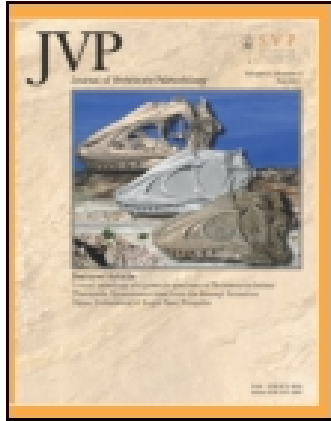


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Lakukullus anatisrostratus, gen. et sp. nov., a new massive nothrotheriid sloth (*Xenarthra*, *Pilosa*) from the middle Miocene of Bolivia

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LAKUKULLUS ANATISROSTRATUS, GEN. ET SP. NOV., A NEW MASSIVE NOTHROTHERIID SLOTH (XENARTHRA, PILOSA) FROM THE MIDDLE MIOCENE OF BOLIVIA

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Xenarthra constitute one of the most representative groups of South American endemic mammals. The armored Cingulata is recorded beginning in the Itaboraian SALMA (lower Eocene; Pujos et al., 2012). Its sister group is Pilosa, which includes Tardi-grada, the sloths, and Vermilingua, the South American anteaters. Sloths appear during the Eocene–Oligocene transition (Tinguirirican SALMA) in Chile, represented by *Pseudoglyptodon* (McKenna et al., 2006). The late Oligocene Deseadan SALMA saw the emergence of Mylodontidae (e.g., *Octodontotherium* and *Orophodon*) and Megalonychidae (e.g., *Deseadognathus*) in Patagonia and the Bolivian altiplano (Pujos et al., 2007). Megatherioidea appear later during the middle Miocene, Megatheriidae in the Santacrucian SALMA (i.e., *Megathericulus*; Pujos et al., 2013), and Nothrotheriidae in the Huayquerian SALMA (i.e., *Mionthropus*; De Iuliis et al., 2011). According to De Iuliis et al. (2011), Nothrotheriidae is supported by 13 unequivocal synapomorphies and includes at least five genera: *Mionthropus*, *Pronothrotherium*, *Thalassocnus*, *Nothrotherium*, and *Nothrotheriops*. Several possible nothrotheriids, generally represented by poor material, have been described from Colombia (*Huilabradys*), Argentina (e.g., *Nothropus*, *Chasicobradys*, *Amphibradys*, and *Xyophorus*), and Bolivia (*Xyophorus* and *Hiskatherium*). Those from Argentina are poorly diagnosed, cannot certainly be differentiated morphologically from other taxa such as *Hapalops*, and are likely invalid. *Nothropus priscus* is exclusive to the Pleistocene of Argentina and is not present in the Amazon (see De Iuliis et al., 2011, for further details).

By its central geographical position in South America, the present territory of Bolivia (Fig. 1) has played an important role in the evolution and diversity of mammals during the Paleogene and Neogene periods (Croft, 2007), although few nothrotheriids have been recorded from this country. St.-André (1996) assigned a dentary and an astragalus to *Xyophorus villarroeli* from the Huayquerian SALMA of Achiri; previously this genus was known from the Santacrucian (Ameghino, 1887, 1891, 1894) and Chasicoan of Argentina with *X. bondesioi* (Scillato-Yané, 1979). A partial skull and mandible of *X. villarroeli* is also recorded from the Laventan SALMA of Quebrada Honda (= *Hapalops angustipalatus* Frailey, 1988; Fig. 3 A–D; see Scillato-Yané and Carlini, 1999, for further details), which also yielded the dentary of the peculiar Megatherioidea *Hiskatherium saintandrei*, recently described by Pujos et al. (2011). Croft et al. (2009) noted the presence of *Xyophorus* cf. *bondesioi* in the Friasian SALMA of Cerdas.

