

A NEW GIANT PORCUPINE (RODENTIA, ERETHIZONTIDAE) FROM THE LATE MIOCENE OF ARGENTINA

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ABSTRACT—An exceptionally well-preserved skull and associated dentary from the Chiquimil locality in the Andalhuala Formation (Huayquerian Age, late Miocene), Santa María Basin, Catamarca Province, northwestern Argentina, represent a new giant porcupine, *Neosteiromys pattoni*, sp. nov. *N. pattoni* is derived relative to *Neosteiromys bombifrons* Rovereto, 1914, the type species of the genus, by having pentalophodont m2–m3, a markedly infected angular region, more prominent masseteric crest, deeper masseteric fossa, and larger auditory bullae. Both species of *Neosteiromys* appear to have been adapted to eat harder, more abrasive food items than those consumed by extant porcupines, as inferred from their stronger masticatory apparatus. They may have inhabited more open environments than those of living Neotropical porcupines.

INTRODUCTION

The Erethizontidae (the New World porcupines) is a primitive clade of Hystricognathi rodents, which probably differentiated early during the evolutionary history of the suborder (Bugge, 1971; Woods, 1972; Bryant and McKenna, 1995; Candela, 1999; but see Huchon and Douzery, 2001). At present, Neotropical porcupines are represented by approximately 15 species strictly adapted to arboreal life, extending from northern Uruguay and Argentina to southern Mexico (Emmons, 1997). The semi-arboreal *Erethizon dorsatum*, the only extant species in temperate North America, is distributed from northern Mexico to Alaska and Canada (Roze, 1989).

Fossil erethizontids were very diverse in Patagonia (southern Argentina) from the late Oligocene to middle Miocene (Ameghino, 1887; Wood and Patterson, 1959; Candela, 1999) and are also known from the middle Miocene of La Venta, Colombia (Walton, 1997). By the late Miocene, the distribution and diversity of the family had changed. Only *Neosteiromys*, the giant porcupine of the New World, from northwestern Argentina (Rovereto, 1914), and *Paradoxomys cancrivorus* from the “Mesopotamian” (northeastern Argentina; Vucetich and Candela, 2001) are recognized. Pliocene and Pleistocene erethizontids from South America belong to the extant genera *Erethizon* and *Coendou* (Lund, 1939; Hoffstetter, 1963; Candela and Reguero, 1998), living in essentially the Brazilian Subregion (sensu Hershkovitz, 1958).

Despite the fact that extinct Erethizontidae are members of many mammal faunas of the South American Cenozoic, until now no single species has been analyzed from a paleobiological perspective. This paper describes a new species of *Neosteiromys* from the late Miocene Chiquimil locality, Catamarca Province, Argentina (Fig. 1). The well-preserved skull and dentary add new information about this relatively poorly known genus. The paleoenvironmental significance of *Neosteiromys* is also discussed in context with other fossil and geologic evidence.

Terminology used for naming the fossettes, flexi, and lophes of the upper cheek teeth follows Candela (1999); names of the fossettids, flexi, and lophids of the lower cheek teeth follow Candela (2000, 2002; Fig. 2). All measurements are in millimeters.

Institutional Abbreviations—MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Argentina); MMH, Museo de Monte Hermoso (Argentina).

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Family ERETHIZONTIDAE Thomas, 1897
Genus *NEOSTEIROMYS* Rovereto, 1914

Type Species—*Neosteiromys bombifrons* Rovereto, 1914.

Referred Species—*Neosteiromys pattoni*, sp. nov.

Distribution—Northwestern Argentina (Catamarca Province), late Miocene (Huayquerian Age).

Diagnosis—*Neosteiromys* differs from all recent and fossil erethizontids in the following features: significantly larger skull and mandible; cheekteeth having thicker enamel without labial cusps and earlier closure of labial flexus; lower molars without lingual cusps and early closure of lingual flexus; P4 subtriangular, protocone and hypocone slightly differentiated; incisors with a deeper implantation; mandible higher and more robust; retro-molar fossa extending farther forward; deeper masseteric fossa; lateral and masseteric crests more prominent; masseteric notch situated at level of p4; skull notably high in the nasofrontal region; rostrum higher; infraorbital foramen smaller in relation to rostrum height and frontally oriented; origin of the ventral zygomatic roots anterior to P4, and posterior zygomatic roots more robust.

Remarks—The genus *Neosteiromys* and its type species *N. bombifrons* were both described by Rovereto (1914). It derives from the Andalhuala Formation (late Miocene, Huayquerian Age; Marshall and Patterson, 1981; but see Bossi et al., 1999) in the Santa María Basin, Catamarca Province. Since the original description of the genus by Rovereto (1914), it has only been briefly mentioned in the literature (e.g., Vucetich, 1986; Vucetich et al., 1993). The material of the new species is better preserved than the type specimen of *N. bombifrons* (the only specimen known, a partial skull and associated dentary) enabling a more comprehensive comparative study of this genus. The diagnosis of *Neosteiromys* proposed here includes the synapomorphies obtained from a recent phylogenetic analysis of the Erethizontidae performed by Candela (2000, 2001) that considered the features present in the new species.

Another potential record for the genus is *Neosteiromys? tordillense* from the Collon Cura Formation (middle Miocene), Cañadón del Tordillo, Neuquen Province, Argentina (Vucetich et al., 1993). The status of this species is uncertain because it is



FIGURE 1. Map showing the geographical location of the Chiquimil locality in the Santa Maria Basin, northwestern Argentina, the type locality of *Neosteiromys pattoni*, sp. nov.

known by only a few isolated cheek teeth that have features in common with both *N. bombifrons* and the Patagonian *Steiromys duplicatus* Ameghino, 1887 (early middle Miocene). Pascual and Bondesio (1981) reported fossils of erethizontids that might be *Neosteiromys* from Santa Isabel Quarry, San Luis Province, Argentina. However, I do not believe they represent *Neosteiromys*. The genus was also reported among the fauna from the Las Playas Formation, at the La Playa locality, Cordoba Province, Argentina, (Kraglievich and Reig, 1954). However, the La Playa material does not even belong to the Erethizontidae (pers. obs.).

