficially whitish), but ventral hairs always gray-based. Pinnae small, not reaching eye when laid

forward. Mystacial and superciliary vibrissae not extending posteriorly beyond pinnae when laid back. Hind foot with conspicuous tufts of long ungual hairs at bases of claws on dI–dV; plantar surface densely covered with distinct squamae distal to thenar pad; hypothenar pad large and distinct; claw of dI extending almost to first interphalangeal joint of dII; claw of dV extending just beyond first interphalangeal joint of dIV. Tail longer than combined length of head and body; distinctly bicolored (dark above, pale below).

Skull with long, stout rostrum flanked by moderately deep zygomatic notches; interorbital region anteriorly convergent, with beaded supraorbital margins; braincase rounded, with more or less distinct temporal crests; lambdoidal and nuchal crests developed in older adults. Posterior margin of zygomatic plate dorsal to M1 alveolus; jugal present and large (the maxillary and squamosal zygomatic processes widely separated, not overlapping in lateral view). Nasals short, not extending posteriorly beyond lacrimals; lacrimals equally sutured to maxillary and frontal bones. Frontosquamosal suture usually colinear with frontoparietal suture. Parietals with broad lateral expansions. Incisive foramina very long, usually extending posteriorly between M1 anterocones or protocones; with subparallel lateral margins. Posterolateral palatal pits large, complex, and recessed in deep fossae; mesopterygoid fossa penetrating anteriorly to or slightly between molar rows; bony roof of mesopterygoid fossa perforated by large sphenopalatine vacuities. Alisphenoid strut usually present (buccinator-masticatory foramen and accessory foramen ovale separate), but strut unilaterally absent on some skulls. Stapedial foramen and posterior opening of alisphenoid canal small; squamosal–alisphenoid groove and sphenofrontal foramen absent; secondary anastomosis of internal carotid crosses dorsal surface of pterygoid plate (= carotid circulatory pattern 3 of Voss, 1988). Postglenoid foramen large and rounded; subsquamosal fenestra large and patent. Periotic exposed posteromedially between ectotympanic and basioccipital but not extending anteriorly to carotid canal; mastoid perforated by small or large posterodorsal fenestra. Capsular process of lower incisor

alveolus indistinct or absent. Superior and inferior masseteric ridges usually conjoined anteriorly as single crest below m1.

Labial and lingual flexi of M1 and M2 not interpenetrating. First upper molar (M1) anterocone not divided into labial and lingual conules (but a small internal fossette obviously derived from the anteromedian flexus is present); anteroloph usually well developed and fused with anterostyle on labial cingulum, separated from anterocone by persistent anteroflexus; protostyle absent; paracone connected by enamel bridge to middle or to posterior moiety of protocone. Second upper molar (M2) protoflexus present but shallow; mesoflexus present as one or more internal fossettes (both conditions occurring on opposite sides of some specimens: e.g., AMNH 64054). Third upper molar (M3) with posteroloph and diminutive hypoflexus (the latter tending to disappear with moderate to heavy wear). Labial accessory root of M1 absent.

First lower molar (m1) anteroconid without an anteromedian flexid; anterolabial cingulum and anterolophid present on all lower molars; ectolophid absent on m1 and m2; mesolophid variably developed on m1 and m2, large and distinct in some specimens but much reduced or absent in others; m2 hypoflexid short. Accessory roots absent on m1; m2 and m3 each with one large anterior root and one large posterior root.

COMPARISONS: "*Oryzomys*" *polius* was consistently recovered as the most basal lineage of clade D and not as the sister group of any other terminal taxon in the phylogenetic analyses of Weksler (2003, 2006). In his original description of "*O.*" *polius*, Osgood (1913) contrasted it with "*O.*" *xantheolus*, a geographically adjacent species, but he emphasized the lack of any close resemblance between them. Indeed, the genera to which we now refer these species are strikingly divergent in several characters.

Among other contrasts, *Eremoryzomys* differs from *Aegialomys* by its much grayer dorsal pelage (the dorsal fur is distinctly yellowish or brownish in *Aegialomys*); larger jugal (the jugal of *Aegialomys* is much smaller); longer incisive foramina (these openings never extend posteriorly between the M1 protocones in *Aegialomys*); shorter palate (the

mesopterygoid fossa never extends anteriorly to the molar rows in *Aegialomys*); alisphenoid strut separating the buccinator–masticatory and accessory oval foramina (the alisphenoid strut is invariably absent and the foramina are confluent in *Aegialomys*); absence of a distinct capsular process of the lower incisor alveolus (the capsular process is well developed in *Aegialomys*); absence of accessory roots on M1/m1 (accessory roots are normally present on these teeth in *Aegialomys*); and presence of the anterolophid on m2 and m3 (the anterolophid is absent on these teeth in *Aegialomys*).

Comparisons with other new genera belonging to clade D, none of which appear to be closely related to *Eremoryzomys*, are summarized in table 2.

ETYMOLOGY: From *eremia* (Greek for a lonely place), in reference to the isolated distribution of this monotypic genus.

Euryoryzomys, new genus

TYPE SPECIES: *Oryzomys macconnelli* Thomas, 1910.

CONTENTS: *emmonsae* Musser et al., 1998; *lamia* Thomas, 1901; *legatus* Thomas, 1925; *macconnelli* Thomas, 1910 (including *incertus* J.A. Allen, 1913, and *mureliae* J.A. Allen, 1915); *nitidus* Thomas, 1884 (including *boliviae* Thomas, 1901); and *russatus* Wagner, 1848 (including *physodes* Brants, 1827, *intermedia* Leche, 1886, *coronatus* Winge, 1887, *kelloggi* Ávila-Pires, 1959, and *moojeni* Ávila-Pires, 1959).

DISTRIBUTION: In moist (evergreen and semi-evergreen) forests throughout the cis-Andean tropical and subtropical lowlands of South America, including Amazonia, the Guianas, southeastern Brazil, eastern Bolivia, northern Argentina, and eastern Paraguay (see Musser et al., 1998: figs. 78, 79).

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage finely grizzled yellowish- to reddish-brown; ventral pelage abruptly paler (superficially whitish), but ventral hairs always gray-based. Pinnae large, reaching eye when laid forward. Mystacial and superciliary vibrissae not extending posteriorly beyond pinnae when laid back. Hind foot with conspicuous tufts of long ungual hairs at bases of claws on dII–dV; plantar surface smooth or sparsely covered with indistinct squamae distal to thenar pad;

hypothenar pad distinct; claw of dI extending just beyond base of phalange 1 of dII; claw of dV extending to middle of phalange 1 of dIV. Tail about as long as combined length of head and body in some species (e.g., *E. nitidus*) but usually longer than head and body in others (e.g., *E. macconnelli*); distinctly bicolored (dark above, pale below).

Skull with long, tapering rostrum flanked by deep zygomatic notches; interorbital region anteriorly convergent, with beaded supraorbital margins; braincase oblong, with weakly developed temporal crests; lambdoidal and nuchal crests developed in older adults. Posterior margin of zygomatic plate usually dorsal to M1 alveolus; jugal present but small in most species, but absent in *E. lamia*. Nasals not extending posteriorly beyond lacrimal bones in some species (e.g., *E. macconnelli*) but often extending beyond lacrimals in others (e.g., *E. lamia*); lacrimals equally sutured to maxillaries and frontals. Frontosquamosal suture usually colinear with frontoparietal suture. Parietals without lateral expansions in some species (e.g., *E. russatus*) or lateral expansions present but usually not very broad (e.g., in *E. macconnelli*). Incisive foramina ranging from moderately short and posteriorly broad (e.g., in *E. macconnelli*) to moderately long and widest near their midlength (e.g., in *E. russatus*), but never extending posteriorly between M1 anterocones. Posterolateral palatal pits small to moderately large, but usually not recessed in distinct fossae; mesopterygoid fossa extending anteriorly between maxillae in some species (e.g., *E. russatus*) but not in others (e.g., *E. macconnelli*); bony roof of mesopterygoid fossa completely ossified or perforated by small (slit-like) sphenopalatine vacuities. Alisphenoid strut usually absent (buccinator-masticatory foramen and accessory oval foramen confluent) in most species but often present in others (e.g., *E. nitidus*). Stapedial foramen, squamosal-alisphenoid groove and sphenofrontal foramen present (= carotid circulatory pattern 1 of Voss, 1988). Postglenoid foramen large and rounded, subsquamosal fenestra large and patent. Periotic exposed posteromedially between ectotympanic and basioccipital, but usually not extending anteriorly to carotid canal; mastoid completely ossified in most fully adult

specimens. Capsular process of lower incisor alveolus well developed in adult specimens of most species but absent in *E. macconnelli* and *E. emmonsae*; superior and inferior masseteric ridges converge anteriorly as open chevron below m1.

Labial and lingual flexi of M1 and M2 not (or shallowly) interpenetrating. First upper molar (M1) anterocone not divided into labial and lingual conules (anteromedian flexus absent); anteroloph well developed and fused with anterostyle on labial cingulum, separated from anterocone by persistent anteroflexus; protostyle absent; paracone connected by enamel bridge to posterior moiety of protocone except in *E. macconnelli* (where the attachment is usually to the middle of the protocone). Second upper molar (M2) protoflexus present; mesoflexus usually present as two internal fossettes. Upper third molar (M3) without posteroloph; hypoflexus well developed (persisting with moderate to heavy wear: e.g., in *E. lamia*) or absent (e.g., in *E. nitidus*). Labial accessory root of M1 usually absent.

First lower molar (m1) anteroconid without an anteromedian flexid; anterolabial cingulum present on all lower molars; anterolophid present on m1 but usually absent on m2 and m3; ectolophid variably present or absent on m1 and m2; mesolophid well developed on m1 and m2; m2 hypoflexid short. Accessory roots usually absent on m1; m2 and m3 each with one large anterior root and one large posterior root.

