A NEW GENUS AND SPECIES OF NOTHROTHERIID SLOTH (XENARTHRA, TARDIGRADA, NOTHROTHERIIDAE) FROM THE LATE MIOCENE (HUAYQUERIAN) OF PERU

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Abstract: The nothrotheriine sloth from riverbank deposits of the Río Acre region of Peru in western Amazonia was originally assigned to *Nothropus priscus* Burmeister, 1882. Although relatively complete, with essentially the pes unknown, its description was accompanied only by limited information on its cranial remains. The remains of this sloth, actually of late Miocene age, were extensively prepared. Subsequent analysis indicates that its original assignment is incorrect and that it belongs to a new genus and species, which is distinguished from other nothrotheriines by the following (among other) features: notably domed braincase; depressed, narrow snout; lack of parietal/alisphenoid contact; ulna with prominently projecting anconeal process; distal position of femoral greater trochanter; medial articular condyle of femur butts against patellar trochlea. Phylogenetic analysis places the new genus and species as sister group to the (*Pronothrotherium* (*Nothrotheriops* + *Nothrotherium*)) clade.

Key words: Tardigrada, Nothrotheriidae, Huayquerian, Río Acre, Amazonia, Peru.

NOTHROTHERIIDAE, together with Mylodontidae, Megalonychidae, and Megatheriidae, are the four main clades of Tardigrada or sloths, sister group to Vermilingua (South American anteaters) in Pilosa. The position of nothrotheriids within Tardigrada is unresolved, with some authors considering them closer to Megatheriidae, and others closer to Megalonychidae (see below).

The nothrotheriid sloth genus *Nothropus* Burmeister, 1882 was erected on the basis of an isolated mandible with teeth from the Pleistocene (Lujanian South American Land Mammal Age (SALMA)) of Argentina that Burmeister (1882) placed in the species *Nothropus priscus* Burmeister, 1882. A second species of *Nothropus*, *N. tarijensis* (Burmeister, 1887), was subsequently recognized by Ameghino (1907), based on a partial lower jaw with teeth that Burmeister (1887) had initially assigned to the more common and better known Pleistocene genus *Nothrotherium* Lydekker, 1889 (= *Coelodon* Lund, 1839). Both specimens of *Nothropus* were characterized by bilophodont, rectangular molariform teeth with a shape and occlusal surface very reminiscent of the morphology in *Nothrotherium*. Unlike the latter

taxon, however, both retained an alveolus for a small anterior caniniform tooth, separated by a diastema from the three posterior molariforms. Such a caniniform tooth is commonly present in other extinct and extant sloths (Grassé 1955; Hoffstetter 1958). Ameghino (1907) noted that the caniniform was smaller in *Nothropus tarijensis*, an adult specimen, than in *N. priscus*, which derived, he believed, from a juvenile. Ameghino (1907) then discussed the possibility that *Nothropus* and *Nothrotherium* may simply represent developmental variants of one another, with the latter form being characterized by an ontogenetically earlier reduction, and eventual loss, of the caniniform. However, Ameghino (1907) made no formal proposal to eliminate the genus *Nothropus*. Rancy (1991) supported the idea that *Nothropus priscus* represents a rare state of *Nothrotherium maquinense* (Lund, 1839), noting a similar occurrence in only one of several individuals of *Nothrotheriops shastensis* (Sinclair, 1905), as McDonald (1995) also noted.

Frailey (1986) reported the discovery of a nothrotheriid ground sloth from riverbank deposits in the Río Acre

region of western Amazonia, Peru. The ground sloth was represented by a single skeleton missing only the left hind limb and both hind feet, and including a nearly complete skull and mandible (LACM 4609/117533; Frailey 1986). Frailey (1986) assigned the material to *Nothropus priscus* based on its retention of a small caniniform tooth (larger than that of *N. tarijensis*) in the mandible and its purportedly Holocene provenance. Subsequent work on this material has questioned both its chronological (Rancy 1991, 1999; Frailey 1995) and taxonomic provenance (Rancy 1991, 1999).

Further collecting in the Río Acre region uncovered 'a rich Miocene vertebrate fauna' (Rancy 1991, p. 91) characteristic of the Huayquerian SALMA (late Miocene, 6.8–9.0 Ma; Flynn and Swisher 1995). It appears likely that Frailey's (1986) nothrotheriid is of similar age (Rancy 1991, 1999; Frailey 1995; see also Cozzuol 2006). Rancy (1991, 1999), based on both age and anatomy, asserted that Frailey (1986) misidentified his specimen as *Nothropus*, suggesting instead that the specimen represents a new, unnamed taxon closely related to the nothrotheriid genus *Pronothrotherium* Ameghino, 1907, a Patagonian taxon from the Huayquerian–Montehermosan SALMAs of South America (Montehermosan = latest Miocene – early Pliocene, 4.0–6.8 Ma; Flynn and Swisher 1995). Rancy (1991) described a second nothrotheriid from Huayquerian SALMA deposits on the upper Acre River. Although noting a series of morphological differences between the new Acre nothrotheriid and Frailey's (1986) specimen, Rancy (1991) suggested that the two may pertain to the same genus and species, but left open the possibility that they represent distinct taxa.