NEOSTEIROMYS PATTONI, sp. nov.

Holotype—MNH 92-1-1, a nearly complete skull with both tooth rows, and left dentary with m1–m3 and the intra-alveolar part of the incisor, both belonging to the same individual.

Hypodigm—Only the holotype.

Etymology—In recognition of Dr. James Patton, because of his contribution to knowledge of South American rodents.

Geographical and Stratigraphic Occurrence—Chiquimil (= Entre Rios) Locality (Fig. 1), Santa María Basin, Santa María Department, Catamarca Province, northwestern Argentina; 'Araucanense' sensu Riggs and Patterson (1939), Andalhuala Formation (Galván and Ruiz Huidobro, 1965), late Miocene, Huayquerian Age (Marshall and Patterson, 1981; but see Bossi et al., 1999).

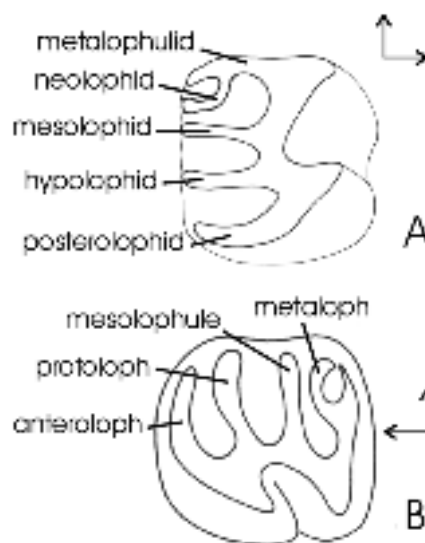


FIGURE 2. Terminology used for upper and lower cheekteeth of the Erethizontidae (after Candela 1999, 2002). **A**, lower molar; **B**, upper molar. Arrows show anterior and labial sides.

Diagnosis—Differs from *Neosteiromys bombifrons* by its narrower rostrum; thinner ventral zygomatic roots; deeper mesopterygoid fossa; larger bullae; lower masseteric notch with respect to the alveolar edge of the mandible; masseteric crest having a more pronounced slope; wider retromolar fossa; masseteric fossa more extended dorsoventrally; deeper anterior portion of the masseteric fossa; angular region markedly lingually inflected; ventral edge of the masseteric crest wider and rounded; lower molars proportionally wider relative to length, without ectostylid or accessory lophid; m2–m3 pentalophodont; m3 proportionally smaller relative to m1–m2, and wider lower incisor.

COMPARATIVE DESCRIPTION

Cranium—The cranium is about forty percent longer than those of the largest living porcupines, *Coendou prehensilis* and *Erethizon dorsatum* (Table 1). The cranial sinuses are inflated, resulting in a dorsal profile that is strongly convex from the nasal tips to the posterofrontal region (Fig. 3A). The highest point of the cranium is at the level of the anterior region of the orbit. The rostrum is long and tall. The nasals are long with the dorsal surface convex, narrowing slightly posteriorly, with straight lateral edges, and posterior margins extending far behind the dorsal zygomatic roots (Fig. 3B). The postorbital process are prominent and located anterior to the midpoint of the orbitotemporal cavity. Viewed dorsally, the right zygomatic arch (the only one preserved) is slightly convex and not divergent posteriorly.

In ventral view, the rostrum is narrower than that of *Neosteiromys bombifrons* (Fig. 3C, G). The diastemal ridges are subparallel, extending from the anterolingual border of the P4 to the level of the anterior border of the ventral zygomatic roots. These roots originate far anterior to the P4 and are slender compared to those of *N. bombifrons*. The masseteric tuberosity is medially and anteriorly located respect to the labial margin of the P4. The toothrows are subparallel. The palate is convex. The mesopterygoid fossa is 'V'-shaped; its apex extends to the level of the middle of the M2, more anterior than in the type species. The pterygoid fossae are narrow and long. The pterygoid plates are almost vertically oriented. The bullae are markedly divergent, laterally compressed, and larger than those of *N. bombifrons*. The dorsal roof of the external auditory meatus is smooth.

TABLE 1. Measurements (in mm) of the skulls and dentary of *Neosteiomys bombifrons* Rovereto, 1914 (MACN 8200), *Neosteiomys pattoni*, sp. nov. (MNH 92-1-1), *Erethizon dorsatum*, and *Coendou prehensilis* (data for *Erethizon* and *Coendou* from Frazier, 1981).

	MACN 8200	MNH 92-1-1	<i>Erethizon</i>	<i>Coendou</i>
Condylbasal length**	150.9	—	108.3	81.3
Bulla-premaxilla length***	144.30	134.11	—	—
Length of diastema	41.47	39.87	—	—
Palatal width at M1*	10.37	8.77	—	—
Palatal width at M3*	—	9.70	—	—
Zygomatic length*	—	61.40	—	—
Nasal length*	—	68.51	—	—
Maximal ventral width of the rostrum	33.33	26.37	—	—
Maximal dorsal width of the rostrum	—	35.81	23.0	18.8
Maximal height of the rostrum	—	72.26	—	—
Width of nasal aperture*	—	25.60	—	—
Width at posterior zygomatic roots*	—	72.42	46.7	71.2
Maximal orbitotemporal length	—	31.87	—	—
Postorbital width	—	45.90	—	—
Width at auditory meatus*	53.80	52.94	45.6	33.6
Bulla length	23.90	27.12	—	—
Mandibular height at m1	31.17	—	—	—
Mandibular height at m2	27.4	—	16	10.5
Mandibular height at posterior edge of m3 (including angular region)	30.26	32.62	—	—
Length of diastema	ca. 17.92	—	—	—

*Measurements following Voss and Angermann (1997), **total skull length for *Erethizon* and *Coendou*; ***measured from the posterior edge of right bulla to anterior edge of premaxilla.

