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Running Header: Thomasomys from northern Peru

Systematic Revision of *Thomasomys cinereus* (Rodentia: Cricetidae), from northern Perú and southern Ecuador with the description of new species.

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ABSTRACT

Thomasomys cinereus is the type species of *Thomasomys*, a rich genus of 44 species distributed along the Andes. Although it was suggested to be a species complex it has not yet reviewed taxonomically. To accomplish that revision, 348 specimens from 34 localities were examined, and 19 meristic variables were measured. A MANOVA found no significant sexual dimorphism in the largest population ($n = 54$, $p > 0.05$). For geographic analysis, 10 operational groups were delimited using geographic discontinuities and a

preliminary analysis of qualitative traits. A covariance matrix of log transformed data was subjected to principal component analysis. In addition, a phylogenetic analysis based on cytochrome b was performed using *Chilomys instans* as outgroup. A plot of PC1 and PC2 shows two partially overlapping groups; a northern group from Piura, Lambayeque, and Cajamarca and the second group mostly from La Libertad and Cutervo (near the type locality). The molecular phylogeny and differences in some discrete characters concur with the existence of these two groups (genetic distance of 5.5%). These evidences suggest the first group may represent a new species. Apparently, the Huancabamba Depression was not an important barrier or speciation driver for these rodents, in contrast to the role of Río Marañón that clearly limit the distribution of *T. cinereus* to the east

INTRODUCTION

Herein, I provide a rediagnosis and description of *Thomasomys cinereus*, including an assessment of geographic variability, and comparisons with related forms from northern Peru.

Ellerman (1941) was the first to recognize a cinereus Group, but his concept was very broadly constructed, and it would include species allocated herein to the "baeops," "incanus," and "cinereus" groups of *Thomasomys* as well as some species of now assigned to *Rhipidomys*, *Wilfredomys*, and *Juliomys*. Therefore, Ellerman (1941)'s concept does not correspond to current taxonomy and is no longer useful. The "cinereus" group, in a more restrictive sense, was then first proposed by Pacheco (2003) and is elaborated here.

Pacheco (2015) provided an updated account on *Thomasomys cinereus*, limiting the distribution from northern Peru in Piura to further south in La Libertad department, and

further east to Cajamarca department. He however stated that the sample from La Libertad differs from specimens from the type locality in several discrete characters, such as a mesopterygoid fossa narrower and more parallel; and warned that the species might be a species complex. No other comment on intraspecific variability was reported. *T. cinereus* is the type species of the genus *Thomasomys*, a rich genus of 44 species distributed along the Andes in South America. However, the species has not yet reviewed taxonomically, limiting the comprehension of the variability and speciation of the genus

MATERIALS AND METHODS

SPECIMENS EXAMINED

We examined a total of 348 specimens of small-bodied *Thomasomys* housed in the following institutions: American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); Museo de la Universidad Nacional de San Agustín, Arequipa (MUSA); Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (MUSM), Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). This morphological material is listed in appendix 1.

MOLECULAR ANALYSIS

We isolated whole DNA of 25 specimens of *Thomasomys cinereus* (from Piura, Cajamarca, Lambayeque, and La Libertad) and one specimen of *N. keaysi* from Pasco

Department (see Appendix 2). DNA was isolated from portions of liver and muscle preserved in alcohol. Whole DNA was extracted using Vivantis DNA isolation kit (Vivantis Technologies, Malaysia) and High Pure PCR Template Preparation Kit (Roche Molecular Systems, Inc., USA). For amplification, we followed Smith and Patton (1991, 1999)'s protocol. Amplifications were performed in 25 μL reactions with GoTaq® G2 Flexi DNA Polymerase (Promega™) and MVZ 05 and MVZ 16 primers (Smith & Patton, 1993). PCR conditions included an initial denaturation step at 94ºC for 4 min, followed by 33 cycles of PCR (denaturation at 93ºC for 1 min, annealing at 45ºC for 1 min, polymerization at 72ºC for 2 min), and a final extension at 72ºC for 10 min. Amplified products were sequenced by an external sequencing service (Macrogen, Inc. Korea). Sequences were edited with CodonCode Aligner 6.0 (http://www.codoncode.com/aligner/) and deposited in GenBank (Appendix 2).