Determining the proper taxonomic allocation of Frailey's (1986) nothrotheriid specimen is important in attempting to understand the phylogenetic, evolutionary and biogeographical history of Nothrotheriidae. This will enhance our knowledge of the evolutionary history of sloths, which were among the most important elements of the South American terrestrial fauna during the Miocene to Pleistocene. Despite the fact that the original *Nothropus* material is younger than the oldest records for *Nothrotherium*, Ameghino (1907) hypothesized that the latter genus was a direct lineal descendent of the former. Paula Couto (1971) suggested subsequently that the two genera were not closely related. His phylogenetic tree derived *Nothropus* and the North American genus *Nothrotheriops* Hoffstetter, 1954 independently from the earlier South American genus *Pronothrotherium,* with *Nothrotherium* descended directly from the even older South American genus *Hapalops* Ameghino, 1887, from the Santacrucian SALMA (early–middle Miocene, 16.3–17.5 MA, Flynn and Swisher, 1995). More recent cladistic studies (Muizon and McDonald 1995; Gaudin and De Iuliis 1999; McDonald and Muizon

2002; Muizon *et al.* 2003; Gaudin 2004), using Frailey's (1986) specimen to represent *Nothropus*, have recognized a clade uniting *Nothrotherium* and *Nothrotheriops* to the exclusion of other nothrotheriids. *Nothropus* has been placed at the base of Nothrotheriidae, either one step closer to (Muizon and McDonald 1995; Gaudin and De Iuliis 1999; Gaudin 2004) or one step further removed (Gaudin 2004) from the *Nothrotherium/Nothrotheriops* clade than *Pronothrotherium*, or as the sister taxon to *Pronothrotherium* (McDonald and Muizon 2002; Muizon *et al.* 2003).

Frailey's (1986) initial description of his putative *Nothropus* specimen (LACM 4609/117533) briefly summarized the morphology of the skull and mandible and covered the dentition in some detail. He did not, however, attempt a detailed skull description, nor did he describe any of the postcranial remains that were discovered with the specimen. Many regions of the skull and postcrania remained inadequately prepared for detailed study. One of the primary goals of the present study is to produce a redescription of LACM 4609/117533. We have conducted extensive additional preparation of the skull, especially in the orbit, nasopharynx, and auditory region. Based on this new preparation, we have prepared a detailed, bone by bone description of the skull and mandible. In addition, we have conducted new preparation on the previously undescribed postcranial material pertaining to LACM 4609/117533 and provide a detailed description of this material.

Based on our study of the newly prepared and described anatomy of LACM 4609/117533, we concur with Rancy (1991, 1999) that the Huayquerian specimen does not belong to the same species as the Lujanian *Nothropus priscus*. Further, we conclude that this specimen is not conspecific with UFAC 1284, the type of Rancy's (1991) unnamed new genus and species, a possibility recognized by this author. We have therefore placed the specimen in a new genus and species, *Mionothropus cartellei*. In the final portion of this report, we attempt to ascertain the phylogenetic position of *Mionothropus* and discuss the implications of the new taxon for the phylogenetic, biogeographical, and evolutionary history of Nothrotheriidae.

Institutional abbreviations. FMNH, Field Museum of Natural History, Chicago, IL, USA; LACM, Los Angeles County Museum of Natural History, Los Angeles, CA, USA; LACMHC, Los Angeles County Museum of Natural History, Hancock Collection, Los Angeles, CA, USA; MCL, Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Minas Gerais, Brazil; UFAC, Universidad Federal do Acre, Rio Branco, Acre, Brazil; MNHN, Muséum national d'Histoire naturelle, Paris, France; ROM, Royal Ontario Museum, Toronto, ON, Canada; YPM, Yale Peabody Museum, New Haven, CT, USA.

SYSTEMATIC PALAEONTOLOGY

XENARTHRA Cope, 1889
TARDIGRADA Latham and Davies in Forster, 1795
(=PHYLLOPHAGA Owen, 1842)
NOTHROTHERIIDAE Gaudin, 1994

Definition. Least inclusive clade including *Thalassocnus* Muizon and McDonald, 1995, *Nothrotheriops*, and *Nothrotherium* (=Nothrotheriinae of Muizon and McDonald 1995; McDonald and Muizon 2002; Muizon *et al.* 2003).