The Laventan SALMA Quebrada Honda vertebrate locality was identified by Hoffstetter (1977). Croft (2007) presented the

most recent list of the vertebrate fauna, which includes the marsupials Didelphimorphia, Paucituberculata, and Sparassodonta, native ungulates Litopterna, Notoungulata, and Astrapotheria, five rodent clades (Dasyproctidae, Eocardiidae, Octodontidae, Echimyidae, and Chinchillidae), and xenarthrans, represented by dasypodids, glyptodontids, and sloths. Three sloths have previously been reported from Quebrada Honda: the nothrotheriid *Xyophorus villarroeli*, the megatherioid *Hiskatherium saintandrei*, and a mylodontid indet. (Takai et al., 1984). Here we describe the fourth sloth, a massive Nothrotheriidae.

Institutional Abbreviations—CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina; FLMNH, Florida Museum of Natural History, Gainesville, U.S.A.; HMS, Harvard Medical School, Boston, U.S.A.; IFEA, Institut Français d'Études Andines, Lima, Peru; MCL, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; MNHN, Muséum national d'Histoire naturelle de Paris, Paris, France; MNHN-Bol-V, Departamento de Paleontología de Vertebrados, Museo Nacional de Historia natural de Bolivia, La Paz, Bolivia; MUSM, Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima, Peru.

Paleontological Abbreviations—c., lower caniniform tooth; HI, hypsodonty index; m., lower molariform tooth; SALMA, South American Land Mammal Age.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

XENARTHRA Cope, 1889

TARDIGRADA Forster in Latham and Davies, 1795

(= PHYLLOPHAGA Owen, 1842)

MEGATHERIOIDEA Gray, 1821

NOTHROTHERIIDAE Gaudin, 1994

NOTHROTHERIINAE Ameghino, 1920

LAKUKULLUS ANATISROSTRATUS, gen. et sp. nov.

(Fig. 2, Table 1)

Holotype—MNHN-Bol-V 006601; nearly complete mandible, right caniniform tooth is broken at the base of the crown and left is missing; condyloid process missing and extremities of angular and coronoid processes incomplete; small parts of ascending ramus and spout have been reconstructed, but the general morphology of the anterior border of the spout is conserved.

Etymology—The generic name from 'Laku'kullu,' 'wild animal of heights' in Aimara, a native Bolivian language, in reference to the locality where the specimen was found. The specific epithet is from the Latin 'anatisrostratum,' 'duck bill' in relation

*Corresponding author.



FIGURE 1. Map showing Bolivian localities where the nothrotheriid sloths *Xyophorus* (e.g., *X. cf. bondesioi* [UAFT V-00871] and *X. villarroeli* [UF 26668]; Fig. 3 C, D) but also *Nothropus*, *Mionothropus*, and *Thalassocnus*. A spout is also present in Megatheriidae such as *Megatherium* (MNHN AYO 101) and *Planops* (FMNH P13148). The spout index (SI) is calculated as the ratio between the maximal spout width and the maximum spout length (measured from the anterior margin of the spout to the posteroventral margin of the mandibular symphysis). Using this method, the SI for *Lakukullus* is 0.76 (Table 1), higher than in *Nothrotherium maquinense* (SI = 0.49) and *Thalassocnus natans* (SI = 0.33). The SI could not be calculated in *Pronothrotherium*, *Mionothropus*, and *Nothropus* because the spout is broken. In occlusal view, the lateral margins of the spout are wide and flat, and rougher than in other nothrotheriid sloths. In medial view, the spout is concave transversely, convex anteroposteriorly, and exhibits a pair of foramina located 15 mm anterior to the alveoli of the caniniform tooth and 12 mm lingual to the lateral margin of the mandible (Fig. 2B, E). In Tardigrada, the mandibular canal ends anterolaterally with the external mental foramina of the mandibular canal. This foramen located on either side of the symphysis is not common in Xenarthra. They are also present in the specimen of *Xyophorus* from Cerdas (UAFT V-000871; F.P., pers. observ.; but not visible in the specimen figured by Croft et al., 2009:fig. 5 A, B) and correspond to the anterior internal openings of the mandibular canal (Fig. 2E). In ventral view, the spout is furrowed posterior to its anterior margin. On each anterior side of the mandible is a large and circular external opening of the mandibular canal, located 12 mm anterior to the anterior border of the c. alveoli, aligned with the anteroposterior axis of the lateral margin of the tooth row.

to the aspect of the spout of this sloth, which is reminiscent of the spatulate bill of an aquatic bird.