We analyzed partial sequences of the mitochondrial cytochrome b gene (Cyt b; 801 bp) of 46 individuals of *Thomasomys cinereus*. We used as outgroups *Chilomys instans* and *Rhipidomys leucodactylus* obtained from GenBank. The accession numbers are listed in Appendix 2. Sequences were manually edited using CodonCode v.6.0 and aligned with Clustal-W implemented into MEGA 7.0.26 (Kumar et al., 2015). We performed a reconstruction phylogenetic tree based on maximum likelihood (ML) and Bayesian inference (BI). To find the best model for the ML and BI under the Akaike information criterion, we used jModelTest 2.1.1 (Darriba et al., 2012). Model of nucleotide substitution TIM2+I+G was selected using the "propose model" routine. The ML analyses were conducted using IQ-tree 3.2 (Nguyen et al., 2015) with the following parameters: rate parameter R: A-C: 4.6960, A-G: 12.6575, A-T: 4.6960, C-G: 1.0000, C-T: 28.4373, G-T: 1.0000; state frequencies: pi(A) = 0.3082, pi(C) = 0.2847, pi(G) = 0.1318, pi(T) = 0.2753,

proportion of invariable sites: 0.3731, and gamma shape alpha: 0.6023. Branch support was estimated calculating a majority-rule consensus tree of 10000 nonparametric bootstrap replicates. BI was performed using MrBayes 3.2.6 (Ronquist et al., 2012); four simultaneous Markov chains were run for 20000000 generations, with a sampling frequency of 1000 generations; the first 25% trees were discarded as ‘‘burn-in.’’ We checked the convergence to stable values using Tracer 1.7 (Rambaut et al., 2018) to bear out the Effective Sample Sizes (ESS) greater than 200 for all parameters. Estimates of evolutionary divergence of sequence pairs between and within *Thomasomys cinereus* were conducted using p-distance by MEGA 7.0.26. Trees were edited using iTOL 4 (Letunic & Bork, 2016).

Morphological Terminology and Morphometric Analysis

Measurements

Skin measurements and weight were transcribed from specimen tags. The head-and-body length (HBL) was estimated by subtracting the tail length (TL) from the total length. However, we sometimes remeasured HF on fluid or dry specimens to check the accuracy of values recorded by the collector, and we used our value rather than the collector’s whenever large discrepancies were found. All external measurements are reported to the nearest millimeter (mm), and all weights to the nearest gram (g).
All cranial and mandibular variables were measured to the nearest 0.1 mm using dial calipers. The variables are illustrated in figures xx and xx and described below:
Greatest length of skull (GSL): measured from the tip of the nasals to the posterior margin of occiput [= to occipitonasal length].

Condyloincisive length (CIL): distance from the greater curvature of an upper incisor to the articular surface of the occipital condyle on the same side.

Condylomolar length (CML): distance from the anterior edge of the first upper molar to the articular surface of the occipital condyle on the same side.

Length of orbital fossa (LOF): greatest distance of the orbital fossa inside the maxillary and squamosal roots of the zygomatic arch.

Length of nasals (LN): the greatest length of either nasal bone.

Diastema length (LD): measured from the crown of the first maxillary molar to the exposed lesser curvature of the upper incisor on the same side.

Length of incisive foramina (LIF): distance from the anterior to the posterior edge of one incisive foramen.

Length of maxillary toothrow (LM): occlusal length of the upper molar row.

Breadth of incisive foramina (BIF): the greatest distance across the incisive foramina.

Breadth of rostrum (BR): the least breadth between the anteroventral edge of the zygomatic plate.

