



A NEW GENUS FOR *Habrothrix angustidens* AND *Akodon serrensis* (RODENTIA, CRICETIDAE): AGAIN PALEONTOLOGY MEETS NEONTOLOGY IN THE LEGACY OF LUND

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ABSTRACT. We describe a new genus of sigmodontine rodent to allocate a fossil species from Lagoa Santa cave deposits, *Habrothrix angustidens* Winge, and a living species from southeastern Atlantic Forest described at the start of the past century, *Akodon serrensis* Thos. Tentatively, both forms are considered as synonyms pending a detailed revision of the genus. The new genus belongs to the *Akodon* Division of the diverse tribe Akodontini where, based on molecular evidence, it is sister to *Thaptomys*, another forest-dwelling akodontine. The new genus is characterized by a unique combination of morphological traits including tail shorter than head-and-body; manual and pedal digits with short claws; skull robust with pointed rostrum, broad and somewhat flat interorbital region with frontal borders divergent posteriorly, and enlarged braincase without crests; large incisive foramina with expanded palatal process of premaxillary; broad mesopterygoid fossa with anterior margin rounded; alisphenoid strut present; carotid arterial circulation pattern primitive; molars noticeably large in relation to the skull and moderately hypsodont; main molar cusps arranged in opposite pairs; first upper molar without anteromedian flexus; length of third lower molar subequal to those of second lower molar; mandible without distinct capsular process; gall bladder present; stomach unilocular and hemiglandular; $2n=46$ (FN=46). The new genus is an Atlantic Forest endemic, indicating that the diversity of Akodontini has been overlooked outside of the Andes.

RESUMEN. Un nuevo género para *Habrothrix angustidens* y *Akodon serrensis* (Rodentia, Cricetidae): de nuevo paleontología y neontología se encuentran en el legado de Lund. Describimos un nuevo género de roedor sigmodontino para ubicar una especie fósil de los depósitos de Lagoa Santa, *Habrothrix angustidens* Winge y una especie viviente del sudeste de la Selva Atlántica descrita en los comienzos de la centuria pasada, *Akodon serrensis* Thos. Tentativamente, ambas formas son consideradas sinónimos a la espera de una revisión detallada de la diversidad del género. El nuevo género pertenece a la División *Akodon* de la diversa tribu Akodontini donde, sobre la base de evidencia molecular, resulta hermano de *Thaptomys*, otro akodontino especialista de selva. El nuevo género se caracteriza por una combinación única de rasgos morfológicos incluyendo una cola más corta que el largo cabeza-cuerpo, garras de los dedos de la mano y el pie cortas, cráneo robusto con

rostro puntiagudo, región interorbitaria ancha y algo chata con los bordes frontales divergentes hacia atrás y caja craneana agrandada y sin crestas, forámenes incisivos expandidos con proceso palatal del premaxilar bien desarrollado, fosa mesopterigoidea ancha con el borde anterior redondeado, barra alisfenoidea presente, patrón de circulación carotídea primitivo, molares notablemente grandes en relación a las proporciones del cráneo y moderadamente hipsodontes, principales cúspides de los molares dispuestas en pares opuestos, primer molar superior carente de flexo anteromediano, largo del tercer molar inferior subigual al del segundo molar inferior, mandíbula sin proyección capsular evidente, vesícula biliar presente, estómago unilocular-hemiglandular, $2n=46$ (FN=46). El nuevo género es endémico de la Selva Atlántica indicando una insospechada diversidad de los Akodontini en regiones extraandinas.

Key words: Akodontini. Atlantic Forest. *Deltamys*. Lagoa Santa. Muroidea.

Palabras clave: Akodontini. *Deltamys*. Lagoa Santa. Muroidea. Selva Atlántica.

INTRODUCTION

During the last 2 decades, several species of sigmodontine rodents named by Winge (1887) based on material from the rich paleontological deposits of Lagoa Santa area (Minas Gerais, Brazil) were recognized as senior synonyms of living entities (e.g., Voss, 1993; Voss and Carleton, 1993; Musser et al., 1998; Pardiñas and Teta, 2011, 2013). These findings, partly based on earlier observations (e.g., Ávila-Pires, 1960; Massoia and Fornes, 1965; Hershkovitz, 1966) helped identify redundancies in sigmodontine classification. In addition, these studies provided new data for understanding the tempo and mode of evolution of this rodent group and its past diversity (Voss, 1988; Voss and Myers, 1991). In fact, of 25 species recorded by Winge (1887) in Quaternary deposits (summarized in Voss and Myers, 1991:table 4), only *Habrothrix angustidens*, *Habrothrix clivigenis*, *Oxymycterus cosmodus*, *Oxymycterus talpinus*, and *Calomys anoblepas*, still remain as presumptively extinct forms (Pardiñas and Teta, 2013).

During the course of our studies of the collections of Lund housed in the Danish city of Copenhagen, once again paleontology meets neontology. *Habrothrix angustidens* Winge, 1887, a putative fossil species recorded from the area of Lagoa Santa, Minas Gerais, Brazil, appears morphologically undistinguishable from *Akodon serrensis* Thomas, 1902, a living form from the Atlantic Forest of Argentina and Brazil. The present paper documents this synonymy—first found and generously commu-

nicated to us by Robert Voss—and proposes a new genus for both forms. The need for a new genus was uncovered by the phylogenetic analyses of D'Elía (2003) and D'Elía et al. (2003), who employed mitochondrial and nuclear DNA sequences and broad taxonomic coverage and recovered *A. serrensis* as sister to *Thaptomys* and not as part of the genus *Akodon*. That hypothesis is here morphologically and karyologically supported and expanded through descriptions and comparisons against related genera that conform the *Akodon* Division (sensu D'Elía, 2003) of the tribe Akodontini (see also D'Elía and Pardiñas, 2015).

MATERIALS AND METHODS

In this report we studied fossil and recent specimens (see **Appendix 1**) housed at the following institutions: American Museum of Natural History, New York, USA (AMNH); The Natural History Museum, London, UK (BMNH); Centro Nacional Patagónico, Puerto Madryn, Argentina (CNP); Field Museum of Natural History, Chicago, USA (FMNH); Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina (MACN); Museu Nacional, Rio de Janeiro, Brazil (MN); Museu de Zoologia, Departamento de Biologia Animal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil (MZUFV); Universitets Zoologisk Museum, Copenhagen, Denmark (ZMK); and voucher specimens CIT and BIO that will be deposited at Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil. Fossil specimens are represented by craniodental fragments; recent specimens are preserved as dry skins, skulls, skeletons and individuals stored in fluid. Most of

the studied material came from several localities in southeastern Brazil, while a few are from Misiones Province in northeastern Argentina (see an annotated gazetteer of recording localities in **Supplementary Material S1**).

Anatomical descriptions and terminology follow Reig (1977), Carleton (1980), Voss (1988), and Carleton and Musser (1989). Standard external measurements (length of head and body; length of tail; length of hind foot with and without claw; length of ear from notch; all in millimeters) and weight (in grams) were transcribed from the specimen labels or museum catalogs as originally recorded by collectors. Craniodental dimensions were taken using a digital caliper and recorded to the nearest 0.01 mm and follow definitions provided by Wekxler and Geise (1996) and Voss et al. (2002). They were, arranged in alphabetical order: breadth across M1s, breadth across occipital condyles, breadth of braincase, breadth of incisive foramina, breadth of M1, breadth of rostrum, breadth of zygomatic plate, condylo-incisive length, depth of incisor, height of skull, height of mandible, least interorbital breadth, length of bulla, length of diastema, length of incisive foramina, length of mandible, length of orbital fossa, length of palatal bridge, length of rostrum, length of maxillary molar row, and zygomatic breadth. Measured specimens were sorted into age categories following toothwear classes defined for *Zygodontomys* by Voss (1991). Because our aim is to provide a general characterization of a new genus, we adopt a univariate statistics approach based on mean values for large samples of adult individuals (toothwear classes 3–5).

Karyotypes from selected specimens (see **Appendix I**) were prepared in the field. Chromosomes at metaphases were obtained via in vitro culture (culture of bone marrow grown in Dulbecco's MEM with 10% fetal bovine serum and colchicine 10^{-6} M), following incubation in KCl 0.075M solution at 37 °C by 40 minutes, centrifuged, fixed in Carnoy solution (methanol: acetic acid, 3:1), dropped onto clean slides and air-dried (Geise, 2014). Conventional coloration with Giemsa 5% was used to observe diploid (2n) and fundamental (FN, excluding sexual chromosomes) numbers and chromosome morphology variation; 50 metaphases of each specimen were analyzed with a Nikon Eclipse 50i photomicroscope under 1000 x magnification. Karyotypes were compared with literature reports. For intergeneric chromosomal comparisons, *Deltamys* sp. (CIT 944, male, Esmeralda, Rio Grande do Sul, Brazil), *Necromys lasiurus* (CIT 952, male, Rio Formoso, Pernambuco, Brazil), *Thalpomys lasiotis* (BIO 288, male, Brasília, Distrito

Federal, Brazil), and *Thaptomys nigrita* (CIT 331, male, Iguape, São Paulo, Brazil), metaphases were also obtained from fibroblast cell cultures derived from ear biopsies grown in Dulbecco's modified Eagle's medium supplemented with 20% fetal calf serum. For all species, GTG-banding was based on routine cytogenetic procedures, and FISH with whole chromosome probes was conducted following Ventura et al. (2009) using the *Akodon paranaensis* chromosome set as paints. FISH with telomeric probes was also performed only on *T. lasiotis* using Telomere PNA FISH Kit/FITC (K 5325-Dako) following the manufacturers' protocol for the purpose of cytogenetic comparisons. After FISH, the slides were counterstained with DAPI diluted in Vectashield (Vector) and analyzed using a fluorescence microscope (Zeiss Axiophot) equipped with software for image capture (MetaSystems).

RESULTS AND DISCUSSION

Taxonomic history

Habrothrix angustidens was described by Winge (1887:28–29) based on fossil remains recovered by the Danish naturalist Peter Lund in Lagoa Santa cave deposits in the first half of the XIX century. Winge (1887) also recognized or named 5 other forms in *Habrothrix*. One of these, *H. clivigenis* was referred to *Akodon* by Trouessart (1898) and remains a putative fossil form. The other 4, *H. cursor*, *H. orycter*, *H. lasiotis*, and *H. lasiurus* are now allocated, respectively, to the recent genera *Akodon*, *Thaptomys*, *Thalpomys*, and *Necromys*. Interestingly, all these genera belong to the tribe Akodontini. This highlights the accurate systematic perception of Winge, despite working mostly with fragmentary fossil material representing a large number of taxonomic groups.

