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Author: Voss, Robert S.

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A New Genus for the "Alfaroi Group" of *Oryzomys* sensu lato (Rodentia: Cricetidae: Sigmodontinae)

ROBERT S. VOSS[1]

ABSTRACT

A new cricetid rodent genus is described for the Alfaroi Group of *Oryzomys* sensu lato. The new genus, which includes seven Mesoamerican species of small oryzomyines, is demonstrably monophyletic and easily diagnosed morphologically from its sister taxon, *Handleyomys*.

INTRODUCTION

Throughout most of the last century, the Neotropical cricetid rodent genus *Oryzomys* included anywhere from 60 to 120 species in five to seven subgenera that collectively ranged from Tierra del Fuego to New Jersey. This expansive concept of *Oryzomys*—as represented, for example, in accounts by Hall and Kelson (1959) and Cabrera (1961)—was substantially reduced by elevating all its constituent subgenera to generic rank (Musser and Carleton, 2005), but the residual polyphyly of the genus was not convincingly documented until Weksler's (2006) landmark phylogenetic analyses. To achieve a monophyletic classification of oryzomyines, Weksler et al. (2006) subsequently named 10 new genera, most of which corresponded to informally recognized species groups of *Oryzomys* sensu lato.

Unfortunately, Weksler et al. (2006) did not provide a generic name for the "Alfaroi Group," a predominantly North American clade that was then under revision by other researchers, who intended to name it themselves. The species that Weksler et al. (2006) construed as members of

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[1] Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History.

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the Alfaroi Group included those recognized by Musser and Carleton (2005) as *O. alfaroi*, *O. chapmani*, *O. melanotis*, *O. rhabdops*, *O. rostratus*, and *O. saturatior*. As an interim solution, Weksler et al. (2006) referred species of the Alfaroi Group to the genus *Handleyomys* based on Weksler's (2006) recovery of a strongly supported clade that included *H. intectus*, *O. alfaroi*, *O. chapmani*, and *O. rostratus*.

Despite the best intentions of all involved, species of the Alfaroi Group have remained in *Handleyomys* for almost two decades. This is an unsatisfactory situation because these taxa differ in numerous external and craniodental characters from the two South American species originally referred to *Handleyomys* by Voss et al. (2002). In effect, *Handleyomys* sensu Weksler et al. (2006) is difficult to diagnose morphologically, and the provisional nature of this usage has resulted in the use of scare quotes ("*Handleyomys*" *alfaroi*, etc.) in various publications (e.g., Patton et al., 2015; Percequillo et al., 2021). Recent phylogenetic analyses of molecular data (Almendra et al., 2018) strongly support monophyly of the Alfaroi Group, document its ancient (>6 My) divergence from *Handleyomys* sensu stricto, and provide compelling phylogenetic justification for its formal taxonomic recognition.

In this report, I provide a new generic name for the Alfaroi Group. Morphological terminology in the following account is defined and illustrated or referenced by Weksler (2006), who also scored several member species for visceral and postcranial-skeletal characters not mentioned in the diagnosis that follows. Morphometric ratios were computed from standard external and craniodental measurements (table 1). Except as noted, synonymies and authorship of taxon names follow Musser and Carleton (2005). Specimens examined for this report are in the American Museum of Natural History (AMNH) and the National Museum of Natural History (USNM).

Family Cricetidae Fischer, 1817

Subfamily Sigmodontinae Wagner, 1843

Tribe Oryzomyini Vorontsov, 1959

Casiomys, new genus

Figures 1, 2

Type species: *Hesperomys* (*Oryzomys*) *alfaroi* J.A. Allen, 1891.

Contents (boldface indicates valid species): ***alfaroi*** J.A. Allen, 1891 (including *agrestis* Goodwin, 1959; *dariensis* Goldman, 1915; *gloriaensis* Goodwin, 1956; *gracilis* Thomas, 1894; *incertus* J.A. Allen, 1908; *intagensis* Hershkovitz, 1940; *palatinus* Merriam, 1901; *palmirae*[2] J.A. Allen, 1912); ***chapmani*** Thomas, 1898 (including *caudatus* Merriam, 1901; *dilutior* Merriam, 1901; *huastecae* Dalquest, 1951); ***guerrerensis***[3] Goldman, 1915; ***melanotis*** Thomas, 1893 (includ-

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[2] The holotype of *palmirae* (AMNH 32224) is composite: the skin is *Casiomys alfaroi*, whereas the skull is *Handleyomys intectus* (Thomas, 1921). To conserve longstanding usage of the latter name, I hereby restrict the holotype to the skin.