Original Determinations—cf. *Hapalops* sp. (MNHN-Bol database).

Collector—Roberto Fajardo (HMS; October 28, 1995).

Type Locality and Age—Quebrada Honda (Hoyadito, level 2; Fig. 1), unnamed formation, Department of Tarija, Bolivia; middle Miocene–Laventan SALMA (see Croft, 2007, and Pujos et al., 2011, for further details).

Diagnosis—Large Nothrotheriidae similar in size to *Thalassocnus*; spout extremely broad in occlusal view, and its lateral margins are wide, flat, and rough, in contrast to the narrower spout of other nothrotheriids; spout index of 0.76 (higher than in *Nothrotherium* and *Thalassocnus*); presence of anterior internal mental foramen on either side of the symphysis (anterior internal openings of the mandibular canal are also present in *Xyophorus*); hypsodonty index of 0.80 (similar to *Mionothropus*); lower caniniform oval, small, anterodorsally oriented as in *Xyophorus*, and strongly compressed anteroposteriorly, much more than in other megatherioid taxa, m3 less compressed than m1 and m2, and lophids extend anterolabially to posterolingually.

Description—The mandible MNHN-Bol-V 006601 from Quebrada Honda corresponds to a large-sized middle Miocene nothrotheriid sloth, much larger than *Xyophorus villarroeli* and *Hiskatherium saintandrei* from the same Bolivian locality (Frailey, 1988; Fig. 3 A–D; Pujos et al., 2011; Fig. 3E, F), and as large as *Thalassocnus natans* MUSM 228 (Muizon et al., 2003) and *Mionothropus cartellei* (De Iuliis et al., 2011). Its general appearance is massive with a shovel-shaped spout. Its small caniniforms and three rectangular molariform teeth with lingual and labial apicobasal sulci on m1 and m2 are typical of Nothrotheriidae (De Iuliis et al., 2011). Small portions of the spout of the holotype are reconstructed, but this does not affect the general aspect of the anterior extremity of the mandible (Fig. 2). The right caniniform tooth is broken at the base of the crown, the left is missing, and labiolingual portions of m3 are missing, as well as

the condyloid process and the extremities of the coronoid and angular processes.

In dorsal view, the spout of the mandible is large and shovel-shaped (Fig. 2B, E), reminiscent of that of some mylodontid such as *Simomyiodon*. In other Nothrotheriidae, the spout is as long but narrower, as in Bolivian specimens referred to *Xyophorus* (e.g., *X. cf. bondesioi* [UAFT V-00871] and *X. villarroeli* [UF 26668]; Fig. 3 C, D) but also *Nothropus*, *Mionothropus*, and *Thalassocnus*. A spout is also present in Megatheriidae such as *Megatherium* (MNHN AYO 101) and *Planops* (FMNH P13148). The spout index (SI) is calculated as the ratio between the maximal spout width and the maximum spout length (measured from the anterior margin of the spout to the posteroventral margin of the mandibular symphysis). Using this method, the SI for *Lakukullus* is 0.76 (Table 1), higher than in *Nothrotherium maquinense* (SI = 0.49) and *Thalassocnus natans* (SI = 0.33). The SI could not be calculated in *Pronothrotherium*, *Mionothropus*, and *Nothropus* because the spout is broken. In occlusal view, the lateral margins of the spout are wide and flat, and rougher than in other nothrotheriid sloths. In medial view, the spout is concave transversely, convex anteroposteriorly, and exhibits a pair of foramina located 15 mm anterior to the alveoli of the caniniform tooth and 12 mm lingual to the lateral margin of the mandible (Fig. 2B, E). In Tardigrada, the mandibular canal ends anterolaterally with the external mental foramina of the mandibular canal. This foramen located on either side of the symphysis is not common in Xenarthra. They are also present in the specimen of *Xyophorus* from Cerdas (UAFT V-000871; F.P., pers. observ.; but not visible in the specimen figured by Croft et al., 2009:fig. 5 A, B) and correspond to the anterior internal openings of the mandibular canal (Fig. 2E). In ventral view, the spout is furrowed posterior to its anterior margin. On each anterior side of the mandible is a large and circular external opening of the mandibular canal, located 12 mm anterior to the anterior border of the c. alveoli, aligned with the anteroposterior axis of the lateral margin of the tooth row.