Winge (1887:28) emphasized the similarities between *H. angustidens* with *H. cursor* but also was impressed by the absence of a capsular projection of the incisors and the smaller size of the former. He specifically highlighted the peculiar condition of the dentition of *H. angustidens*, and most remarkably, mentioned the difficulty of distinguishing the enamel from the dentine on the occlusal surfaces. Winge (1887:pl. II, figure 9) illustrated 2 remains belonging to *H. angustidens*, both from Lapa da Serra das Abelhas; an anterior skull fragment and a right

mandible. Shortly after, Trouessart (1898:536) listed *H. angustidens* under *Akodon*; this action must be viewed as a taxonomic act without major implications because this author transferred to this genus all the *Habrothrix* species of Winge plus a wide array of sigmodontine forms.

In 1902 Oldfield Thomas received from Brazil a large mammal collection made by Alphonse Robert in the Serra do Mar of the Brazilian state of Paraná. Thomas (1902:61) recognized one sigmodontine as new and described it as *Akodon serrensis* with type locality at “Roça Nova... at an altitude of about 1000 meters” (Thomas, 1902:59). Thomas also received in the same collection specimens of *A. cursor*, and he directly compared both species. *Akodon serrensis* was characterized basically on coloration traits and said to be intermediate in size between *A. azarae* (= “*arenicola*” in the original work) and *A. cursor*. Thomas (1902:61) also noted “molars very large in proportion, as large as those of the much bigger species *A. cursor*,” however, he did not make any mention about their morphology.

Miranda Ribeiro (1905:188) added a new name to the nominal forms allied to *A. serrensis*. Based on a single female from Retiro de Ramos (also known as Retiro do Ramos), Rio de Janeiro, Brazil, he erected [*Hesperomys*] (*A.*) *serrensis* var. *leucogula*, a subspecies characterized by a more olive dorsal coloration, a yellowish-ochraceous belly, and a narrow pure white band in the lower part between the chin and the anterior limbs.

The XXth century passed without major systematic or nomenclatural modifications. While *H. angustidens* was basically forgotten, *A. serrensis*—including *H. (A.) serrensis leucogula*—was maintained under *Akodon* from the time of the catalog of Gyldenstolpe (1932) up to the more recent treatments (e.g., Musser and Carleton, 2005; Patton et al., 2015). Hershkovitz (1990a:14) ranked *leucogula* as a valid and different species from *serrensis*, including both forms in an informal group that he named *Akodon mollis* size class. Other researchers addressed morphological and chromosomal considerations of *A. serrensis* populations, especially in southern Brazil. In part, these studies were triggered by a misunderstanding

involving several species of the *A. cursor* group (sensu Smith and Patton, 2007) and *A. serrensis*. This contorted history, which started when Liascovich and Reig (1989) erroneously referred one Argentinean *Akodon* specimen to *A. serrensis* and reported for it a diploid complement of 44, was fully resolved by Christoff et al. (2000; see also Pardiñas et al., 2003; Gonçalves et al., 2007). It is of interest to transcribe a paragraph of Liascovich and Reig (1989:394) in order to reflect the understanding of *A. serrensis* at that time: “*Akodon serrensis* is similar to *A. cursor* in size and color pattern, and the two species are difficult to distinguish based on external characters. Fresh skins of *A. serrensis* have a conspicuously more ochraceous venter, especially evident in the anal region; however, even this distinction must be confirmed by examination of a large series of specimens. The skulls of both species also are similar in having long, narrow rostra, moderately inflated frontal regions, short zygomatic plates, a reduced interparietal, and elongated palatal foramina that reaches the level of the protocone of M1. The main differences between the two species are: the nasals are longer and project farther behind the maxillo-frontal suture in *A. cursor*; the zygomatic plate is much deeper in *A. serrensis*; the palate is shorter in *A. cursor*, its posterior border terminating anterior to the level of the alveoli of M3; the molars are narrow, elongated, and larger in *A. serrensis*; and the mandible in *A. cursor* is slender and elongated with a more posteriorly projecting condylar process and a more inflated capsular projection (root of incisor).” It is difficult to know how influential it was that one of the specimens used by Liascovich and Reig (1989) was, in reality, an *Akodon paranaensis* (see Pardiñas et al., 2003; Gonçalves et al., 2007). Despite having the holotype of *A. serrensis* in hand, these authorities failed to distinguish these species. This necessitates that we call attention to the similarity of *A. serrensis* and other species of the *cursor* group of *Akodon* (e.g., *cursor*, *montensis*, *paranaensis*).

However, a new scenario emerged from molecular studies. D’Elía et al. (2003:358) explicitly called attention to the generic position of *A. serrensis* as follows: “A novel finding of our

study with respect to akodontine systematics is the placement of *Akodon serrensis* well outside the *Akodon* clade... *A. serrensis* appears as sister to the monotypic genus *Thaptomys*, and this clade is sister to the genus *Necromys*... The phylogenetic position of *Akodon serrensis* is surprising because to the best of our knowledge nobody has cast doubt upon the inclusion of *A. serrensis* within the genus *Akodon*... We will not make any taxonomic judgment about this topology until further studies... are carried out. However, a combined analysis of nuclear and mitochondrial DNA sequences points in the same direction." In fact, D'Elía (2003:319) revisited this topic in a combined cytb and IRBP analysis "Ten extra steps are needed to force *A. serrensis* within the *Akodon* clade. *Akodon serrensis* appears to be sister to the monotypic genus *Thaptomys* (node 18), although this relationship is weakly supported (JK<50%, BS=1). This clade is sister to the clade *Thalpomys-Necromys*. Further studies, including morphological comparisons and the sequencing of additional specimens, are needed to determine if *A. serrensis* should be placed on its own genus or in *Thaptomys*." Despite the relevance, these findings were basically ignored in the chromosomal research developed with *Akodon* species in southeastern Brazil (e.g., Ventura et al., 2006; Hass et al., 2008; Bonvicino, 2011). More recently, analyzing cytb over a taxonomically diverse sample of *Akodon*, Smith and Patton (2007:848) corroborated the separate position of *serrensis* although they highlighted its alternative relationship to *Akodon* + *Deltamys* rather than *Thaptomys*.

The taxonomic hypothesis that *H. angustidens* and *A. serrensis* were congeners was achieved by R. Voss after a restudy of the type material of both forms. According to him "The type series of *Habrothrix angustidens* consists of subfossil cranial fragments and disassociated hemimandibles from several caves in the vicinity of Lagoa Santa... All of this material qualifies as syntypes because Winge did not designate a holotype... Altogether, this material... preserves the entire upper and lower dentition, the left zygomatic plate, diastema, palate, interorbital region, and mandibles. We compared this material side-by-side with

a complete topotypical cranium of *Akodon serrensis* (ZMUC 1257) and found these two taxa to be phenotypically indistinguishable. In addition to qualitative resemblances, the few measurements that we were able to take from the lectotype of *angustidens* all fall within the range of variation seen in the topotypic series of *serrensis*... The only possible taxonomic conclusion is that *angustidens* and *serrensis* are synonyms" (R. Voss, in litt. November 4, 2008; **Supplementary Material S2**).

SYSTEMATICS

Family Cricetidae Fischer, 1817

Subfamily Sigmodontinae Wagner, 1843

Tribe Akodontini Vorontsov, 1959

Castoria, gen. nov.

Figs. 2-5; Tables 1-3

Synonymy.—

Habrothrix sensu Winge (1887:28), part, not *Habrothrix* Wagner, 1843

Akodon sensu Thomas (1902:61), part, not *Akodon* Meyen, 1833

Hesperomys sensu Miranda Ribeiro (1905:188), part, not *Hesperomys* Waterhouse, 1839

Type species.— *Habrothrix angustidens* Winge, 1887.

Etymology.— In homage to Castor Cartelle, a contemporary paleontologist (born in Ourense, Spain in 1938) studying Quaternary Brazilian mammalian fauna who effectively resurrected in Brazil the genus and figure of Peter W. Lund (see Cartelle, 2002). Continuous efforts of Cartelle over the last 4 decades have enlarged our knowledge of biotic evolution in tropical areas through the excavation, cleaning, sorting, and study of a huge quantity of osteological material recovered from karstic caves in northeastern Brazil.

Geographic distribution.— Known from southeastern Brazil and the northeastern tip of Argentina, roughly between 20° to 30° S and mostly restricted to an elevational range above 800 m (**Fig. 1; Supplementary Material S1**).