Fifth lumbar (17th thoracolumbar) vertebra with well-developed anapophysis. Hemal arch between second and third caudal vertebrae with or without posterior spinous process. Supratrochlear foramen of humerus present.

Stomach without extension of glandular epithelium into corpus. Male accessory reproductive glands not dissected, unknown. Distal bacular cartilage of glans penis large and trifid (with robust central digit); shelf of nonspinous tissue on crater rim does not conceal bacular mounds; dorsal papilla spineless; urethral processes without subapical lobules.

COMPARISONS: Weksler's (2003, 2006) phylogenetic analyses of morphological and molecular characters consistently recovered

Euryoryzomys (represented by “*Oryzomys*” *lamia*, “*O.*” *macconnelli*, and “*O.*” *russatus*) as a member of clade B together with *Hylaeamys*, *Transandinomys*, *Nephelomys*, *Oecomys*, *Handleyomys*, and the “*alfaroi* group”. Within clade B, however, the relationships of *Euryoryzomys* were not consistently indicated by different analytic permutations. Whereas some analyses suggested that this genus may be the sister group of *Mindomys* + *Oecomys*, others recovered it as a basal lineage or as the sister group of *Transandinomys*, but none of these alternatives was strongly supported. Phenetically, *Euryoryzomys* resembles other lowland moist-forest taxa that also have large pinnae, short outer digits on the hind foot, and that normally lack accessory roots on M1/m1. Comparisons of *Euryoryzomys* with *Hylaeamys* and *Transandinomys* are of special interest because the species that we assign to these genera have traditionally been treated as members of the so-called “*capito*” complex of *Oryzomys* sensu lato (Musser et al., 1998).

Although fully adult specimens of *Euryoryzomys* are usually larger than those of *Hylaeamys* (see measurement data summarized by Musser et al., 1998) and tend to have brighter (tawny or ochraceous versus brownish) dorsal fur, these genera are externally similar and are often confused in the field. Among the integumental contrasts summarized by Musser et al. (1998: table 52), tail coloration most consistently distinguishes *Euryoryzomys* (their “*nitidus* group”) from *Hylaeamys* (their “*megacephalus*” and “*yunganus*” groups): In *Euryoryzomys*, the tail is almost always distinctly bicolored, whereas it is indistinctly bicolored or unicolored (all-dark) in *Hylaeamys*.

Euryoryzomys also differs strikingly from *Hylaeamys* by its primitive pattern of carotid circulation (pattern 1 of Voss, 1988), which includes both the supraorbital and infraorbital branches of the stapedia artery. The supraorbital branch leaves a prominent translucent groove across the squamosal and alisphenoid on the inside of the braincase and exits the skull via the sphenofrontal foramen; both of these osteological features are lacking in *Hylaeamys*, almost all specimens of which clearly lack the supraorbital branch of the

stapedial artery (pattern 2 of Voss, 1988). Illustrations of these alternative conditions as expressed by representative species of *Euryoryzomys* and *Hylaeamys* are provided in Musser et al. (1998: fig. 27).

The only other cranial trait that usefully distinguishes these genera is mastoid fenestration. The occipital surface of the mastoid capsule that houses the paraflocculus is completely ossified in almost all examined specimens of *Euryoryzomys*, but it is prominently fenestrated in most specimens of *Hylaeamys*. Illustrations of these contrasting character states, exemplified by other taxa but resembling the conditions seen in *Euryoryzomys* and *Hylaeamys*, are provided in Weksler (2006: fig. 22).

Fully adult specimens of *Euryoryzomys* average larger than those of *Transandinomys*, but they are otherwise similar in most external features. Indeed, the integumental pigmentation of *T. talamancae* strikingly resembles that of *Euryoryzomys*. Apparently, the only nonmetric external feature by which *Euryoryzomys* and *Transandinomys* can be distinguished is the length of the superciliary vibrissae. These tactile hairs, rooted just above the eye, extend well behind the pinnae in both species of *Transandinomys*, although they are much longer in *T. bolivaris* than in *T. talamancae* (see Musser et al., 1998: fig. 53). By contrast, the superciliary vibrissae do not extend beyond the posterior margins of the pinnae in examined specimens of *Euryoryzomys*.

Euryoryzomys and *Transandinomys* also differ in several dental traits. Of these, the most striking concerns the upper second molar (M2) mesoflexus, which is consistently represented by two internal fossettes (labial and medial) in *Euryoryzomys*, whereas only a single internal fossette represents the M2 mesoflexus in *Transandinomys* (see Musser et al., 1998: figs. 29, 151). On the upper third molar (M3), the hypoflexus tends to be deeper and more persistent in *Euryoryzomys* than it is in *Transandinomys*, but this trait is not sufficiently constant to permit unambiguous identifications by itself. On the second lower molar (m2), however, the hypoflexid is distinctively shorter in *Euryoryzomys* (see Musser et al., 1998: fig. 32A,B) than it is in *Transandinomys*

(see Musser et al., 1998: fig. 64, left and middle).

REMARKS: This clade has usually been called the “*nitidus* group” by authors (e.g., Weksler, 1996; Musser et al., 1998; Percequillo, 1998; Patton et al., 2000), but we designate *macconnelli* as the type species of *Euryoryzomys* because it is represented by more complete character data than any of the other congeneric forms whose relationships have been analyzed to date. Although only three of the species that we refer to *Euryoryzomys* were analyzed by Weksler (2003, 2006), more taxonomically inclusive phylogenetic studies based on morphological data also support generic monophyly (Weksler, 1996). This clade is likewise recovered by parsimony analyses of cytochrome *b* sequence data that exclude third-position transitions and by neighbor-joining and maximum-likelihood analyses when transversions are weighted more heavily than transitions (Bonvicino and Moreira, 2001).

ETYMOLOGY: From *eurus* (Greek for far-reaching or far-spread), in reference to the extensive distribution of this genus.

Hylaeamys, new genus

TYPE SPECIES: *Mus megacephalus* Fischer, 1814.

CONTENTS: *acritus* Emmons and Patton, 2005; *laticeps* Lund, 1840 (including *saltator* Winge, 1888, and *seuanezi* Weksler et al., 1999); *megacephalus* Fischer, 1814 (including *capito* Olfers, 1818, *cephalotes* Desmarest, 1819, *velutinus* J.A. Allen and Chapman, 1893, *goeldii* Thomas, 1897, and *modestus*, J.A. Allen, 1899); *oniscus* Thomas, 1904; *perenensis* J.A. Allen, 1901; *tatei* Musser et al., 1998; and *yunganus* Thomas, 1902.

DISTRIBUTION: In moist (evergreen and semi-evergreen) forests of cis-Andean tropical and subtropical lowlands and foothills (to about 1500 m above sea level) from Venezuela and the Guianas southward throughout Amazonia and the Atlantic rainforest to Paraguay and northern Argentina. Numerous records from drier landscapes (e.g., in the Chaco and Cerrado) are probably all from gallery forests or relictual moist forest fragments formerly continuous with either Amazonian or coastal Brazilian rain forests.

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage finely grizzled-brownish, typically drab grayish-brown in young adults but often tawny or buffy in mature specimens; ventral pelage usually abruptly paler (superficially whitish), but ventral hairs always gray-based. Pinnae large, extending to eye when laid forward. Mystacial and superciliary vibrissae not extending posteriorly beyond pinnae when laid back. Pes with tufts of long unguis hairs at bases of claws on dII–dV (also on dI of *H. acritus*); plantar surface smooth or sparsely covered with indistinct squamae distal to thenar pad; hypothenar pad distinct in most species but often very small in *H. megacephalus* and sometimes absent in *H. yunganus*; claw of dI extending just beyond base of phalange I of dII; claw of dV extending almost to first interphalangeal joint of dIV. Tail usually about as long as or slightly shorter than combined length of head and body; unicolored (all dark) or weakly bicolored (dark above, pale below) near base.

Skull with moderately long, tapering rostrum flanked by deep zygomatic notches; interorbital region usually convergent anteriorly with weakly beaded supraorbital margins (some specimens of *H. laticeps* and *H. megacephalus* have almost hourglass-shaped interorbits with squared dorsolateral margins); braincase oblong, usually with distinct temporal crests; lambdoidal and nuchal crests developed in older adults. Posterior margin of zygomatic plate usually dorsal to M1 alveolus; jugal present but small (maxillary and squamosal zygomatic processes overlapping in lateral view but not in contact). Nasals short, not extending posteriorly beyond lacrimal; lacrimals equally sutured to maxillary and frontal bones in some species (e.g., *O. yunganus*) or sutured primarily to maxilla in others (e.g., *O. megacephalus*). Parietals with small lateral expansions. Incisive foramina short, not extending posteriorly between M1 alveoli, and broader posteriorly than anteriorly. Posterolateral palatal pits variable in size, number, and morphology, but usually large and recessed in shallow fossae; mesopterygoid fossa usually not extending anteriorly between maxillae; roof of mesopterygoid fossa completely ossified or perforated by small (slit-like) sphenopalatine vacuities. Alisphre-

noid strut absent (buccinator–masticatory foramen and accessory oval foramen confluent). Stapedial foramen and posterior opening of alisphenoid canal large, squamosal–alisphenoid groove and sphenofrontal foramen absent (= carotid circulatory pattern 2 of Voss, 1988). Postglenoid foramen large and rounded; subsquamosal fenestra large and patent. Periotic exposed posteromedially between ectotympanic and basioccipital but usually not extending anteriorly to carotid canal; mastoid perforated by conspicuous posterodorsal fenestra. Distinct capsular process of lower incisor alveolus absent; superior and inferior masseteric ridges converge anteriorly as open chevron below m1.

