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Artículo

BACULAR MORPHOLOGY OF SEVEN SPECIES OF HIGH ANDEAN RODENTS FROM COLOMBIA (RODENTIA: SIGMODONTINAE)

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ABSTRACT. We describe and compare the bacular morphology of the high Andean rodents *Thomasomys laniger*, *T. niveipes*, *T. princeps*, *Chilomys instans*, *Microryzomys minutus* and *Neomicroxus bogotensis* distributed in Chingaza National Natural Park in the Colombian Cordillera Oriental. We also describe the baculum of *Thomasomys aureus* from two localities from the Cordillera Central. Our analyses used 16 penises from adult specimens, which were cleared and double stained with alizarin and alcian blue. Each of the seven species exhibited a tridigitate complex-penis with clear bacular morphological differences among them. Within the genus *Thomasomys*, bacula of *T. aureus* and *T. princeps* were substantially different, especially in the size and the shape of the base. Likewise, *T. laniger* showed marked differences in comparison to *T. niveipes*, contrasting with the latter by an expanded head and digits of the trident of similar size. The baculum of *C. instans* was similar to those of *Thomasomys,* with its wide base and distally expanded head. Both *M. minutus* together with *N. bogotensis* had the smallest bacula studied. The baculum of *M. minutus* has a wide and flat base and that of *N. bogotensis* is slender with a narrow and shallow base; neither set of attributes was seen in the other species analyzed. The differences found within these species led us to conclude that bacular morphology holds great potential to understand both taxonomic boundaries as well as evolutionary trends among sigmodontine rodents.

RESUMEN. Morfología del báculo de siete especies de roedores altoandinos de Colombia (Rodentia: Sigmodontinae). El presente trabajo describe y compara la morfología del báculo de los roedores altoandinos *Thomasomys laniger*, *T. niveipes*, *T. princeps*, *Chilomys instans*, *Microryzomys minutus* y *Neomicroxus bogotensis* distribuidos en la Cordillera Oriental colombiana dentro del Parque Natural Nacional Chingaza. Adicionalmente, describimos y analizamos el báculo de *Thomasomys aureus* en dos localidades de la Cordillera Central colombiana. Se diafanizaron 16 penes de individuos adultos con alcian-blue y alizarina para un análisis detallado. Nuestros resultados mostraron que las siete especies exhibieron diferencias morfológicas presentando un báculo complejo con tres dígitos. Dentro del género *Thomasomys*, las especies *T. aureus* y *T. princeps* mostraron una gran diferenciación en sus báculos de acuerdo al tamaño y a la forma de la base. Así mismo, la especie *T. laniger* presentó diferencias marcadas con *T. niveipes* como una cabeza ensanchada y los dígitos del tridente de tamaño

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similar, condiciones opuestas a las de *T. niveipes*. El báculo de *C. instants* presentó similitudes morfológicas con los del género *Thomasomys*, con una base ancha y una cabeza ensanchada. Por otra parte, *M. minutus* y *N. bogotensis* presentaron los báculos de menor tamaño. El báculo de *M. minutus* tiene una base amplia y plana, y el de *N. bogotensis* es delgado con una base angosta y poco profunda; ninguno de estos conjuntos de atributos fue observado en las demás especies estudiadas. Finalmente, las diferencias encontradas en estas especies nos permiten concluir que la morfología del báculo presenta un gran potencial para entender tanto límites taxonómicos como tendencias evolutivas entre los roedores sigmodontinos.

Key words: Bacular morphology. *Chilomys. Microryzomys. Neomicroxus. Thomasomys.*

Palabras clave: *Chilomys. Microryzomys.* Morfología del báculo. *Neomicroxus. Thomasomys.*

INTRODUCTION

The mammalian baculum (os priapi) is the penis bone found in some to most members of five mammalian orders: Carnivora, Chiroptera, Lipotyphla, Primates and Rodentia. This element is highly diverse morphologically, varying considerably among genera but remaining relatively constant within a given species (Thomas, 1915; Romer, 1970; Patterson and Thaeler, 1982). Although its adaptive function remains contentious, bacular diversification appears to be driven by sexual selection and is thus implicated in speciation (Hosken and Stockley, 2004; Stockley et al., 2013). In rodents, in particular, studies have emphasized bacular structure as an important reproductive component in their evolutionary and taxonomic diversification (Wade and Gilbert, 1940; Blair, 1942; Anderson, 1960; Burt, 1960; Hooper and Musser, 1964; Lidicker, 1968; Bradley and Schmidly, 1987; Pessôa et al., 1996; Pessôa and Strauss, 1999; Bezerra, 2005; Rocha-Barbosa, 2013).

