



The presence of an atavistic caniniform alveolus in *Nothrotherium maquinense* (Xenarthra, Folivora, Nothrotheriidae)

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Received: 8 January 2026 / Accepted: 24 April 2026
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Abstract

Sloths (Folivora) display remarkable morphological diversity yet share a highly conserved dental formula, whose occasional deviations offer key insights into their evolutionary history. Among nothrotheriids, Neogene species retained upper and lower caniniforms, whereas these teeth were lost in Pleistocene genera. Here we describe, for the first time, a poorly developed alveolus interpreted as an atavistic upper caniniform alveolus in an individual of *Nothrotherium maquinense* from the Late Pleistocene of Bahia, Brazil. Computed tomography and X-ray imaging confirm its internal anatomy and rule out taphonomic or pathological origins. The alveolus occupies the precise position of the caniniform in Neogene nothrotheriids and exhibits similar morphology, suggesting a partial re-expression of a lost ancestral trait. Beyond its developmental implications, this observation may offer additional context for interpreting the taxonomy of *Nothropus*, traditionally defined based on the presence of a lower caniniform alveolus. The occurrence of similar atavistic structures in related taxa indicates that this feature alone may be insufficient for diagnosis and warrants reevaluation within a broader evolutionary framework.

Keywords Atavism · Morphology · *Nothropus* · Sloths · Teeth

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Introduction

Folivora (sloths) comprises one of the most iconic groups of placental mammals, being a fundamental component of the Cenozoic South American native fauna (Patterson and Pascual 1968; Gaudin and Croft 2015). It is the sister group of Vermilingua (anteaters), and together they form Pilosa, which in turn is the sister group of Cingulata, the clade that includes armadillos, pampatheres, and glyptodonts. These groups collectively comprise Xenarthra, one of the major clades of Placentalia (Gibb et al. 2016; Foley et al. 2023). According to the most recent phylogenetic inferences, including both morphological and molecular data, Folivora consists of three main clades: Megalocnoidea, the Antillean sloths; Mylodontoidea, including Choloepodidae, Scelidotheriidae, and Mylodontidae; and Megatherioidea, encompassing Bradypodidae, Megalonychidae, Megatheriidae, Nothrotheriidae, and a few other taxa—mostly from the Santacrucian South America Land Mammal Age (SALMA), Early Miocene—whose relationships with megatherioid clades remain uncertain (Tejada et al. 2024; Boscaini et al. 2025).

Sloths were much more diverse in the past, with their fossil record encompassing about a hundred genera (McKenna and Bell 1997, and numerous described subsequently). They underwent several episodes of extinctions throughout the Cenozoic (McDonald and De Iuliis 2008; Varela et al. 2019), with the most drastic being the Late Pleistocene megafaunal extinction, which nearly decimated them, leaving only the two extant genera, *Bradypus* Linnaeus, 1758 and *Choloepus* Illiger, 1811 (McDonald and De Iuliis 2008; Boscaini et al. 2025).

Sloths are also known for exhibiting considerable ecomorphological diversity, expressed in their broad range of body sizes, substrate preferences, and substrate uses (Toledo et al. 2017; Boscaini et al. 2025). As for dietary adaptations, sloths are slightly more homogeneous, with most taxa being strictly herbivorous, or nearly so. A range of dietary modes can be recognized, from strict browsers to strict grazers, including various degrees of mixed feeding (Bargo et al. 2006; Dantas et al. 2023). However, the inclusion of hard food items such as roots, tubers, fruits, or seeds by some Antillean sloths and *Megalonyx jeffersonii* (Desmarest, 1822) is supported by the functional analysis of the mandible and dentition (Varela et al. 2023b), and isotope data have also been interpreted as indicating some degree of meat consumption in *Myiodon darwini* Owen, 1840 (Tejada et al. 2021).

In sloths, the first upper and lower teeth are usually referred to as caniniforms (Cf/cf, respectively; Pujos et al. 2012), although this is merely an interpretation of function and they are not homologous to true canines in other placental mammals. Moreover, Cf/cf teeth vary in morphology, and can assume either a truly caniniform, a molariform, or an incisiform shape (Gaudin 2004). The remaining upper and lower teeth are usually referred to as molariforms (Mf/mf; respectively, Pujos et al. 2012). Even though the homology of individual teeth across taxa can be contentious, particularly that of the Cf (Hautier et al. 2016; Tejada et al. 2024), the ancestral sloth dental formula was inferred as comprising five upper and four lower teeth (i.e., 5/4), a condition retained in nearly all sloths throughout their evolutionary history (Hautier et al. 2016; Delsuc et al. 2019).

Notwithstanding, some deviations of this ancestral dental formula also evolved in sloths. In the oldest purported sloth genus, *Pseudoglyptodon* Engelmann, 1987, the last Mf is absent, whereas in *Myiodon darwini* Owen, 1840, and in some specimens of *Paramyiodon harlani* (Owen, 1840), the Cf is absent, leading to two different instances of a 4/4 dental formula (Casali et al. 2022). In other taxa, both Cf and cf. are missing, thus resulting in a 4/3 dental formula. This condition is observed in

the mylodontoid *Octomyiodon robertoscagliai* Scillato-Yané, 1977, in the megatheriid (or nothrotheriid) genus *Thalassocnus* McDonald & Muizon, 2002, and in at least some Pleistocene representatives of Nothrotheriidae.