Chronological distribution.— Late Pleistocene? –Recent. Fossils were found in 5 cave deposits – Lapa do Capão Secco, da Cerca Grande, a chamber near Escrivania, Quebra Chavelha, and Serra das Abelhas– in the area of Lagoa Santa, Minas Gerais, Brazil (Winge, 1887). Absolute radiometric dates performed on fossils and breccias excavated by Lund from Lagoa Santa indicate an array of ages

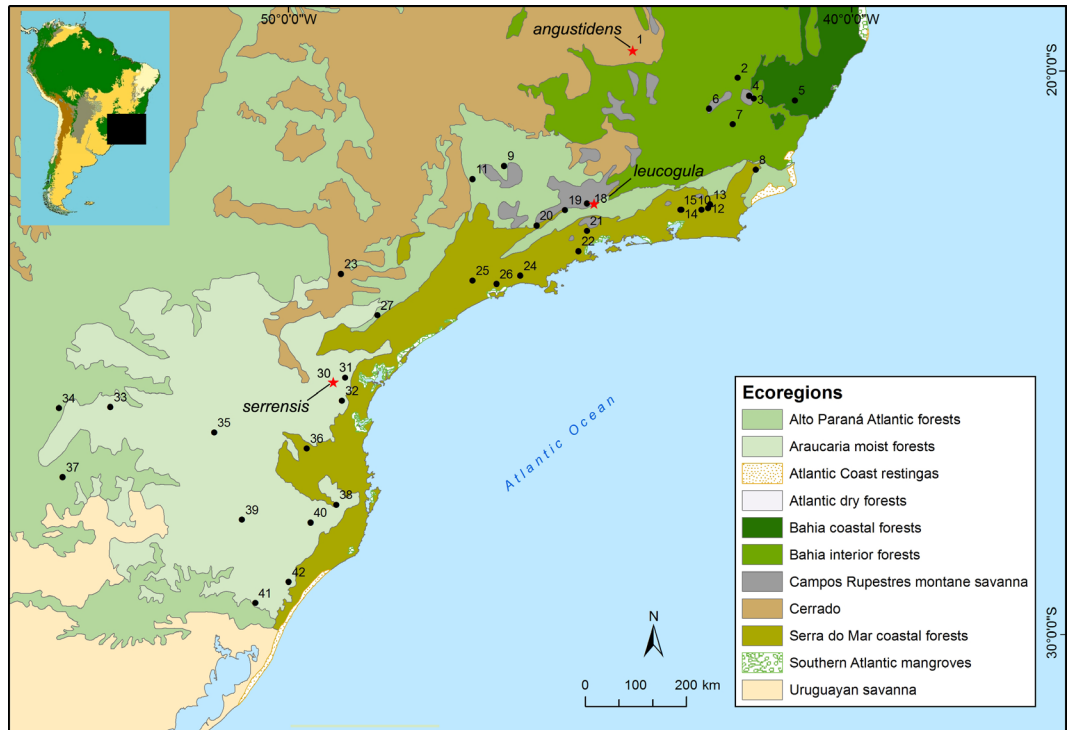
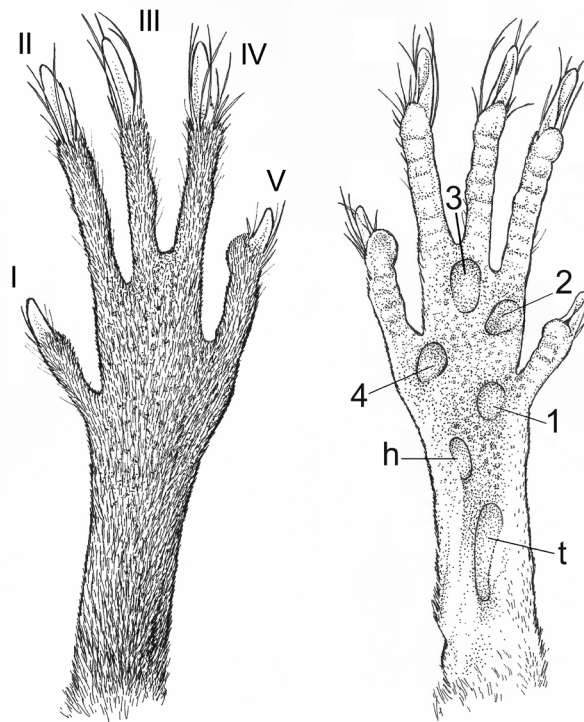


Fig. 1. Locality records for *Castoria* gen. nov.; type localities of available nominal forms are indicated. See **Supplementary Material S1** for a geographic gazetteer.



covering at least the last 0.5 MA (e.g., Auler et al., 2006).

Contents.— Tentatively, the genus is considered to be composed by one species, *Castoria angustidens* (Winge, 1887), nov. comb. Neither morphology nor metrics (**Table 1**) allow us to distinguish, at the specific level, the anterior skull portion that represents *H. angustidens* from those of living populations traditionally ascribed to *A. serrensis*. In fact, an exploratory multivariate analysis based on principal components placed the lectotype of *H. angustidens* within the morphospace of recent Brazilian specimens of *A. serrensis* (**Supplementary Material S3**). Minor differences between the fossil *H. angustidens* fragment—particularly the

Fig. 2. Dorsal and plantar view of left hind foot of *Castoria* gen. nov., based on an adult female from RP 2, 6 km NE Arroyo Paraíso, Misiones, Argentina (CNP 449). Abbreviations are: I–V, digits; 1–4, interdigital tubercles; h, hypothenar; t, thenar.



Fig. 3. *Castoria* gen. nov., based on an adult male from Fazenda da Neblina, Parque Estadual da Serra do Brigadeiro, Brazil (MZUFV 1635): skull in right lateral (top), dorsal (left) and ventral (right) views, and right dentary in labial view. Scale = 5 mm.

narrow condition of the molar tooththrow—and recent *A. serrensis* individuals are here attributed to age variation. Given the broad geographic range of this genus and modest morphometric segregation (results not shown; see also Kosloski, 1997), the variation of *Castoria* is a topic that deserves further study. The names *serrensis* Thomas, 1902 and *leucogula* Miranda Ribeiro, 1905 are available.

Morphological diagnosis.— Rodents of the subfamily Sigmodontinae (sensu Reig, 1980) with the following combination of characters: small-medium size (head-and-body length ~95 mm; condylo-incisive length ~25 mm); tail shorter than head-and-body (~85% of head-and-body length); manual and pedal digits with short claws covered by long and sparse ungual tufts; pelage soft and long; skull robust with pointed rostrum, broad and somewhat flat interor-

bitral region with frontal borders moderately divergent backwards, and enlarged braincase without patent crests; broad, anteriorly rounded, and slanting zygomatic plate; zygomatic arches with their lower border parallel with respect to the alveolar plane; long incisive foramina, anteriorly constricted, with expanded palatal process of premaxillary; short, broad, and flat bony palate; broad mesopterygoid fossa with anterior margin rounded; alisphenoid strut present; tegmen tympani overlapping squamosal with the participation of a distinct posterior suspensory process of the latter bone; carotid arterial circulation pattern primitive; bullae short and rounded; upper incisors opisthodont; molars noticeable large in relation to the cranium proportions, terraced, enlarged, and moderately hypsodont; main molar cusps arranged in opposite pairs; M1 without anteromedian flexus with large procingulum and marked trilophodont pattern; M3 with cylindrical outline; m1 with anteromedian flexid weakly present and procingulum anterior-posteriorly compressed; m1–2 with small ectolophids present and mesolophids probably fused to metaconids; length of m2 slightly shorter than those of m1; length of m3 subequal than those of m2; lower incisor alveolus without distinct capsular process on lateral dentary surface; gall bladder present; stomach unilocular and hemiglandular; diploid number (2n) = 46 and fundamental number (FN) = 46.

Morphological description.—The following description is based on representative samples from localities in Minas Gerais and Rio de Janeiro states in Brazil and 2 individuals from Argentina. It aims to provide a general characterization of the genus. Additional morphological details and measurements can be found in Hershkovitz (1998:215–218).

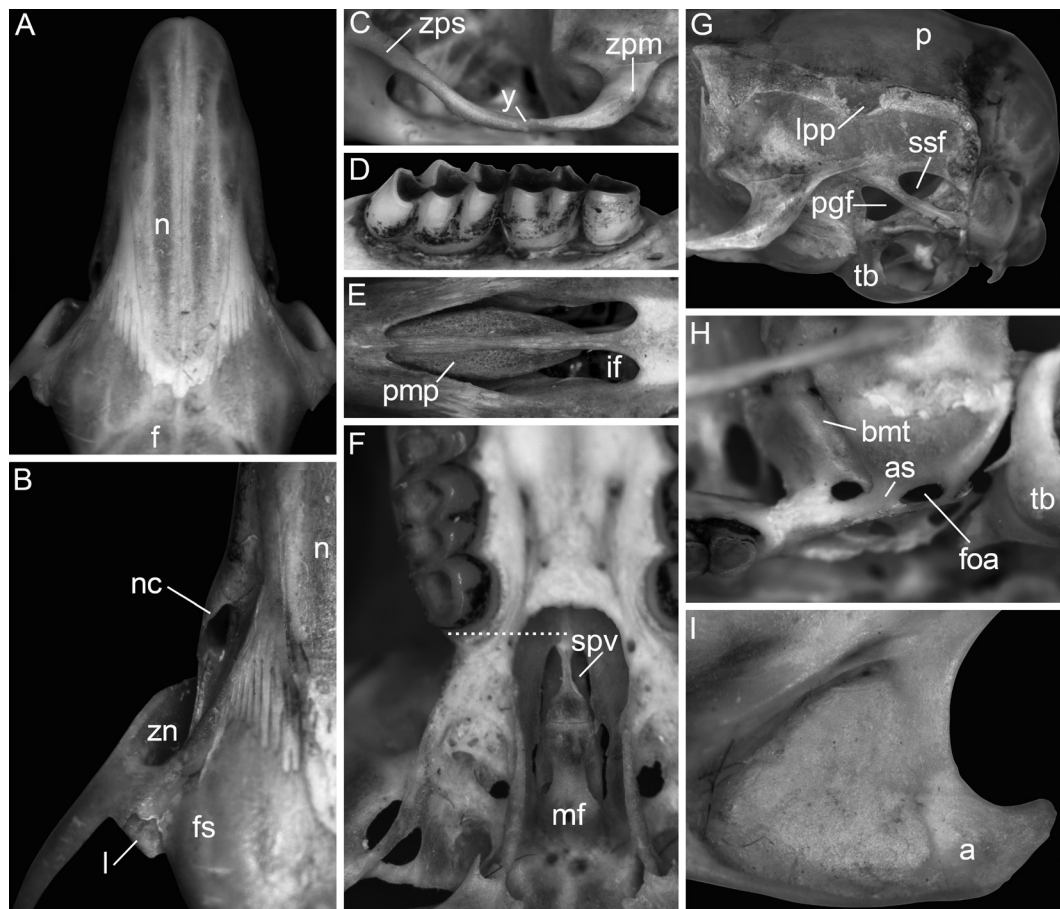


Fig. 4. Selected anatomical features of the skull and dentition of *Castoria* gen. nov., based on adult individuals MZUFV 1630, 1655, 2555, and CNP 449: A) rostrum in dorsal view; B) maxillary-frontal area in dorsal view; C) left zygomatic arch in lateral view; D) left upper tooththrow (note the hypsodonty); E) incisive foramina; F) mesopterygoid and parapterygoid fossae (the dashed line highlights the short condition of the palate); G) posterior portion of the skull in lateral view; H) alisphenoid-squamosal area; I) angular process of the mandible in lingual view. Abbreviations are: a, angular process of the mandible; ab, auditory bulla; as, alisphenoid strut; bmt: buccinatory-masticatory thorough; f, frontal; fs, frontal sinus; if, incisive foramen; j, jugal; zn, zygomatic notch; l, lachrymal; lpp, lateral projection of the parietal; mf, mesopterygoid fossa; n, nasal; nc, nasolachrymal capsules; p, parietal; pgf, postglenoid foramen; pmp, premaxillary process; spv: sphenopalatine vacuities; ssf, subsquamosal fenestra; zpm, zygomatic process of the maxillary; zps, zygomatic process of the squamosal.