Breadth of palatal bridge (BPB): measured between the protocones of first maxillary molars.

Breadth of first upper molar (BM1): measured across the protocone-paracone cusp pair of the first upper molar.

Breadth of nasals (BN): the greatest distance across both nasal bones.

Least interorbital breadth (LIB): the least distance across the frontal bones between the orbital; fossae.

Zygomatic breadth (ZB): the greatest distance across the zygomatic arches.

Braincase breadth (BB): measured immediately posterodorsal to the squamosal roots of the zygomatic arches.

Breadth of zygomatic plate (BZP): the distance between the anterior and posterior edges of the zygomatic plate.

Depth of incisor (DI): distance between greater and lesser curvature of the upper incisor.

Height of braincase (HBC): distance from the top of the braincase to the ventral surface of the basisphenoid and basioccipital bones.

AGE CRITERIA.

A relative estimate of age is based on molar toothwear. Five categories are here defined, in essence equivalent to the scheme presented by Voss (1991) for his revision of *Zygodontomys*.

TWC 0: M3 incompletely erupted,

TWC 1: M3 essentially unworn, basisphenoid-presphenoid suture unossified.

TWC 2: M3 little worn (some dentine exposed), paracone tuberculate and prominent, paraflexus distinct, basisphenoid-presphenoid suture at least partially ossified.

TWC 3: M3 worn, occlusal surface flat or concave but hypoflexus still distinct; M1-2 moderately worn, primary cusps separate, distinct, but not prominent; flexus distinct.

TWC 4: M1-M3 worn, occlusal surface essentially flat or concave, hypoflexus obliterated; All analysis were based only on TWC 3 and 4, considered adult specimens.

Anatomical terminology follows Brown (xx) for external characters; Reig (1977), Carleton and Musser (1989) and Hershkovitz (1993) for dentition; Bugge (1970) for the cephalic arteries, Wahlert (1985) for the cranial foramina, Howell (1926) for postcranial; and Carleton and Musser (1984) and Voss (1988) for general features of muroid anatomy;

and Pacheco (2003, 2015) for anatomical features of thomasomyines. For teeth morphology nomenclature follows Reig (1980), Carleton & Musser (1983, 1989) and Hershkovitz (1962). Descriptions of right upper and right lower molar rows were used.

Statistical Analyses: Variables were assessed for univariate normality with Shapiro-Wilk tests. Sexual dimorphism was tested with a multivariate analysis of variance (MANOVA) based on the largest available population sample from northern Peru (Nfemales = 31, Nmales = 36), but no significant differences were found ($\lambda = 0.388$, $p > 0.05$). Therefore, the sexes were combined for subsequent morphometric analyses. Statistical analysis for geographic variation was performed with specimens of age classes III and IV; all of which were considered adults (Voss, 1991; Rengifo and Pacheco, 2015). We used measurements to produce orthogonal morphological axes using principal component analysis (PCA) on a covariance matrix using non-transformed data. We also produced a discriminant analysis with estimation of canonical functions (Strauss, 2010). Later a MANOVA was performed to evaluate statistical differences between closely related species as determined by phylogenetic analysis. All analyses were executed in SPSS v 23 and graphics in SigmaPlot v10.

RESULTS

Thomasomys cinereus (Thomas, 1882)

Olive-gray Thomasomys

Figures 1

H[*esperomys*]. (*Rhipidomys*) *cinereus* Thomas, 1882:108; type locality "Cutervo, 9,200′ [2,804 m]" Cajamarca, Peru.

Hesperomys (*Vesperimus*) *cinereus*: Thomas, 1884:449; name combination.

Hesperomys (*Thomasomys*) *cinereus*: Coues, 1884:1275; name combination.

Peromyscus (*Thomasomys*) *cinereus*: Trouessart, 1898:512; name combination.

Thomasomys cinereus: Thomas, 1906:443; first use of current name combination.