In lateral view, the rostrum is very high. Scars on the lateral side of the rostrum indicate a very large area of origin for the masseter medialis pars anterior extending over all the rostrum (Woods, 1972). The dorsal zygomatic root is subvertically oriented, and its origin is located at the level of the P4, behind the origin of the ventral zygomatic root. The infraorbital foramina are in a frontal plane. In lateral view, the anterior part of the zygomatic arch is wider than the posterior part. The maxillary-jugal suture is located just behind the dorsal and ventral zygomatic roots. The posterior zygomatic roots are very strong and wider anteroposteriorly. The sphenopalatine foramen is situated above the M2–M3. The orbital cavity is small in relation to the skull length. The squamosal crest is well developed, limiting the posterior border of the orbitotemporal fossa (origin of the orbital division of temporal muscle; Woods, 1972), which is anteriorly bounded by the postorbital process.

The infraorbital foramen is small in relation to the height of the rostrum because the frontal aspect of the dorsal zygomatic root is very large. The nasal orifice is sub-quadrangular and very large (Fig. 3D). The lateral side of the rostrum shows the mark of the alveoli of the incisor, indicating its implantation above M1, as in *N. bombifrons* (Fig. 3E). Its degree of curvature indicates a proodont orientation, like that of the type species.

Mandible—The preserved portion of the dentary is tall and strong (Fig. 4A–C, Table 1). The ascending ramus extends far dorsally relative to the tooth row. The mandibular body is wide and convex labially. The posterior end of the masseteric notch (insertion of the pars anterior of the medial masseter) is located just above the midpoint of the mandibular height (lower than in *N. bombifrons*, Fig. 4D–F), and at the level of the m1, indicating that the whole notch was at the level of posterior end of p4, as in the type species. The masseteric crest is prominent, mainly its anterior region, descending from the masseteric notch with a higher slope than that of the type species. Posteriorly, the masseteric crest becomes less evident along the ventral border of the angular region of the mandible, widening in a large area for insertion of the masseter superficialis. The masseteric fossa is very deep and more extended dorsoventrally (between the basis of the coronoid process to masseteric crest) than that of the type species. The lateral crest is prominent, extending from the masseteric notch to the basal border of the coronoid process. Unlike the condition observed in living porcupines, there is no fossa for insertion of the pars posterior of the medial masseter (Woods,

1972). The retromolar fossa extends anteriorly to the level of m1–m2, and is wider than that of *N. bombifrons*. The alveolar sheath of the incisor is very broad, been clearly distinctive from the angular region of the mandible. Unlike *N. bombifrons*, this region of the mandible is markedly lingually inflected. On the labial side of the dorsal region of the mandibular ramus, a strong prominence indicates the position of the base of the incisor. The post-condyloid process is located behind this swelling.

Upper Dentition—The upper cheek teeth are characterized by shallow fossettes, thick enamel, absence of cusps, and early closure of the labial flexus (Fig. 5A; Table 2). The P4 is pentalophodont and subcircular in occlusal view. The protocone and hypocone differ little from each other. The hypoflexus of the left P4 is lingually closed, the hypoflexus of the right P4 remains as a shallow, narrow groove. The hypoflexus/hypofossette is connected to the parafofsette. The protocone is continuous with the anteroloph, forming a subcircular border. The protoloph extends from the mure, slightly oblique anterolabially, to the labial side of the teeth. The mesolophule is also slightly oblique anterolabially. The metaloph is well developed; the posterofossette is suboval.

As in *N. bombifrons* (Fig. 5C, D; Table 2), the M1 and M2 are wider than long, with a noticeable angle between the protocone and the anteroloph. The M1 is pentalophodont. The bottom of the hypoflexus is lingually open and is continuous with the parafofsette; it is also connected with the bottom of the mesofossette by a narrow and shallow groove. The protoloph and mesolophule are transversely oriented. The metaloph is well developed, more than the type species, bounding a narrow and long posterofossette. The M2 is larger than the M1 (Table 2). The posterofossette is suboval in occlusal view. The hypoflexus is nearly closed and, unlike the type species, is not connected with the bottom of the parafofsette. The M3, also pentalophodont, is equal in size with the M1, although narrower posteriorly. Like the M2, the hypoflexus is not connected to the parafofsette. The hypoflexus is lingually closed. The hypocone is more labially located than those of the M1–M2.

Lower Dentition—The m1–m3 are characterized by shallow fossettids, thick enamel, absence of cusps, and early closure of the lingual flexus (Fig. 5B; Table 3). The m1 is quite wider than longer. The protoconid is labially convex. The hypoconid is labially located relative to the protocone and the two are divided by a broad hypoflexus. The ectolophid is well developed; in its