Castoria includes small-medium sized sigmodontine rodents (Tables 1 and 2) characterized by a darker general coloration above and below, short mystacial vibrissae, short claws, and a moderately long tail although shorter than the combined length of head and body. The dorsal and ventral colors are subtly delimited with weak countershading (Supplementary Material S4). The skins exhibit thick, soft fur (guard hairs ~9 to 12 mm); the cuticle pattern of guard hairs was described as narrow and leaf-shaped; medullar pattern of these same hairs were a mixture

of alveolar and striped types, with three to four layers of cells of irregular shape (Silveira et al., 2013). The dorsal fur is dark yellowish- to orangish-brown; the ventral surface is washed with bright buff or tawny over dark-gray hair bases. The eyes are small. The mystacial vibrissae are short, not extending posteriorly much beyond the base of the pinnae; genal vibrissae are present. The ears are medium in size, rounded, and internally and externally covered by brown hairs. The tail is dark brown, unicolored, and sparsely haired, covered by sets of 3 somewhat



Fig. 5. Occlusal view of upper left (above; MZUFV 1234, 1242, 1630, 1076) and lower left (below; MZUFV 1234, 1242, MN 69813, MZUFV 1076) tooththrows in *Castoria* gen. nov., arranged from left to right by increased wear. Scale = 1 mm.

hispid hairs per scale, each dorsal hair covering 2–3 scale-rows; apical tuft absent. The manus and pes in *Castoria* are covered with short hairs, with their basal portion brown and apical portion whitish. The claws, basally open on the pes, are inconspicuous and dorsally covered by several whitish or darker unguis hairs slightly surpassing their apices. The plantar surface is naked, pigmented, and slightly squamated (sensu Pacheco, 2003). The pes has 6 pads, 4 interdigital and 2 plantar, the thenar and hypothenar; the thenar pad is enlarged and narrow; the hypothenar pad is subequal in size to the 1st interdigital pad; dIII and dIV are the largest, subequal in size and showing a slightly syndactylous condition (Fig. 2).

The skull in dorsal view is characterized by a flat, broad appearance with a pointed rostral region and

Table 1

Selected measurements (in mm) of the lectotype of *Habrothrix angustidens* (ZMK 1/1845:13246), the type series of *Akodon serrensis* (BMNH 3.7.1.66–BMNH 3.7.1.73, ZMK 1257; mean, minimum–maximum and sample size in parenthesis), and the holotype of *Akodon serrensis leucogula* (MN 2513).

	<i>H. angustidens</i>	<i>A. serrensis</i>	<i>A. s. leucogula</i>
Length of head and body ^a	–	92, 85 - 105 (8)	105
Length of tail ^a	–	78, 70 - 85 (8)	73
Hind foot with claws ^b	–	24, 23 - 25 (8)	24 ^a
Ear ^a	–	17, 17 - 18 (8)	–
Condylus-incisive length	–	23.7, 22.5 - 24.8 (8)	25.8
Length of diastema	6.3	6.8, 6.3 - 7.5 (9)	7.1
Length of upper molars	4.9	4.9, 4.8 - 5.2 (9)	4.6
Breadth of M1	1.2	1.2, 1.1 - 1.2 (9)	1.6
Length of incisive foramina	5.9	5.8, 5.5 - 6.1 (9)	5.6
Breadth of rostrum	4.4	4.5, 4.2 - 4.7 (9)	4.6
Breadth of palatal bridge	2.6	2.8, 2.5 - 3.3 (9)	–
Breadth of zygomatic plate	2.2	2.4, 2.2 - 2.6 (9)	2.7
Least interorbital breadth	5.2	5.4, 5.2 - 5.6 (9)	5.3
Breadth of braincase	–	12.2, 11.7 - 12.7 (9)	11.1
Depth of incisor	1.2	1.2, 1.1 - 1.3 (9)	–
Length of orbital fossa	–	8.0, 7.7 - 8.4 (9)	8.2

^a Measured by collector.

^b Measured from dry skin.

Table 2

Descriptive statistics (in mm; mean \pm standard deviation, range, and sample size in parenthesis) for 2 samples of adult individuals of *Castoria angustidens* nov. comb., from Brazil (see **Supplementary Material S1** for additional data about these localities); PE=Parque Estadual; PN=Parque Nacional.

	Fazenda da Neblina, PE da Serra do Brigadeiro				Vale das Antas, PN da Serra dos Órgãos			
	females		males		females		males	
Length of head and body	98.70 \pm 26.90	84.00 – 113.00 (10)	96.67 \pm 27.88	83.00 – 116.00 (9)	100.03 \pm 14.09	84.00 – 116.00 (31)	102.20 \pm 12.20	87.00 – 119.00 (40)
Length of tail	89.80 \pm 23.38	83.00 – 95.00 (10)	83.33 \pm 23.15	74.00 – 95.00 (9)	84.10 \pm 12.30	60.00 – 96.00 (29)	85.10 \pm 10.18	70.00 – 101.00 (39)
Length of hind foot with claw	25.57 \pm 6.31	24.00 – 28.00 (7)	25.50 \pm 7.07	24.00 – 29.00 (6)	25.77 \pm 3.30	16.00 – 31.50 (30)	25.36 \pm 2.60	22.00 – 28.00 (39)
Length of hind foot without claw	23.29 \pm 5.51	22.00 – 25.00 (7)	23.33 \pm 6.26	22.00 – 26.00 (6)	23.87 \pm 3.46	14.00 – 29.00 (30)	23.18 \pm 3.05	19.00 – 25.00 (40)
Length of ear	17.20 \pm 2.58	14.00 – 20.00 (10)	16.71 \pm 3.30	16.00 – 18.00 (7)	15.80 \pm 3.90	11.00 – 22.00 (30)	16.81 \pm 4.42	11.00 – 23.00 (40)
Weight	29.67 \pm 10.42	19.00 – 38.00 (6)	28.50 \pm 9.82	21.00 – 39.00 (6)	24.48 \pm 4.13	17.00 – 36.00 (30)	25.47 \pm 7.54	15.00 – 60.00 (38)
Breadth across M1s	5.67 \pm 1.26	5.36 – 5.99 (10)	5.58 \pm 1.06	5.24 – 5.97 (9)	5.74 \pm 3.95	5.42 – 6.09 (27)	5.66 \pm 4.73	5.19 – 6.27 (34)
Breadth across occipital condyles	6.55 \pm 1.01	6.23 – 6.82 (10)	6.49 \pm 0.78	6.16 – 6.84 (9)	6.55 \pm 3.81	5.95 – 7.00 (27)	6.49 \pm 4.49	6.07 – 7.41 (33)
Breadth of braincase	11.68 \pm 0.58	11.11 – 12.15 (10)	11.67 \pm 1.19	11.31 – 12.32 (8)	11.48 \pm 2.89	11.03 – 12.01 (27)	11.42 \pm 3.66	10.90 – 11.91 (33)
Breadth of incisive foramina	2.13 \pm 2.27	1.95 – 2.39 (10)	2.09 \pm 2.09	1.77 – 2.25 (9)	2.17 \pm 4.61	1.85 – 2.49 (27)	2.09 \pm 5.32	1.76 – 2.33 (34)
Breadth of M1	1.25 \pm 2.53	1.14 – 1.37 (10)	1.27 \pm 2.33	1.12 – 1.42 (9)	1.30 \pm 4.77	1.18 – 1.46 (27)	1.30 \pm 5.45	1.14 – 1.43 (34)
Breadth of rostrum	5.09 \pm 1.44	4.69 – 5.62 (10)	4.99 \pm 1.25	4.50 – 5.55 (9)	4.99 \pm 4.10	4.12 – 5.58 (27)	5.03 \pm 4.84	4.40 – 5.66 (34)
Breadth of zygomatic plate	2.82 \pm 2.09	2.45 – 3.30 (10)	2.56 \pm 1.97	1.76 – 2.97 (9)	2.76 \pm 4.51	2.28 – 3.29 (27)	2.75 \pm 5.21	2.40 – 3.06 (34)
Condylol-incisive length	25.39 \pm 4.53	23.51 – 27.24 (10)	24.74 \pm 4.83	23.28 – 26.36 (9)	25.46 \pm 0.81	23.47 – 27.47 (27)	25.47 \pm 1.54	23.26 – 26.76 (33)
Height of skull	8.26 \pm 0.54	7.94 – 8.69 (10)	8.22 \pm 0.27	8.00 – 8.40 (9)	8.25 \pm 3.49	7.84 – 8.59 (27)	8.24 \pm 4.30	7.85 – 8.61 (34)
Height of mandible	6.28 \pm 1.11	5.67 – 6.66 (10)	6.28 \pm 0.86	5.80 – 6.67 (9)	6.40 \pm 3.59	5.78 – 6.94 (25)	6.38 \pm 4.40	5.77 – 6.94 (32)
Least interorbital breadth	5.54 \pm 1.30	5.21 – 5.86 (10)	5.47 \pm 1.08	5.24 – 5.70 (9)	5.38 \pm 4.02	5.05 – 5.94 (27)	5.34 \pm 4.78	4.81 – 5.76 (34)
Length of bulla	4.77 \pm 1.52	4.55 – 5.06 (10)	4.79 \pm 1.03	4.45 – 5.07 (8)	4.86 \pm 4.12	4.47 – 5.42 (27)	4.79 \pm 4.88	4.23 – 5.27 (34)
Length of diastema	7.26 \pm 0.87	6.76 – 7.98 (10)	7.02 \pm 0.67	6.56 – 7.52 (9)	7.39 \pm 3.66	6.60 – 8.20 (27)	7.39 \pm 4.45	6.61 – 8.00 (34)
Length of incisive foramina	5.96 \pm 1.21	5.45 – 6.66 (10)	5.75 \pm 1.03	5.39 – 6.22 (9)	5.87 \pm 3.93	5.34 – 6.53 (27)	5.87 \pm 4.70	4.97 – 6.44 (34)
Length of mandible	14.02 \pm 1.22	13.34 – 14.86 (10)	13.49 \pm 1.45	12.47 – 14.06 (9)	13.85 \pm 2.18	13.11 – 14.77 (25)	13.90 \pm 3.13	13.14 – 14.79 (32)
Length of orbital fossa	8.52 \pm 0.54	8.07 – 9.29 (10)	8.26 \pm 0.30	7.92 – 8.58 (9)	8.24 \pm 3.49	7.73 – 8.78 (27)	8.31 \pm 4.29	7.74 – 8.92 (34)
Length of palatal bridge	4.32 \pm 1.66	3.65 – 4.55 (10)	4.39 \pm 1.40	4.02 – 4.72 (9)	4.53 \pm 4.18	3.74 – 5.07 (27)	4.58 \pm 4.92	4.15 – 6.25 (34)
Length of rostrum	11.06 \pm 0.60	10.00 – 12.13 (10)	10.71 \pm 0.78	9.54 – 11.69 (9)	11.19 \pm 2.09	10.23 – 12.16 (21)	10.98 \pm 3.54	9.17 – 11.91 (31)
Length of maxillary molar row	4.96 \pm 1.47	4.41 – 5.16 (10)	5.02 \pm 1.21	4.69 – 5.32 (9)	4.99 \pm 4.09	4.70 – 5.28 (27)	4.98 \pm 4.84	4.73 – 5.28 (34)
Zygomatic breadth	14.57 \pm 2.14	13.60 – 15.35 (10)	14.21 \pm 1.99	13.52 – 14.69 (8)	14.30 \pm 1.80	13.60 – 15.06 (23)	14.28 \pm 2.81	13.54 – 15.18 (30)