Labial and lingual flexi of M1 and M2 not (or shallowly) interpenetrating except in *H. tatei* (which has more deeply interpenetrating flexi). First upper molar (M1) anterocone not divided into labial and lingual conules (anteromedian flexus absent); anteroloph well developed and fused with anterostyle on labial cingulum, separated from anterocone by anteroflexus in minimally worn dentitions; protostyle absent; paracone connected by enamel bridge to posterior moiety of protocone. Second upper molar (M2) protoflexus present or absent; mesoflexus present as single internal fossette in some species (e.g., *H. megacephalus*) or as two fossettes (e.g., in *H. yunganus*). Third upper molar (M3) without posteroloph; hypoflexus deep and persistent in some species, shallow and transitory in other. Labial accessory root of M1 absent.

First lower molar (m1) anteroconid without an anteromedian flexid; anterolabial cingulum present on all lower molars; anterolophid usually distinct on m1 but absent on m2 and m3; ectolophid often present on m1 and m2; mesolophid present and distinct on m1 and m2; m2 hypoflexid usually short in some species (e.g., *H. yunganus*) but usually long in others (e.g., *H. megacephalus*). Accessory roots absent on m1; m2 and m3 each with one large anterior root and one large posterior root.

Fifth lumbar (17th thoracolumbar) vertebra usually without anapophysis. Hemal arch between second and third caudal vertebrae without posterior spinous process. Supratrochlear foramen of humerus present.

Stomach without extension of glandular epithelium into corpus. One pair of preputial glands present. Distal bacular cartilage of glans penis large and trifid (with robust central digit); shelf of nonspinous tissue on crater rim does not conceal bacular mounds; dorsal papilla spineless; urethral processes without subapical lobules.

COMPARISONS: Weksler's (2003, 2006) phylogenetic analyses of morphological and molecular characters consistently recovered *Hylaeamys* (represented by "*Oryzomys*" *megacephalus*, and "*O.*" *yunganus*) as part of clade B along with *Euryoryzomys*, *Transandinomys*, *Nephelomys*, *Oecomys*, and *Handleyomys*. Phenetically, *Hylaeamys* is most similar to two other genera that contain species formerly referred to the so-called "*capito* complex" of *Oryzomys* sensu lato (Musser et al., 1998), namely *Euryoryzomys* and *Transandinomys*. Because comparisons with *Euryoryzomys* have already been provided in the account for that genus (above), only comparisons with *Transandinomys* are discussed here.

Hylaeamys is similar to *Transandinomys* in size and in most qualitative external features, but its superciliary vibrissae are shorter, not extending posteriorly behind the pinnae. Although *T. talamancae* has much shorter superciliary vibrissae than *T. boliviae* (see Musser et al., 1998: fig. 53), these tactile hairs extend posteriorly behind the pinnae in both species of *Transandinomys* and are diagnostically longer than they are in *Hylaeamys*. Otherwise, the two genera are difficult (if not impossible) to distinguish per se based on integumental comparisons.

In cranial features, the two genera are most readily distinguished by their alternative patterns of carotid circulation. Whereas *Hylaeamys* possesses only the infraorbital branch of the stapedial artery, *Transandinomys* also has an intact supraorbital branch. The presence of the latter vessel is indicated by a translucent groove across the internal surfaces of the squamosal and alisphenoid bones and by the presence of a sphenofrontal foramen. Both of these osteological markers are constant features of examined skulls of *Transandinomys*, but they are just as consistently absent in *Hylaeamys* (see Musser et al., 1998: fig. 151).

Hylaeamys and *Transandinomys* do not appear to differ consistently in any other character that we have been able to score in all member species. However, the potential diagnostic value of an anapophysis on the fifth lumbar (17th thoracolumbar) vertebra, a process that is usually absent in *H. megacephalus* but present in *T. talamancae*, merits evaluation as postcranial skeletal material becomes available for other congeneric taxa.

REMARKS: The monophyly of *Hylaeamys* is not supported by analyses of morphological character data (Weksler, 2006: figs. 34, 35) or mtDNA sequences (Bonvincino and Moreira, 2001). Instead, compelling evidence for generic monophyly comes primarily from nuclear sequences (Weksler, 2003). Because the latter are only available from two species (*H. megacephalus* and *H. yunganus*), our concept of *Hylaeamys* is primarily based on the absence of the supraorbital branch of the stapedia artery. This trait was optimized as an unambiguous synapomorphy of *H. megacephalus* + *H. yunganus* in Weksler's combined analyses of morphological and IRBP characters; within clade B, it is uniquely shared by the species that we refer to *Hylaeamys*.

ETYMOLOGY: For the hylaea, Humboldt's name for the the rainforested lowlands of cis-Andean South America, the principal habitat of species belonging to this clade.

Mindomys, new genus

TYPE SPECIES: *Nectomys hammondi* Thomas, 1913.

CONTENTS: *hammondi* Thomas, 1913.

DISTRIBUTION: Currently known from just nine specimens, eight of which were collected in the vicinity of Mindo in the western Andean foothills of Pichincha province, Ecuador. Another specimen, labeled as having been collected in the eastern (Amazonian) lowlands of Ecuador, represents a remarkable and somewhat problematic range disjunction. In consequence, the geographic distribution of this taxon is difficult to interpret.⁵

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage coarsely grizzled yellowish-brown; ventral pelage abruptly paler (whitish or yellowish superficially) in most specimens, but ventral hairs always gray-based. Pinnae small, not reaching eye when laid forward. Mystacial and

superciliary vibrissae very long, extending posteriorly well beyond caudal margins of pinnae when laid back. Pes with sparse tufts of rather short unguis hairs at bases of claws on dII–dV; plantar surface sparsely covered with indistinct squamae distal to thenar pad; hypothenar pad present and distinct; claw of dI extending to or just beyond first interphalangeal joint of dII; claw of dV extending to middle of phalange 2. Tail unicolorous (all dark), and much longer than combined length of head and body.

Skull with long, stout rostrum flanked by very shallow zygomatic notches; interorbital region anteriorly convergent, with strongly beaded supraorbital margins; braincase elongate, with well-developed temporal, lambdoidal, and nuchal crests developed in older adults. Posterior margin of zygomatic plate dorsal to M1 alveolus; jugal present and large (the maxillary and squamosal zygomatic processes widely separated, usually non-overlapping in lateral view). Nasals not extending posteriorly beyond lacrimal bones; lacrimals equally sutured to maxillary and frontal bones. Frontosquamosal suture anterior to

⁵ The eight specimens of "*Oryzomys*" *hammondi* from Mindo (0°02'S, 78°48'W, 1264 m above sea level; Paynter, 1993) were taken by three different collectors—G. Hammond, L. Söderström, and R.S. Voss—from 1913 to 1980; seven of these specimens are at the BMNH and the eighth is at the UMMZ. The single Amazonian record is based on MCZ 52543, an adult female whose skin label states that it was collected by the Olallas (a family of professional collectors) on 27 July 1929 at "Concepción, Oriente, Ecuador". According to Paynter (1993), Concepción is at 0°48'S, 77°25'W, about 50 km NE of Tena between 300 and 500 m above sea level in Napo province. Several aspects of these distributional data are problematic. First, we are not aware of any other species of small nonvolant native mammal that occurs below about 1500 m on both sides of the Ecuadorean Andes. Second, the lowlands and foothills around Tena have been intensively worked over for many years by numerous collectors, none of whom have taken additional material of this species. Thus, there is some reason to question whether *Mindomys* really occurs in Amazonia. Additionally, it is not known if Mindo represents the upper or the lower limit of the elevational distribution of this taxon in western Ecuador, or if Mindo is somewhere in the middle of its elevational range. If *Mindomys* is predominantly a lowland taxon, then it might more appropriately be classified as a trans-Andean rather than as an Andean clade (sensu Weksler, 2006). Only future fieldwork can resolve such uncertainties, which are obviously relevant to reconstructing oryzomyine historical biogeography.

frontoparietal suture (dorsal facet of frontal in broad contact with squamosal). Parietals with broad lateral expansions. Incisive foramina short, not extending posteriorly to level of M1 alveoli, usually widest posteriorly and converging anteriorly (teardrop-shaped). Posterolateral palatal pits small and unrecessed in some specimens but larger and recessed in moderately deep fossae in others; mesopterygoid fossa extending anteriorly between maxillae but not between molar rows; bony roof of mesopterygoid fossa usually completely ossified (some specimens have very narrow sphenopalatine vacuities flanking the presphenoid or the presphenoid/basisphenoid suture). Alisphenoid strut absent (buccinator-masticatory foramen and accessory oval foramen confluent). Stapedial foramen, squamosal-alisphenoid groove, and sphenofrontal foramen present (= carotid circulatory pattern 1 of Voss, 1988). Postglenoid foramen small and dorsoventrally compressed; subsquamosal fenestra vestigial (not patent) or absent. Periotic broadly exposed posteromedially between ectotympanic and basioccipital, extending anteriorly to carotid canal; mastoid completely ossified, not fenestrated. Distinct capsular process of lower incisor alveolus absent; superior and inferior masseteric ridges converge anteriorly as open chevron below m1.

Labial and lingual flexi of M1 and M2 interpenetrating. First upper molar (M1) anterocone not divided into labial and lingual conules (anteromedian flexus absent); anteroloph well developed, fused with anterostyle on labial cingulum, and separated from anterocone by persistent anteroflexus; proto-style absent; paracone connected by enamel bridge to posterior moiety of protocone. Second upper molar (M2) protoflexus absent; mesoflexus present as two internal fossettes. Third upper molar (M3) with posteroloph and persistent hypoflexus. Labial accessory root of M1 absent.

Lower first molar (m1) anteroconid without an anteromedian flexid; anterolabial cingulum present on m1 and m2, occasionally absent on m3; anterolophid present on m1 but absent on m2 and m3; ectolophid present on m1 but not on m2 and m3; mesolophid well developed on all lower molars; m2 hypoflexid short.

Accessory roots absent on m1; m2 and m3 each with one large anterior root and one large posterior root.

Postcranial skeletal characters unknown.

Stomach without extension of glandular epithelium into corpus. Male reproductive tracts not examined.