Rodents are the largest extant mammalian order and the Cricetidae subfamily Sigmodontinae is the most diverse subfamily in South America (Reig, 1986; Musser and Carleton, 2005; D'Elía and Pardiñas, 2015). Currently, molecular data have reinforced the independence of Sigmodontinae from the North American cricetids (Neotominae and Tylominae) (Jansa and Weksler, 2004; Vilela et al., 2014). An early hypothesis posited a basic separation between the New World cricetids, separating the North American groups with a simple penis from those in South America with a complex penis (Hooper, 1959; Hooper and Musser, 1964, Hershkovitz, 1966; Reig, 1980). More recent evidence, however, has rejected this hypothesis (Spotorno et al., 1990; Spotorno, 1992). While most sigmodontines do have a complex penis, exceptions to this standard pattern are known (e.g., *Abrothrix* and *Punomys*; Spotorno, 1992).

Within sigmodontines, the genera *Chilomys*, *Microryzomys*, *Thomasomys*, and *Neomicroxus* are confined to the central and northern Andes. In Colombia, the first three of these genera are distributed through each cordilleran branch while *Neomicroxus* is limited only to the Cordillera Oriental (Cuervo Díaz et al., 1986; Alvarado-Serrano and D'Elía, 2015; Carleton, 2015; Pacheco, 2015a, b). Each of these genera has had a complex taxonomic history, due to difficulty in species diagnosis or changes in generic allocation through time. Despite the utility of the baculum in species and subspecies delimitation (Anderson, 1960; Pessôa and Reis, 1992; Pessôa and Strauss, 1999; Rocha-Barbosa, 2013), only few taxonomic and descriptive studies have concerned Colombian species. Among the species we describe herein, *Thomasomys aureus* and *T. hylophilus* were included in the study by Hooper and Musser (1964) and both *Microryzomys minutus* and *Neomicroxus bogotensis* by Díaz de Pascual and Péfaur (1982).

Herein we describe the bacular morphology of seven species of high Andean rodents in Colombia: *Thomasomys aureus*, *T. niveipes*, *T. laniger*, *T. princeps*, *Chilomys instans*, *Microryzomys minutus* and *Neomicroxus bogotensis*. Likewise, we compare and discuss the morphological variation of this bone with other genera and related species within Sigmodontinae. Finally, we examine age-related interspecific and intraspecific variation of the baculum based on tooth-wear classes. We end by emphasizing the relevance of the baculum in taxonomic approaches contributing to the knowledge of the high Andean rodents.

MATERIALS AND METHODS

We examined the bacula of adult specimens of *T. aureus* (n = 2), *T. laniger* (n = 3) *T. niveipes* (n = 3), *T. princeps* (n = 2), *C. instans* (n = 1), *M. minutus* (n = 3) and *N. bogotensis* (n = 2) collected on the eastern flank of the Cordillera Oriental of Colombia in Cundinamarca, municipio Fómeque in Chingaza National Natural Park (PNN) (**Appendix 1**). We also examined the baculum of *T. aureus* (n = 2) collected in the Cordillera Central.

We extracted the phallus at its base from fluid preserved material originally fixed in 10% formalin, and then cleared and double-stained with alcian blue-alizarin following Wassersug (1976). We then described each baculum in its dorsal, ventral, lateral, and proximal views (as per Anderson, 1960) and obtained 6 measurements (modified from Hooper, 1958; Bezerra, 2005): total bacular length (TBL), shaft length (SL), medial digit length (MD), lateral digit length (LD), trident length (TRL) and width of base (WB). Measurements were taken under a stereo microscope using ruler with a precision of 0.1 mm.

Our descriptions and comparisons of bacula among genera and species followed Hooper and Musser (1964) for *Thomasomys* and Díaz de Pascual and Péfaur (1982) for *M. minutus* and *N. bogotensis*. We generated univariate Boxplots to compare mean values and the variation of the bacular measurements among species. Finally, we examined intraspecific developmental (age-related) differences in bacular morphology of *T. laniger*, *T. niveipes* and *M. minutus* based on the five tooth-wear classes (TWC) proposed by Voss (1991), which are described as follows: TWC 1: M3 incompletely erupted or unworn; TWC 2: M3 fully erupted exhibiting a slight to moderate wear, the occlusal surface still tubercular; TWC 3: M3 well worn, occlusal surface flat or concave, M1-2 tubercular, anteroloph of M2 distinct; TWC 4: M3 flat or concave, M1-2 almost worn or quite flat, but no bellow the widest part of the crown; TWC 5: M1-3 worn flat or concave bellow the widest part of crown.

RESULTS

Baculum morphology

The baculum of each species is composed of a bony shaft and a cartilaginous distal trident, but each exhibits a distinctive morphology. Generally, the base is convex in dorsal view and deeply concave in ventral view, wide relative to the shaft, and tapers distally along the bone (**Figs. 1** and **2**). The medial digit of the trident is longer than lateral ones in most species except *T. niveipes* and *C. instans*, where both medial and lateral digits are similar in length (**Figs. 1D** and **2A**). Of the species we examined, *Thomasomys princeps* had the longest baculum, and both *M. minutus* and *N. bogotensis* had the smallest (**Table 1**).