Nothrotheriidae presents one of the most intriguing patterns of dental formula variation, with Neogene taxa (e.g., *Pronothrotherium typicum* Ameghino, 1907, *Mionthropus cartellei* De Iuliis et al., 2011, *McDonaldocnus bondesioi* (Scillato-Yané, 1979), *Lakukullus anatisrostratus* Pujos et al., 2014) having caniniform teeth, which are separate from the molariforms by a well-developed diastema, whereas the Cf/cf are absent in the Pleistocene genera *Nothrotherium* Lydekker, 1889 and *Nothrotheriops* Hoffstetter, 1955. In *Nothropus* Burmeister, 1882, a third and more contentious Pleistocene genus, mandibles exhibit cf. alveoli, purportedly vestigial (Quiñones et al. 2017). In addition to that, a well-developed Cf was observed in the maxilla of a juvenile specimen of *Nothrotheriops texanus* (Sinclair, 1905), which represents an instance of atavism (McDonald 1995). Unlike vestigiality, which corresponds to the persistence of a functionless remnant of a trait that no longer serves the biological role it once fulfilled in ancestral forms, atavism represents the rare recurrence of a trait in some individuals of a population after its loss for many generations within a given evolutionary lineage (Dhawan et al. 2023).

Because they are related to development, the study of atavistic and vestigial structures is vital to elucidating the origin and biological function of traits that have been lost during the evolutionary history of a group. For instance, investigations into the developmental origin of the human appendix—formerly considered useless—have revealed its role as an important immune organ (Dhawan et al. 2023). Other well-documented examples of atavisms across vertebrates include the presence of hindlimbs in whales and teeth in birds (Bejder and Hall 2002; Abouheif et al. 2013). Furthermore, a better understanding of these traits has important phylogenetic implications and may help to avoid misinterpretations of ontogenetic anomalies that could otherwise be mistaken for synapomorphies or novel characters.

Accordingly, the present study aims to report the occurrence of a poorly developed atavistic caniniform alveolus in the nothrotheriid *Nothrotherium maquinense* (Lund, 1839). This specimen, recovered in Gruta dos Brejões, Morro do Chapéu, Bahia, Brazil (Fig. 1), represents the first evidence of this morphology in this species, adds to our understanding of the dental evolution in Nothrotheriidae, and provides insights into the taxonomic validity of the genus *Nothropus*.

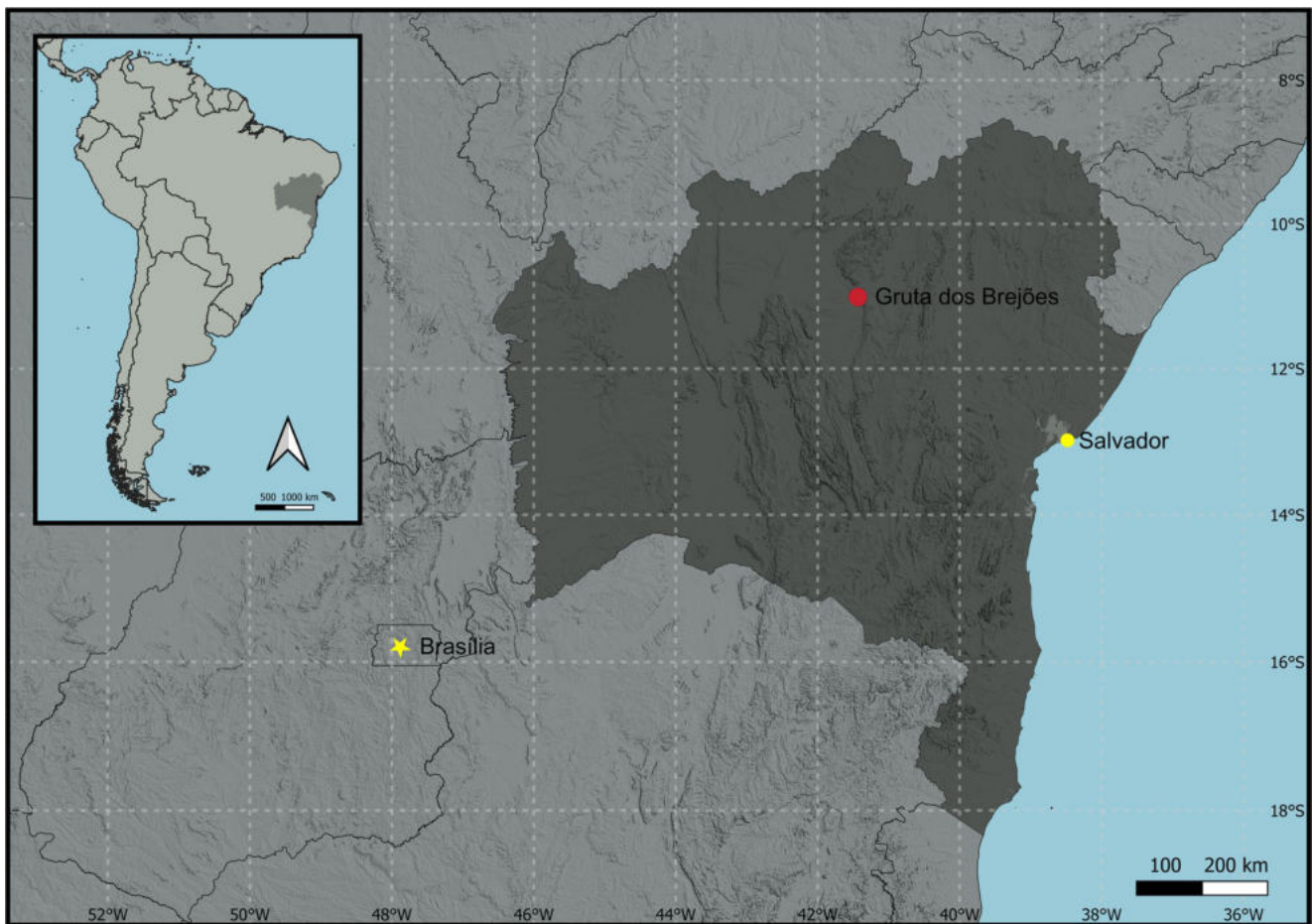


Fig. 1 Map indicating the locality where the fossil specimen of *Nothrotherium maquinense* (MCL 1021) was collected, marked by a red dot (Gruta dos Brejões, Morro do Chapéu, Bahia, Brazil). The state of Bahia is shown in dark grey. Black lines in the inset map on the left

indicate country borders, whereas those in the larger map indicate Brazilian state borders. For reference, Salvador (capital of Bahia) is indicated by a yellow dot, and Brasília (capital of Brazil) by a yellow star

Materials and methods

In addition to digital photographs, cranial images of the anterior fragment of the specimen were obtained using a portable X-ray machine (Poskom, Seoul, South Korea). The images were taken using the ventrodorsal, dorsoventral, laterolateral, anteroposterior, and oblique views, with parameters of 60 kV and 0.8 mAs. The Focus Detectors (Carestream Health, NY, USA) were used, measuring 35 × 43 cm.