TYPE: A specimen in the British Museum of Natural History (BMNH 81.9.7.29) collected at Cutervo, Departamento Cajamarca, 9200 f., Chota, Departamento Cajamarca, Peru. The type is a female specimen preserved as alcoholic with skull removed.

DISTRIBUTION: *Thomasomys cinereus* is restricted to southern Ecuador and northwestern Peru, west of the Río Marañón, from 1,198 to 3,100 m.

EMENDED DIAGNOSIS: Pelage long and soft, above ashy gray, thick and tapering tail; unusual hairiness of ears, feet and tail (no penciled). Nasals long, expanded anteriorly and tapering backward, extending slightly behind of premaxilla and surpassing the maxillary-frontal suture. Zygomatic notch slightly deep; zygomatic plate moderately broad, anterior edge slightly sloped forward. Incisive foramina large, rather broad, oblongue-shaped, with smooth and uniform borders, extending posteriorly to procingulum of first molar or between them. Carotid circulation primitive. Alisphenoid strut present. Paraoccipital process short. Anterolabial cingulum of m3 absent or poorly developed Thomas provides figures of the skull and feet of *cinereus* holotype.

Type's measurements: HBL 4.75" (120.7), TL 5.0" (127), FL 1.14" (29), EARL .64" (16.3), GSL 1.3" (33), ML .22"(6), BRW 19, DL 9, IOB 5

DESCRIPTION: Medium sized (adult head and body length 107– 146 mm) with long, soft, and dense dorsal fur. Dorsal coloration grizzled ashy gray, hairs being slate colored at base and white at tips, sprinkled with longer and blackish hairs. Ventral pelage grayish white, hairs also slate-colored at base, and moderately countershaded with dorsal pelage. Mystacial vibrissae moderately long, extending slightly beyond posterior margin of

pinnae when bent; genal 1 vibrissae absent. Tail comparatively thick, indistinctly bicolored, and lacks terminal white tip; it ranges from shorter to longer than head and body (96–145%). Hindfeet moderately long (28– 32 mm) with metatarsals covered by pure white shining hairs; hands also whitish. Digit I of pes (hallux) moderately long, its claw extending close or to interphalangeal joint of dII. Digit V of pes long, with claw extending about half length of phalanx 2 of dIV. Skull moderately long (condyloincisive length 29.3–32.3 mm) with relatively long and broad rostrum, nasals well expanded anteriorly, and no rostral tube. Interorbital region narrow or moderate, hourglass in shape with rounded margins. Zygomatic plates moderately broad, subequal to length of M1, and vertical. Zygomatic arches converge anteriorly to moderate degree. Incisive foramina oval but elongated, and long, reaching anterior margins of M1s or slightly between them. Mesopterygoid fossa broad, wider anteriorly or with margins subparallel; medial process usually present. Auditory bullae small and uninflated. Carotid circulatory pattern primitive (stapedial foramen, groove on inner surface of squamosal and alisphenoid, and sphenofrontal foramen present). Upper molars moderately hypsodont, without interpenetration of flexi. Maxillary toothrow moderately long, ranging from 4.8– 5.6 mm. Upper incisors orthodont. M1 lacks accessory labial root, and m1 with distinct anteromedian flexid. Capsular process absent.

COMPARISONS: *T. cinereus* is the type for the genus, comparisons are needed with T. *silvestris*, *T. caudivarius*, proposed as members of the "cinereus" group (Pacheco 2015).

natural history: This species inhabits humid montane forests or Yungas of northern Peru where specimens have been caught on the ground among dense shrubs and on the forest floor. One female (LSUMZ 27081) from Piura was pregnant with three embryos in August (dry season). Several males with scrotal testes were caught at the same place from

late July and early August. Known ectoparasites of *T. cinereus* include the flea *Plocopsylla kilya* (Schramm and Lewis 1987) and a staphylinid beetle, *Amblyopinus piurae* (Seevers 1955). P. T. Johnson (1972) and Durden and Musser (1994) reported *T. cinereus* as the host for the anopluran louse *Hoplopleura angulata*, but this allocation is corrected here to *T. ischyrus* (see that account).