COMPARISONS: Weksler (2006) recovered "*Oryzomys*" *hammondi* either as the most basal oryzomyine lineage (as in fig. 1) or as a member of clade B. Within clade B, "*O.*" *hammondi* was sometimes recovered as the sister taxon to *Oecomys*, but its relationships were unresolved in other analytic permutations. Because the phylogenetic position of "*O.*" *hammondi* was not strongly supported in any analysis, no compelling evidence exists for the membership of this taxon in any monophyletic group less inclusive than the tribe Oryzomyini. The following comparisons are therefore motivated in part by historical concepts of taxonomic affinity.

Among other characters, *Mindomys* differs from both *Nectomys* (the genus to which *hammondi* was originally referred by Thomas [1913]) and *Oryzomys* (the genus to which *hammondi* was transferred by Hershkovitz [1948]) by its much longer vibrissae (the vibrissae do not extend posteriorly behind the pinnae in *Nectomys* or *Oryzomys*); possession of a distinct hypothenar pad on the hind foot (the hypothenar is absent or vestigial in *Nectomys* and *Oryzomys*); unwebbed pedal digits (*Nectomys* and *Oryzomys* have partially webbed hindfeet); very long fifth digit (the claw of dV does not extend beyond the first interphalangeal joint in *Nectomys* or *Oryzomys*); much shallower zygomatic notches; much larger jugals; small, simple, unrecessed posterolateral palatal pits (*Nectomys* and *Oryzomys* have large, complex posterolateral palatal pits that are deeply recessed in conspicuous fossae); complete stapedial circulation (the stapedial circulation is absent in *Nectomys* and *Oryzomys*); absence of accessory roots on M1 and m1 (upper and lower first molars have accessory roots in *Nectomys* and *Oryzomys*); and possession of an ectolophid on m1 (*Nectomys* and *Oryzomys* lack ectolophids). Given the large number of additional characters by which *Mindomys* differs individually from *Nectomys* (represent-

ed by *N. squamipes* in Weksler [2006: table 5]) and *Oryzomys* (represented by *O. couesi* and *O. palustris*), the morphological distinctness of these taxa is not arguable.

Several authors (Ray, 1962; Hershkovitz, 1970; Steadman and Ray, 1982) have suggested a close relationship between "*Oryzomys*" *hammondi* and extinct Antillean giant rats of the genus *Megalomys*. We have not examined material of *Megalomys*, but Musser and Carleton's (2005) statements that its metatarsal pads are vestigial, that accessory roots are present on M1 and m1, and that it has a derived carotid circulation suggests that the genus is a member of clade D and not, in fact, a close relative of *Mindomys*.

Mindomys appears to differ consistently from *Oecomys* (a speciose genus that exhibits taxonomic variation in many characters) by its much smaller interdigital pads on the hind foot (the interdigital pads are very large in *Oecomys*); indistinct plantar squamae (the sole of the hind foot is entirely smooth in *Oecomys*); sparse tufts of short ungual hairs on pedal digits II–V (ungual tufts are denser and longer in *Oecomys*); much longer rostrum (all species of *Oecomys* have short rostrums); frontosquamosal suture anterior to the frontoparietal suture (the two sutures are more nearly colinear in *Oecomys*); shorter palate (the mesopterygoid fossa does not extend anteriorly between the maxillae in *Oecomys*); small, simple, unrecessed posterolateral palatal pits (*Oecomys* has large, often complex posterolateral palatal pits that are usually deeply recessed in conspicuous fossae); more lophodont upper molars (the labial and lingual flexi do not interpenetrate deeply on the upper molars of *Oecomys*); suppression of the protoflexus on M2 (the protoflexus is distinct on unworn M2s in *Oecomys*); absence of a paralophule on M2 (a distinct paralophule is present on the M2 of all examined species of *Oecomys*); and absence of an anterolabial cingulum from m3 (the anterolabial cingulum is distinct on the unworn m3 of *Oecomys*).

REMARKS: Hershkovitz (1948) designated *hammondi* as the type species of *Macruroryzomys*, but the latter was not diagnosed and the name is therefore unavailable (Pine and Wetzel, 1975). Although Hershkovitz (1970)

acknowledged this situation, he effectively did nothing to correct it, so *Macruroryzomys* remains a nomen nudum.

The possibly basal position of this extraordinary rat within the oryzomyine radiation, together with its enigmatic distribution and the absence of preserved tissues suitable for DNA extraction and sequencing, will hopefully impel future collectors to make special efforts to obtain more material.

ETYMOLOGY: For Mindo, a tiny agricultural community in the western Andean foothills of Pichincha province, Ecuador.

Nephelomys, new genus

TYPE SPECIES: *Hesperomys albigularis* Tomes, 1860.

CONTENTS: *albigularis* Tomes, 1860; *auriventer* Thomas, 1899; *caracolus* Thomas, 1914; *childi* Thomas, 1895 (including *oconnelli* J.A. Allen, 1913); *devius* Bangs, 1902; *keaysi* J.A. Allen, 1900 (including *obtusirostris* J.A. Allen, 1900); *levipes* Thomas, 1902; *maculiventer* J.A. Allen, 1899; *meridensis* Thomas, 1894; *moerex* Thomas, 1914; *nimbosus* Anthony, 1926; *pectoralis* J.A. Allen, 1912; and *pirvensis* Goldman, 1913.

DISTRIBUTION: In humid montane ("cloud") forests between about 900 and 3500 m above sea level from Bolivia northward along the Andes and Central American cordilleras to Costa Rica, and eastward along the Caribbean coastal mountains to eastern Venezuela (Percequillo, 2003).

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage finely grizzled yellowish- to reddish-brown; ventral pelage abruptly paler (gray-based whitish) in some species, but not in others (which have gray-based ochraceous underparts); with irregular patches of self-whitish fur variably present on throat, chest, abdomen, and/or groin in some species. Ears small, not quite extending to eye when laid forward. Mystacial vibrissae usually extending posteriorly for several millimeters beyond caudal margins of pinnae when laid back, but superciliary vibrissae shorter (not extending beyond pinnae). Pes with conspicuous tufts of long ungual hairs at bases of claws on dII–dV; plantar surface smooth, without plantar squamae; hypothenar pad large and distinct; claw of dI extending to or just beyond middle of

phalange 1 of dII; claw of dV extending to or just beyond first interphalangeal joint of dIV. Tail longer than combined length of head and body, weakly to distinctly bicolored (dark above, pale below).

Skull with long, stout rostrum flanked by relatively shallow to moderately deep zygomatic notches; interorbital region variable, hourglass-shaped with rounded supraorbital margins in some species (e.g., *N. albigularis*) but anteriorly convergent with beaded interorbital margins in others (e.g., *N. auriventer*); braincase rounded, usually with indistinct temporal crests in species having rounded supraorbital margins but with better-developed temporal crests in species having beaded supraorbital margins; lambdoidal and nuchal crests moderately developed in older adults. Posterior margin of zygomatic plate dorsal to M1 alveolus; jugal bone present but small in most species (the maxillary and squamosal zygomatic processes overlapping in lateral view but not in contact; *N. auriventer*, however, has a large jugal). Nasals usually not extending posteriorly beyond lacrimals; lacrimals sutured equally to maxillae and frontals in some species (e.g., *N. albigularis*) or primarily to maxillae in others (e.g., *N. moerex*). Frontosquamosal suture usually colinear with frontoparietal suture. Parietals with or without large lateral expansions (variable within and among species). Incisive foramina long (extending posteriorly to or between the alveoli of M1) and usually widest at midlength (e.g., in *N. levipes*) or much shorter (never approaching the molar rows) and wider posteriorly than anteriorly (e.g., in *N. moerex*). Posterolateral palatal pits usually large, complex, and recessed in deep fossae (but much reduced and inconspicuous in *N. caracolis* and *N. nimbosus*); mesopterygoid fossa extending anteriorly between maxillae in most species, but often extending between toothrows in *N. levipes*; bony roof of mesopterygoid fossa completely ossified or perforated by small sphenopalatine vacuities. Alisphenoid strut usually absent (buccinator-masticatory foramen and accessory oval foramen confluent) in most species, but strut usually present in *N. moerex* and variably present in others (*N. auriventer*, *N. levipes*, and *N. keaysi*). Stapedial foramen, squamosal-

alisphenoid groove and sphenofrontal foramen present (= carotid circulatory pattern 1 of Voss, 1988). Postglenoid foramen large and rounded; subsquamosal fenestra large and patent in most species but much narrower in *N. auriventer*. Periotic exposed posteromedially between ectotympanic and basioccipital but usually not extending anteriorly to carotid canal; mastoid completely ossified (e.g., in *N. auriventer*) or usually fenestrated (e.g., in *N. levipes*). Capsular process of lower incisor alveolus indistinct or absent; superior and inferior masseteric ridges converge anteriorly as open chevron below m1.

Labial and lingual flexi of M1 and M2 interpenetrating. First upper molar (M1) anterocone divided into labial and lingual conules by distinct anteromedian flexus; anteroloph well developed and fused with anterocone by persistent anteroflexus; protocone absent; paracone connected by enamel bridge to posterior moiety of protocone. Second upper molar (M2) protoflexus present; mesoflexus present as single internal fossette. Third upper molar (M3) posteroloph present; hypoflexus shallow and transitory (disappearing with moderate wear). Labial accessory root of M1 absent.

First lower molar (m1) anteroconid usually without an anteromedian flexid (a shallow median crease visible on some newly erupted teeth is quickly obliterated by wear); anterolabial cingulum present on all lower molars; anterolophid usually distinct on unworn m1 but absent on m2 and m3; ectolophid present or absent on m1 and m2 (variable within and among species); mesolophid present and distinct on m1 and m2; m2 hypoflexid short. Accessory labial root of m1 usually present, accessory lingual root absent; m2 and m3 each with one large anterior root and one large posterior root.

Fifth lumbar (17th thoracolumbar) vertebra usually with anapophysis. Hemal arch between second and third caudal vertebrae without posterior spinous process. Supratrochlear foramen of humerus present.