The horizontal ramus is robust, convex labially in anterior view (Fig. 2G), and widest posteriorly to m2. Its ventral margin is nearly horizontal, as in *Mionothropus* and *Xyophorus* (UAFT V-000871). A deep anteroposterior groove borders the tooth row labially and extends posteriorly to the c. (Fig. 2 A–C, E). The buccinator fossa is well marked in Megalonychidae and

Mylodontidae. This fossa is deep in *Lakukullus*, very shallow in *Hiskatherium* and *Mionothropus*, and very deep in *Xyophorus*, particularly in MNHN-Bol-V 009867 from Quebrada Honda referred to *X. villarroeli* (Fig. 3D, E). The posterior external opening for the mandibular canal is oval and wide, and opens anterolaterodorsally as in *Hiskatherium*.

The angular process presents the same general appearance as in other Nothrotheriidae, although its distal extremity is longer and more pointed in *Thalassocnus*, *Mionothropus*, and *Xyophorus* (UAFT V-000871) than in *Lakukullus*. The angular process is entirely ventral to the tooth row, as in other Nothrotheriidae. The condyloid process is missing, but its base is preserved, which indicates that the condyle was well dorsal to the tooth row, as in all nothrotheriids. The posterior border between the angular and condyloid processes is concave rather than vertical in the direction toward the condyle, as in strongly hypsodont sloths such as the megatheriid *Megatherium* and *Planops* and in contrast with poorly hypsodont forms such as *Pronothrotherium*. In lateral view, the angle between horizontal ramus and the anterior margin of the ascending ramus is approximately 115° (Fig. 2A, C, F), as in *Xyophorus* and *Nothrotheriops*. The angle is smaller in *Thalassocnus natans* (105°) and larger in *Mionothropus cartellei* (125°). The lateral surface of the ascending ramus bears a large masseteric fossa onto which the temporalis muscle inserts dorsally and the deeper parts of the masseter muscle insert ventrally. The dorsolateral surface of the angular process bears the insertion of the muscle masseter pars superficialis. The internal surface of the angular process is deeply concave and served for the insertion of the muscle pterygoid medius (Fig. 2H). The posterior internal opening of the mandibular canal, poorly preserved, lies at the height of the middle of the crown of m3 (Fig. 2B, E, H). A deep and thin sulcus (2.0 × 24.0 mm), possibly for the passage of an artery, extends anteroventrally from the base of the condyloid process to the center of the angular process on the medial surface (Fig. 2H). This sulcus has not been reported in any other sloth.

The lower dentition of *Lakukullus* comprises a caniniform and three molariform teeth, which is considered as the plesiomorphic dental formula for sloths (Pujos et al., 2012). This new middle Miocene nothrotheriid sloth is strongly hypsodont, with a hypsodonty index (HI) of 0.80, calculated according to the method used by Bargo et al. (2006) and applied to most megatherioid genera by Pujos et al. (2011). The HI of *Lakukullus* is slightly lower than that of *Mionothropus* and higher than that of all other Nothrotheriidae with the same dental formula (e.g., *Nothropus* and *Pronothrotherium*). The HI of *Hiskatherium* with four lower molariform teeth (also present in *Diabolootherium* for the Quaternary of Peru; Pujos et al., 2007) is higher (0.93).