REMARKS: Thomas (1882) described *T. cinereus* based mostly on external morphology and basic morphometric values, but it remained for Voss (1993) to detail descriptions of key external, cranial, dental, and soft characters. Pacheco (2003) confirmed these reported attributes and expanded on additional characters of the species. The holotype specimen is a subadult, age class 2, with zygmotic notches comparatively deep and incisive foramen long that penetrates M1. In adult specimen the incisive foramen do not extend conspicuosly beyong M1, but this characteristic is more common in juveniles and subadults.

Thomas (1884) identified a specimen, obtained by M. C. Jelski for the Warsaw Museum, from Maraynioc (near Chanchamayo), Junín department, as *Hesperomys* (*Vesperimus*) *cinereus*. However, this record is not included for the species because its description does not fit typical *T. cinereus* and I have not had the opportunity to examine the specimen. Osgood (1914b) also reported some specimens from near Uchco, Amazonas, as the subspecies *T. cinereus ischyrus*, but the taxon *ischyrus* is now regarded as a different species (Pacheco 2003; Musser and Carleton 2005). Osgood (1914) also reported *Thomasomys cinereus* from Mountains East of Balsas, Amazonas, but these were reported as *T. c. eleusis* by Thomas (1926) and treated as *T. eleusis* (Pacheco 2015). Previous records of the species from Ecuador (Musser and Carleton 1993) were based on the inclusion of *caudivarius* as a subspecies (following Cabrera 1961), but L. Luna and Pacheco (2002) treated this taxon as a valid species. Other Colombian records of the

allegedly *T. cinereus* (from Antioquia [Hooper and Musser 1964] and Huila [Carleton 1973]) are likely based on misidentified specimens because these localities are far from the currently known distribution of the species. As a consequence, the descriptions of glans penis morphology (Hooper and Musser 1964) and stomach morphology (Carleton 1973) intended for *T. cinereus* do not correspond to this species. Similarly, Vorontsov (xx) described the morphology of *T. cinereus* based probably on the same series or on the specimen FMNH 72396, also from San Antonio, Colombia, which was exchanged with the Zoological Institute, USSR. Rather, Pacheco (2003) reported on these morphological attributes based on correctly allocated specimens. The sample from La Libertad differs from specimens from the type locality in several discrete characters, such as a narrower and parallel mesopterygoid fossa. *T. cinereus* was suggested to be also a complex of separate species (Pacheco 2015). The karyotype is unknown.

The specimen of *Thomasomys cinereus* LSUMZ 20313 (Esselstyn (2017) has a wrong locality and coordinates. Mr. Thomas K.R. collected several specimens of *T. cinereus* from "33 road km SW Chiriaco" and others from "33 road km SW Huancabamba", both from Piura. Obviously, the first coordinate is a typo with a wrong coordinate point in Amazonas region. This wrong locality would be the single locality of *T. cinereus* from Amazonas department, far from other known records. I have published an account about *T. cinereus* in the II SAM volume (Patton et al. Eds). See my account in Pacheco (2015) for the right distribution of the species. In case the locality is correct, I would doubt the specimen is *T. cinereus*.

The specimen AMNH 73127, 73129 were collected from Seques, Lambayeque by Watkins in his way to Taulis. Currently, Lambayeque has no single locality with the name of Seques, but Cajamarca does. In province of San Miguel, district of La Florida there are

places known as Pampa de Seques and Mountain of Seques (http://escale.minedu.gob.pe/documents/10156/1367930/ugel_santa_cruz.pdf) with approximate coordinates : -6.890384°, -79.088967°. It is more likely Watkins has collected in these places, but coordinates were later calculated without proper precision. Our specimens from Cañaris and Palomapampa are the first from Lambayeque region. The same would apply also to specimens of *T. taczanowskii* collected by Watkins in Seques.