In order to complement and compare the images obtained by X-ray, we used 3D Computed Tomography (CT) images of the partial skull. Cranial images were obtained by a single experienced operator, trained by a radiologist. The cone-beam computed tomography (CBCT) images were acquired using the Carestream[®] 9600 machine (Carestream Health, NY, USA), with parameters of 140 kHz, 95 kV, 4 mA, an exposure time of 40 s, a voxel size of 150 μm, and a field of view (FOV) of 8 cm x 8 cm. All images were converted to DICOM format (Digital Imaging and Communication in

Medicine) and processed using Carestream[®] CS 3D Imaging software. The fossil was positioned in the perpendicular median sagittal plane during the procedure.

For comparisons, additional fossil materials were studied—*Nothrotherium maquinense*: MCL 1020 and MCL 2825; *Nothrotheriops texanus*: UF 83700; *Pronothrotherium typicum*: MACN-Pv 8141. Comparisons with *Nothropus* were based on literature illustrations (Quiñones et al. 2017). Other sources were consulted for comparison of the Cf alveolus or the maxillary morphology in Nothrotheriidae (Reinhardt 1878; Stock 1925; Lull 1929; Paula Couto 1959; 1971; De Iuliis et al. 2011; Pujos et al. 2014; Gaudin et al. 2020; Pujos et al. 2023).

Institutional abbreviations: MACN-Pv, Colección Paleovertebrados, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; MCL, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; MNHN-Bol-V, Departamento de Paleontología de Vertebrados,

Museo Nacional de Historia Natural de Bolivia, La Paz, Bolivia; UF, University of Florida, Florida Museum of Natural History, Gainesville, USA.

Systematic Paleontology

Superorder Xenarthra Cope, 1889
 Order Pilosa Flower, 1883
 Suborder Folivora Delsuc, Catzefflis, Stanhope, and Douzery, 2001
 Superfamily Megatherioidea Cabrera, 1929
 Family Nothrotheriidae Ameghino, 1820

Genus *Nothrotherium* Lydekker, 1889

Type species: *Nothrotherium maquinense* (Lund, 1839)

Temporal and geographic occurrence: Middle to Late Pleistocene (Bonaerian–Lujanian SALMAs) of Argentina, Brazil, and Uruguay (Auller et al. 2006; Brandoni and Vezosi 2019).

Nothrotherium maquinense (Lund, 1839)

Referred material: MCL 1021, two skull fragments of a subadult individual. The first (MCL 1021/01), consists of most of the skull vault, preserving nearly complete frontal and parietal bones, a small part of the right pterygoid, most of the right squamosal and mastoid (including the petrosal bone), and the right occipital condyle associated with a small portion of the exoccipital (Fig. 2). The second fragment (MCL 1021/02) corresponds to the anterior part of the skull, which retains most of the palate and dentition. The lateral and dorsal walls of the snout are largely missing, except for part of the lateral exposure of the right maxilla (Fig. 3).

Locality and age: Gruta dos Brejões, Morro do Chapéu, Bahia, Brazil (Fig. 1). The material is likely from a Late Pleistocene age. Although a direct radiocarbon date of this specimen is currently unavailable, a coprolite attributed to *Nothrotherium maquinense* from the same locality was dated as Late Pleistocene (Auller et al. 2006).

Description

The preserved portion of the cranial vault indicates an elongate, subcylindrical skull, as is typical of Pleistocene nothrotheriids (Paula Couto 1971). In dorsal view (Fig. 2a), the interfrontal, interparietal, and frontoparietal sutures are not fully fused, indicating that the specimen represents a subadult individual. In this view, the frontal bones are almost entirely preserved, lacking only their anteriormost portions.

The postorbital processes of the frontals are weakly developed, as in MCL 1020/01. Still in dorsal view, the frontal region appears markedly tubular, whereas the skull becomes more globose posteriorly, expanding laterally at the level of the parietals. The right parietal is nearly complete, missing only the posteromedial portion, whereas the entire posterior region of the left parietal is absent. The base of the right zygomatic process of the squamosal is preserved and indicates that this process was not laterally expanded and was most likely anteriorly directed, as in MCL 1020/01—a synapomorphy of nothrotheriids (Gaudin 2004; Casali et al. 2022).

In ventral view (Fig. 2b, e), the basicranium and most of the auditory region are not preserved, with the exception of, on the right side, part of the pterygoid, the mastoid region (including the petrosal), and the tympanohyal, which forms the anterior portion of an anteroposteriorly elongate stylohyal fossa. The stylomastoid foramen and canal can also be discerned lateral to it. In the squamosal, posterior to the base of the zygomatic process, a partially preserved lateral bulge is indicated, which accommodated the epitympanic sinus. This bulge is also observed in other specimens of *Nothrotherium maquinense* (e.g., MCL 1020/01), in *Nothrotheriops* spp., and in *Pronothrotherium typicum*, but is absent in *Mionothropus cartellei* (De Iuliis et al. 2011). In the frontal region, given the incomplete preservation of the basicranium, the trabecular structure associated with the frontal sinus, part of the vomer, and the internal wall of the cranial vault are exposed. The preserved portion of the pterygoid likely corresponds to the lateral wall of the inflated pterygoid sinus, as seen in MCL 1020/01, but its poor preservation does not allow any further description. In this view, the occipital condyle is anteromedially directed, exhibiting a rounded lateral margin and a nearly straight medial outline.