Table 3

Morphological comparisons of selected traits among *Castoria* gen. nov. and other related sigmodontines of the *Akodon* Division.

Characters	<i>Castoria</i>	<i>Akodon</i> (<i>cursor</i> group)	<i>Deltamys</i>	<i>Necromys</i> (excluding <i>amoenus</i> and <i>urichi</i>)	<i>Thalpomys</i>	<i>Thaptomys</i>
Head and body length as % total length	~85%	~80%	~85%	~55–60%	~60%	~35%
Countershading	weak	moderate	weak	moderate	strong	weak
Rostrum	long and narrow	long and narrow	short and narrow	short and broad	short and broad	short and broad
Interorbital region	broad	moderate	narrow	broad	broad	broad
Frontals	convergent with sharp margins	“hourglass,” with rounded margins	“hourglass,” with rounded margins	convergent with beaded margins	convergent with ledged margins	convergent with rounded margins
Free upper border of zygomatic plate	yes	yes	no	yes	yes	no
Premaxillary process	> ½ of the incisive foramen length	< ½ of the incisive foramen length	> ½ of the incisive foramen length	< ½ of the incisive foramen length	< ½ of the incisive foramen length	> ½ of the incisive foramen length
Alisphenoid strut	present	present	absent	present	?	present
Middle lacerate foramen	open	open	close	open	open	close
Subsquamosal [ssf] / postglenoid [pgf] fenestrae size	ssf ~ pgf	ssf ~ pgf	ssf ~ pgf	ssf < pgf	ssf ~ pgf	ssf << pgf
Capsular process	absent	absent	absent	present	present	present
Molar design main cusps	opposite	alternate	opposite	opposite	alternate	alternate
Anteromedian flexus	absent	present	present	absent	present	present
Procingulum m1	compressed	not compressed	compressed	not compressed	not compressed	not compressed
m2 / m3 in length	m2 ~ m3	m2 > m3	m2 > m3	m2 >> m3	m2 >> m3	m2 > m3
Gall bladder	present	present or absent	present	present or absent	present	absent

a rounded braincase (Fig. 3). The nasals are pointed and usually slightly projecting beyond the anterior margin of the premaxillary (Fig. 4A). The rostrum is flanked by shallow but distinct zygomatic notches (Fig. 4B); the frontal sinuses are inflated and the interorbital region is broad, with rounded supra-orbital margins in young and adult specimens (older animals develop small, sharp, convergent postorbital edges). The zygomatic arches are delicate, widest across the squamosal roots; they converge anteriorly and their midportions run parallel to the alveolar plane; the jugal is well developed (Fig. 4C). The braincase is large, smooth, and globose; the lambdoid crests are developed only in older individuals. The interparietal varies in size and form, being typically rhomboidal and compressed. The zygomatic plate in lateral view has a straight anterior margin that aligns vertically or slopes slightly backward; the origin of the superficial masseter is marked by a scar (not a tubercle) that is just below and slightly behind the anteroventral margin of the zygomatic plate. The foramina of the carotid circulation consist of pattern 1 (sensu Voss, 1988); a thick alisphenoid strut is present, and the subsquamosal fenestra is large (Figs. 4G and 4H). The incisive foramina are long (extending between the M1 anterocones) and characterized by a constricted anterior portion (at or near the premaxillary-maxillary sutures) and a markedly inflated premaxillary process (Fig. 4E); the palate is broad and uncomplicated by keels or deep lateral grooves; and the mesopterygoid fossa extends anteriorly to or between the M3s (Fig. 4F). There are no large posterolateral palatal pits, just tiny foramina flanking the mesopterygoid fossa. The mesopterygoid roof is perforated by very narrow but long sphenopalatine vacuities (Fig. 4F). The auditory bullae are small and flask-shaped, with broad bony Eustachian tubes.

The mandible is relatively robust, moderately low and elongated; the lower border of the ramus bends upward and backward behind the level of the m2 and descends again behind the m3. The mental foramen opens on the dorsolateral surface of the diastema. The alveolus of the lower incisor is contained in a ridge, not a distinct process, on the lateral surface of the mandible behind the base of the coronoid process. The angular process is pointed and bent upwards (Fig. 4I).

The upper incisors are opisthodont in orientation, with yellow-orange enamel bands, straight or very slightly inclined in frontal view and sharp, not inclined medially in ventral view (cf. Voss, 1988:376-377). The exterior edge of the upper incisors shows a thick enamel band; the dentine lake is straight

(sensu Steppan, 1995:figure 10). The molars are very narrow in proportion to their length, with a marked unilateral tubercular hypsodonty (sensu Hershkovitz, 1962:89; Fig. 4D). They are also characterized by the opposite pattern of the main cusps, strongly bi-level (subadults) to terraced (adults) coronal surface (sensu Hershkovitz, 1962:86), simplification, and a tendency to retain little occlusal detail even in young animals; the cusps and lophs wear rapidly away, exposing large dentine basins (Fig. 5). The latter feature, shared with other akodontines (e.g., *Akodon*, *Oxymycterus*), makes it necessary to study a series of individuals of different ages in order to adequately assess dental variation. The upper molar tooth-rows are parallel or slightly convergent backwards in adult and old-adult specimens. The M1 is typically composed by 3 subequal "lobules" characterized by central basins and abrupt posterior walls inclined backwards. The procingulum lacks any trace of an anteromedian flexus and shows a well-developed surface occlusal area. The paracone "lobule" is the largest because it likely involves the mesoloph plus the paralophule; a trace of the latter is present as an acute posterior edge. The proto- and hypoflexus are subequals and scarcely developed, while para- and metaflexus are moderately directed backwards, with their internal margins reaching the middle line of the molar; the mures flanked by these flexus are particularly enlarged, lingually disposed, and longitudinally oriented. No evidence of a free posteroloph was detected in any studied specimen. The M2 shows a tetralophodont pattern with anteroloph and posteroloph obsolescent in young individuals to bilophodont in adults. The metacone "lobule" is smaller than the paracone one. The M3 is certainly complex in juveniles, with an internal enamel ring of equivocal identity (mesofossette?) and reduced hypoflexus and posterior lobe. In subadult to adult individuals, M3 acquires a cylindrical outline without internal accidents. We documented a deformation of the occlusal figure of the upper molars by the differential wear of labial and lingual sides as a consequence of age; whereas the labial portion is partially eroded to the coronal base, the lingual remains with persistent striae and thicker enamel. Lower molars are characterized by occlusal simplicity in subadult and adult individuals, a compressed procingulum mostly fused with the remainder portion of the m1, and a large m3 subequal to or even exceeding the m2 in length.

On the basis of 9 individuals, *Castoria* has 13 thoracic ribs, 13 thoracic vertebrae, 6 lumbar vertebrae, and 29-30 caudal vertebrae. The sacrum involves 3 subequal and squared sacral vertebrae. The neural spine of the axis is enlarged anteriorly-posteriorly

and is fan-shaped. The neural spine of the 2nd thoracic vertebra is enlarged, twice or more as long as nearby spines. The caudal vertebrae lack hemal arches but hemal processes are present starting between the 3rd and 4th caudal vertebrae, becoming most pronounced between the 5th and 6th, and then decreasing in size.

Gross stomach morphology in *Castoria* conforms with the unilocular-hemiglandular type (sensu Carleton, 1973:figure 2), a widespread condition in sigmodontine rodents. The bordering fold bisects the stomach on a line from the incisura angularis to a point opposite it on the greater curvature (**Supplementary Material S5**). Animals from Rio de Janeiro, São Paulo, and Misiones indicate that a gall bladder is present (cf. Geise et al., 2004; this paper).

Cytogenetics.— The specimens of *Castoria angustidens* cytogenetically analyzed (**Appendix 1**) presented the same karyotype, with $2n=46$ and $FN=46$ (**Supplementary Material S6**); the autosomes comprising 21 acrocentric pairs and 1 small metacentric pair (the smallest of the complement). The X chromosome is a medium-sized acrocentric, and the Y one of the smallest of the complement, also acrocentric. This karyotype was previously recorded for specimens collected in states of Rio de Janeiro (Geise et al., 1998; Olifiers et al., 2007), Paraná (Barros-Battesti et al., 1998; Hass et al., 2008), Santa Catarina (Testoni et al., 2012), Minas Gerais (Moreira et al., 2009), and Espírito Santo (Bonvicino et al., 2002). Cytogenetic information is lacking for Argentinean populations; the animal referred to *A. serrensis* by Liascovich and Reig (1989) and characterized as having $2n=44$ ($FN=44$) was correctly reidentified as *Akodon paranaensis* by Christoff et al. (2000).