Thomasomys XX new species

Figs. xx

Thomasomys cinereus

Holotype.— An adult male (age class 4/f/n) preserved as skin, skull, and carcass, and muscle tissue preserved in alcohol 96°, deposited at Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM xxxx); collected on xxx by Víctor Pacheco under field catalog number VPT

DISTRIBUTION: Department of Piura, Peru, on montane forests of the western slopeand in, Loja, Ecuador. Most localities are placed on the headwaters of the río Huancabamba, a tributary of the Río Chamaya on the north of the Huancabamba depression. However, southern localities are on the left margin of the río Chotano, also a tributary of the Río Chamaya, and not extending south of the Río Maichil (Cajamarca) and Río Reque (Lambayeque). Includes Pagaibamba with Cañaris.

DIAGNOSIS: Nasal bones shorter, extending posteriorly to level of maxillo-frontal-lacrimal intersection or more anterior; interorbital region moderately broad; incisive foramina short, rhomboid shape, and usually not extending to M1; molar tooth row shorter; M3 reduced; the zygomatic arch with a more triangular shape; and mesopterygoid fossa wide and lyre shaped.

DESCRIPTION: A large series from Cruz Blanca Piura have extensive variation in color pelage, ranging from dark to more brownish, venter color also change from more whitish to even brownish. It apparently represents individual variation since I could not correlated those pattern either to sex, 1age or local variation. Those from Huancabamba appears more uniform, have shorter ear. The dorsal profile of skull is slightly rounded, never straight, and slightly bumped at the interorbital region level. The coronoid process

long, slender and curved backward. Angular process well developed, at level of the condyle process or more usually slightly anterior to it. Ventral border of mandible deeply concave. The m1 with distinctly broader hypoflexid, m3 have more a triangular occlusal view, due to the less developed hypoconid.

Paraflexus oriented backward following the mure; Protoflexus on M2 absent, enterostyle on M2 absent, protostyle on M1 absent. Paraloph on M2 goes backward from the paracone to the root of mesoloph.

Main conulids prismatic and alternate, hypoflexid narrow and directed backward

COMPARISONS: Compared with *Thomasomys cinereus*, specimens of *T. piuranus* can be unambiguously identified based on skin and skull features. It differs from *cinereus* in nasals more expanded anteriorly; nasals shorter, extending posteriorly to level of maxillary-frontal suture or slightly in front; incisive foramina smaller [72% of diastema length, but needs X] and narrower; the anterior third finely narrow, anterior edge delicately rounded; posterior two thirds wider, converging slightly to the posterior edge, extending in front of first molar, rarely reaching the anterior edge of molar. Zygomatic notch shallow, spine barely projecting frontward. Jugals more robust; Paraoccipital process longer and slender distinctly projecting from the periotic. Molar tooth row smaller.

Specimens from Huancabamba exhibit ventral surface grayish with wash of light brown, while in *cinereus* s.s. the ventral surface is brown grayish, less countershading with dorsal surface; a darker wide middorsal band is more conspicuous in piuranus, and only incipient in *cinereus*.

REMARKS: The FM series from Canchaque are from 1198 m, unusually low for a *Thomasomys*.

SPECIES EXAMINED: Peru: Piura, El Tambo, 3100 m, 79 33' W, 5 21'35"S

(USNM 304535, 304536, 304537); Huancabamba, Sondorillo, Ulpamache[o] (USNM 551643). MUSM 511

The specimens from Huancabamba fits with piuranus in skull. Those from Canchaque also but show some variations: nasals usually level to mfl, in some preorbital not very swollen; postglenoid appears smaller; incisive foramina short but usually more lanceolate shape rather than rhomboideal.. The specimen MUSM 511 fits with piuranus based on nasal, interorbital region and size.