In lateral view (Fig. 2c–d), it can be seen that the ventral and anterior parts of the frontal are not preserved. The frontals are dorsally and laterally flat, and supraorbital foramina (=foramina for the frontal diploic vein) are present on both sides of the skull. The nearly continuous suture with the lateral portion of the parietal and with the squamosal is posterodorsally oriented. In contrast to the frontal, the parietal region is globose, rendering the posterior portion of the skull higher at the anterior part of the parietal, as in MCL 1020/20. Posterior to that, the parietal strongly descends posteriorly, resulting in a condition in which it would have been much higher than the supraoccipital (not preserved), a character used to differentiate *Nothrotherium* and *Nothrotheriops* (Paula Couto 1971).

In right lateral view (Fig. 2c), the partially preserved squamosal is broad, as in MCL 1020/10 and MCL 2825. The anterior portion of the zygomatic process and most of the bulge for the epitympanic sinus are missing. Dorsal to

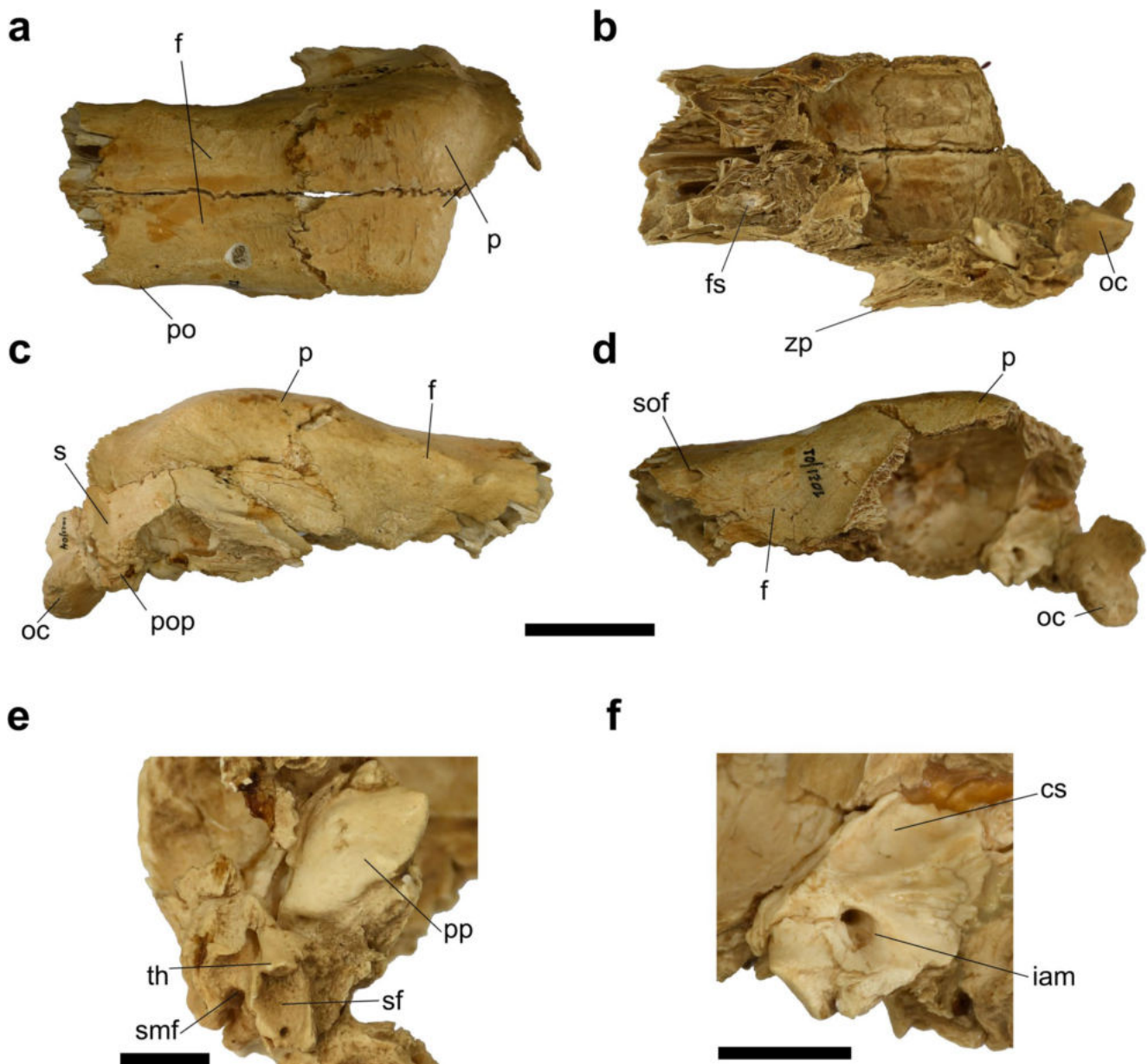


Fig. 2 Posterior fragment of the skull of *Nothrotherium maquinense* (MCL 1021/01) in dorsal (**a**), ventral (**b**), right lateral (**c**), and left lateral (**d**) views; close-up of the right ear region in ventral (**e**) and medial (**f**) views. Scale bars equal 3 cm in **a-d**, and 1 cm in **e-f**. Abbreviations: **cs**, cerebellar surface; **f**, frontal; **fs**, frontal sinus; **iam**, internal acoustic

meatus; **oc**, occipital condyle; **p**, parietal; **po**, postorbital process of frontal; **pop**, paroccipital process; **pp**, promontorium of the petrosal; **s**, squamosal; **sf**, stylohyal fossa; **smf**, stylomastoid foramen; **sof**, supra-orbital foramen of frontal; **th**, tympanohyal; **zp**, zygomatic process of the squamosal

the base of the zygomatic process, the bone is perforated by several nutrient foramina. Ventrally, the squamosal contacts the preserved portion of the pterygoid; anterodorsally, it contacts the frontal; posterodorsally, the parietal; and posteriorly, it is fused to the mastoid, forming a rugose paroccipital process ventrally. Posterior to this region, the right occipital condyle is projected posteroventrally, showing an oval outline. Dorsal to it there is a small plate of the exoccipital that formed the dorsal margin of the foramen magnum. In left lateral view (Fig. 2d, f), the squamosal is

not preserved, allowing observation of the medial surface of the petrosal, in which the opening of the internal acoustic meatus is evident. Dorsal to it, lies a broad cerebellar surface.