The form of the alveolar portion of right caniniform indicates that it is reduced, with long axis mesiodistal and anterodorsally inclined (Fig. 2D, E), as in *Xyophorus* but slightly bigger than in *Xyophorus*, *Mionothropus*, and *Nothropus*. In other nothrotheriids (i.e., *Thalassocnus*, *Nothrotheriops*, and *Nothrotherium*), c. is lost. In occlusal view, c. of *Lakukullus* is separated to the m1 by a long diastema (9.0 mm) and positioned labially, in contrast to the condition in other nothrotheriids and the megatherioid *Planops martini*. A similar diastema is present in *Xyophorus*, *Hapalops*, and *Mionothropus*; it is slightly larger in *Pronothrotherium* and shorter in *Huilabradys*.

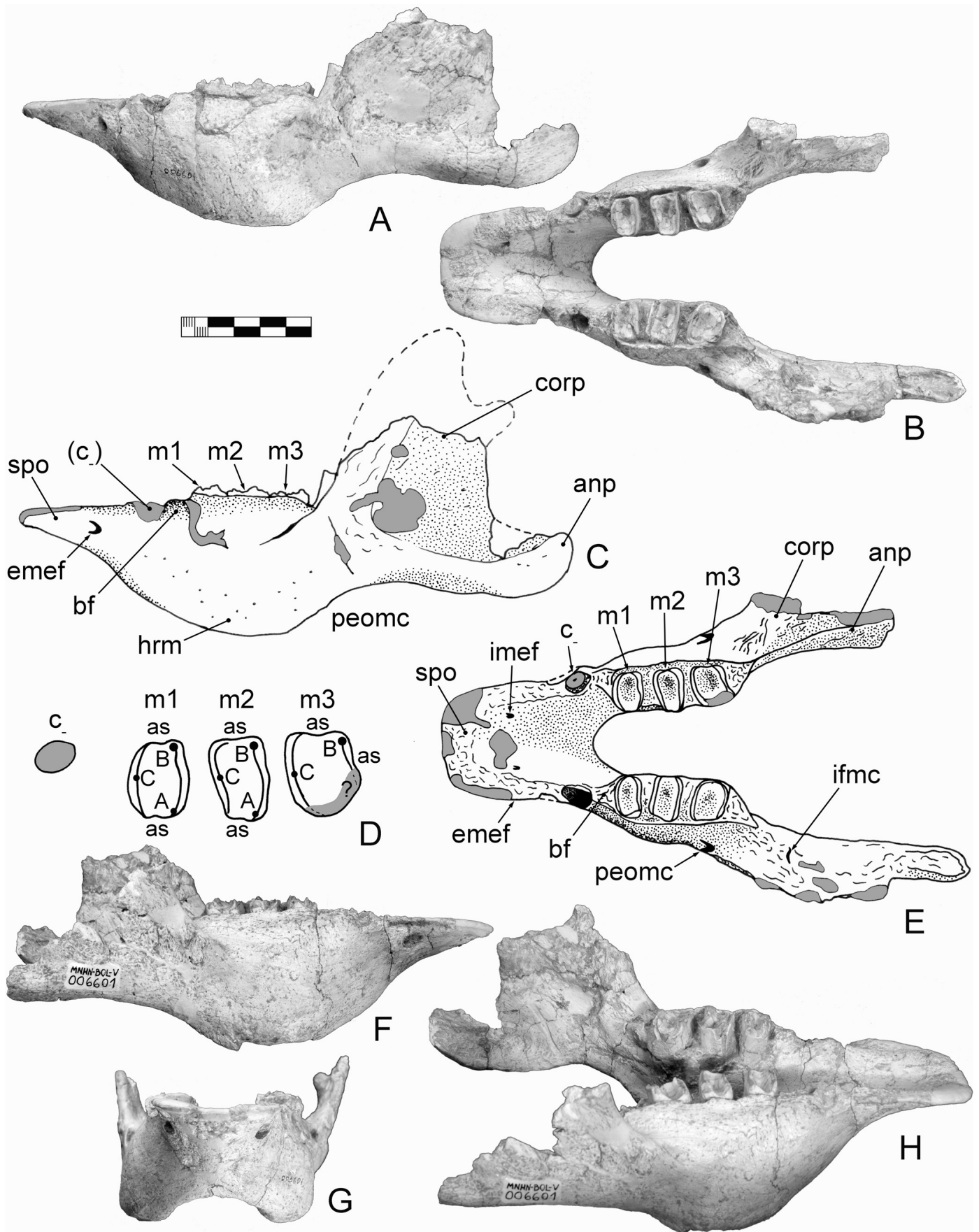
The three molariforms (m1–m3) of *Lakukullus* have a similar general morphology, with a mesial and distal lophid separated by a labially open transverse valley. Cusp C (following the terminology of Bargo et al., 2009; see also Pujos et al., 2011) is located at the center of the mesial lophid and cuspids B (distolabial) and A (distolingual) at the extremities of the distal lophid (Fig. 2D). The crown of the m3 is incomplete, so cusp A is not observable. The molariforms of Nothrotheriidae exhibit lingual and labial apicobasal sulci. Unlike other nothrotheriid genera,