Stomach without extension of glandular epithelium into corpus. Macroscopic preputial glands absent. Distal bacular cartilage of glans penis large and trifid (with robust central

TABLE 3
Selected Morphological Comparisons Among New Genera from Clade B

	<i>Euryoryzomys</i>	<i>Hylaeamys</i>	<i>Nephelomys</i>	<i>Transandinomys</i>
Superciliary vibrissae:	short (not extending posteriorly beyond pinnae)	short (not extending posteriorly beyond pinnae)	short (not extending posteriorly beyond pinnae)	long (extending posteriorly behind pinnae)
Ears:	large (extending anteriorly to eye)	large (extending anteriorly to eye)	small (not extending anteriorly to eye)	large (extending anteriorly to eye)
Tail:	distinctly bicolored	unicolored or indistinctly bicolored	distinctly or indistinctly bicolored	unicolored or bicolored
Claw of dIV:	reaches middle of phalange 1 of dIV	almost reaches end of phalange 1 of dIV	reaches end of phalange 1 of dIV	almost reaches end of phalange 1 of dIV
Carotid circulation:	pattern 1 (squamosal-alisphenoid groove and sphenofrontal foramen present)	pattern 2 (squamosal-alisphenoid groove and sphenofrontal foramen absent)	pattern 1 (squamosal-alisphenoid groove and sphenofrontal foramen present)	pattern 1 (squamosal-alisphenoid groove and sphenofrontal foramen present)
Mastoid:	not fenestrated	fenestrated	fenestrated in some species, not in others	fenestrated in one species, not in the other
M1 anterocone:	undivided	undivided	divided	undivided
M2:	with two internal fossettes	with one or two internal fossettes	with one internal fossette	with one internal fossette
m2 hypoflexus:	short	short or long	short	long

digit); shelf of nonspinous tissue on crater rim does not conceal bacular mounds; dorsal papilla spineless; urethral processes without subapical lobules.

COMPARISONS: Phylogenetic analyses of nuclear gene sequences and morphology consistently recovered *Nephelomys*, represented by "*Oryzomys*" *albigularis* and "*O.*" *levipes* in Weksler (2003, 2006), as a member of clade B along with *Euryoryzomys*, *Handleyomys*, *Hylaeamys*, *Oecomys*, and *Transandinomys* (as in fig. 1). Within clade B, the relationships of *Nephelomys* were often unresolved, but some analytic permutations weakly supported a sister-group relationship with *Transandinomys*. Comparisons between *Nephelomys* and *Transandinomys* are summarized below, whereas comparisons among *Nephelomys* and other new taxa belonging to clade B are summarized in table 3.

Species of *Nephelomys* are larger-bodied than species of *Transandinomys*, a contrast that is apparent in most external dimensions. The adult hind foot (including claws), for example, averages about 32 mm or more

in species of *Nephelomys*, whereas this dimension averages about 30 mm or less in *Transandinomys* (see measurements in Musser et al., 1998). In addition, species of *Nephelomys* have relatively shorter superciliary vibrissae, smaller pinnae, longer fifth pedal digits, and longer tails than *Transandinomys* (see the diagnoses of both taxa for ratios or landmark comparisons that document these differences).

The most conspicuous qualitative craniodental difference between *Nephelomys* and *Transandinomys* concerns the anterocone of M1, which is deeply divided into labial and lingual conules by a persistent anteromedian flexus in the former genus. By contrast, the anterocone of M1 is undivided and no trace of an anteromedian flexus is present in *Transandinomys*. The size difference between these genera indicated by external dimensions is also apparent in craniodental comparisons: length of the maxillary toothrow, for example, consistently averages >5.5 mm in species of *Nephelomys*, but this measurement averages <4.7 mm in species samples of *Transandi-*

nomys. The accessory root(s) that are usually present on m1 in *Nephelomys* are apparently never developed in *Transandinomys*.

Due to morphological variation among congeneric taxa (as noted above in this account and below in the account that follows), consistent differences between *Nephelomys* and *Transandinomys* are not apparent in any other characters that we have been able to score in all member species. However, the potentially diagnostic value of preputial morphology deserves future study. Among the material dissected by Voss and Linzey (1981), a single pair of large preputial glands was found in *Transandinomys talamancae* (represented by their Panamanian specimens of "*Oryzomys capito*"), but no macroscopic preputial glands were detected in *Nephelomys devius* (represented by their specimens of "*Oryzomys albigularis*"); unfortunately, no additional species from either genus were included in that study and none have been dissected by other investigators.

REMARKS: All of the taxa that we refer to *Nephelomys* were treated as synonyms or subspecies of "*Oryzomys*" *albigularis* by Hershkovitz (1944: 72) and Cabrera (1961: 380–383), but subsequent karyotypic and morphological research has shown that most of these are valid species (Gardner and Patton, 1976; Patton et al., 1990; Aguilera et al., 1995; Márquez et al., 2000; Percequillo, 2003). Of the characters that Weksler (2006) identified as unambiguous synapomorphies of "*O.*" *albigularis* + "*O.*" *levipes*, only the divided anterocone of M1 seems to be exhibited consistently by other species of *Nephelomys*. Although no additional analytic results are currently available to support generic monophyly, we are not aware of any evidence that contradicts this hypothesis.

ETYMOLOGY: From *nephelê* (Greek for clouds or mist), in reference to the cloud-forest habitat of these montane species.

Oreoryzomys, new genus

TYPE SPECIES: *Oryzomys balneator* Thomas, 1900.

CONTENTS: *balneator* Thomas, 1900 (including *hesperus* Anthony, 1924).

DISTRIBUTION: In humid montane ("cloud") forest on the Andean slopes of southern Ecuador and northern Peru.

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage dark olive-brown; ventral pelage abruptly paler (superficially whitish or yellowish), but ventral hairs mostly gray-based (a few specimens have irregular gular and/or pectoral patches of self-whitish fur). Pinnae small, not reaching eye when laid forward. Mystacial vibrissae extending posteriorly beyond caudal margins of pinnae when laid back against cheeks; superciliary vibrissae shorter, not extending to caudal margins of pinnae when laid back. Pes with conspicuous tufts of long unguis hairs at bases of claws on dII–dV; plantar surface covered with distinct squamae distal to thenar pad; hypothenar pad present and distinct; claw of dI extends to middle of phalange 1 of dII; claw of dV extends to first interphalangeal joint of dIV. Tail unicolored (all-dark) or indistinctly bicolored basally, much longer than combined length of head and body.

Skull with short, narrow rostrum flanked by shallow zygomatic notches; interorbital region hourglass shaped, with rounded supraorbital margins; braincase rounded and globose, without temporal, lambdoidal, or nuchal crests. Posterior margin of zygomatic plate usually anterior to M1 alveolus. Jugal absent (maxillary and squamosal zygomatic processes in contact). Nasals extending posteriorly beyond lacrimals; lacrimals small, equally sutured to maxillary and frontal bones. Frontosquamosal suture usually colinear with frontoparietal suture. Parietals with or without small lateral expansions. Incisive foramina short, sometimes extending posteriorly to but not between M1 alveoli, and widest posteriorly (with anteriorly convergent lateral margins). Posterolateral palatal pits large and recessed in shallow fossae; mesopterygoid fossa extending anteriorly between maxillae but not between molar rows; bony roof of mesopterygoid fossa usually perforated by narrow sphenopalatine vacuities (the type of *balneator* has a completely ossified mesopterygoid roof). Alisphenoid strut absent (buccinator–masticatory foramen and accessory foramen ovale confluent). Stapedial foramen, squamosal–alisphenoid groove and sphenofrontal foramen present (= carotid circulatory

pattern 1 of Voss, 1988). Postglenoid foramen large and rounded, subsquamosal fenestra large and patent. Periotic broadly exposed posteromedially between ectotympanic and basioccipital, extending anteriorly to carotid canal; mastoid perforated by conspicuous posterodorsal fenestra. Capsular process of lower incisor alveolus strongly developed below base of coronoid process; superior and inferior masseteric ridges converge anteriorly as open chevron below m1.

Labial and lingual flexi of M1 and M2 not interpenetrating. First upper molar (M1) with anterocone divided into labial and lingual conules by anteromedian flexus; anteroloph well developed and fused with anterostyle on labial cingulum, separated from anterocone by persistent anteroflexus; protostyle absent; paracone connected by enamel bridge to anterior moiety of protocone. Second upper molar (M2) protoflexus present; mesoflexus usually present as single internal fossete. Third upper molar (M3) without a posteroloph, but with persistent hypoflexus. Labial accessory root of M1 absent.

Lower first molar (m1) anteroconid without a distinct anteromedian flexid (an indistinct flexid visible in some newly erupted dentitions is presumably obliterated with light wear); anterolabial cingulum present on all lower molars; anterolophid distinct on unworn m1 but absent on m2 and m3; ectolophid absent on all lower molars; mesolophid present and distinct on m1, reduced or absent on m2; m2 hypoflexid short. Accessory roots absent on m1; m2 and m3 each with one large anterior root and one large posterior root.

Postcranial skeletal characters unknown.

Stomach with extension of glandular epithelium into corpus. Distal bacular cartilage of glans penis large and trifid (with a robust central digit); nonspinous tissue on crater rim concealing bacular mounds; dorsal papilla nonspinous; urethral processes without subapical lobules.

COMPARISONS: "*Oryzomys*" *balneator* was consistently recovered as a member of clade C in the phylogenetic analyses of Weksler (2003, 2006). Although a sister-group relationship between *Oreoryzomys* and *Microryzomys* was moderately well supported in some analyses, *Oreoryzomys* was recovered as the sister taxon

of *Neacomys* (albeit with only trivial support) in other analytic permutations. In effect, its relationships within clade C remain to be resolved convincingly, and comparisons with all three member genera (including *Oligoryzomys*) seem appropriate.