The anterior portion of the skull of the studied specimen (MCL 1021/02) preserves most of the palate, which is strongly rugose and perforated, as in all sloths (Gaudin 2004; Casali et al. 2022). In ventral view (Fig. 3a), the anterior part of the palate is poorly preserved, although the sulci associated with the paired anterior palatal foramina can still

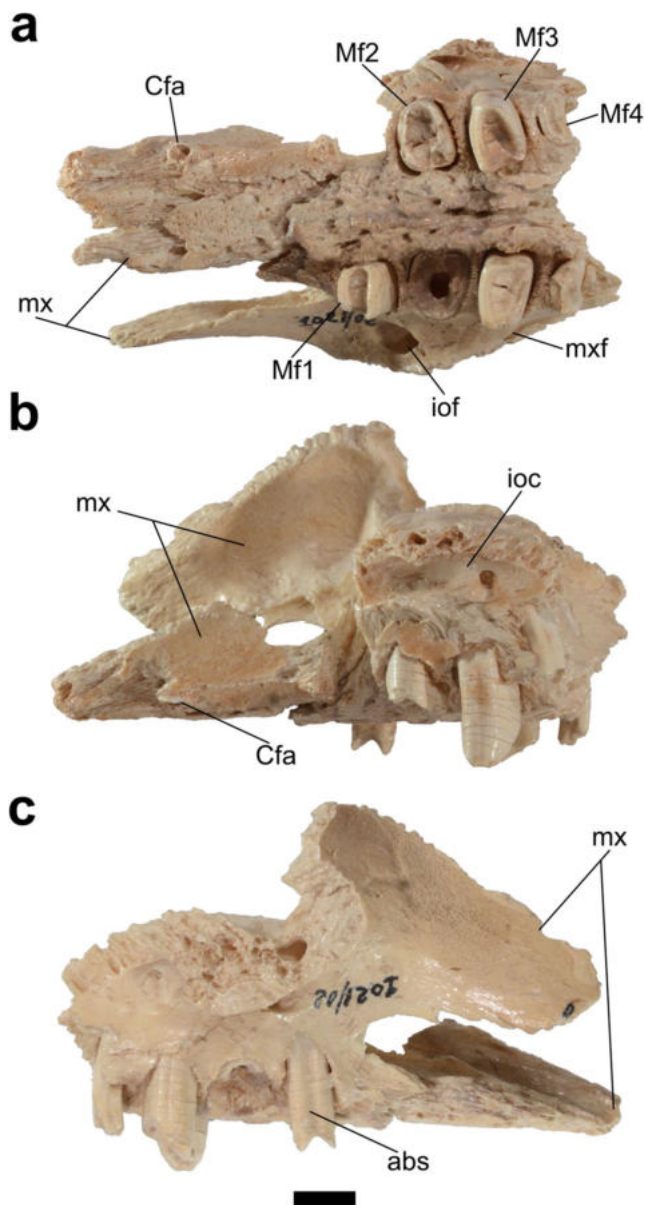


Fig. 3 Anterior fragment of the skull of *Nothrotherium maquinense* (MCL 1021/02) in ventral (**a**), left lateral (**b**), and right lateral (**c**) views. Scale bar equals 1 cm. Abbreviations: **abs**, apicobasal sulcus; **Cfa**, upper caniniform alveolus; **ioc**, infraorbital canal; **iof**, infraorbital foramen; **Mf1–Mf4**, upper molariforms 1–4; **mx**, maxilla; **mxl**, maxillary foramen

be discerned in the maxilla. A conspicuous opening is also present on the left side, purportedly a Cf alveolus, which is discussed in greater detail below. The right upper molariform tooththrow is preserved, although the Mf2–Mf3 are damaged, with Mf2 lacking most of the crown. The left upper molariform tooththrow is also preserved and nearly complete, missing only Mf1; however, the posterior and medial margins of its alveolus are retained. As in MCL 1020/01, Mf1–Mf3 are subtrapezoidal. Mf1 exhibits nearly equivalent mesiodistal and mediolateral dimensions, whereas Mf2—and especially

Mf3—are clearly wider than long. Mf4 is also wider than long, reniform in shape, and smaller in both mesiodistal and mediolateral dimensions relative to the other Mf. This teeth morphology is typical of nothrotheriids (Gaudin 2004; Casali et al. 2022). Lingual and labial apicobasal sulci are also present in Mf teeth, representing another characteristic feature of these taxa (De Iuliis et al. 2011; Pujos et al. 2014, 2023). In the lateral portion of the right maxilla, the anterior opening of the infraorbital canal (i.e., the infraorbital foramen) is located between Mf1 and Mf2, whereas the posterior opening of this canal (i.e., the maxillary foramen) lies at the level of the distal margin of Mf3.

In lateral views (Fig. 3b–c), the apicobasal sulci on the labial side of the molariform teeth are also evident. In left lateral view (Fig. 3b), damage exposes the infraorbital canal, revealing that it is slightly curved, with convex dorsal and concave ventral margins. The lateral margin of the opening located anterior to the left Mf1 is also visible in this view. In right lateral view (Fig. 3c), the preserved dorsolateral portion of the maxilla indicates that this bone was long and high, and the broad, rounded suture with the lacrimal (not preserved) resembles that observed in MCL 1020/01.