Phylogeny.— Phylogenetic analyses of combined molecular markers (e.g., D'Elía, 2003; D'Elía et al., 2003; Smith and Patton, 2007) showed that *Castoria* belongs to the *Akodon* Division of the tribe Akodontini, a well-supported clade composed by the recent genera *Akodon*, *Deltamys*, *Necomys*, *Podoxymys*, *Thalpomys*, and *Thaptomys* (D'Elía, 2003; Leite et al., 2015). Within the *Akodon* Division, its position varies depending upon the molecular markers used, taxonomic sampling, and the type of analysis conducted. In fact, in those studies with moderate taxonomic coverage (e.g., excluding Vilela et al., 2014), *Castoria* was recovered as sister to a clade including *Akodon* + *Deltamys* (Smith and Patton, 2007; Ventura et al., 2013; Abreu et al., 2014; Pardiñas et al., 2014b), but elsewhere, it appears as sister to *Thaptomys* (e.g. D'Elía, 2003; D'Elía et al., 2003), or as sister to *Deltamys* (Fabre et al., 2012; Leite et al., 2015). Despite its uncertain position, no study has

recovered *Castoria* within or as sister to the genus *Akodon*. This finding supports the hypothesis that this lineage deserves generic recognition.

Comparisons.— The fact that *A. serrensis* remained allocated as a species of *Akodon* for more than a century is a clear signal of the strong morphological similarity between these 2 genera. In addition, some character traits that were used as evidence of the distinctiveness of some genera of the *Akodon* Division, such as the morphology of the male accessory glands (see Reig, 1987), were—and remain—unknown for *A. serrensis*. *Castoria* is smaller than *Akodon cursor* or *Akodon montensis* and can be externally distinguished by its shorter manual claws and overall darker coloration. The relative size of molar tooththrows, noticeably larger in *Castoria* than in *Akodon* (as Gyldenstolpe, 1932:104 highlighted), the general morphology of the interorbital region—flat and divergent posteriorly in *Castoria* and smooth and hourglass-shaped in *Akodon*, and the marked differences in the development of the premaxillary process as seen through the openings of the incisive foramina—more inflated and extended in *Castoria* than in *Akodon*, are the main cranial features separating these genera (**Fig. 6**). However, there are more trenchant differences between *Castoria* and *Akodon* in molar morphology. *Castoria* displays a conspicuous pattern of opposite main cusps in contrast to *Akodon* where these elements are moderately alternating; in addition, the former lacks the anteromedian flexus that typically characterizes the M1 procingulum in *Akodon* species (**Table 3; Fig. 7**). An additional important trait to distinguish *Castoria* from species of the *cursor* group of *Akodon*, which are sympatric with *Castoria*, is the morphology of the incisive foramina. In *Castoria*, the foramina are constricted anteriorly, anterior to the premaxillary-maxillary suture. In *Akodon*, the margins are not constricted, and the lateral margins of the foramina are convex and wider medially, resembling parentheses and showing no changes in curvature (**Fig. 6**; see also **Supplementary Material S7**). However, this degree of morphological differentiation is considered as interspecific variation within the genera *Handleyomys* (cf. Voss et al., 2002:22) and *Drymoreomys* (Percequillo et al., 2011:371).

Thaptomys appears as the sister taxon for *Castoria* in some molecule-based phylogenies (e.g., D'Elía, 2003). Both share weak pelage countershaping and inflation of the premaxillary process. However, morphological differences are strong. *Castoria* has a moderately long tail and rostrum, contrasting with the shorter condition of both in *Thaptomys*. *Castoria* has a well-developed upper free margin of

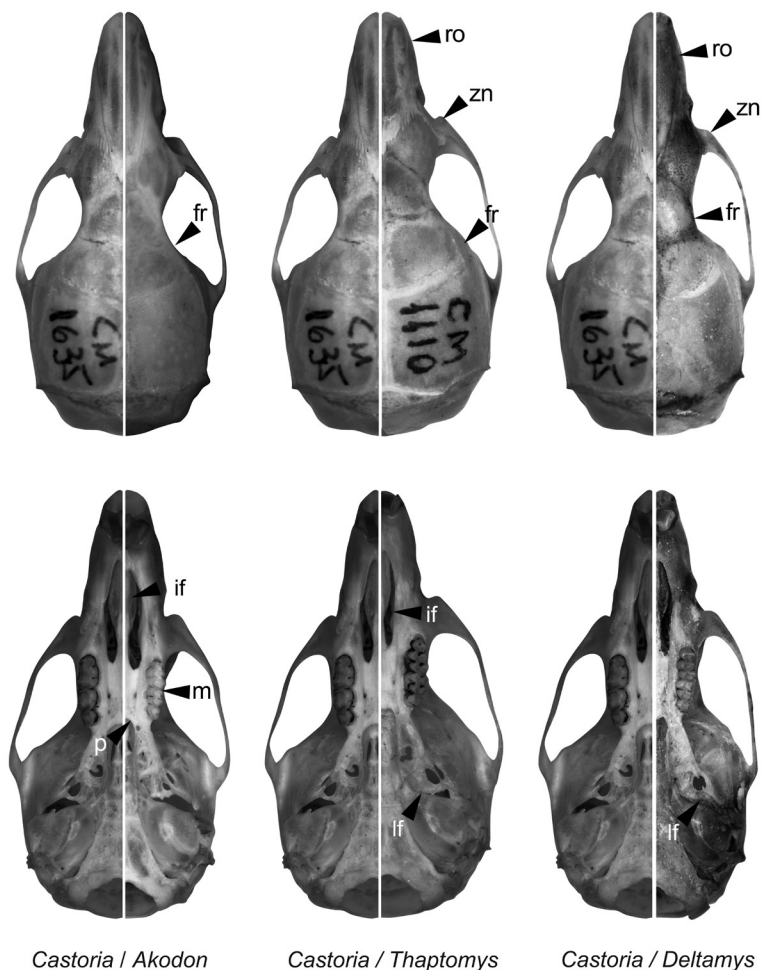


Fig. 6. Selected aspects of qualitative anatomy contrasted in the skulls of *Akodon*, *Thaptomys*, *Deltamys*, and *Castoria* gen. nov., scaled to the same length. The figure portrays contrasts between the characteristics of these genera and *Castoria* as follows: *Akodon* has rounded interorbital margins on frontals (fr), smaller tooththrow (m), and shorter palate (p); *Thaptomys* has a shorter rostrum (ro), less developed zygomatic notches (zn), rounded interorbital margins, shorter incisive foramina (if), and more ossified lacerate foramen (lf); *Deltamys* has a shorter rostrum, less developed zygomatic notches, rounded interorbital margins, and an almost completely ossified lacerate foramen.

the zygomatic plate whereas *Thaptomys* does not. *Castoria* lacks the defined capsular projection of the lower incisor root characterizing the mandible of *Thaptomys*. A gall bladder is present in *Castoria* and absent in *Thaptomys*. Molar morphology in *Thaptomys* is very similar to that in *Akodon*, so that *Castoria* differs from *Thaptomys* in all the respects noted earlier regarding *Akodon*.

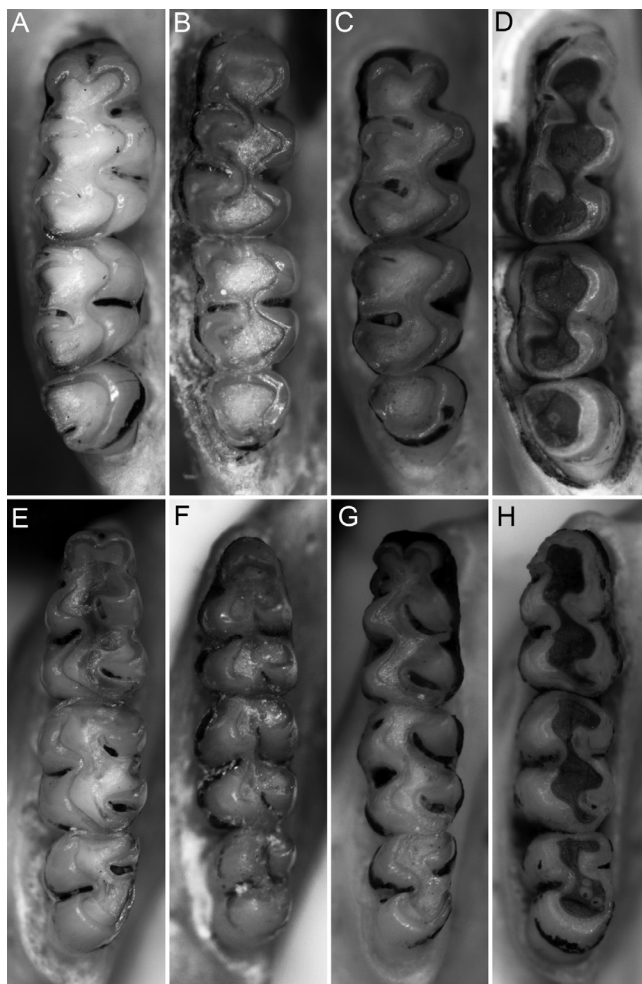
Although *Castoria* differs in numerous aspects with respect to *Deltamys*, both share weak countershading, a moderately long tail, and the general “soricine” external aspect. Their skulls are easily distinguished by the pointed rostrum and broad interorbital region of *Castoria* versus the comparatively shortened rostrum and narrow interorbital region of *Deltamys*. In addition, *Castoria* has a broad zygomatic plate and an alisphenoid strut whereas *Deltamys* has a narrow plate without free upper margin and lacks

the alisphenoid strut. In keeping with the molecular phylogenetic hypothesis of Smith and Patton (2007), which recovered *Castoria* close to *Deltamys*, these genera show many similarities in molar occlusal morphology (Fig. 7). In particular,

both have the main cusps arranged in opposite pairs, the tendency to a trilophodont M1 in adults, and an anteriorly-posteriorly compressed procingulum that coupled with its coalescence to the metaconid produce on the m1 a nearly bilophodont pattern.