[3] A synonym of *chapmani* according to Carleton and Musser (2005), but see Almendra et al. (2014, 2018).

ing *colimensis* Goldman, 1918); ***rhabdops*** Merriam, 1901 (including *angusticeps* Merriam, 1901); ***rostratus*** Merriam, 1901 (including *carrorum* Lawrence, 1947; *megadon* Merriam, 1901; *salvadorensis* Felton, 1958; *yucatanensis* Merriam, 1901); and ***saturatior*** Merriam, 1901 (including *hylocetes* Merriam, 1901).

DISTRIBUTION: Species of *Casiomys* range from central Mexico southward in forested lowland and montane habitats throughout most of Central America (Almendra et al., 2018: fig. 1) to northwestern South America (Weksler, 2015: map 161). As currently recognized, only *C. alfaroi* occurs in South America.

TABLE 1. Morphological measurement abbreviations used in this report. (For measurement definitions and illustrated endpoints, see Voss et al., 2024: 38–40).

HBL	Head-and-body length
LT	Length of tail
HF	Length of hind foot
CIL	Condyloincisive length
LD	Length of diastema
LIF	Length of incisive foramina
LR	Length of rostrum

MORPHOLOGICAL DIAGNOSIS: Small (<50 g) oryzomyines with soft (nonspinous), grizzled-brownish dorsal fur; ventral fur abruptly paler and superficially whitish, but uniformly gray-based from chin to anus in most specimens (a small patch of pure-white fur is sometimes present on the chin and throat). Pinnae large (reaching the eyes when folded forward), darker than the surrounding fur of the head, and sparsely covered with short hairs. Mystacial vibrissae long, extending several millimeters beyond the posterior margins of the pinnae when laid back against the head. Hind foot long and narrow, with unwebbed (or inconspicuously webbed) digits,[4] of which dII–dIV are much longer than dI and dV (the claw of dI does not extend more than halfway along the first phalange of dII, and the claw of dV does not extend past the end of phalange 1 of dIV); plantar surface smooth over heel and proximal metatarsus but squamous distally (among the plantar pads); hypothenar pad consistently present;[5] ungual tufts dense, silvery, and usually longer than claws on dII–dV. Tail only slightly longer than head and body in some species (e.g., *alfaroi*, with mean LT/HBL = ca. 1.07) but substantially longer in others (e.g., *rhabdops*, with mean LT/HBL = ca 1.24), sparsely haired (visibly scaly from base to tip), and lacking a terminal tuft or pencil of long hairs; indistinctly bicolored proximally in some species (e.g., *saturatior*) but distinctly bicolored in others (e.g., *melanotis*). Mammae always eight, in inguinal, abdominal, postaxial, and pectoral pairs.

Skull with relatively long rostrum (mean LR/CIL = 0.38–0.40 in all species) flanked by deep zygomatic notches. Interorbital region convergent anteriorly, with beaded supraorbital margins; supraorbital beads continuous with indistinct temporal ridges; nuchal crest absent; lambdoidal crests small and inconspicuous. Zygomatic plate broad, with rounded (never angular or spinous) anterodorsal margin; posterior margin anterior to or level with M1 alveoli. Jugal small, narrowly separating zygomatic processes of maxillary and squamosal. Nasals extend posteriorly

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[4] When present, webs occur only between dIII and dIV, and they never extend more than halfway along the first phalanges of those digits.

[5] Contra Weksler and Percequillo (2011: key couplet 30).

FIG. 1. Dorsal, ventral, and lateral cranial views of *Casiomys alfaroi* (AMNH 142435) from Cañas Gordas, Puntarenas, Costa Rica. All views ×3.

FIG. 2. Occlusal views of upper (**A**) and lower (**B**) molar rows of *Casiomys alfaroi* (AMNH 142435). Both views ca. ×25.

between or slightly beyond lacrimals. Frontosquamosal suture and frontoparietal suture roughly colinear (dorsal facet of frontal seldom contacts squamosal). Parietal extension onto lateral braincase usually small. Incisive foramina consistently more than half as long as diastema, but shorter in some species (e.g., *alfaroi*, with mean LIF/LD = 0.59) than in others (e.g., *chapmani*, with mean LIF/LD = 0.68); foramina not extending to or between M1 alveoli in fully adult specimens. Posterolateral palatal pits large and often complex (consisting of multiple perforations recessed in a common fossa). Mesopterygoid fossa usually not penetrating between maxillae and never between M3s; mesopterygoid roof perforated by distinct sphenopalatine vacuities flanking the basisphenoid-presphenoid suture.[6] Alisphenoid strut bilaterally absent (buccinator-masticatory and oval foramina confluent) in almost all examined specimens.[7] Osteological traces of carotid circulation include large stapedial foramen, internal squamosal-alisphenoid groove, and sphenofrontal foramen (carotid circulatory pattern 1; Voss, 1988) in some species (*alfaroi*, *melanotis*, *rhabdops*, *rostratus*); or stapedial foramen, squamosal-alisphenoid groove, and sphenofrontal foramen absent (carotid circulatory pattern 3) in others (*chapmani*, *guerrerensis*, *saturatior*). Postglenoid foramen and subsquamosal fenestra consistently present, widely open, and separated by hamular process of squamosal. Capsular process of lower incisor alveolus indistinct in some species (e.g., *alfaroi*) but large and strongly projecting in others (e.g., *chapmani*).