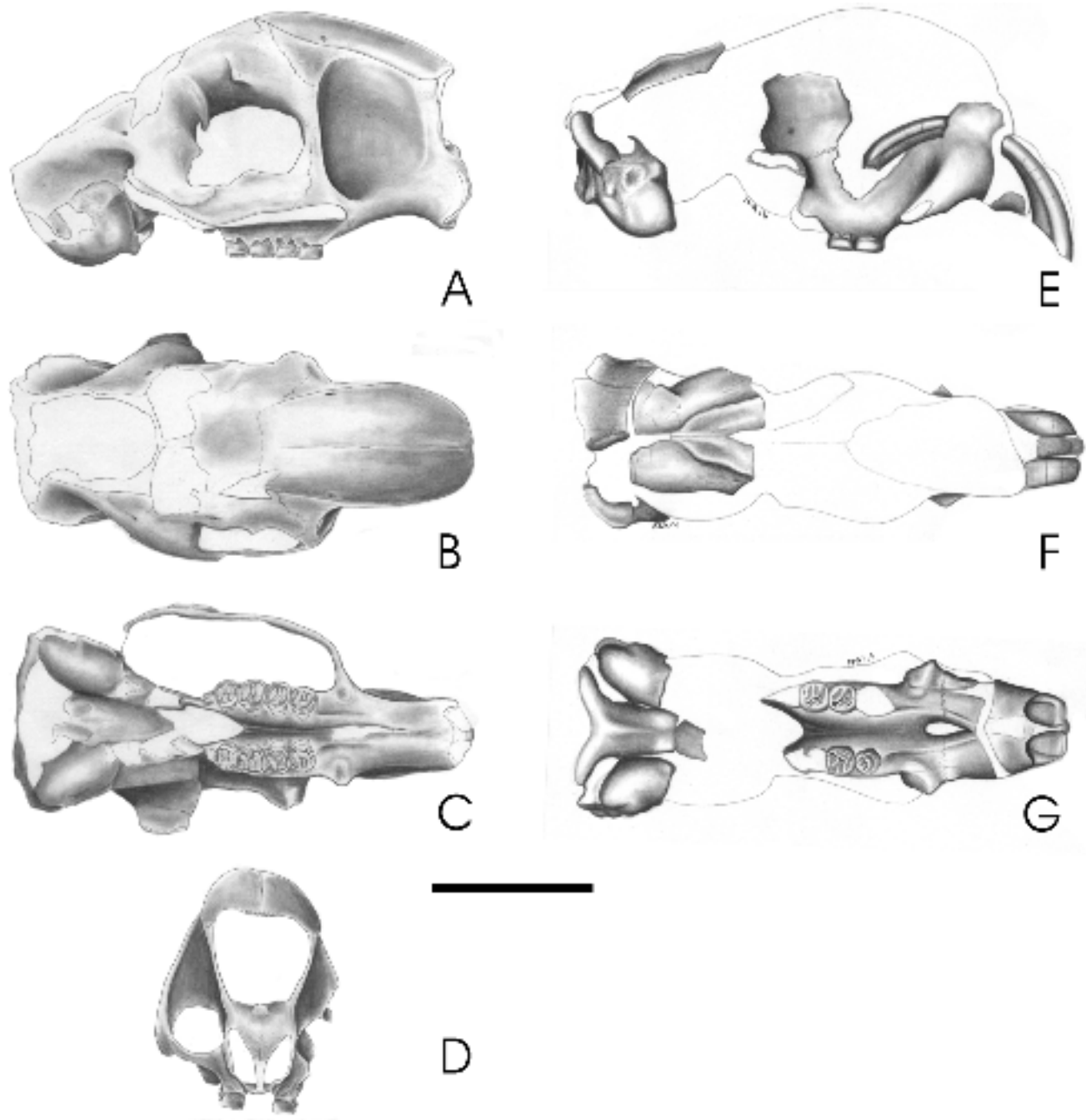


FIGURE 3. A–D, *Neosteiromys pattoni*, sp. nov. (holotype MNH 92-1-1), skull in lateral (A), dorsal (B), ventral (C), and anterior (D) views. E–G, *Neosteiromys bombifrons* Rovereto, 1914 (holotype MACN 8200), skull in lateral (E), dorsal (F), and ventral (G) views. Scale equals 5 cm.

middle portion, among the labial ends of the meso- and hypolophid, is a small spur. An incipient neolophid is linked to the metalophid.

The m2 is larger than the m1 (Table 3), and differs from the m1 and from the m2 of *N. bombifrons* (Fig. 5D) by the presence of the well developed neolophid. A thin wall extends from the posterolophid to the hypolophid, separating the posterofossettids into two parts, a smaller labial and a larger lingual fossettids. The m1–m2 lack ectostylids and accessory lophids, both present in *N. bombifrons* (the latter placed behind the mesolophid).

The m3 is smaller than m2 and it narrows posteriorly. A thin wall extends from the mesolophid and hypolophid, separating

the mesofossettids into a small labial and a large lingual fossettids. The hypoflexus is very short and shallow.

The lower incisor (only its intra-alveolar portion is preserved) is deeper than wide, it has a flat anterior surface and is somewhat wider than that of the type species.

DISCUSSION

Differences Between the Two Species of *Neosteiromys*

The differences between the type specimen of *N. bombifrons* and the type specimen of *N. pattoni* (see Diagnosis) do not cor-