The GTG-banding patterns of *Castoria* chromosomes allowed the identification and pairing of all homologues (Supplementary Material S6), and therefore, comparisons with the GTG-banded chromosomes of *Akodon paranaensis* (2n=44 and FN=44; reported in Ventura et al., 2009). Chromosome painting using *A. paranaensis* (APA) revealed that a tandem rearrangement, in which chromosome 7 of *A. paranaensis* is homologous to two chromosome pairs (16 and 21) of *Castoria angustidens*, explains their differences in 2n and FN. Meanwhile, analyzed species of *Akodon* share the sequences of APA 7 conserved as one chromosome (see Ventura

Fig. 7. Upper right (above) and lower left (below) molar toothrows in occlusal view in *Akodon*, *Deltamys*, *Thaptomys*, and *Castoria* gen. nov.: A, E, *Akodon montensis* (CNP 4112); B, F, *Deltamys kempfi* (CNP 4141); C, G; *Thaptomys nigrita* (MZUFV 1112); D, H, *Castoria* (MZUFV 1234 [upper], MN 69804 [lower]). Not to scale.



et al., 2009). Comparisons of karyotypes among *C. angustidens* and other closely related akodontines (*Deltamys*, *Necomys*, *Thalpomys* and *Thaptomys*), showed that two groups besides *Akodon* can also be delimited with respect to APA 7. The first group unites *Castoria* and *Thaptomys*, both with homologous sequences of chromosome 7 of *A. paranaensis* reorganized into two acrocentric chromosomes (data not shown). The second group comprises *Deltamys* sp., *Necomys lasiurus* and *Thalpomys lasiotis*, which present the 2 chromosome pairs homologous to APA 7 (as *Castoria* and *Thaptomys*), but also presents an exclusive association of chromosomes APA 7 and APA 8. *Castoria* presents a distinct pattern and nature of heterochromatin, distributed in large and positive pericentromeric blocks after telomeric FISH with (TTAGGG) n sequences as probes (Ventura et al., 2006, as *Akodon serrensis*). *Thalpomys lasiotis* also exhibits a pericentromeric region rich in (TTAGGG) n -like sequences (for CBG-banding patterns see Yonenaga-Yassuda et al., 1987, as *Akodon reinhardtii*, and Andrade et al., 2004); this homoplasial feature in light of currently understood phylogenetic relationships, suggests that accumulation of the (TTAGGG) n -like repetitive sequences could lead to generic-level differentiation in the Akodontini.

Natural History.— *Castoria* has been recorded in at least 44 localities, almost all in the Atlantic Forest of Brazil (41) and Argentina (3), encompassing 7 ecoregions (**Supplementary Material S1**). Little is known about its natural history. The principal vegetation where *Castoria* is recorded is humid mountain forest, including those with *Araucaria augustifolia* (**Supplementary Material S8**). The elevational range for *Castoria* collection localities is from 300 to 2100 m (correlation between latitude and elevation was $r=0.5$; **Supplementary Material S9**). Usually *Castoria* is interpreted as an element of montane

fauna (Gonçalves et al., 2007; Abreu et al., 2014). Paglia et al. (2012) reported the diet of this rodent as insectivorous/omnivorous, although the basis for this assessment is unknown. Morphometric analysis of the appendicular skeleton suggests that this species uses terrestrial locomotion (Coutinho et al., 2013). Vieira and Monteiro-Filho (2003) captured this mouse exclusively on the ground. Miranda Ribeiro (1905) indicates that *Castoria* inhabits “galerias subterraneas,” that according to Voss (1993:35) possibly correspond to “shallow tunnels under matted roots and moss” and piles of litter in thickets of *Chusquea*. The species was the most frequently trapped small mammal in the Parque Estadual do Desengano, a disturbed montane forest (~1000-1425 m elevation) in the northern portion of Rio de Janeiro (Modesto et al., 2008). *Castoria angustidens* was also the dominant species among recorded sigmodontines in

an elevational transect of Parque Estadual da Serra do Brigadeiro from 1200 to 1800 m, particularly at middle to upper elevations (1450-1800 m; Moreira et al., 2009). In Parque Nacional de Itatiaia, it was trapped in montane forests and “campos de altitude” up to ~2100 m (Geise et al., 2004). Captive animals fed mainly on pulp of fruits and also on small to medium-sized seeds of a wide array of plant species from the Atlantic Forest (Vieira et al., 2003). A rich assemblage of parasites, including Acari, Anoplura, and Siphonaptera has been recorded from Brazilian individuals (Barros-Battesti et al., 1998; Linardi and Guimarães, 2000; Moraes et al., 2003). Teixeira et al. (2014) recorded natural spillover infection between this species and the Jaborá strain of hantavirus, whose primary host is *Akodon montensis*. According to these authors, spillover infection in secondary hosts, including *C. angustidens* and *A. paranaensis*, may play an important role in maintaining the hantavirus sylvatic cycle during periods of low prevalence in primary hosts.

Biogeography.— *Castoria* is distributed in south-eastern Brazil, from Espírito Santo to Rio Grande do Sul, and in Misiones, northeastern Argentina. Its distributional range overlaps those of other akodontine rodents, such as *Blarinomys breviceps*, *Brucepattersonius* spp., and *Thaptomys nigrata*. Unlike those taxa and other Atlantic Forest sigmodontines, *Castoria* is much restricted to a narrow coastal fringe at relatively high elevations (500-1600 m) in well conserved forest remnants. Most of the recorded localities are located within Serra do Mar coastal forests and Araucaria Moist forests ecoregions (Olson et al., 2001; Pardiñas et al., 2015). The Serra do Mar is recognized as one of the more remarkable centers of endemism in South America, with evidence from plants (especially of the families Myrtaceae, Lauraceae, Melastomataceae, and Orchidaceae), birds, butterflies, amphibians, and mammals (Da Silva, 2000a and references therein). Araucaria Moist forests spread from middle-level plateaus of ~500 m to the high slopes (1600 m) of the Serra da Mantiqueira. Among 352 plant species recorded in this region, 47 (13.3%) are endemic; this moist forest is also recognized as an important endemic bird area (Da Silva, 2000b). *Castoria* has been recorded from the Bahia Coastal and Interior Forests and at ecotones with the Alto Paraná Atlantic forests. At a regional scale, at least other 2 genera, *Delomys* and *Juliomys*, have similar distributions, with populations mostly restricted to these same ecoregions (see Pavan and Leite, 2011; Gonçalves and Oliveira, 2014). The genera *Delomys* and *Juliomys* comprise both widely distributed species as well as more elevationally restricted taxa. This pattern highlights the impor-

tance of montane topographies in the evolution of sigmodontines of the Atlantic Forest (Gonçalves and Oliveira, 2014) and identifies this area as a major center of diversification of this subfamily (Smith and Patton, 1999).

Conservation.— *C. angustidens* was categorized as “Least Concern” by the IUCN. Several arguments were used to justify this placement, including its wide distribution, presumed large populations, its presence in a number of protected areas (e.g., Parque Estadual do Desengano, Parque Estadual da Serra do Brigadeiro, Parque Nacional de Itatiaia, Parque Nacional da Serra dos Órgãos, Parque Nacional da Bocaina), and because “it is unlikely to be declining at nearly the rate required to qualify for listing in a threatened category” (<http://www.iucnredlist.org/details/full/756/0>). However, it is likely that some populations of this species have been negatively affected by habitat destruction and forest fragmentation.

Remarks.— Our systematic hypothesis involves fossil (*H. angustidens*) and recent materials (*A. serrensis*). This kind of taxonomic work is obviously limited owing to the anatomical incompleteness and absence of genetic information for the fossils. However, as discussed several times revisiting the Lund collections (Voss, 1993; Voss and Carleton, 1993; Pardiñas et al., 2008), fossils of Lagoa Santa often preserve enough information to make confident inferences regarding both genus and species (**Supplementary Material S2 and S10**).

Winge’s description of *H. angustidens* was explicitly based on multiple specimens, none of which was designated as type (Winge, 1887:28-29). Therefore, all of those specimens must be considered syntypes in accordance with Article 72.1.1 of the Code (ICZN). We designate as lectotype of *H. angustidens*—according to Article 74.1—the cranial anterior fragment illustrated by Winge (1887:II, figure 2); this fossil was recently numbered in ZMK collections as 1/1845:13246 and is associated with Winge’s handwritten label saying “*Habrothrix angustidens* Tegnet [figured] ?Lapa da Serra das Abelhas” (**Supplementary Material S10**). In addition, a photograph of this specimen was published in the catalog of Hansen (2012:58–59).

The lectotype of *H. angustidens* comes from “Lapa da Serra das Abelhas,” and like other fossils of the same provenience (e.g., the types of *H. orycter* or *H. clivigenis*) is fragmentary and stained yellowish by superficial concretions. Several of the caves worked by Lund—including Serra das Abelhas—were destroyed by human activities over the last 170 years; however, a few, such as Cerca Grande

located about 16 km NW Lagoa Santa city, where *H. angustidens* was also recorded, still remain. It is noteworthy that, despite extensive surveys of modern mammal fauna made by Lund around Lagoa Santa, *Castoria* was not detected (cf. Voss and Myers, 1991). In fact, the nearest record for the species is from Fazenda da Neblina in the Parque Estadual da Serra do Brigadeiro (Moreira et al., 2009), ca. 200 km SE of Lagoa Santa. The Lapa da Serra das Abelhas sigmodontine assemblage includes 8 taxa without recent records of occurrence near Lagoa Santa, including *Castoria*, *Delomys*, *Euryoryzomys*, *Juliomys*, *Sooretamys*, and *Thaptomys* (Winge, 1887; Pardiñas and Teta, 2013). The taxonomic structure of this assemblage is characterized by elements presently restricted to Atlantic Forest in mixture with Cerrado species, a non-analogue fauna probably triggered by cooling episodes during the Late Pleistocene (Voss and Carleton, 1993; Cartelle, 1999; Pardiñas and Teta, 2013).

The cursory indication by Hershkovitz (1990a:14) concerning the synonymy of *A. serrensis* and *Akodon pervalens* Thomas, 1925, a poorly known form with type locality at Caraparí (Tarija, Bolivia), must be dismissed. *A. pervalens*—judging from examination of its holotype and paratype—looks like a true *Akodon*, phenotypically similar to species of the *A. cursor* species group as earlier suggested by Myers (1989). Although the holotype of *A. pervalens* is old (see Jayat et al., 2007:210) and some of its cranial and dental features (e.g., broad interorbital region, nasals tapering forward, absence of anteromedian flexus on M1) recall those of older *A. serrensis*, these are only general resemblances produced by aging (**Supplementary Material S7**).