m3 of *Lakukullus* lacks a lingual sulcus, but its distal surface bears a sulcus. The m1 and m2 are rectangular, anteroposteriorly compressed (Fig. 2B, D, E). The mesial lophid of m1 is convex mesially and the distal lophid slightly convex distally. The lophids of m2 are rectilinear and converge slightly labially. The transverse axis of m1–m2 is nearly perpendicular to the anteroposterior axis of the tooth row, but that of m3 is oriented mesiolabially to linguodistally, so that m3 gives the appearance of having rotated counterclockwise. The general appearance of these three molariform teeth looks like most Nothrotheriidae, such as *Thalassocnus*, *Mionothropus*, *Pronothrotherium*, and *Xyophorus*. However, in *Lakukullus*, the anteroposterior compression of m1 and m2 is more important than in other megatherioid taxa, including *Xyophorus villarroeli* and *Hiskatherium saintandrei*, from the same locality in Bolivia.

DISCUSSION AND CONCLUSION

Lakukullus anatisrostratus, gen. et sp. nov., is a nothrotheriid sloth based on the presence of a small caniniform separated by a diastema from the first molariform and three quadrangular or rectangular molariforms bearing two transverse lophids and usually lingual and labial apicobasal sulci (De Iuliis et al., 2011). The dentition of *Lakukullus* resembles that of *Huilabradys* in general form, the former genus differs considerably in other respects from the type of the latter. In contrast to other nothrotheriids, the m3 of *Lakukullus* bears labial and distal apicobasal sulci. The presence of a distal sulcus is autapomorphic in this genus. Most notable is the presence of wide and spatulate symphyseal spout (SI = 0.76). The spout in other nothrotheriids is considerably narrower, as exhibited, for example, in *Thalassocnus* (see Muizon et al., 2004) and *Mionothropus* (De Iuliis et al., 2011). The presence of a wide spatulate spout is typical of Mylodontinae and is accompanied by a lateral displacement of the most anterior caniniform tooth but also an increase in the size of the most anterior tooth. An uncommon feature of *Lakukullus* is the presence of an anterior internal mental foramen on each side of the symphysis, apertures that correspond to anterior internal openings of the mandibular canal. This character is also present in *Xyophorus*. The lower dentition of *Lakukullus* includes a reduced c. moved laterally, in relation to the enlargement of the spout, and separated to the molariforms by a diastema. In the megalonychid *Eucholoeps*, the spout is narrow but the c. is large and laterally displaced. The occlusal morphology of the molariforms resembles that of the megalonychid *Eucholoeps* (Bargo et al., 2009), suggesting that an orthal component was also predominant in *Lakukullus* during mastication. The prominent insertion areas on the ascending ramus and angular process suggest a powerful masticatory musculature. The combination of a wide symphysis, a reduced caniniform, molariform teeth that favor orthal mastication, and a strong musculature suggest that *Lakukullus* was a leaf eater, as suggested by Bargo et al. (2009) for most Miocene megatherioids or at least an indiscriminant feeder compared with other nothrotheres with a narrow spout that may have been able to more selective feeders. The existence of *Lakukullus* in the Laventan SALMA of southern Bolivia increases the paleobiodiversity of Nothrotheriidae during the Miocene in Central South America.