As noted by Musser and Carleton (2005), *Oreoryzomys* and *Microryzomys* exhibit noteworthy similarities, but they also differ in many characters. Among the most useful morphological features for distinguishing these taxa, the pelage of *Oreoryzomys* is distinctly countershaded (the pelage is not countershaded in *Microryzomys*); the claw of pedal digit V extends only to the first interphalangeal joint of dIV (the claw of dV extends well beyond the first interphalangeal joint of dIV in *Microryzomys*); the tail is unicolored or indistinctly bicolored basally (the tail is more or less distinctly bicolored in *Microryzomys*); the premaxillae do not extend as far posteriorly as the nasals do (the premaxillae and nasals extend posteriorly to about the same extent in *Microryzomys*); the incisive foramina do not extend posteriorly between the M1 alveoli (as they usually do in *Microryzomys*); the foramen magnum is more caudally oriented (versus more ventrally oriented in *Microryzomys*); and the anteroconid of m1 is undivided (the anteroconid of m1 is deeply divided into anterolabial and anterolingual conulids by a persistent anteromedian flexid in *Microryzomys*).

Oreoryzomys differs from *Neacomys* by its soft fur (*Neacomys* has spiny fur); much longer tail (the tail of *Neacomys* seldom exceeds the combined length of head and body); shallower zygomatic notch (the zygomatic notch is moderately deep in *Neacomys*); hourglass-shaped interorbital region with rounded supraorbital margins (the interorbital region is anteriorly convergent with beaded supraorbital margins in *Neacomys*); absence of the jugal (the jugal is small but present in *Neacomys*); and shorter palate (the mesopterygoid fossa extends anteriorly between the maxillary bones in *Oreoryzomys* but not in *Neacomys*). We observed additional character differences between *Oreoryzomys* and some species of *Neacomys*, but none that appear to represent generically consistent distinctions.

Oreoryzomys differs from *Oligoryzomys* by its unicolored or indistinctly bicolored tail (the tail is distinctly bicolored in *Oligoryzomys*); premaxillae that do not extend as far posteriorly as the nasals do (the premaxillae and nasals extend posteriorly to about the same level in *Oligoryzomys*); shallower zygomatic notch (the zygomatic notch is moderately deep in *Oligoryzomys*); shorter palate (the mesopterygoid fossa does not extend anteriorly between the maxillae in *Oligoryzomys*); more deeply excavated parapterygoid fossae (the flat parapterygoid fossae of *Oligoryzomys* are almost level with the palate); smaller sphenopalatine vacuities (these openings are very large in *Oligoryzomys*); complete stapedia circulation (the dorsal ramus of the stapedia artery is absent in *Oligoryzomys*); more posterior position of the masseteric crest (which extends anterior to m1 in *Oligoryzomys*); absence of spines on the dorsal papilla of the gland penis (the dorsal papilla is spinous in examined species of *Oligoryzomys*); and extension of glandular epithelium into the gastric corpus (the gastric corpus is entirely lined by cornified epithelium in examined species of *Oligoryzomys*).

REMARKS: The available morphological character data for *Oreoryzomys* is incomplete because postcranial skeletons and male accessory reproductive gland dissections are currently unavailable. Although new morphological information from these (and other) systems might help resolve the relationships of this genus within clade C, the trenchant differences it exhibits with other member taxa suggests that such resolution will not affect its status as a distinct clade. *Oreoryzomys* is currently unrepresented by sequence data from any gene other than IRBP, hence the lack of prior information concerning phylogenetic relationships in published molecular studies of oryzomyines (e.g., Myers et al., 1995; Bonvincino and Moreira, 2001).

ETYMOLOGY: From *oros* (Greek for mountain), in reference to the montane distribution of this distinctive taxon.

Sooretamys, new genus

TYPE SPECIES: *Mus angouya* Fischer, 1814.

CONTENTS: *angouya* Fischer, 1814 (including *buccinatus* Olfers, 1818; *angouya*

Desmarest, 1819; *leucogaster* Wagner, 1845; *ratticeps* Hensel, 1872; *rex* Winge, 1887; *paraganus* Thomas, 1924; and *topicus* Thomas, 1924).

DISTRIBUTION: In tropical and subtropical moist forests of the Atlantic littoral in southeastern Brazil and in interior subtropical moist forests of eastern Paraguay and northern Argentina.

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage coarsely grizzled-brownish (the overall effect varying from drab grayish-brown to warm reddish- or yellowish-brown); ventral pelage abruptly paler (superficially whitish or yellowish), but ventral hairs always gray-based. Pinnae small, not reaching eye when laid forward. Mystacial vibrissae extending posteriorly well beyond pinnae when laid back against cheeks; superciliary vibrissae much shorter, not extending posteriorly to caudal margins of pinnae. Pes with conspicuous tufts of long unguis hairs at bases of claws on dI-dV; plantar surface densely covered with distinct squamae distal to thenar pad; hypothenar pad present and distinct; claw of dI extending to middle of phalange 1 of dII; claw of dV extending to or just beyond first interphalangeal joint of dIV. Tail unicolored (all dark) in most specimens and much longer than combined length of head and body.

Skull with long, broad rostrum flanked by deep zygomatic notches; interorbital region hourglass-shaped, with squared supraorbital margins; braincase oblong and usually without distinct temporal crests, but lambdoidal and nuchal crests often well developed in older adults. Posterior margin of zygomatic plate dorsal to M1 alveolus. Jugal present but not large (the maxillary and squamosal zygomatic processes overlapping in lateral view but not in contact). Nasals short, not extending posteriorly beyond lacrimals; lacrimals equally sutured to maxillary and frontal bones. Frontosquamosal suture colinear with frontoparietal suture in most specimens. Parietals with broad lateral expansions. Incisive foramina long, usually extending posteriorly to or between M1 alveoli; usually widest at mid-length and tapering symmetrically anteriorly and posteriorly. Posterolateral palatal pits large, usually complex, and recessed in deep

fossae; mesopterygoid fossa penetrating anteriorly between maxillae but not between molar rows; bony roof of mesopterygoid fossa perforated by large sphenopalatine vacuities. Alisphenoid strut absent (buccinator–masticatory foramen and accessory foramen ovale confluent). Stapedial foramen and posterior opening of alisphenoid canal small; squamosal–alisphenoid groove and sphenofrontal foramen absent; secondary anastomosis crosses dorsal surface of pterygoid plate (= carotid circulatory pattern 3 of Voss, 1988). Postglenoid foramen large and rounded; subsquamosal fenestra large and patent. Periotic exposed posteromedially between ectotympanic and basioccipital but usually not extending anteriorly to carotid canal; mastoid perforated by conspicuous posterodorsal fenestra. Capsular process of lower incisor alveolus strongly developed posteroventral to base of coronoid process; superior and inferior masseteric ridges converge anteriorly as open chevron below m1.

Labial and lingual flexi of upper molars not (or shallowly) interpenetrating. First upper molar (M1) anterocone not divided into labial and lingual conules (anteromedian flexus absent); anteroloph well developed and fused with anterostyle on labial cingulum, separated from anterocone by persistent anteroflexus; protostyle present but often inconspicuous; paracone connected by enamel bridge to middle or to anterior moiety of protocone. Second upper molar (M2) protoflexus present; mesoflexus usually present as two internal fossettes. Third upper molar (M3) with posteroloph and persistent hypoflexus. Labial accessory root of M1 absent.

First lower molar (m1) anteroconid without an anteromedian flexid; anterolabial cingulum present on all lower molars; anterolophid present on m1 but indistinct or absent on m2 and m3; ectolophid variably developed on m1 and m2; mesolophid present and distinct on m1 and m2; m2 hypoflexid short. Accessory labial root of m1 usually present, accessory lingual root usually absent; m2 and m3 each with one large anterior root and one large posterior root.

Fifth lumbar (17th thoracolumbar) vertebra with well-developed anapophysis. Hemal arch between second and third caudal verte-

brae with posterior spinous process. Supratrochlear foramen of humerus absent.

Stomach without extension of glandular epithelium into corpus. One pair of preputial glands present. Distal bacular cartilage of glans penis large and trifid (with robust central digit); nonspinous tissue of crater rim does not conceal bacular mounds; dorsal papilla spineless; urethral processes without subapical lobules.

COMPARISONS: “*Oryzomys*” *angouya* was consistently recovered as an isolated lineage within clade D by Weksler (2003, 2006), but some analyses of mtDNA sequences weakly support a sister-group relationship with *Cerradomys* (see Bonvicino and Moreira, 2001; Bonvicino, 2003). The hypothesis that *Sooretamys* and *Cerradomys* might be sister taxa was not explicitly stated by Musser et al. (1998), but it is implicit in their concept of the “*subflavus* group” of *Oryzomys* sensu lato. Despite such indications, we are not aware of any compelling morphological evidence that *Sooretamys* and *Cerradomys* are more closely related to one another than they are to other members of clade D; indeed, they are strikingly divergent in many respects.

Among other anatomical contrasts, *Sooretamys* differs from *Cerradomys* by its much longer vibrissae (the mystacial vibrissae of *Cerradomys* do not extend posteriorly beyond the pinnae); unicolored tail (the tail is more or less bicolored in *Cerradomys*); hourglass-shaped interorbital region with squared supraorbital margins (the interorbital region is anteriorly convergent and the supraorbital margins are strongly beaded in *Cerradomys*); lack of distinct temporal crests (temporal crests are well developed in *Cerradomys*); lack of a labial accessory root on M1 (a labial accessory root is present on M1 in *Cerradomys*); lack of a lingual accessory root on m1 (a lingual accessory root is present on m1 in *Cerradomys*); lack of a supratrochlear foramina of the humerus (this foramen is present in *Cerradomys*); and a trifid bacular cartilage bearing a robust central digit (the bacular cartilage is bifid because the central digit is vestigial or absent in *Cerradomys*).

REMARKS: The assumption that all of the nominal taxa currently synonymized with *S.*

angouya are conspecific has not been tested by any revisionary study.