Species of *Thomasomys* all have a baculum with a wide and convex base (dorsally), a robust shaft and a distal rounded tip (head), although there are clear differences between them. The bacular bony shaft of *T. princeps* is slightly bowed to the dorsal side and terminates in a round expanded head (**Fig. 1A**); ventrally, the base is deeply concave, ending laterally in two pronounced projections. In dorsal view, its base forms an inverted Gaussian bell curve about 50% of SL and with broad lateral processes. The trident is 33% of SL with the medial digit blunt and larger than the laterals, which are slightly curved laterally. In comparison, the baculum of *T. aureus* is smaller. The bony shaft is also gently curved dorsally with the head enlarged, although less so than in *T. princeps* (**Fig. 1B**); however, in ventral view its morphology is similar to *T. princeps* (compare **Fig. 1B** to **1A**). The base is 70% of SL, and its strongly concave form delineates two robust lateral processes proximally oriented, giving the base an M-shape in dorsal aspect. The size of the trident is 50% of SL, and the medial digit is longer than lateral ones, which are directed sideways.

The baculum of *T. laniger* is not bowed, and the head is rounded and large as in *T. princeps* (**Fig. 1C**). The inverted dome base is not constrained laterally and is wide (close to 65%) in proportion to SL; the lateral processes of the base are dorsally sharp and ventrally reduced or only weakly developed. Proximately, the base

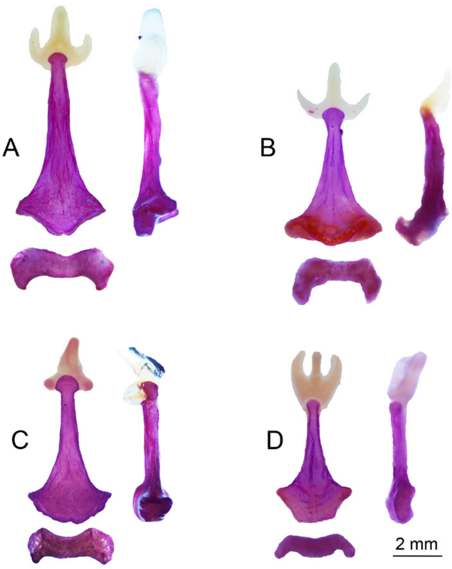

Fig 1. Bacular morphology of *Thomasomys* species. A, *T. princeps* (ICN 21743); B, *T. aureus* (ICN 12196); C, *T. laniger* (ICN 21736); D, *T. niveipes* (ICN 21741). In each section, a dorsal view is on the left, lateral on the right, and proximal below.

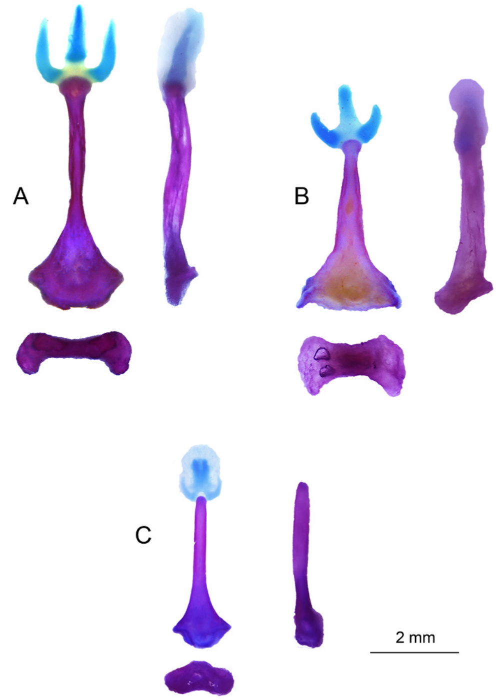

Fig 2. Bacular morphology of the species: A, *Chilomys instans* (ICN 21712); B, *Microryzomys minutus* (ICN 21721); C, *Neomicroxus bogotensis* (ICN 21731). In each section, a dorsal view is on the left, lateral on the right, and proximal below.

Table 1

Means of 6 bacular and 2 external measurements of *Thomasomys aureus* [ICN 12196, 15181: Caldas and Risaralda, Colombia; FMNH 75588: Cuzco, Peru (Hooper and Musser, 1964)], *T. princeps* (ICN 21742, 21743), *T. hylophilus* [FMNH 92555: Boyacá, Colombia (Hooper and Musser 1964)], *T. laniger* (ICN 21736, 21737, 21738), *T. niveipes* (ICN 21739, 21740, 21741), *Chilomys instans* (ICN 21712), *Microryzomys minutus* (ICN 21721, 21723, 21725) and *Neomicroxus bogotensis* (ICN 21728, 21731). Variable abbreviations: bacular – TBL = total bacular length, SL = shaft length, MD = medial digit length, LD = lateral digit length, TRL = trident length, and WB = width of base (WB); external – HBL = head and body length and W = weight.