The vertebrate locality of Quebrada Honda is essential for reconstructing the paleomammalian fauna during the Miocene of South America and correlating the austral Patagonian faunas to tropical vertebrate association such as that of La Venta in Colombia. Frailey (1988) noted the first record of Tardigrada in this locality, assigning remains (FLMNH 26668) to the Patagonian megatherioid *Hapalops angustipalatus*. However, reconsideration of the systematic status of these remains by



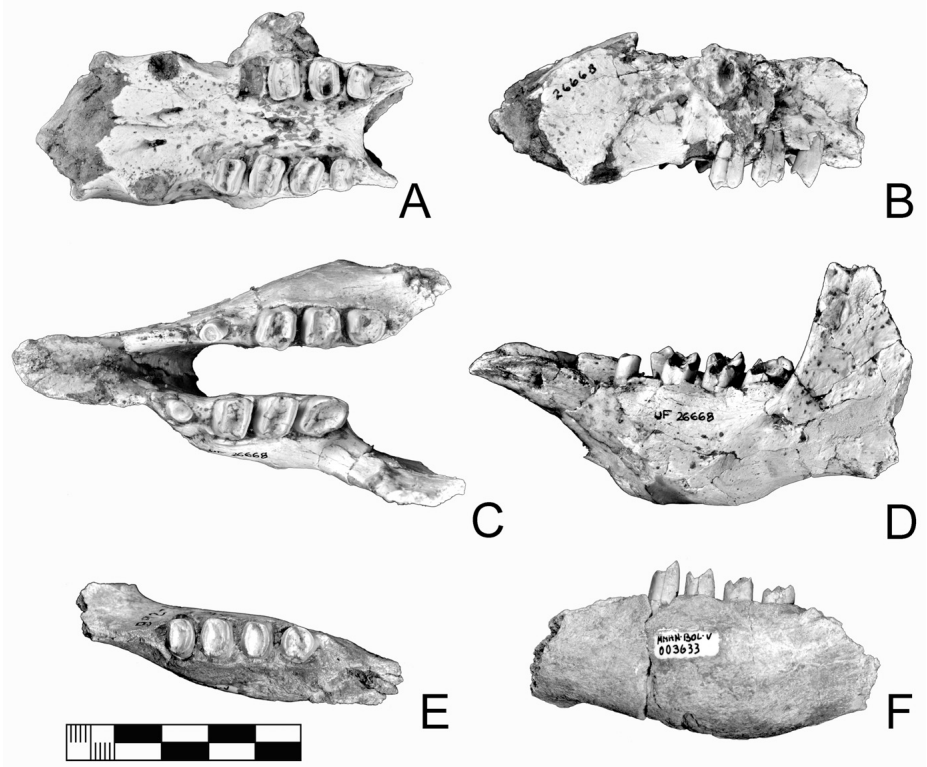


FIGURE 3. Photographs in occlusal (A, C, and E) and left lateral (B, D, and F) views of the anterior portion of the rostrum and mandible of *Xyophorus villarroeli* (FLMNH 26668; A–D) and left dentary of *Hiskatherium villarroeli* (MNHN-Bol-V 003633; E, F) from Quebrada Honda (Frailey, 1988; Pujos et al., 2011). Scale bar equals 50 mm.