ETYMOLOGY: From *sooretama*, the old Tupian name for the Atlantic rainforest region of eastern Brazil (Por, 1992).

Transandinomys, new genus

TYPE SPECIES: *Oryzomys talamancae* J.A. Allen, 1891.

CONTENTS: *bolivaris* J.A. Allen, 1901 (including *castaneus* J.A. Allen, 1901; *rivularis* J.A. Allen, 1901; *bombycinus* Goldman, 1912; *alleni* Goldman, 1915; and *orinus* Pearson, 1939); and *talamancae* J.A. Allen, 1891 (including *mollipilosus* J.A. Allen, 1899; *magdalenae* J.A. Allen, 1899; *villosus* J.A. Allen, 1899; *sylvaticus* Thomas, 1900; *panamensis* Thomas, 1901; *medius* Robinson and Lyon, 1901; and *carrikeri* J.A. Allen, 1908).

DISTRIBUTION: In tropical lowland and premontane trans-Andean rain forests (to about 1500 m above sea level) from northeastern Nicaragua throughout much of Costa Rica and Panama to Colombia, western Ecuador, and northern Venezuela (see Musser et al., 1998: figs. 50, 66).

MORPHOLOGICAL DIAGNOSIS: Dorsal pelage finely grizzled brownish (in *T. bolivaris*) or tawny (in *T. talamancae*); ventral pelage abruptly paler (superficially whitish), but ventral hairs uniformly gray-based over throat, chest, abdomen, and groin. Pinnae large, reaching eye when laid forward. Mystacial vibrissae long (extending posteriorly to or slightly beyond caudal margins of pinnae when laid back against cheeks in *T. talamancae*) or very long (extending well behind pinnae in *T. bolivaris*); superciliary vibrissae extending behind pinnae in both species (but much longer in *T. bolivaris* than in *T. talamancae*). Pes with conspicuous tufts of long ungual hairs at bases of claws on dII–dV; plantar surface entirely smooth (in *T. bolivaris*) or sparsely covered with indistinct squamae distal to thenar pad (in *T. talamancae*); hypothenar pad present and distinct; claw of dI extending almost to middle of phalange 1 of dII; claw of dV extending almost to first interphalangeal joint of dIV. Tail about as long as or slightly longer than combined length of head and body; unicolored

in *T. bolivaris* but often distinctly bicolored (dark above, pale below) in *T. talamancae*.

Skull with long, tapering rostrum flanked by moderately deep zygomatic notches; interorbital region anteriorly convergent, with beaded supraorbital margins; braincase rounded, with moderately well-developed temporal crests; lambdoidal and nuchal crests developed in older adults. Posterior margin of zygomatic plate usually dorsal to M1 alveolus. Jugal present but small (maxillary and squamosal zygomatic processes overlapping in lateral view but not in contact). Nasals not extending posteriorly beyond lacrimals; lacrimals equally sutured to maxillary and frontal bones. Frontosquamosal suture usually colinear with frontoparietal suture. Parietals with broad lateral expansions (in *T. talamancae*) or lateral expansions reduced or absent (in *T. bolivaris*). Incisive foramina short (not extending posteriorly between the alveoli of M1) and usually wider posteriorly than anteriorly (teardrop-shaped). Posterolateral palatal pits usually simple and recessed (if at all) in shallow fossae; mesopterygoid fossa usually not extending anteriorly between maxillae; bony roof of mesopterygoid fossa completely ossified or perforated by small sphenopalatine vacuities. Alisphenoid strut absent (buccinator–masticatory foramen and accessory oval foramen confluent). Stapedial foramen, squamosal–alisphenoid groove, and sphenofrontal foramen present (= carotid circulatory pattern 1 of Voss, 1988). Postglenoid foramen large and rounded, sub-squamosal fenestra usually large and patent. Periotic exposed posteromedially between ectotympanic and basioccipital but not extending anteriorly to carotid canal; mastoid usually unfenestrated in *T. bolivaris* but fenestrated in *T. talamancae*. Capsular process of lower incisor alveolus indistinct or absent; superior and inferior masseteric ridges converge anteriorly as open chevron below m1.

First upper molar (M1) anterocone not divided into labial and lingual conules (anteromedian flexus absent); anteroloph well developed, fused with anterostyle on labial cingulum, separated from anterocone by persistent anteroflexus; protostyle absent; paracone usually connected by enamel bridge to posterior end of protocone. Second upper

molar (M2) protoflexus present; mesoflexus present as single internal fossette. Third upper molar (M3) posteroloph absent; hypoflexus shallow and transitory (usually disappearing with moderate wear). Labial accessory root of M1 absent.

First lower molar (m1) anteroconid without an anteromedian flexid; anterolabial cingulum present on all lower molars; anterolophid distinct on m1 but absent on m2 and m3; ectolophid often present on m1 and m2; mesolophid present on m1 and m2; m2 hypoflexid long and deep, almost bisecting tooth. Accessory labial and lingual roots absent on m1; m2 and m3 each with one large anterior root and one large posterior root.

Fifth lumbar (17th thoracicolumbar) vertebra with well-developed anapophysis. Hemal arch between second and third caudal vertebrae without posterior spinous process. Supratrochlear foramen of humerus present.

Stomach without extension of glandular epithelium into corpus. Distal bacular cartilage of glans penis large and trifid (with robust central digit); shelf of nonspinous tissue on crater rim does not conceal bacular mounds; dorsal papilla spineless; urethral processes without subapical lobules.

COMPARISONS: Weksler (2003, 2006) consistently recovered *Transandinomys* (represented by "*O.*" *talamancae*) as a member of clade B together with *Euryoryzomys*, *Handleyomys*, *Hylaeamys*, *Nephelomys*, and *Oecomys* (as in fig. 1). Within clade B, *Transandinomys* was variously recovered by different analytic permutations as the sister taxon of *Euryoryzomys*, of *Nephelomys*, or of *Handleyomys intectus* + *Nephelomys*. Comparisons of *Transandinomys* with *Euryoryzomys*, *Hylaeamys*, and *Nephelomys* have already been provided in the accounts for those genera, salient aspects of which are summarized in table 3. The morphology of *Handleyomys intectus* (redescribed by Voss et al., 2002) is sufficiently distinctive that direct comparisons seem unnecessary in this context.

REMARKS: Although *Transandinomys bolivar* and *T. talamancae* are phenetically similar (as remarked by Musser et al., 1998: 323), no analytic results are currently available to support the monophyly of this genus. The only unambiguously derived trait that appears

to be uniquely shared by these species is their possession of unusually long supraorbital vibrissae, a character that was not scored for phylogenetic analysis by Weksler (2006).

ETYMOLOGY: For the trans-Andean distribution of these species.

DISCUSSION

Given the analytic results in hand (Weksler, 2003, 2006), several phylogenetically defensible nomenclatural options could be adopted. One would be to keep all of the species currently referred to *Oryzomys* sensu lato in a single genus that would necessarily also include all the descendants of their most recent common ancestor (the root node in fig. 1). However, the oldest available name for this clade is *Holochilus* (see table 1), so *Oryzomys* would effectively disappear from binomial usage, as would *Neacomys*, *Nectomys*, *Oecomys*, and many other well-established names.

Other options would involve naming fewer new genera than the 10 proposed herein by combining clades for which there is any evidence of a sister-group relationship. For example, one might combine the "*albigularis* group" (our *Nephelomys*) with "*Oryzomys*" *bolivar* and "*O.*" *talamancae* (together comprising our *Transandinomys*) to form one new genus instead of two new genera. However, doing so would effectively formalize a weakly supported hypothesis and obscure the useful fact that each of these groups is a morphologically diagnosable and ecogeographically distinct collection of species. Because weakly supported groups are more likely to be rejected by future taxonomic studies than well-supported groups, and because biologists need names for clades with distinct morphologies and distributions, two new names rather than one better serve the larger community of zoological researchers in this case and in others like it discussed by Weksler (2006: 75–77).

Thanks to ongoing revisionary research and the advent of character-based phylogenetic analyses, complex patterns of muroid rodent relationships are now emerging from the fog of prephylogenetic nomenclature. The abandonment of traditional usage for *Oryzomys* is

a necessary consequence of advancing knowledge about how species are actually related to one another, a process previously exemplified by the restriction of such long-abused names as *Rattus* and *Peromyscus* to smaller groups of closely related species (e.g., by Musser, 1981; Carleton, 1989). In both of those cases, the result was a richer lexicon of generic names that enabled muroid researchers in Asia and North America to communicate more effectively about a wide range of biological topics than they had previously been able to do. We expect that a similar benefit will now accrue to muroid researchers in the Neotropics.

ACKNOWLEDGMENTS

We thank Paula Jenkins (at the Natural History Museum, London), Bruce Patterson (Field Museum of Natural History, Chicago), and Jim Patton (Museum of Vertebrate Zoology, Berkeley) for timely specimen loans that helped us evaluate character variation in several taxa that are not well represented at the AMNH. Al Gardner, Guy Musser, and Jim Patton read a preliminary draft of our manuscript and provided thoughtful reviews that helped us improve the text, but they are not responsible for any factual errors or flawed arguments that might remain uncorrected herein. Mary Knight kindly checked our Greek etymologies, for which we thank her, too.