Species	**TBL**	**SL**	**MD**	**LD**	**TRL**	**WB**	**HBL**	**W (g)**
T. aureus	6.6	4.5	2.1	1.3	2.4	3.1	141.5	84
T. aureus Cuzco, Peru	12.6	8.1	4.5	1.2	-	-	-	-
T. princeps	9.8	7.5	2.3	1.8	2.6	3.5	161	121
T. hylophilus	5.3	4.3	1.0	0.4	-	-	-	-
T. laniger	6.8	5.3	1.5	1	2.0	3.3	110	34.2
T. niveipes	6.1	4.4	1.7	2.0	2.1	2.6	113	44.5
C. instans	7.1	5.3	1.8	1.8	2	1.7	82	15
M. minutus	3.6	2.6	1.0	0.7	1.2	1.6	74	14.6
N. bogotensis	3.4	2.5	0.9	0.7	1	0.9	66	14.4

is broader on the sides than in the medial part. The trident is 35% of SL, with the medial digit projecting well beyond the lateral ones.

The penis bone of *T. niveipes* is the smallest of the genus *Thomasomys* (**Table 1**). The shaft is thinner dorsoventrally and slightly bowed to the dorsal side (**Fig. 1D**). The distal portion of the shaft lacks a distinct head. The base is 60% of SL and is shaped as an inverted dome constrained on the ends; ventrally, well-developed lateral processes form a concavity on the base with a medial bulge. One of three bacula we examined exhibited a medial constriction on the shaft. The cartilaginous trident is long in proportion to SL (about 45%); both enlarged lateral digits are similar in size to the blunt medial digit.

Chilomys instants has a thin and sinoid-curved shaft (**Fig. 2A**). It tapers drastically from the base to the distal part where it terminates in an enlarged head similar to the condition observed in species of *Thomasomys*. Its base is deeply concave and narrow, about 35% of SL; well-developed and blunt lateral processes are apparent in ventral view. Proximately the base is slender and its width is much the same over its extension. The trident is 32% of SL with its digits of comparable proportions (**Table 2**); lateral digits are thicker and pointed, while medial digit is slim and blunter.

The bacular shaft of *Microryzomys minutus* is straight, tapering distally and terminating in a weakly developed head (**Fig. 2B**). There is a slight expansion along the medial part of the bony shaft. The base is flattened in dorsal view and concave in ventral view, and rather wide (close to 60% in proportion to SL). The lateral processes of the base (seen from ventral view) are developed. Proximately, the base is constricted in the center, wider on the extremes with half-straight borders. The trident is about 45% of SL and the medial digit protrudes beyond the lateral ones (**Fig. 2B**; **Table 2**).

Neomicroxus bogotensis has a slender, cylindrical and straight baculum (**Fig. 2C**). The distal tip lacks a distinct head and the base is triangular and narrow (35% of SL), and quite concave in ventral view. The lateral processes are very weakly developed. In proximal view, the base is oval-shaped gently concave. The trident is 45% of SL; the medial digit is stubby and protrudes over the lateral digits, which are thin and pointed (**Fig. 2C**).

Interspecific differences among the 7 species are readily apparent by visual comparison of **Figs. 1** and **2**. In the majority of the boxplots (**Fig. 3**), perhaps unsurprisingly the larger-bodied species *T. princeps*, *T. aureus*, *T. laniger* and *T. niveipes* have higher mean values for each bacular variable than do the smaller *M. minutus* and *N. bogotensis*. As an exception, the small-bodied *C. instans* had values similar to those of *T. laniger* and *T. niveipes*. Overall, the boxplots for each bacular measurement show similar trends across all species except for the LD where there is a marked variation within *Thomasomys* species.

Intraspecific variation

Although every individual we examined was an adult, we observed some differences in bacular morphology in ossification and development of both the cartilaginous trident and bony shaft across 4 (2-5) of the 5 tooth-wear classes (TWC). For *T. laniger*, ossification in trident cartilage is apparent in ICN 21737 (TWC 3) but more strongly visible in ICN 21738 (TWC 4) (**Fig. 4A**). However, the bony shaft has become completely ossified by TWC 3 regardless the slight variation along the margin of the base. For *T. niveipes*, the younger, TWC 2 specimen (ICN 21740) shows no sign of ossification of the trident cartilage nor has the bony shaft completed ossification, while limited trident ossification and complete shaft ossification are apparent in the TWC 3 specimen (ICN 21739) (**Fig. 4B**). In the baculum of *M. minutus*, ossification of the trident at age class TWC 3 (ICN 21723) is not visible, contra observations for both *T. laniger* and *T. niveipes* at the same TWC. By TWC 5 (ICN 21725) in *M. minutus* (**Fig. 4C**), however, advanced ossification encompassing half of the lateral digits is evident in the trident and the shaft has reached a much more robust, complete development.