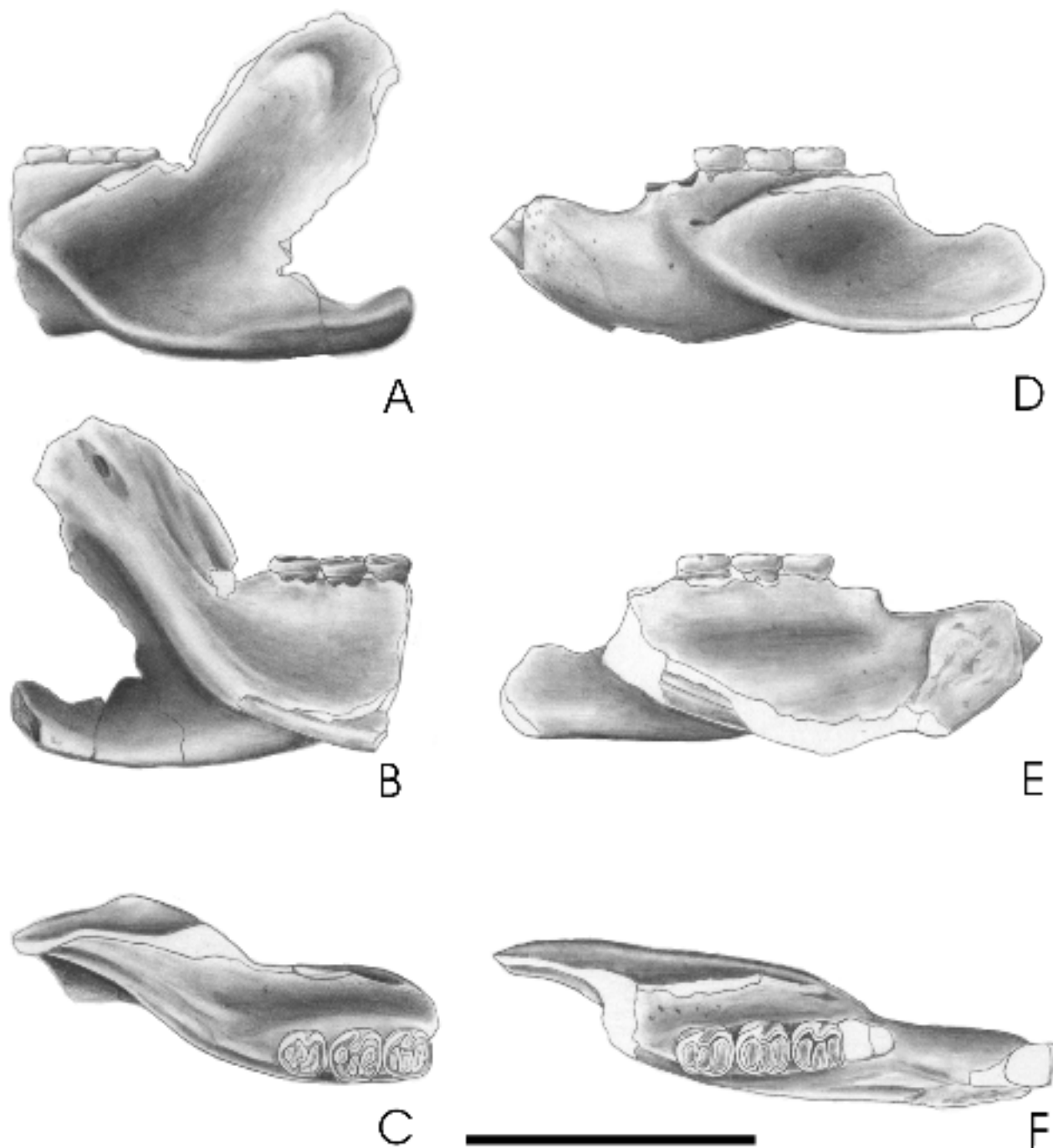


FIGURE 4. **A–C**, *Neosteiromys pattoni*, sp. nov. (holotype MNH 92-1-1), left dentary in labial (**A**), lingual (**B**), and occlusal (**C**) views. **D–F**, *Neosteiromys bombifrons* Rovereto, 1914 (holotype MACN 2800), left dentary in labial (**D**), lingual (**E**), and occlusal (**F**) views. Scale equals 5 cm.

respond to intraspecific variability. The differences between them (e.g., width of the rostrum and the ventral zygomatic roots, depth of the mesopterygoid fossa, relative size of the bullae; width of retromolar fossa; extension of the masseteric fossa; inflection of the angular region; ventral edge of the masseteric crest; proportions of the lower molars; presence of ectostylid; number of lophids; relative size of m3 and the incisors) are not found within any extant species, such as *Coendou prehensilis* or *Coendou insidiosus* (pers. obs.), and are even more pronounced than those observed between many of the extant species of *Coendou* (see Voss and Angermann, 1997). Furthermore, the species of *Neosteiromys* differ in several dental features, whereas living species

in the same genus, such as those of *Coendou*, show a conservative molar morphology. The lower molars of *N. pattoni* differ from those of *N. bombifrons* in lacking an ectostylid and accessory lophid, m1–m3 wider than long, and pentalophodont m2–m3. In the upper cheekteeth of *N. bombifrons*, the hypoflexus is connected to the parafofsette, while in *N. pattoni* this connection tends to disappear in M2–M3. In *N. pattoni*, the metaloph and the posteroloph are always joined, as well as the mesolophule and the mure, while both connections may be absent in *N. bombifrons*. Because the configuration of the metaloph and mesolophule could be affected by wear, additional specimens are required in order to assess the diagnostic value of these differences.