Upper incisors strongly opisthodont. Upper molar rows parallel. Labial and lingual flexi of upper molars not interpenetrating. Mesolophs consistently present and well developed (fused with mesostyle on labial cingulum) on first and second upper molars (M1 and M2), vestigial but sometimes distinct on M3. M1 anterocone not divided into anterolabial and anterolingual conules (anteromedian flexus absent); M1 anteroloph well developed, fused with parastyle on labial cingulum; M1 paracone connected by enamel bridge to posterior moiety of protocone. M2 protoflexus absent or indistinct even on unworn teeth; M2 mesoflexus present as one or two internal fossettes (varies within species). M3 posteroloph absent; M3 hypoflexus vestigial

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[6] Contra Weksler and Percequillo (2011: key couplet 30).

[7] But bilaterally present in the holotypes of *guerrerensis* (USNM 127517) and *saturatior* (USNM 76183).

but often present on lightly worn teeth. Accessory labial root of M1 consistently present in most species (but apparently geographically variable in *rhabdops*).

First lower molar (m1) anteroconid undivided (anteromedian flexid absent or indistinct); anterolabial cingulum usually present on all lower molars (occasionally indistinct on m2 and m3). Anterolophid often present on m1, but consistently absent on m2 and m3. Ectolophid often present on m1 in some species (e.g., *alfaroi*), but almost always absent on m2 and m3. Mesolophid well developed on m1 and m2 (but indistinguishably fused to entoconid with only moderate wear). Labial accessory root of m1 consistently present; lingual accessory root present in most species (with four m1 roots), but apparently absent in *rhabdops* (with three-rooted m1); m2 and m3 each with two anterior roots and one posterior root (three total on each tooth).

KARYOTYPES: According to Almendra et al.'s (2018: supplementary data 7) compilation of karyotypic data from several original sources—some of which remain unpublished—the species herein referred to *Casiomys* have 54 to 64 diploid chromosomes, and 62 to 116 autosomal arms ($2n$ = 54–64, FN = 62–116).

COMPARISONS: *Casiomys* and *Handleyomys* can be unambiguously distinguished by several external and craniodental traits (table 2). Pelage countershading refers to the contrast between dorsal and ventral color zones, which is abrupt in *Casiomys* (with grizzled-brownish dorsal fur and superficially whitish ventral fur) but not in *Handleyomys* (with dark, dull, grayish-brown dorsal fur and dull-grayish ventral fur; Voss et al., 2002). Although tail length varies among species of *Casiomys*, mean ratios of tail to head-and-body length are always greater than one (LT/HBL = 1.07–1.24); by contrast, tails are on average shorter than the combined length of head and body (LT/HBL = ca. 0.93) in both species of *Handleyomys* (Voss et al., 2002: table 3). Like most other oryzomyines, species of *Casiomys* have eight mammae in inguinal, abdominal, postaxial, and pectoral pairs (see Voss and Carleton [1993: fig. 8] for a diagram of these mammary loci), whereas species of *Handleyomys* have only six mammae because the pectoral pair is absent.

In dorsal cranial view, the zygomatic notch is deep in *Casiomys* because the free anterodorsal margin of the zygomatic plate projects anteriorly well beyond the dorsal root of the maxillary zygomatic process, but the zygomatic notch is visibly shallower in *Handleyomys*, which has a correspondingly shorter anterodorsal projection of the zygomatic plate (Voss et al., 2002: fig. 8). As in most other oryzomyines, the interorbital region is anteriorly convergent ("cuneate") and the supraorbital margins are beaded in all species of *Casiomys*, whereas the interorbital region is symmetrically constricted ("hourglass-shaped") and the supraorbital margins are rounded in *Handleyomys* (Voss et al., 2002: fig. 9). In ventral cranial view, the most conspicuous difference between these genera concerns the roof of the mesopterygoid fossa, which is consistently perforated by sphenopalatine vacuities that flank the basisphenoid-presphenoid suture in *Casiomys*. By contrast, the roof of the mesopterygoid fossa is completely ossified in *Handleyomys*, which lacks distinct sphenopalatine vacuities (Voss et al., 2002).