DISCUSSION

In each species studied, the morphology of the baculum conforms the tridigitate complex-pe-

Table 2

Diagnostic characters of the bacula of *Thomasomys aureus*, *T. laniger*, *T. niveipes*, *T. princeps*, *Chilomys instans*, *Microryzomys minutus* and *Neomicroxus bogotensis*. Additionally, we include characters of *T. aureus* FMNH 75588 (Cuzco, Peru) and, *T. hylophilus* FMNH 92555 (Boyacá, Colombia) based on Hooper and Musser 1964. Abbreviations in the table: SL = shaft length.

Species	Shape of the base	Shape of the base (proximal view)	Concavity of the base (ventral view)	Shape of the distal part	Trident shape
T. princeps	Wide (50% of SL) with Gaus Bell shape	Robust, curved ends with lateral processes half-pointed	Deep	Moderately expanded	Medial digit protrudes
T. aureus (Colombia)	Wide (70% of SL) with an M shape	Robust, straight ends with lateral processes half-pointed	Deep	Moderately expanded	Medial digit protrudes
T. aureus (Peru)	Triangular base/ double headed shaft			Heart-shaped	Medial digit protrudes
T. hylophilus	Slightly laterally constrained	Dorsoventrally fine		Slightly expanded	Medial digit almost twice as large as the laterals
T. laniger	Wide (65% of SL) inverted dome	Robust. Wider at the ends than in the center, lateral processes slightly developed	Slightly deep	Expanded	Medial digit protrudes
T. niveipes	Wide (60% of SL) constrained inverted dome.	Slender. Wider at de middle, it reduces in size at the ends. Developed lateral processes	Slightly deep	Not expanded	Digits of the same size
C. instansts	narrow (35% of SL)	Slim, similar width over its extension. Blunt lateral processes	Deep	Expanded	Digits of the same size
M. minutus	Straight and wide (60% of SL)	Robust. Half-straight ends, squeezed in the center	Deep	Not expanded	Medial digit protrudes
N. bogotensis	Triangular and narrow (35% of SL)	Robust. Oval shaped, not developed lateral processes	Slightly deep	Not expanded	Bulky medial digit protrudes