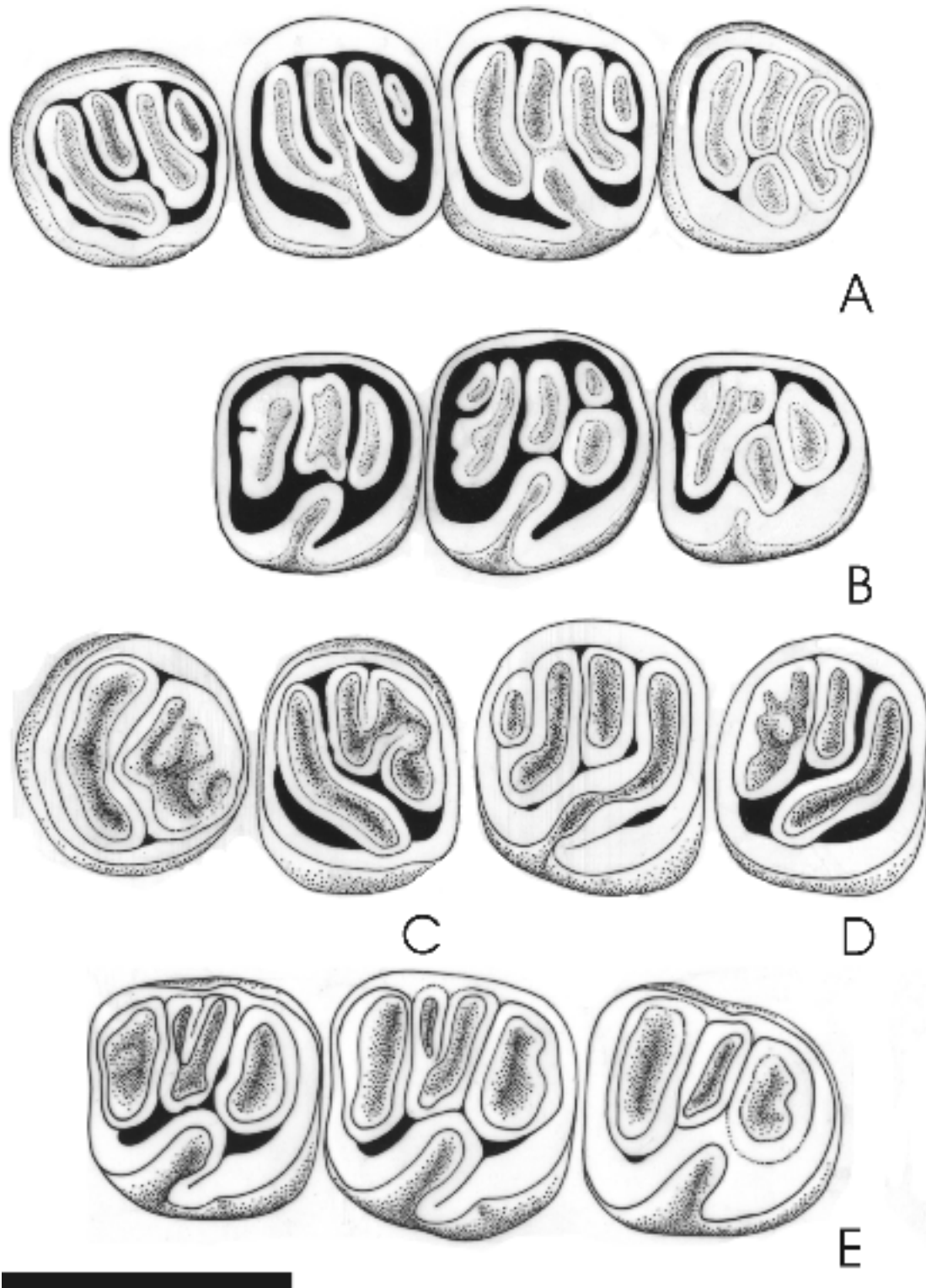


FIGURE 5. **A–B**, *Neosteiomys pattoni*, sp. nov. (holotype MNH 92-1-1), occlusal views of left P4–M3 (**A**), and left m1–m3 (**B**). Anterior to left. **C–E**, *Neosteiomys bombifrons* Rovereto, 1914 (holotype MACN 2800), occlusal views of left P4–M1 (**C**), right M1–M2 (**D**), and left m1–m3 (**E**). Scale equals 1 cm.

It is worth noting that the differences between the type specimen of *N. bombifrons* (with scarcely worn cheek teeth), and the type specimen of *N. pattoni* (with more worn cheek teeth) do not correspond to ontogenetic variation. *Erethizon dorsatum* re-

places the DP4 when it is about two years old (Sotton, 1971; Roze, 1989). In that ontogenetic stage, extant porcupines have nearly reached their definitive size and show the distinctive features of the adult stage. The type specimens of both *N. bombi-*

TABLE 2. Measurements (in mm) of the upper dentition of the holotypes of *Neostiromys bombifrons* Rovereto, 1914 (MACN 8200, including the isolated right M3 and right P4) and *Neostiromys pattoni*, sp. nov. (MNH 92-1-1). **APD**, maximum anteroposterior diameter; **TD**, maximum transverse diameter.

	MACN 8200	MNH 92-1-1
APD incisor	11.50	—
TD incisor	8.81	—
Length P4-M3	—	30.67
Length M1-3	—	22.96
APD P4	8.57	7.98
TD P4	8.57	8.10
APD M1	7.35	7.28
TD M1	8.94	8.64
APD M2	8.26	7.72
TD M2	9.69	9.02
APD M3	8.16	7.25
TD M3	8.70	8.20

frons and *N. pattoni* have replaced the DP4 and the P4 is completely erupted and generally similar in overall size (the skull of the type species of *N. bombifrons* is somewhat longer, Table 1). Upon this basis, it can be assumed that the characters of both specimens correspond to the adult stage and, hence, their dissimilarities do not reflect different ontogenetic stages. In addition, most of the characters distinguishing *N. bombifrons* from *N. pattoni* are not modified in extant erethizontids after the complete eruption of the P4 and p4, such as: position of the masseteric notch in relation to alveolar edge; size of m3 with respect to m1–m2; degree of lingual inflexion of the angular region of the mandible; depth of the mesopterygoid fossa of the skull; and size of the bullae.

N. pattoni has some derived characters relative to those of *N. bombifrons*, such as pentalophodonty of m2–m3, markedly inflected angular region, more prominent masseteric crest, deeper masseteric fossa, and larger bullae (Candela, 2000, 2001). This suggests that the morphology of *N. bombifrons* is closer to the ancestral condition of the genus.

Phylogenetic and Biogeographic Considerations

One of the distinguishing characteristics of *Neostiromys* is its large size, exceeding all other erethizontids. The pronounced height of the skull at the orbitonasal region, resembling some *Coendou* species, is also distinctive. In connection with this, Rovereto (1914:75) pointed out that the skull of *N. bombifrons* is characterized by the “prominencia arqueada y saliente que ofrece su parte antero-superior, casi como en el cuandú viviente *Coendus prehensilis*” (“arched and salient prominence of its antero-superior part, almost like in the extant coendu *Coendus*

TABLE 3. Measurements (in mm) of the lower dentition of the holotypes of *Neostiromys bombifrons* Rovereto, 1914 (MACN 8200, including the isolated left p4) and *Neostiromys pattoni*, sp. nov. (MNH 92-1-1). Abbreviations as in Table 2.