REFERENCES

- Aguilera, M., A. Pérez-Zapata, and A. Martino. 1995. Cytogenetics and karyosystematics of *Oryzomys albigularis* (Rodentia, Cricetidae) from Venezuela. *Cytogenetics and Cell Genetics* 69: 44–49.
- Bonvicino, C.R. 2003. A new species of *Oryzomys* (Rodentia, Sigmodontinae) of the *subflavus* group from the Cerrado of central Brazil. *Mammalian Biology* 68: 78–90.
- Bonvicino, C.R., and M.A.M. Moreira. 2001. Molecular phylogeny of the genus *Oryzomys* (Rodentia: Sigmodontinae) based on cytochrome *b* DNA sequences. *Molecular Phylogenetics and Evolution* 18: 282–292.
- Brooks, D.M., R.J. Baker, R.J. Vargas, M. T. Tarifa, H. Aranibar, and J.M. Rojas. 2004. A new species of *Oryzomys* (Rodentia: Muridae) from an isolated pocket of Cerrado in eastern Bolivia. *Occasional Papers Museum of Texas Tech University* 241: 1–11.
- Cabrera, A. 1961. Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Ciencias Zoológicas)* 4(2): 309–732.
- Carleton, M.D. 1989. Systematics and evolution. In G.L. Kirkland, Jr., and J.N. Layne (editors), *Advances in the study of Peromyscus*: 7–141. Lubbock: Texas Tech University Press.
- Carleton, M.D., and G.G. Musser. 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. *Bulletin of the American Museum of Natural History* 191: 1–83.
- Ellerman, J.R. 1941. The families and genera of living rodents, vol. 2. Family Muridae. London: British Museum (Natural History).
- Emmons, L.H., and J.L. Patton. 2005. A new species of *Oryzomys* from eastern Bolivia. *American Museum Novitates* 3478: 1–26.
- Emmons, L.H., V. Chávez, N. Rocha, B. Phillips, I. Phillips, L.F. del Aguila, and M. Swarner. In press. The non-flying mammals of Parque Nacional Noel Kempff Mercado, Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental*.
- Gardner, A.L., and J.L. Patton. 1976. Karyotypic variation in oryzomyine rodents (Cricetinae) with comments on chromosomal evolution in the Neotropical cricetine complex. *Occasional Papers of the Museum of Zoology Louisiana State University* 49: 1–48.
- Goldman, E.A. 1918. The rice rats of North America (genus *Oryzomys*). *North American Fauna* 43: 1–100.
- Gyldenstolpe, N. 1932. A manual of Neotropical sigmodont rodents. *Kungliga Svenska Vetenskapsakademiens Handlingar* 11: 1–164.
- Hall, E.R., and K.R. Kelson. 1959. The mammals of North America, 2 vols. New York: Ronald Press.
- Hershkovitz, P. 1944. A systematic review of the Neotropical water rats of the genus *Nectomys* (Cricetinae). *Miscellaneous Publications Museum of Zoology, University of Michigan* 58: 1–88, pls. I–IV, gazetteer, + folding map.
- Hershkovitz, P. 1948. Mammals of northern Colombia preliminary report no. 3: water rats (genus *Nectomys*), with supplemental notes on related forms. *Proceedings of the United States National Museum* 98: 49–56.
- Hershkovitz, P. 1970. Supplementary notes on Neotropical *Oryzomys dimidiatus* and *Oryzomys hammondi* (Cricetinae). *Journal of Mammalogy* 51: 789–794.
- Langguth, A., and C.R. Bonvicino. 2002. The *Oryzomys subflavus* species group, with descrip-

- tions of two new species (Rodentia, Muridae, Sigmodontinae). *Arquivos do Museu Nacional, Rio de Janeiro* 60: 285–294.
- Márquez, E.J., M. Aguilera M., and M. Corti. 2000. Morphometric and chromosomal variation in populations of *Oryzomys albigularis* (Muridae: Sigmodontinae) from Venezuela: multivariate aspects. *Zeitschrift für Säugetierkunde* 65: 84–99.
- McFarlane, D.A., and A.O. Debrot. 2001. A new species of extinct oryzomyine rodent from the Quaternary of Curaçao, Netherlands Antilles. *Caribbean Journal of Science* 37: 182–184.
- Morgan, G.S. 1993. Quaternary land vertebrates of Jamaica. In R.M. Wright and E. Robinson (editors), *Biostratigraphy of Jamaica*. Geological Society of America Memoir 182: 417–442. Boulder, CO: Geological Society of America.
- Musser, G.G. 1981. Results of the Archbold expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. *Bulletin of the American Museum of Natural History* 168: 225–334.
- Musser, G.G., and M.D. Carleton. 1993. Family Muridae. In D.E. Wilson and D.M. Reeder (editors), *Mammal species on the world*, 2nd ed.: 501–755. Washington, DC: Smithsonian Institution Press.
- Musser, G.G., and M.D. Carleton. 2005. Superfamily Muroidea. In: D.E. Wilson and D.M. Reeder (editors), *Mammal species of the world*, 3rd ed., vol. 2: 894–1531. Baltimore: Johns Hopkins University Press.
- Musser, G.G., M.D. Carleton, E.M. Brothers, and A.L. Gardner. 1998. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): diagnoses and distributions of species formerly assigned to *Oryzomys* “capito”. *Bulletin of the American Museum of Natural History* 236: 1–376.
- Musser, G.G., and M.E. Holden. 1991. Sulawesi rodents (Muridae: Murinae): morphological and geographical boundaries of species in the *Rattus hoffmanni* group and a new species from Pulau Peleng. *Bulletin of the American Museum of Natural History* 206: 322–413.
- Musser, G.G., and C. Newcomb. 1983. Malaysian murids and the giant rat of Sumatra. *Bulletin of the American Museum of Natural History* 174: 327–598.
- Myers, P., B. Lundrigan, and P.K. Tucker. 1995. Molecular phylogenetics of oryzomyine rodents: the genus *Oligoryzomys*. *Molecular Phylogenetics and Evolution* 4: 372–382.
- Osgood, W.H. 1913. New Peruvian mammals. *Field Museum of Natural History Zoological Series* 10: 93–100.
- Patton, J.L., and M.S. Haffner. 1983. Bio-systematics of the native rodents of the Galapagos Archipelago, Ecuador. In R.I. Bowman, M. Benson and A.E. Leviton (editors), *Patterns of evolution in Galapagos organisms*: 539–568. San Francisco: Pacific Division American Association for the Advancement of Science.
- Patton, J.L., M.N.F. da Silva, and J.R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bulletin of the American Museum of Natural History* 244: 1–306.
- Patton, J.L., P. Myers, and M.F. Smith. 1990. Vicariant versus gradient models of diversification: the small mammal fauna of eastern Andean slopes of Peru. In G. Peters and R. Hutterer (editors), *Vertebrates in the tropics*: 355–371. Bonn: Museum Alexander Koenig.
- Paynter, R.A., Jr. 1993. *Ornithological gazetteer of Ecuador*, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).
- Percequillo, A.R. 1998. *Sistemática de Oryzomys Baird, 1858 do Leste do Brasil (Muroidea, Sigmodontinae)*. Unpublished Master’s thesis, Universidade de São Paulo.
- Percequillo, A.R. 2003. *Sistemática de Oryzomys Baird, 1858: definição dos grupos de espécies e revisão taxonômica do grupo albigularis (Rodentia, Sigmodontinae)*. Unpublished Doctoral thesis, Universidade de São Paulo.
- Pine, R.H., and R.M. Wetzel. 1975. A new subspecies of *Pseudoryzomys wavrini* (Mammalia: Rodentia: Muridae: Cricetinae) from Bolivia. *Mammalia* 39: 649–655.
- Por, F.D. 1992. *Sooretama, the Atlantic rainforest of Brazil*. The Hague: SPB Academic Publishers.
- Ray, C.E. 1962. *Oryzomyine rodents of the Antillean Subregion*. Unpublished Doctoral thesis, Harvard University.
- Sánchez, H.J., J. Ochoa, G., and R.S. Voss. 2001. Rediscovery of *Oryzomys gorgasi* (Rodentia, Muridae), with notes on taxonomy and natural history. *Mammalia* 65: 205–214.
- Steadman, D.W., and C.E. Ray. 1982. The relationships of *Megaoryzomys curioi*, an extinct cricetine rodent (Muroidea: Muridae) from the Galápagos Islands, Ecuador. *Smithsonian Contributions to Paleobiology* 51: 1–23.
- Tate, G.H.H. 1932. The taxonomic history of the South and Central American cricetid rodents of the genus *Oryzomys*. Part 1: subgenus *Oryzomys*. *American Museum Novitates* 579: 1–18.

- Thomas, O. 1894. Descriptions of some new Neotropical Muridae. *Annals and Museum of Natural History* ser. 6, vol. 14: 346–366.
- Thomas, O. 1913. New mammals from South America. *Annals and Magazine of Natural History* ser. 8, vol. 12: 567–574.
- Voss, R.S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History* 188: 259–493.
- Voss, R.S. 1993. A revision of the Brazilian muroid rodent genus *Delomys* with remarks on “thomasomyine” characters. *American Museum Novitates* 3073: 1–44.
- Voss, R.S., and M.D. Carleton. 1993. A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an analysis of its phylogenetic relationships. *American Museum Novitates* 3085: 1–39.
- Voss, R.S., and A.V. Linzey. 1981. Comparative gross morphology of male accessory glands among Neotropical Muridae (Mammalia: Rodentia) with comments on systematic implications. *Miscellaneous Publications Museum of Zoology, University of Michigan* 159: i–iv, 1–41.
- Voss, R.S., M. Gómez-Laverde, and V. Pacheco. 2002. A new genus for *Aepeomys fuscatus* Allen, 1912, and *Oryzomys intectus* Thomas, 1921: enigmatic murid rodents from Andean cloud forests. *American Museum Novitates* 3373: 1–42.
- Weksler, M. 1996. Revisão sistemática do grupo de espécies *nitidus* do gênero *Oryzomys* (Rodentia: Sigmodontinae). Unpublished Master’s thesis, Universidade Federal do Rio de Janeiro.
- Weksler, M. 2003. Phylogeny of Neotropical oryzomyine rodents (Muridae: Sigmodontinae) based on the nuclear IRBP exon. *Molecular Phylogenetics and Evolution* 29: 331–349.
- Weksler, M. 2006. Phylogenetic relationships of oryzomyine rodents (Muroidea: Sigmodontinae): separate and combined analyses of morphological and molecular data. *Bulletin of the American Museum of Natural History* 296: 1–149.