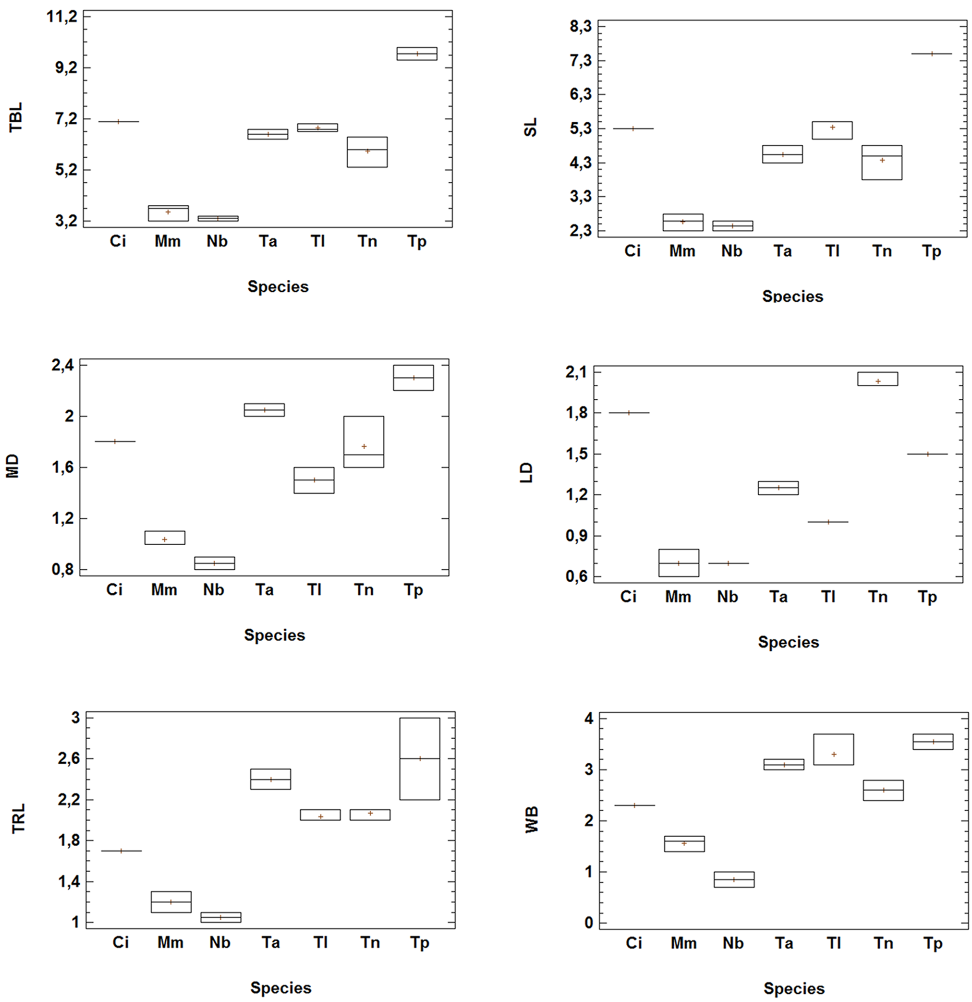

Fig. 3. Boxplots of the 6 bacular measurements (in mm) of *Chilomys instans* (Ci), *Microryzomys minutus* (Mm), *Neomicroxus bogotensis* (Nb), *Thomasomys aureus* (Ta), *T. laniger* (Tl), *T. niveipes* (Tn) and *T. princeps* (Tp). Abbreviations of the measurements: total bacular length (TBL), shaft length (SL), medial digit length (MD), lateral digit length (LD), trident length (TRL) and width of base (WB).

nis of most sigmodontines (Burt, 1960; Hooper and Musser, 1964; Bezerra, 2005). Four of the 7 species we examined (*Thomasomys laniger*, *T. niveipes*, *T. princeps* and *Chilomys instans*) are described here for the first time. Among this assemblage of high Andean rodents, we found diverse bacular morphology as previously described in other rodent taxa (Hooper and Musser, 1964; Díaz de Pascual and Péfaur, 1982; Voss, 1988).

The bacula of *Thomasomys* species exhibit substantial intrageneric differences in both size and structural details (**Table 2**; **Figs. 1-3**). Similar variation is the norm in many other rodent genera such as *Peromyscus* (Blair, 1942), *Proechimys* (Pessôa and Reis, 1992), *Abrothrix* (Spotorno, 1992) and *Ctenomys* (Rocha-Barbosa et al. 2013), to name a few. In addition, we can differentiate the species of *Thomasomys* by their size (**Table 1**). The largest-bodied *Thomasomys*, *T. princeps* and *T. aureus* show a deep concavity on the base in ventral view, a character less apparent in the smaller *T. laniger* and *T. niveipes* (**Fig. 1**; **Table 2**). And, although, *T. laniger* and

Fig 4. Age-related intraspecific bacular variation of A) *Thomasomys laniger* (top to bottom: ICN 21737, 21738), B) *T. niveipes* (Top to bottom: ICN 21740, 21739) and C) *Microryzomys minutus* (ICN 21723, 21725) based on the tooth-wear classes (TWC) proposed by Voss (1991).

T. niveipes have similar body sizes, their bacula exhibit marked differences in the morphology of the trident (**Fig. 1C**-**D**). Furthermore, with the limited data available for this highly speciose genus, *T. niveipes* has unique bacular characters, such as trident digits of the same size and the lack of an expanded head on the shaft (**Fig. 1D**; **Table 2**).

Thomasomys aureus is broadly distributed along the Andes from western Venezuela to the west-central Bolivia; in Colombia, this species is mapped from both the eastern and central part of the country (Pacheco, 2015b). The morphology of the baculum of our Colombian specimens of *T. aureus* is different from that described by Hooper and Musser (1964:35) for specimens from Amacho, Quispicanchi, Cuzco, Peru (FMNH 75588). The baculum of the Peruvian specimen is larger in size (**Table 1**), its cartilaginous trident is more than half the size of the bony shaft, its base is triangular and prominent proximally and the shaft head is heart-shaped. Morphologically, *T. aureus* exhibits variation between isolated populations and is consider a species complex (Pacheco, 2015b). The differences found in bacular morphology between populations from Colombia (ICN 15181, 12196) and Peru (FMNH 75588) may signal species-level recognition, a hypothesis suggested by Pacheco (2015b) and one that warrants further investigation.

Following Cabrera (1961), *Thomasomys princeps* has been considered a subspecies of *T. aureus* by most subsequent authors (Musser and Carleton, 1993, 2005; Voss, 2003). However, as recognized by Thomas (1900), Pacheco (2003, 2015b) separated *T. princeps* from *T. aureus* and considered *T. princeps* a valid species occurring in the Cordillera Oriental of Colombia. Our specimens (ICN 21742, 21743) match the diagnostic characters described for *T. princeps* (Pacheco, 2015b), including its larger size in respect to *T. aureus*. Our data on bacular differences described herein provides support for Pacheco's systematic decision. Most notably, bacular differences between *T. princeps* and *T. aureus* (Colombia) involve shaft length and trident (shorter in *T. aureus*) and both the form and width of the base (**Fig. 1A**-**B**; **Table 2**).