	MACN 8200	MNH 92-1-1
APD incisor	10.66	ca. 11.01
TD incisor	7.35	8.48
Length of m1–m3	26.22	23.18
APD p4	8.62	—
TD p4	7.31	—
APD m1	8.29	7.37
TD m1	8.15	7.80
APD m2	8.79	7.87
TD m2	8.70	8.40
APD m3	8.8	7.50
TD m3	8.33	7.44

prehensilis”). *Neostiromys* shares numerous characters with *Coendou*: frontally oriented infraorbital foramen; dorsal zygomatic roots subvertically oriented (both features preserved only in *N. pattoni*); and dorsal roof of the external auditory meatus smooth or slightly rough (see Voss and Angermann, 1997:fig. 15). Also, the frontal bones at the level of the postorbital constriction are greatly wider than the nasals in *Neostiromys*, *Coendou*, and *Erethizon*, unlike the condition in Patagonian fossil erethizontids such as *Steiromys*. On the other hand, *Neostiromys* differs from extant porcupines in a number of features: smaller orbitotemporal region relative to skull length (measured from the posterior edge of dorsal zygomatic root to anterior edge of posterior zygomatic root); longer and deeper rostrum; ventral zygomatic root more anterior than the anterior alveolar edge of P4; posterior zygomatic root more anteroposteriorly developed; bullae compressed and divergent, higher mandible; lack of insertion fossa for the pars posterior of the masseter medialis; position of masseteric notch far above the middle of mandible height; and larger incisors in relation to the cheekteeth and more deeply implanted. *Neostiromys* shares some of these features with Patagonian porcupines (e.g., *Steiromys*).

This mosaic of features in *Neostiromys* has led to the idea that it is the link between the Patagonian *Steiromys* and the extant porcupines *Coendou* and *Erethizon* (Rovereto, 1914). Yet, in a phylogenetic analysis of the erethizontids, two major clades were recognized, the Erethizontinae (= Coendinae of Candela 2000, 2001) representing the living genera from the Neotropics and North America, and the Steiromyinae, composed exclusively of extinct taxa (Candela, 2000, 2001; Fig. 6). In this latter group,

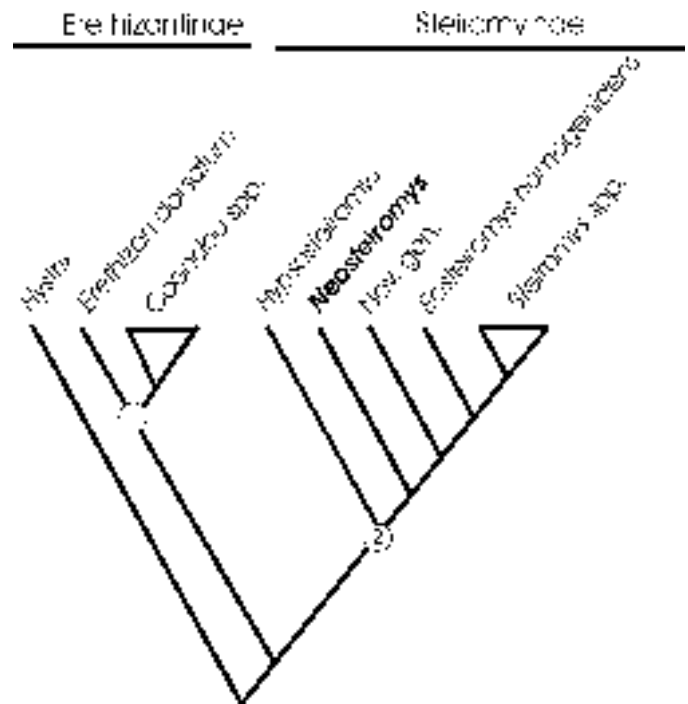


FIGURE 6. Phylogenetic position of *Neostiromys* as determined by the presence of character states used by Candela (2000, 2001). Node 1 (Erethizontinae): alveolar sheath not abruptly separated from the angular region; masseteric notch placed in the middle or slightly over the mandibular body and at level of m1–m2; presence of the insertion fossa of the medial masseter pars posterior; pterygoid shelf well developed, masseteric crest poorly developed; base of the incisor implanted posterolaterally to m3; orbitotemporal region long relative to cranium length; pterigoidea fossa very wide. Node 2 (Steiromyinae) deep masseteric fossa; lateral border of incisory foramen posteriorly divergent toward premaxilla-maxilla suture, well developed postorbital process; width of alisphenoid; incisors large in relation to size of cheekteeth.

Neosteiromys was the sister taxon of the early to middle Miocene Patagonian clade that includes *Eosteiromys* and *Steiromys*. If the phylogenetic analysis is correct, the shared characters of *Neosteiromys* and living porcupines represent homoplasy and inflation of the cranial sinuses developed independently in different taxa of the family at different times during their evolutionary history. According to the phylogenetic hypothesis of Candela (2000, 2001), and taking into account that the age of the oldest fossils provide minimum ages for cladogenetic events, *Neosteiromys* and the Patagonian clade must have differentiated by at least the early Miocene. Consequently, the late Miocene *Neosteiromys* is a survivor of an lineage for which no older records are currently known. The other late Miocene erethizontid, *Paradoxomys cancrivorus* (Cione et al., 2000), was tentatively assigned to the Erethizontinae clade (Vucetich and Candela, 2001). If true, the contemporaneous *Neosteiromys* and *P. cancrivorus* represent different clades that separated very early in the evolutionary history of the family. *P. cancrivorus* is the southernmost member of the Erethizontinae, a group otherwise restricted in South America to the Brazilian Subregion (Hershkovitz, 1958). The phylogenetic affinities and geographical and temporal occurrences of *Neosteiromys* and *P. cancrivorus* support the hypothesis that the northeastern and northwestern regions of Argentina had differentiated biogeographically by at least the late Miocene (Pascual et al., 1996). The Paraná Seaway (middle Miocene) could have formerly been a barrier, precluding the interaction between the Erethizontidae and Steiromyinae.