Thomasomys XX new species

Holotype.— An adult male (age class 4/f/n) preserved as skin, skull, and carcass, and muscle tissue preserved in alcohol 96°, deposited at Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM xxxx); collected on xxx by Víctor Pacheco under field catalog number VPT

DIAGNOSIS.- This is a species of Thomasomys relatively small; incisive foramen narrow and long extending to reach M1; mesopterygoid fossa narrow and parallel; posterior border of palatal bone lacks a posterior process; toothrow length small;M3 reduced.

DISTRIBUTION AND SYMPATRY.- The localities are only on the western side of the Andes, located in La Libertad department (Sayapullo and Cachicadan) and in a single locality in Cajamarca department (Cachil). All these localities are at south of the Río Jequetepeque, and south of the Río Crisnejas.

MEASUREMENTS OF HOLOTYPE: HBL, xxxx Measurements of additional specimens are provided in table 1.

COMPARISONS (Table 2):

DISCUSSION

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REFERENCES

Baker, R.J., M. Hamilton, and D.A. Parish. 2003. Preparation of mammalian karyotypes under field condition. Occasional Papers of Museum of Texas Tech University 228: 1–8.

Baker, R.J., and R.D. Bradley. 2006. Speciation in mammals and the genetic species concept. Journal of Mammalogy 87: 643–662.

Bradley, R.D., and R.J. Baker. 2001. A test of the genetic species concept: cytochrome b sequences and mammals. Journal of Mammalogy 82: 960–973.

Brito, nidos

Cabrera, A. 1961. Catálogo de los Mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ciencias Zoológicas 42: xxii + 309-732.

Carleton, M. D., & G. G. Musser. 1995. Systematic studies of oryzomyine rodents (Muridae: Sigmodontinae): definition and distribution of Oligoryzomys vegetus (Bangs, 1902).-Proceedings of the Biological Society of Washington 108:338-369.

da Silva, J.M.C., A.B. Rylands, and G.A.B. Fonseca. 2005. O destino das áreas de endemismo. Megadiversidade 1: 124–131.

Esselstyn J (2017). LSUMZ Mammals Collection. Louisiana State University Museum of Natural Science. Occurrence dataset https://doi.org/10.15468/wxiqf6 accessed via GBIF.org on 2019-03-15. https://www.gbif.org/occurrence/45912597

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 Zoology Louisiana State University 49: 1-48.

Luna W, L.

Moreno, P. Ecuador

Pacheco, V., et al. 2009. Diversidad y endemismo de los mamíferos del Perú. Revista Peruana de Biología 16: 5–32.

Pacheco V. 2015. Genus *Thomasomys* Coues, 1884, pp. 617-682. In J.L. Patton, U.F.J. Pardiñas, and G. D’Elía, eds. Mammals of South America. Volume 2, Rodents. The University of Chicago Press, Chicago, IL.

Patterson, B.D., D.F. Stotz, and S. Solari. 2006. Mammals and birds of the Manu Biosphere Reserve, Peru. Fieldiana Zoology 110: 1–49.

Voss, R.S. 1991. An introduction to the Neotropical muroid rodent genus *Zygodontomys*. Bulletin of the American Museum of Natural History 244:1–113.

Steppan

Parada

Lee

FIGURE CAPTIONS

Figure 1. Skull and mandible of specimen of *Thomasomys cinereus* from Cajamarca, Monteseco

APPENDIX 2

SPECIES EXAMINED: **Peru**: *Cajamarca*, "35 mi. WNW Cajamarca"= Monteseco (MUSM VPT 1640, 1650, 1629; MVZ 137937--137939), Taulis (AMNH 73136, 73147); Lambayeque [Cajamarca], Seques (AMNH 73127, 73129); MVZ and MUSM. . Total, AMNH 73129 AND MVZ 137938 were compared to types.

MUSM 511, Piura, Ayabaca, Huamba,

Figure 1.


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