Pacheco (2105b) noted that the baculum described by Hooper and Musser (1964) under the name *T. laniger* (FMNH 92555: Muzo, Boyacá, Colombia) was actually that of a misidentified *T. hylophilus*. The baculum of the specimens of *T. laniger* we examined is clearly different from that described by Hooper and Musser. *Thomasomys hylophilus* has the smallest baculum of any *Thomasomys* heretofore examined (**Table 1**; Hooper and Musser 1964), and the poorly developed lateral processes are unique. Our description of the baculum here of *T. laniger* is thus the first reported for this species.

Cabrera (1961) listed *niveipes* Thomas as a junior synonym of *T. laniger* Thomas but Musser and Carleton (1993) recognized *T. niveipes* as a valid species. Subsequently, Gómez-Laverde et al. (1997) in a detailed morphological, karyotypic and ecological study provided clear support for these two taxa as distinct species. Our morphological comparisons of bacula from these two taxa provide further support for their species status (**Fig. 1C**-**D**; **Table 2**).

The diverse morphology found in the bacula of species of *Thomasomys* (**Fig. 1**) demonstrates the utility of this structure as a specific diagnostic character set, even in a highly variable group. To date, however, only 5 of the 15 species of *Thomasomys* known to occur in Colombia have bacular descriptions, and even fewer descriptions are available for other species in the genus distributed outside of Colombia. Given the species-specific differences we detail here, we believe a review of bacular morphology for all *Thomasomys* species will provide very useful data in further delineating the species-level taxonomy of the genus.

The genus *Chilomys* is closely related to *Thomasomys* (Pacheco, 2003), and the baculum of *C. instants* shares characters found also in *Thomasomys*, such as an expanded head and a deep ventral concavity. Contrary to most of *Thomasomys* species, however, the trident of *C. instans* has digits of the same size otherwise known in *T. niveipes*. A slender shaft, narrow base and radical reduction of the bone from the base are distinctive characteristics of *C. instants* baculum. *Chilomys instans* is widely distributed from the Andes of central Ecuador through the three cordilleras of Colombia (Pacheco, 2015a). Substantial character variation across this range led Pacheco (2003, 2015a) to suggest that *C. instants*, as currently understood, may be a composite of several distinct taxa. Comparison of bacular characteristics for additional samples of this species in Ecuador and elsewhere in Colombia may prove helpful in delineating this composite nature.

The flat and broad base of *Microryzomys minutus* are characters not shared with the other species we examined. Our material exhibits similar characteristics to those described by Díaz de Pascual and Péfaur (1982) for specimens of this species from the Páramo region of Mérida, Venezuela. For example, the lateral digits are partially ossified, the base of the shaft is large, and LTB is short (**Fig. 2B**; **Table 2**). Our Colombian specimen is, however, not exactly like that from Venezuela. For example, our specimen lacks the median notch on the base characterizing the Venezuelan material (Díaz de Pascual and Péfaur, 1982: fig. 3). As currently understood, *M. minutus* is a species with a very wide distribution, and with gaps along the Colombian Cordillera Oriental through the Venezuelan Andes. Although, Carleton and Musser (1989) found no distinguishable geographic subspecies, the bacular differences found in populations closely distributed could suggest the species has either an interspecific variation or that their populations correspond to composite species. A detailed review of the bacula among the populations over this large range is needed to clarify the significance of dissimilarities we describe here. A characteristic of most, but not all, oryzomines is a trident that is greater than or equal to half of SL and the central digit is usually longer (Hooper and Musser, 1964: table 2), a feature that typifies the baculum of *M. minutus* where the trident is 60% of SL. In other oryzomines, such as *Aegialomys xanthaeolus*, *Cerradomys subflavus*, *Handleyomys alfaroi*, *H. chapmani*, *H. rostratus*, *Melanomys*, *Nesoryzomys*, *Pseudoryzomys* and *Sigmodontomys alfari*, the cartilage is reduced and the central digit is less robust than laterals (Hooper and Musser, 1964: fig. 2; Patton and Hafner, 1983).