Analysis of the purported alveolus

Anteriorly to the left Mf1 alveolus there is a rounded opening with walls reaching 36 mm of anteroposterior diameter and 26 mm of mediolateral diameter, and an internal opening of 12 mm of diameter (Fig. 4a). This opening presents a slightly raised and rugose border that resembles the tooth socket—which is formed by alveolar bone—surrounding the edges of Mf alveoli (Fig. 4a). The homologous region on the right side of the palate is not preserved, therefore, not allowing for evaluating the presence of a symmetric counterpart of this opening. The most superficial bony layer posterior to this opening is well-preserved, but the surface medial and anterior to it are damaged (Fig. 4a). The anatomical position of such opening coincides exactly with that of the Cf of Neogene nothrotheriids (e.g., *Pronothrotherium typicum*, *Mionothropus cartellei*, and *Mcdonaldocnus bondesioi*). As observed in the computed tomography images (Fig. 4b), the cavity is straight, anteriorly oriented, with an opening with a rugose border that resembles that of a Cf alveolus. Moreover, this opening extends dorsally, matching the morphology observed in the thecodont tooth sockets of the other teeth, which are deep and accommodate the teeth well within the jaw.

We also explored the possibility of taphonomic causes for the presence of this structure. Circular to oval holes in fossil bones are often attributed to vertebrate feeding traces or invertebrate scavenging (e.g., Zonneveld et al. 2015; Fernandez-Jalvo and Andrews 2016; Zonneveld et

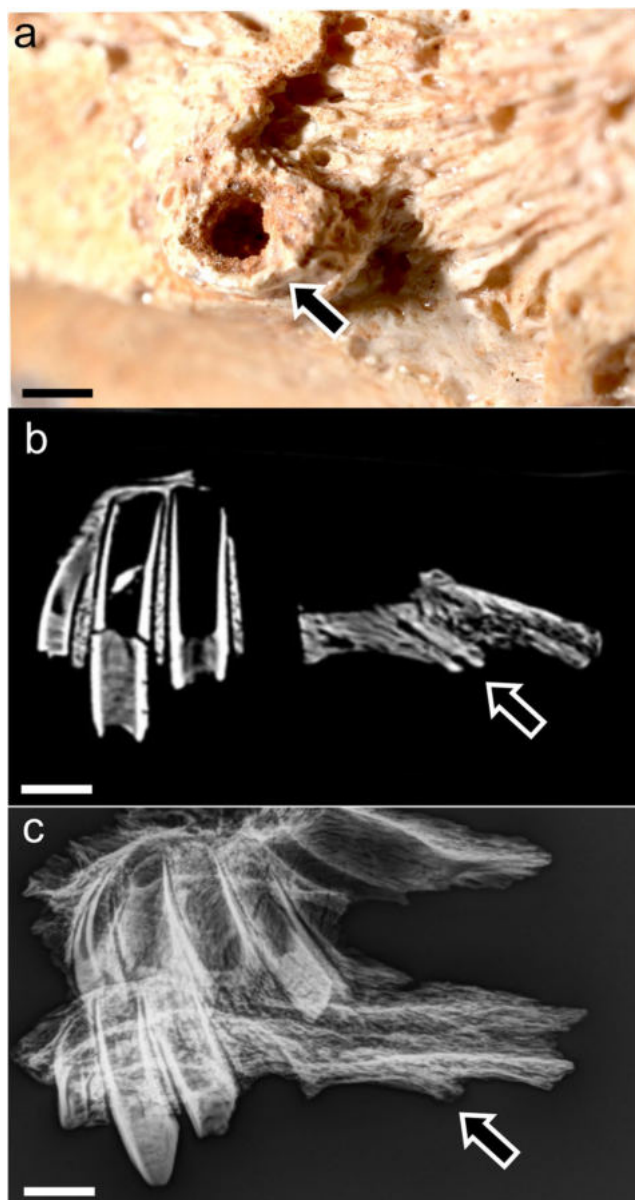


Fig. 4 Atavistic caniniform alveolus in *Nothrotherium maquinense*, indicated by arrows. **a.** close-up view of the alveolus; **b.** computed tomography, with the cut line passing along the middle of the left toothrow, showing the orientation and depth of the caniniform alveolus; **c.** x-ray in oblique (lateroventral) view, highlighting the absence of morphological alterations nearby or associated with the alveolus. The anterior portion of the skull is directed to the right. Scale bars equal 2.5 mm in **a** and 1 cm in **b-c**

al. 2022). The cavity examined here, however, lacks several features typically associated with vertebrate tooth marks, such as an opening with jagged edges indicative of brittle deformation, a puncture outline that reflects the morphology of the tooth, and associated traces pits, scores, furrows, or fractures (Mikulás et al. 2006; Andrés et al. 2012; Sala et al. 2014; Arriaza et al. 2021). Moreover, its straight, obliquely oriented shape, with an opening located at the

top of a slightly raised area (Fig. 4a-b), and lacking filling, bioglyphs or branching, does not resemble common continental bone-boring ichnotaxa produced by invertebrates (e.g., *Cubiculum*, *Karethraichnus*, *Clavichnus*, *Munitusichnus*, *Osedacoides*) (e.g., Xing et al. 2016; Parkinson 2016; Höpner and Bertling 2017; Zonneveld et al. 2022; Trifilio et al. 2023).

Lastly, the maxillary structure could, alternatively, be interpreted as pathological. However, we rule out this possibility due to the absence of two key diagnostic features of destructive pathological processes (Ortner 2003; Waldron 2009): (i) smooth or rounded edges, and (ii) evidence of osteoblastic activity within the lesion, typically manifested as rounded margins or new bone formation at the edges (Fig. 4a-c). Furthermore, although the oval, slightly depressed shape resembles a cloaca (a pus-draining channel in bone infections), radiographic image (Fig. 4c) reveals no bone sclerosis—increased radiopacity—a hallmark of this condition (Rothschild and Martin 2006).