FINAL CONSIDERATIONS

Castoria belongs to a clade of akodontine genera historically understood as a part of *Akodon* (cf. Reig, 1987), which has recently been reorganized into several genera (for a review, see D'Elía and Pardiñas, 2015). Morphological differences among *Akodon*, *Deltamys*, *Thalpomys*, *Thaptomys*, *Necromys*, and *Castoria*, as well as more controversial forms such as *Microxus*, are typically subtle (**Table 3**). This seems to be a signature of the *Akodon* Division, one that prevented the recognition of these different genera for most of the XXth century.

Since the 1970s, several distinctive lineages formerly subsumed in *Akodon*—directly or under subgeneric combinations—have been

progressively elevated to full generic rank. Paradigmatic cases were *Abrothrix* (now included in a different tribe) and *Thaptomys*, but also more recently *Thalpomys* and *Deltamys*. Reig (1987:358) anticipated these changes when he wrote “I tentatively recognize a central genus *Akodon*, subdivided into five subgenera... I do not deny, however, that more detailed and comprehensive further studies could eventually elevate some of these taxa to generic level.” These generic partitions within *Akodon* were possible because of the accumulation of morphological and karyological information and were then consolidated by DNA-based phylogenetic analyses (e.g., Hershkovitz, 1990b; Smith and Patton, 1993, 1999, 2007; Geise et al., 2001; D'Elía, 2003; D'Elía et al., 2003; Pardiñas et al., 2005; Jayat et al., 2010). It is interesting to point out that at least two putative genus-rank groupings remain subsumed under *Akodon* despite clear morphological indications about their singularities; these are *Microxus* and *Hypsimys* (see Reig, 1987:359–360; Ventura et al., 2000:497; Voss, 2003:20–21). Perhaps their retention in *Akodon* is more the result of historical inertia than of unequivocal phylogenetic support (see Patton et al., 1989; Smith and Patton, 2007). An example of such progress is the recent finding that *Akodon bogotensis* and *Akodon latebricola* are neither *Akodon* nor Akodontini (Alvarado-Serrano and D'Elía, 2013). The naming of *Neomicroxus* demonstrates that the content of *Akodon*, as presently understood containing about 38 living species (Pardiñas et al., 2015), requires detailed morphological and molecular scrutiny.

Castoria adds a new piece to Akodontini historical biogeography. In fact, the exclusion of the Abrotrichini (see Smith and Patton, 1999), the inclusion of Scapteromyini (see Smith and Patton, 1999; D'Elía et al., 2005), and the elevation to genera of several erstwhile subgenera or species (*Deltamys*, *Gyldenstolpia*; D'Elía et al., 2003; Pardiñas et al., 2008) have reshaped our vision about this diverse tribe. Of the 15 genera currently recognized (see Patton et al., 2015), three are Atlantic Forest endemic, *Blarinomys*, *Brucepattersonius*, and *Thaptomys*. *Castoria* offers further evidence for a potential area of endemism in southeastern Brazil, a

picture also supported by several genera of non-akodontine sigmodontine rodents (Smith and Patton, 1999; Pardifias et al., 2014a; Prado et al., 2014) and echimyid rodents (Upham and Patterson, 2015:Fig. 1).

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APPENDIX 1

Studied specimens belong to the following mammal collections: AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, UK; CNP, Colección de Mamíferos del Centro Nacional Patagónico, Chubut, Argentina; FMNH, Field Museum of Natural History, Chicago, USA; MACN, Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MN, Museu Nacional, Rio de Janeiro, Brazil; MZUFV, Museu de Zoologia, Departamento de Biologia Animal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil; ZMK, Universitets Zoologisk Museum, Copenhagen, Denmark. Symbols denote specific studies carried out on each specimen (*=measured; ^k=karyotyped).

Akodon montensis (n=46): Argentina, Misiones, Balneario Municipal de Aristóbulo del Valle sobre el arroyo Cuña Pirú, 10 km NN W Aristóbulo del Valle (CNP 1785, 1786, 1789, 1790, 1794, 1795, 1796, 1797, 1798, 1799, 1800, 1802, 1804, 1805, 1807, 1808, 1809, 1810, 1811, 1812, 1813, 1814, 1815, 1818, 1819, 1821, 1825, 1829, 1831, 1833, 1835, 1838, 1844, 1845, 1847), Reserva Privada de Usos Múltiples Guaraní (CNP 4243, 4244, 4245, 4247, 4248, 4249, 4250, 4251, 4252, 4253, 4254).

Castoria angustidens nov. comb. (n=123): Argentina, Misiones, Reserva Privada de Vida Silvestre Urugua-í (MACN 22246), RP 2, 6 km NE Arroyo Paraíso (CNP 449*). Brazil, Minas Gerais, Parque Estadual da Serra do Brigadeiro, Fazenda da Neblina (MZUFV 520*, 551*, 1076, 1148*, 1150*, 1151*, 1153*, 1154*, 1155*, 1156*, 1215*, 1220*, 1234, 1242, 1266*, 1281*, 1298*, 1630, 1635, 1653, 1655, 2555; UFMG 1858*, 1859*, 1860*, 1861*, 1862*), Parque Estadual da Serra do Brigadeiro, Serra das Cabeças (MZUFV 1243*, 1248*, 1250*, 1267*, 1280*, 1286*, 1287*, 1294*, 1295*). Lapa da Serra das Abelhas (ZMK 1/1845:13246* [lectotype of *H. angustidens*]; CNP 4267 [lectotype: cast of upper molar row], CNP 4268 [paralectotype: cast of lower molar row]); Paraná, Roça Nova (BMNH 3.7.1.66*-3.7.1.73*, ZMK 1257*); Rio de Janeiro, Parque Nacional da Serra dos Órgãos, Vale das Antas (MN 69807^k, 69808*, 69809*, 69810*, 69811*, 69812*^k, 69813*, 77085*, 77099^k, 77100*, 77101*, 77102*, 77104*, 77105*, 77108*, 77111*, 77112*, 77113*, 77116*, 77117^k, 77119*, 77121*, 77122*, 77123*, 77078^k, 77079^k, 77081*, 77082*, 77084^k, 81130*, 81131*, 81133*, 81134*, 81135*, 81136*, 81137*, 81138*, 77086*, 77087^k, 77088*, 77090*, 77091*, 81144*, 77096*, 81147*, 81148*, 81150*, 81151*, 81152*, 81153*, 81154*, 81155*, 81156*, 81157*, 81158*, 81159*, 81160*, 81161, 81162*, 81163*, 81164*, 81165*, 81166*, 81168*, 81169*, 81170*, 81171*, 81172*, 77097^k, 81175*), Sítio Xitaca, Debossan, Nova Friburgo (MN 35912*, 35920*, 35921*, 35923*, 35924*, 35926*), Parque Nacional do Itatiaia (MN 69803*), Retiro de Ramos (MN 2513* [holotype of *H. serrensis leucogula*]), Visconde de Mauá (MN 69804*); São Paulo, Fazenda Intervales (FMNH 143275).

Deltamys kempi (n=6): Argentina, Buenos Aires, La Balandra (CNP 581, 893, 3086, 3087, 4141), General Lavalle (CNP 2377).

Necomys lactens (n=5): Argentina, Jujuy, Bárcena, ca. 3 km S sobre RN 9 (CNP 1486), Abra de la Ciénega Negra (CNP 1487), San Francisco (CNP 3032, 3037, 4124).

Necomys lasiurus (n=8): Argentina, Santiago del Estero, Estación Experimental INTA "La María" (CNP 2358); Chaco, 5 km NW Puerto Las Palmas (CNP 3036, 3049); Misiones, Estancia Santa Inés (CNP 3038, 3041, 3043, 3045, 3048).

Necomys obscurus (n=5): Argentina, Buenos Aires, Arroyo de las Brusquitas (CNP 891, 2380, 3039, 3047), Estación Experimental INTA "Balcarce" (CNP 3053).

Thaptomys nigrita (n=23): Argentina, Misiones, Balneario Municipal de Aristóbulo del Valle sobre el arroyo Cuña Pirú, 10 km NN W Aristóbulo del Valle (CNP 1788, 1791, 1816, 1826, 1827, 1828, 1832, 1839, 1846, 1929, 1931), Refugio Moconá (CNP 1938, 3008, 3010, 3011), Asentamiento Aborigen Kaaguy Poty, 1 km NNW intersección RP 7 y arroyo Cuña Pirú (CNP 1979, 2370, 2371, 2372), Posada Las Malvinas (CNP 3526), Reserva Privada de Vida Silvestre Urugua-í (CNP 3875). Brazil: Minas Gerais, Parque Estadual da Serra do Brigadeiro, Fazenda da Neblina (MZUFV 1110, 1112)

SUPPLEMENTARY MATERIAL ONLINE

S1. Gazetteer of the recording localities for the genus *Castoria*.

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup1.doc

S2. Study notes on *Habrothrix angustidens* and *Akodon serrensis* made by R. S. Voss in November, 2008.

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup2.doc

S3. Principal component analysis of all age classes of Brazilian specimens of *Castoria*, including the lectotype of *Habrothrix angustidens*.

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup3.doc

S4. External appearance of *Castoria angustidens*, nov. comb.

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup4.doc

S5. Gastric morphology of *Castoria angustidens*, nov. comb.

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup5.doc

S6. Chromosomes of *Castoria angustidens*, nov. comb.

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup6.doc

S7. Comparison of the holotypes of *Akodon pervalens* and *A. serrensis*.

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup7.doc

S8. Habitat of *Castoria angustidens*, nov. comb. at Itamonte, Brazil.

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup8.doc

S9. Joint distribution of latitude and elevation for *Castoria angustidens*, nov. comb. collection localities.

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup9.doc

S10. Lectotype of *Castoria angustidens*, nov. comb. (ZMK 1/1845:13246).

https://www.sarem.org.ar/wp-content/uploads/2016/06/SAREM_MastNeotrop_23-1_Pardinas-sup10.doc