The baculum of *Neomicroxus bogotensis* is easily distinguished from the rest of species we studied (**Fig. 2C**). Hooper and Musser (1964: 27) described the baculum of *N. bogotensis*, but the specimen they examined was young and, as a result, does not match well to what we found here. Our specimens are similar to that described by Díaz de Pascual and Péfaur (1982) for *N. bogotensis* in the páramo of Mérida although a few differences are apparent, such as the curvature of the bony shaft and the lack of ossification of the three cartilaginous digits in our material (**Fig. 2C**; **Table 2**). These differences in cartilage ossification, however, may only be age-related, since age is a factor in ossification (Murakami and Mizuno, 1984). The genus *Neomicroxus* has only been recently recognized (Alvarado-Serrano and D'Elía, 2013), and comprises only two species restricted to the northern Andes. These species have been previously allocated to the akodontine genus *Akodon* (including *Microxus*), but the current tribal allocation of *Neomicroxus* is uncertain (D'Elía, 2015; Alvarado-Serrano and D'Elía, 2015). The baculum of *N. bogotensis* does lack the medial notch at the base of the shaft that otherwise characterizes those species of akodontines for which the baculum has been described (Hershkovitz, 1962; Hooper and Musser, 1964; Bezerra, 2005; Gonçalves et al., 2005). It is thus possible that bacular characters can be added to the list of attributes diagnosing *Neomicroxus*, and perhaps will be found useful in the search for phylogenetic ties between this genus and other sigmodontines.

Bacular morphology among related taxa may vary according to body size (head and body length or weight) or vary independently of size (Patterson and Thaeler, 1982; Lessa and Cook, 1989; Ramm, 2007). Among the sigmodontine taxa we examined, larger-bodied species do have longer and generally more robust bacula, but this relationship is not absolute. For example, while the larger *T. niveipes* has a shorter baculum than that of the slightly longer *T. laniger*, the baculum of the small-bodied *C. instans* is comparable in length to species of greater body size (**Table 1**; **Fig. 4**).

Finally, our data confirm to what is known about ossification increasing with age, as it also does with size (Morris, 1972). The proximal and central portions of the bacular shaft ossify first in the neonate, and the cartilaginous trident (distal portion) begins to ossify later in puberty (Ruth, 1934; Murakami and Mizuno, 1984). We observed similar developmental changes in the ossification of the baculum shaft and cartilage in adults of different age categories (TWC). It is important to mention that the variation shown in the shape of the trident of *T. niveipes* (ICN 21739) is possibly due to the conditions in which the specimens were preserved and the way the sample was fixed. The different samples observed lead us to conclude that cartilage only ossifies when specimens have reached an older stage of adulthood. Consequently, to consider the ossification of digits of the trident as a diagnostic character, as shown in other studies (Anderson, 1960; Díaz de Pascual and Péfaur, 1982), may be spurious unless the specimen's age is specified.

The penis bone has proven to be a useful structure in taxonomy and systematics (Blair, 1942; Lidicker, 1968; Simson et al., 1995; Pessôa et al., 1998, Bezerra, 2005; Rocha-Barbosa et al., 2013). Our results support the potential taxonomic value of this bone at the generic and specific levels, especially in groups where there is high morphological variation in craniodental characters. Although our study does not evaluate intraspecific variation across different populations, this topic requires further investigation given the scarcity of information available and the high diversity of rodent still unknown. Even though recent molecular studies combined with taxonomic and systematic approaches have been helpful in species diagnosis, we highlight the morphological implications and research of other structures such as the baculum in order to provide suitable information for species definition. Furthermore, studies based on bacular morphology can contribute in the exploration of other biological aspects of rodents, such as sexual selection and reproductive biology (Ramm, 2007; Simmsons and Firman, 2013;

Stockley et al., 2013), important attributes that are largely unknown for most species.

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APPENDIX 1

List of localities and specimens examined:

CUNDINAMARCA, Municipio Fómeque, PNN Chingaza, Sector Laguna Verde-Laguna Seca, 3445 m, 4°41'03.1" N, 73°45'58.9" W: *Neomicroxus bogotensis* (ICN 21728, 21731); *Microryzomys minutus* (ICN 21721, 21725); *Chilomys instants* (ICN 21712); *Thomasomys niveipes* (ICN 21739, 21740, 21741). Sector Las Ciervas, 3171 m, 4°37'47.2" N, 73°43'57.9" W: *M. minutus* (ICN 21723); *Thomasomys laniger* (ICN 21737). Sector Monterredondo, Encenillo Forest, 3182 m, 4°35'51.4" N, 73°43'10.7" W *Thomasomys laniger* (ICN 21736, 21738); *Thomasomys princeps* (ICN 21742, 21743).

CALDAS, Municipio Manizales, Vereda Las Palomas, El mirador, Río Blanco Reserve, 2640 m, 5º4'20.1" N; 75º25'10.6 W: *Thomasomys aureus* (ICN 15181).

RISARALDA, Pereira, Corregimiento La Florida, La Pastora, PNN Ucumarí, 2650 m, 4º42'00.0" N; 75º28'59.8" W: *T. aureus* (ICN 12196).