Discussion

The identification of the rounded opening observed in the specimen of *Nothrotherium* studied here as an atavistic Cf alveolus is supported by its anatomical position and morphology, and most importantly, by the occurrence of a comparable structure in earlier members of Nothrotheriidae. The position of the alveolus is consistent with that observed in the Neogene nothrotheriids, and its external morphology—with a rugose alveolar edge—resembles that seen in the maxilla of the holotype of *Pronothrotherium* (MACN-Pv 8141; Gaudin et al. 2020) and in the mandible of *Lakukullus anatisrostratus* (MNHN-Bol-V 006601, Pujos et al. 2014). A similar morphology is also observed along the edge of the rudimentary alveolus present in the mandible of the holotype of *Nothropus tarijensis* (Burmeister, 1887) (MACN-Pv 1112; Quiñones et al. 2017: fig. 5). Also, the anteroventral inclination of the alveolar cavity is similar to that observed in *Nothrotheriops texanus* (UF 83700) (McDonald 1995). Lastly, the alveolus is positioned within the jaw in a typical thecodont fashion, consistent with the pattern of tooth implantation observed in the other teeth of this specimen. Given that the tooth socket forms alongside each new tooth (Tencate and Mills 1972), it remains unclear whether, in life, this atavistic alveolus—together with the presence of periodontal ligaments—also housed an atavistic tooth that was subsequently lost post mortem, or whether only the alveolus itself was produced atavistically during tooth ontogeny. Alternative hypotheses for the circular opening not representing an alveolus, such as taphonomic artifacts, or a pathological origin, have been excluded; thus,

the interpretation of this structure as a homologous alveolus represents the most plausible explanation for the observed anatomy. This suggests that the developmental potential for Cf formation persisted in derived nothrotheriids, at least in some individuals.

Among sloths, a fully formed atavistic Cf was reported for the maxilla of a juvenile individual of *Nothrotheriops texanus* from the Early Pleistocene of Florida (McDonald 1995), differing from the poorly developed and toothless alveolus described here. Atavistic alveoli for canines and incisors have also been reported for a juvenile of *Acratocnus ye* MacPhee et al. 2000 (Gaudin and Scaife 2022). Like MCL 1021, the teeth were absent in the Antillean specimen; however, in contrast, the alveolus in *Acratocnus ye* is associated with an early ontogenetic stage, similarly to what was observed in *Nothrotheriops*, whereas in the *Nothrotherium* specimen of this study, the alveolus is present in a subadult individual.

Despite the conserved dental formula of sloths (5/4), the homology of individual teeth has historically been inferred based solely on positional evidence and inferred function of the teeth. However, Hautier et al. (2016) provided compelling evidence that, at least among extant genera, the Cf is not homologous: in *Choloepus*, it corresponds to a permanent canine, whereas in *Bradypus*, it is homologous to a deciduous canine. Following their interpretation, it has been proposed that Cf/cf in general should not be assumed to be homologous among sloths (Tejada et al. 2024). However, sufficient evidence required to test this broader hypothesis is currently lacking for fossil sloths, and the non-homology of *Bradypus* teeth may simply result from the paedomorphic condition of this genus (Gaudin 2004). Until further evidence becomes available, the most parsimonious hypothesis is that the teeth of fossil sloths are homologous to those of the extant *Choloepus*. If true, this further suggests that positional correspondence likely reflects genuine homology rather than convergence as a general rule, despite some intriguing exceptions, such as that observed in *Bradypus*.

The ancestral condition in Nothrotheriidae included the presence of Cf/cf teeth, as observed in *Pronothrotherium typicum*, *McDonaldocnus bondesioi*, *Mionothropus cartellei*, and *Lakukullus anatisrostratus* (Pujos et al. 2014; De Iuliis et al. 2011; Gaudin et al. 2020). These teeth, however, differ markedly from the Cf/cf observed in other derived Megatherioidea, being considerably smaller, similar to those of some early-diverging megatherioids (Gaudin 2004; Casali et al. 2022).

Although dietary reconstructions for fossil taxa are inherently challenging, most megatherioid sloths are interpreted as browsers (Casali et al. 2023; Boscaini et al. 2025; and references therein). However, such homogeneity in dietary classifications may result from simplifying assumptions.

For instance, Varela et al. (2023b) showed that the forces exerted by the mandible in *Neocnus* cf. *dousman* MacPhee et al., 2000, *Acratocnus ye*, and *Megalonyx jeffersonii* are consistent with the processing of hard food items such as roots, tubers, fruits, and seeds, rather than with strictly browsing habits. Based on isotope data and measurements of relative muzzle width, *N. maquinense* has been classified as a browser (Dantas and Santos 2022; Dantas et al. 2023), and coprolite analyses have documented the inclusion of leaves, but also seeds in its diet (Duarte and de Souza 1991). Additionally, biomechanical analyses of the mandible of *N. maquinense* suggested the capacity to process hard food items; however, the authors emphasized that the evaluated specimen was a subadult individual, which may have exhibited incomplete development of the skull and masticatory musculature, thereby limiting broader interpretations (Varela et al. 2023b). It is also noteworthy that the ingestion of hard food items has been suggested for *Thalassocnus*, which, like *Nothrotherium*, lacks the Cf/cf. In the former taxon, however, the hard items could have included mollusks and crustaceans, complementing the consumption of seagrasses (Varela et al. 2023b).

Another possible factor related to the evolution of Cf/cf teeth is sexual selection. Sexual dimorphism in the size of caniniforms is well documented in *Lestodon armatus* Gervais, 1855 and *Paramylodon harlani* (Owen, 1840), with males bearing larger caniniforms than those of females (McDonald 2006; Varela et al. 2022). For the latter taxon, wear patterns are also sexually dimorphic. The condition in Nothrotheriidae remains poorly understood, as the Neogene taxa in which Cf/cf is present are known from a limited number of specimens, whereas taxa represented by more abundant material (i.e., *Nothrotherium* and *Nothrotheriops*) generally lack these teeth. However, if the caniniforms observed in known Neogene specimens could be taken as representative of both sexes, its small size—and eventual loss in Quaternary forms—may suggest the absence of strong sexual selection acting on this structure in the lineage.