Paleoenvironmental Significance

The Santa María Basin is situated on the eastern margin of the Argentine Andes in northeastern Sierras Pampeanas (Fig. 1). This basin is bounded by the Sierra de Quilmes to the west and the Cumbres Calchaquíes and the Sierra Aconquija to the east. At present, rainfall rarely exceeds 200 mm/yr, the main vegetation type is steppe, characterized by low bushes and scattered cacti (Cabrera and Willink, 1973), and the extant rodent fauna is relatively depauperate (e.g., *Ctenomys*, *Microcavia*, *Galea*, *Eligmodontia*).

Knowledge of the ecology of the extant porcupines (*Erethizon* and *Coendou*) provides a basis to interpret the paleoecology of *Neosteiromys*. Living Neotropical porcupines are strictly adapted to arboreal life and inhabit different types of forests, although some species, such as *C. prehensilis*, also live in more open areas (Anderson, 1997; Emmons, 1997). They feed mainly on fruits, seeds, buds, and soft leaves (Charles-Dominique et al. 1981; Emmons, 1997). In contrast, *E. dorsatum* is semi-arboreal, and is mostly found in temperate woodlands, but it is also present in the taiga and Arctic tundra (Roze, 1989). *Erethizon dorsatum* is a generalist, feeding mainly on harder food (bark, coniferous leaves, and seeds; Roze, 1989) than Neotropical species.

The masticatory apparatus of *Neosteiromys* differs from those of extant porcupines. In *Neosteiromys*, the temporal and masseter muscles would have been stronger, as indicated by more robust sagittal and temporal crests (origin of the main part of the temporal muscle; Woods, 1972) and the posterior zygomatic roots (origin of the orbital part of the temporal muscle). The pars anterior of the medial masseter was also probably more developed in *Neosteiromys* than in the extant species, as indicated by the larger rostral fossa and deeper masseteric fossa. The whole medial side of the posterior region of the mandible of *N. pattoni* is manifestly inflected, more than in *E. dorsatum*, suggesting greater development of the masseter superficialis. This increase of the mass of the adductor muscles could be attributable to scaling effects related to larger size, as observed in the caviomorph *Ctenomys* (Vasallo, 1998). The force exerted by these adductor jaw muscles (F_i) affects the out-force at the tip of the

incisors (F_o). The out-force is also affected by the proportions between the in-lever arm (L_i) and out-lever arm (L_o) as follows: $F_o = F_i \cdot L_o/L_i$ (Lessa, 1990). Out-lever and in-lever arms are measured as the distances between the lower jaw condyle and the tip of the incisors, and the in-force (F_i), respectively. In rodents, as in mammals in general, positive rostral allometry results in a relatively longer L_o (Vasallo 2000; Mora et al., 2003). An increase in L_o would result in a decreased F_o . However, in *Neosteiromys*, as in other caviomorphs (Vasallo, 2000; Mora et al., 2003), the forward displacement of the origin and insertion of the muscles results in an increase of L_i compensating for changes in the out-lever arm, and maintaining in this way an isometric relationship between in-lever and out-lever arms. In fact, in *Neosteiromys*, the origin and insertion areas of the main masticatory muscles are more anteriorly located relative to the incisors, the retromolar fossa (insertion of the orbital part of the temporal muscle) is more anteriorly extended than that of *Coendou* and *Erethizon*, the ventral zygomatic root (of origin of the masseter superficialis) originates more anteriorly relative to the P4, and the masseteric notch (insertion of the anterior pars of the masseter medialis) is more anteriorly located (below p4) than that of *Coendou* and *Erethizon* (below m1–m2). Thus, *Neosteiromys* seems to preserve the mechanical function of the incisors in spite of the change of the skull proportions in relation to living porcupines. In addition, the upper incisors of *Neosteiromys* are more proodont, stronger, and more deeply implanted (above M1) than those of extant porcupines (above or in front of P4), and probably had a more efficient scraping function. Some features of the cheek teeth of *Neosteiromys* (thick enamel, the trend to close the flexus, and absence of cusps) would have favored the grinding action of the occlusal surfaces. Consequently, both species of *Neosteiromys* appear to have been adapted to eat harder, more abrasive food items than those consumed by extant porcupines.

Interestingly, the paleoenvironmental study by Kleinert and Strecker (2001) on sedimentary characteristics and paleosols of the Andalhuala Formation in the Santa María Basin indicated a mixture of humid and arid conditions. They also noted that stable carbon isotope values indicate the presence of both C3 and some C4 plants (the latter are better adapted to water stress). Several other vertebrates from the Andalhuala Formation add evidence about the paleoenvironment. Some of the taxa are generally believed to have been adapted to open environments more so than wooded areas. Octodontidae rodents can be indicators of relative arid and dry conditions (Vucetich, 1986), the eumysopine echimyid *Reigechimys* also suggests open areas (Verzi et al., 1994), and argyrolagid marsupials were probably adapted to arid, open environments (Pascual and Bond, 1986). However, other taxa indicate closed, more tropical habitats. For example, the armadillo *Paraeuphractus* is closely related to the tropical to subtropical *Euphractus*. The anteaters *Neotamandua* (Myrmecophagidae) and *Paleomyrmidon* (Cyclopidae) suggest the existence of forested environments similar to the present Chaco (Scillato-Yané, 1986). The presence of capybara (Hydrochoeridae) implies permanent bodies of water. The tortoise *Geochelone gallardoi* is thought to have been adapted to forested habitats with higher annual precipitation than those of the present day (Gasparini, 1986).

The presence of wooded areas is concordant with geological evidence that the aridification of the Santa María Basin occurred in the Pliocene (Kleinert and Strecker, 2001), caused by uplift of surrounding orographic ranges and formation of a rain shadow effect within the basin. In summary, paleontological and geological evidence indicates that environmental conditions in the Santa María Basin during the late Miocene were more humid than at present, probably characterized by wet-dry seasonality, which allowed the coexistence of forested and open areas, similar to the

present Chaco or humid savannas. The masticatory complex of *Neosteiromys* suggests that this genus would have been adapted to eat harder and more abrasive food items than those consumed by any living species, a specialization probably related to living in more open areas than tropical or subtropical forests.

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