Scillato-Yané and Carlini (1999) and Pujos et al. (2011) resulted in reassignment to *Xyophorus villarroeli*, which had been described by St.-André (1996) in the Huayquerian Bolivian locality of Achiri. Pujos et al. (2011) described a second megatherioid from Quebrada Honda, *Hiskatherium saintandrei*, which is characterized among other features by four lower molariform teeth, a derived dental formula also present in *Diabolotherium nordenskiöldi*, a Megatherioidea of uncertain affinities from the Lujanian SALMA of Peru and Chile (Pujos et al., 2007). Material collected in Quebrada Honda and housed in MNHN of La Paz include a large quantity of cranial and postcranial remains belonging to Megatherioidea (more than 30 specimens under study by Pujos and colleagues) and confirms the presence of Mylodontidae previously mentioned by Takai et al. (1984). Nothrotheriidae are present in Bolivia beginning at the base of the middle Miocene through *Xyophorus* cf. *bondesioi* in the Friasian SALMA of Cerdas (Croft et al., 2009); they are then recorded from the Laventan SALMA of Quebrada Honda (*X. villarroeli* and *Lakukullus anatisrostratus*). *Xyophorus* appears during the early Miocene Santacrucian SALMA of Patagonia and is recorded from the Friasian and Colloncuran SALMAS in Bolivia (Cerdas) and Argentina (Brandoni, 2013), respectively.

As with most native South American mammals, nothrotheriid sloths appear earlier in the south of the continent before populating regions farther north. The diversity of sloths in Quebrada

TABLE 1. Measurements (in mm) of *Lakukullus anatisrostratus*, sp. nov., from the middle Miocene of Quebrada Honda.

Holotype—MNHN-Bol-V 006422	
Diameters of c. (MD × LL)	8.1 × 6.0
Diameters of m1 (MD × LL)	10.3 × 14.3
Diameters of m2 (MD × LL)	10.2 × 15.5
Diameters of m3 (MD × LL)	13 × ~16
Length of the tooth row (from mesial margin of the c. to labial margin of the m3)	60
Length of the molariform series (m1–m3)	42.3
Maximum height of the ramus (at m2)	48.2
Maximum width of the ramus (at m2)	25
Transversal diameter between the labial surfaces of the m1	52.3
Maximal length of the dentary (from the anterior margin of the spout to the posterior margin of the angular process)	200
Maximum width of the spout	5.5
Maximum length of the spout (from the anterior margin of the spout to the posteroventral margin of the mandibular symphysis)	7.2
Hypsodonty index (HI = 48.2/60)	0.80
Spout index (SI = 5.5/7.2)	0.76

Abbreviations: LL, labiolingual; MD, mesiodistal (or transverse).

← FIGURE 2. Photographs and drawings of *Lakukullus anatisrostratus*, gen. et sp. nov. (MNHN-Bol-V 006601), in lateral (A, C, and F), occlusal (B, E), anterior (G), and dorsolateral (H) views, as well as an enlargement (×2) of the teeth in occlusal view to appreciate the dental cusps and lopheids (D). **Abbreviations:** A, cuspid A (distolingual); **anp**, angular process; **as**, apicobasal sulcus; B, cuspid B (distolabial); **bf**, buccinator fossa; C, cuspid C (mesial); **c.**, lower caniniform tooth; **corp**, coronoid process; **emef**, external mental foramina; **hrm**, horizontal ramus; **ifmc**, internal foramen of the mandibular canal; **imf**, internal mental foramina; **m1–m3**, three lower molariform teeth; **peomc**, posterior external opening of the mandibular canal; **spo**, spout. Scale bar equals 50 mm.

Honda is somewhat unexpected, given that, except in Santacrucian SALMA of Argentinean Patagonia (Bargo et al., 2012), it is uncommon to find together in a single locality four genera belonging to at least two main sloth clades and three small- to medium-sized sloths that might have competed in similar ecological niches.

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