This does not preclude the possibility that *Nothrotherium* exhibited sexual dimorphism in other traits, as reported for other sloths, including overall body size, cranial robustness, and muzzle morphology (e.g., De Iuliis and Cartelle 1999; McDonald 2006; Miño-Boilini and Zurita 2015; Boscaini et al. 2019). However, for the closely related genus *Nothrotheriops*, sexual dimorphism appears to be either absent or, if present, very subtle (McDonald 2006; Potter and Prothero 2025). In any case, the evolutionary advantages associated with the presence, loss, or recurrence of Cf/cf teeth remain unclear, and further developmental and ontogenetic studies may help clarify their functional and palaeobiological implications within a phylogenetic framework.

Alternatively, it could be hypothesized that, as for *Bradypus*, the Cf of nothrotheriids might represent deciduous teeth, which might have facilitated their loss in Quaternary forms. Observing caniniform teeth in juvenile Quaternary nothrotheriids would lend support to this speculative scenario. However, the maxilla of a fetus of *Nothrotherium* already shows a complete absence of caniniform teeth (Pujos et al. 2023), suggesting either that, if a Cf was present, it occurred only at an earlier ontogenetic stage, or, more likely, that the Cf is absent in *Nothrotherium* even during early stages of development, except under exceptional atavistic conditions such as the one reported here.

Beyond its anatomical and developmental significance, this finding may also bear on the systematics of Nothrotheriidae. The observations presented here may have important implications for the taxonomic validity of the genus *Nothropus*, which has been recognized as distinct primarily on the basis of the presence of a cf. alveolus in the mandible of specimens referred to this taxon. Accordingly, if atavistic expressions of caniniforms can occur in the maxillae of *Nothrotherium* and *Nothrotheriops* (McDonald 1995; this study), the occurrence of similar morphologies in the mandibles assigned to *Nothropus* may suggest that it may be synonymous with either *Nothrotherium* or *Nothrotheriops*, rather than representing a distinct genus. Given recent evidence suggesting the presence of *Nothrotheriops* in South America based on non-dental specimens, and the existence of other poorly documented species of *Nothrotherium* (i.e., *Nothrotherium torresi* and *Nothrotherium roverei*) (Brandoni and McDonald 2015; Brandoni and Vezzosi 2019; Varela et al. 2023a), the validity of *Nothropus* should be critically reevaluated. Moreover, the recovery of additional material of *Nothropus* will require examination under this developmental perspective and may help clarify whether these features represent true taxonomic distinctions or intraspecific variation within *Nothrotherium* or *Nothrotheriops*.

It should be noted that our findings are based on a single specimen, which precludes any assessment of the frequency of occurrence of this feature within the species, but given the absence in every other specimen so far assigned to *Nothrotherium*, it is likely a rare condition. In contrast, and rather intriguingly, all known mandibles of *Nothropus* exhibit the cf. alveolus. Moreover, the absence of teeth preserved within this alveolus further restricts the inferences that can be drawn, and it remains possible that the atavism is limited to the development of the tooth socket itself rather than the reappearance of a functional tooth. Additional material will be necessary to fully understand the nature, distribution, and evolutionary significance of this condition.

Conclusions

The presence of a Cf alveolus in *Nothrotherium* likely represents an atavistic expression of a lost ancestral dental condition, supported by its anatomical position, morphology, and comparisons with earlier members of the family that also exhibit that feature. Although distinct from conditions observed in other sloths, the consideration and subsequent rejection of taphonomic and pathological explanations render the hypothesis of an atavistic, poorly developed alveolus, the most plausible interpretation. This specimen provides further evidence that lost morphological traits may occasionally partially reemerge during the evolution of a lineage. The occurrence of atavistic caniniforms among nothrotheriids also calls into question the taxonomic validity of *Nothropus*, highlighting the need for a critical reevaluation of this genus. Accordingly, further developmental and ontogenetic studies of dental evolution in sloths may help clarify the evolutionary history of the group, as well as the functional significance of Cf/cf teeth in feeding mechanics and their implications for sloth paleobiology.

Acknowledgements We thank the Pontifícia Universidade Católica de Minas Gerais, Museu de Ciências Naturais PUC Minas with a special thanks to Dr. Castor Cartelle Guerra for providing access to the specimen used in this study and to the collection. We thank Radius Odonto Clinic for granting us access to the computed tomography equipment. We also thank Zoovet Veterinary Clinic for lending the portable X-ray device, as well as Wendy Vieira and Pablo Pezoa. We are also indebted to Donato Martucci and Gabriel M. A. Campos for their assistance with CT scan software.

Author contributions All authors contributed to the study conception and design. D.M.C., G.M., R.P.D., and L.V. analyzed, described, and illustrated the fossil material. Computed tomography and X-ray images were taken by C.G.C., I.L.A.L., and F.R.M., and were analyzed by F.R.M. F.H.M.B. and F.P.M. conducted evaluations regarding taphonomic and pathological aspects of the material. H.G.M. and R.E.N. performed comparisons with *Nothrotheriops* material. The first draft of the manuscript was written by D.M.C., and all authors reviewed, and contributed significantly to the final version of the manuscript. All authors read and approved the final manuscript.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614). D.M.C. research is currently funded by the grant #2022/00044-7, São Paulo Research Foundation (FAPESP). We thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the doctoral scholarship for C.G.C. G.M. is currently funded by the São Paulo Research Foundation (FAPESP) under grant numbers 2022/00171-9 and 2022/12395-9. F.P.M. is currently funded by the São Paulo Research Foundation (FAPESP) under grant numbers 2024/03599-5.

Data availability Computed tomography DICOM files (.dcm) and X-ray images generated during this study are available in GitHub digital repository, and can be accessed with the link: https://github.com/danielmcasali/Nothrotherium_vestigial_alveolus.

Declarations

Competing interests The authors declare no competing interests.

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