Opisthodonty, which refers to upper-incisor curvature, has been differently defined by authors. According to the terminology suggested by Thomas (1919), opisthodont upper incisors are those in which the anterior angle formed by the chord of the exposed greater curvature of that tooth with the occlusal plane of the molars is less than 90°, and orthodont incisors are

TABLE 2. Morphological differences between *Casiomys* and *Handleyomys*.

	Casiomys	*Handleyomys*
Pelage countershading	distinct	indistinct
Tail ratio (LT/HBL)[a]	>1.0	<1.0
Mammae	eight	six
Zygomatic notches	deep	shallow
Interorbital region	anteriorly convergent, with beaded supraorbital margins	hourglass shaped, with rounded supraorbital margins
Sphenopalatine vacuities	present	absent
Upper incisors	strongly opisthodont	weakly opisthodont
Upper molar flexi	not interpenetrating	interpenetrating

[a] Inequalities based on species' mean values (a few, possibly mismeasured, specimens have atypical tail:head-and-body ratios).

those in which this angle is about equal to 90°. By this definition, the upper incisors of both *Casiomys* and *Handleyomys* are opisthodont, but whereas those of *Casiomys* are strongly opisthodont, those of *Handleyomys* more closely approach the orthodont condition. Weksler (2006: table 5, character 52), who used alternative definitions of these terms suggested by Hershkovitz (1962), classified the upper incisors of "*Oryzomys*" *alfaroi*, "*O.*" *chapmani*, and "*O.*" *rhabdops* as opisthodont and those of *H. intectus* as orthodont.

Lastly, *Casiomys* and *Handleyomys* differ conspicuously in molar occlusal morphology. The upper and lower molars of *Casiomys* closely resemble those of *Oryzomys palustris* (and many other oryzomyines), in which the labial flexi (paraflexus, mesoflexus, metaflexus) and lingual flexi (protoflexus hypoflexus) of the upper teeth extend only to the dental midline and do not interpenetrate; the same is true of the labial and lingual flexids of the lower teeth. By contrast, the labial and lingual flexi of the upper molars and the labial and lingual flexids of the lower molars interpenetrate deeply in *Handleyomys*, a morphology that Voss et al. (2002) termed incipient lophodonty.

REMARKS: Molecular and chromosomal data compiled and analyzed by Almendra et al. (2018) suggest that the diversity of *Casiomys* is underestimated by the species recognized as valid in this report. Michael D. Carleton and the late Guy G. Musser were actively working on a taxonomic revision of the Alfaroi Group for several years, but their project remains uncompleted. Hopefully, others will take up the challenge of revising the species-level classification of this interesting Mesoamerican radiation.

SPECIMENS EXAMINED:[8] ***Casiomys alfaroi***—COSTA RICA: Puntarenas, Cañas Gordas (AMNH 142424–142426, 142430, 142431, 142433–142435, 142438, 142439, 142497), Finca Helechales (USNM 547952[f], 548022[f], 548023[f]). ***C. chapmani***—MEXICO: Hidalgo, 2.5 km E Tlanchinol (AMNH 283668[f]); Veracruz, Jalapa (USNM 93375), Jico (USNM 55023, 55025, 55030, 55059), Mirador (USNM 58552), Las Minas (USNM 329796–329803). ***C. guerrerensis***—MEXICO: Guerrero, Omilteme (USNM 126942, 127503, 127517, 127518, 127521). ***C. melano-***

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[8] Skins and skulls except as noted. Fluids (f) were examined for plantar morphology and/or mammae.

tis—MEXICO: Nayarit, 2 mi E Jalcocotán (USNM 523606–523610, 523612, 523615). ***C. rhabdops***—GUATEMALA, Alta Verapaz, Chelemha (USNM 570002[f], 570009[f], 570013[f]); Quetzaltenango, Calel (USNM 76804–76808, 76812–76814, 76818); Sololá, San Lucas Tolimán (AMNH 75067). ***C. rostratus***—MEXICO: Puebla, Metlaltoyuca (USNM 93108, 93109, 93111–93115, 93117, 93120, 93121); San Luis Potosí, El Salto (USNM 329792, 329793). ***C. saturatior***—MEXICO: Chiapas, Tumbala (USNM 76183, 76327, 76334, 76359, 76360); GUATEMALA: Alta Verapaz, Chelemha (USNM 570010[f]); Zacapa, Sierra de las Minas (USNM 570129[f]).

Etymology: From the Greek κάσις (*kasis*, a sibling), in allusion to the sister-group relationship between this genus and *Handleyomys*.

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