Diagnosis. Sloths with caniniform (when present) positioned approximately midway on maxilla between anterior edge and M1; molariforms quadrate, rectangular or trapezoidal with transverse width less than two times mesiodistal length, with longitudinal grooves on lingual and labial surfaces; sagittal crest rudimentary or absent; postorbital process of jugal reduced or absent; hypoglossal foramen recessed dorsally, lies at same level as jugular foramen; occipital condyles sessile, with posterior edges at the same level as or anterior to posterior edge of foramen magnum; mastoid process (= paroccipital process of Wible and Gaudin 2004) bulbous, expanded mediolaterally; dorsally directed branch of the occipital artery perforates mastoid process, emerging in a foramen on the dorsal side of the mastoid process (foramen apparently absent (lost?) in *Nothrotherium*); Glaserian fissure opens into weak groove on ventral or posteroventral surface of entoglenoid process; coronoid process of mandible without medial ridge along anterior edge; radial bicipital tuberosity projecting mainly posteriorly; pronator teres insertion at proximal one-third of radial diaphyseal length (=relatively elongated distal radial diaphysis); cuneiform proximodistally deep, nearly rectangular in dorsal view; ungual process of ungual phalanx of manual digit two semicircular in cross section and not triangular as in other manual unguals; astragalus with medial trochlea enlarged and modified into an odontoid process; calcaneum with tuber calcis enlarged mediolaterally and anteroposteriorly (diagnosis modified from McDonald and Muizon 2002; characters added from Gaudin (2004) and present study).

NOTHROTHERIINAE Ameghino, 1920

Definition. Least inclusive clade including *Mionothropus, Pronothrotherium, Nothrotheriops,* and *Nothrotherium* (=Nothrotheriidae of Gaudin 2004).

Diagnosis. Vomer with enormous exposure in nasopharyngeal roof, expanded posteriorly to cover presphenoid and much of basisphenoid and contacting the pterygoid posterolaterally; vomer marked by deep, elongated, asymmetrical ventral keel extending into the nasopharynx; parietal with anteroventral process contacting alisphenoid (absent in *Mionothropus*, in some *Nothrotheriops* parietal does not reach alisphenoid); pterygoid does not participate in roof of tympanic cavity; stylohyoid fossa elongated anteroposteriorly (but circular in *Mionothropus*); lateral bulge at base of zygomatic root for epitympanic sinus; root of zygoma on squamosal directed anteriorly; ventral nuchal crest hypertrophied; external occipital protuberance in line with ventral nuchal crest; coronoid process of mandible short and broad, ratio of maximal height to anteroposterior length measured at mid-height <1.0; femur flattened anteroposteriorly, transverse width at midshaft much greater than anteroposterior depth; greater trochanter of femur even with crest between head and greater trochanter, so crest nearly normal to long axis of diaphysis; femoral trochlea (patellar surface) separated from lateral condylar surface; femoral trochlea (patellar surface) and medial condylar surface separate, but the facets abut against each other in *Mionothropus*; patella long and narrow (but not in *Mionothropus*); metatarsal V with mediolateral expansion.

Genus MIONOTHROPUS gen. nov.

Type species. *Mionothropus cartellei* sp. nov.

Derivation of name. 'Mio' is a reference to the Miocene provenance of the holotype, 'nothropus' refers to the initial allocation of the holotype to this genus from the South American Pleistocene.

Diagnosis. As for type species.

Distribution. Huayquerian SALMA (late Miocene) of Río Acre region on the border of Peru and Brazil (Rancy 1991, 1999; Frailey 1995).

Mionothropus cartellei sp. nov.
Text-figures 1–18

1986 *Nothropus priscus* Frailey, p. 34, figs 29–32.

Derivation of name. The specific epithet honours Dr Castor Cartelle of the Museu de Ciencias Naturais da Pontifícia Universidade Católica de Minas Gerais, and formerly of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil, for his contributions to the study of South American palaeontology, and particularly fossil sloths, and for his collaboration and friendship with GDI.

Holotype. LACM 4609/117533 (= *Nothropus priscus* Frailey, 1986).

Localities and horizon. Type locality LACM 4609, on the Río Acre marking the border between Brazil and Peru; Iñapari formation, Member A (Frailey 1986), late Miocene Huayquerian SALMA (Rancy 1991, 1999; Frailey 1995).

Diagnosis. Skull with distinctive domed braincase and depressed, narrow snout; vomerine keel straight, though offset, somewhat to the right of the midline anteriorly, and very deep, at its deepest over two-thirds the depth of the choanae; open grooves leading to the foramen ovale and foramen rotundum exposed in the roof of the naso-pharynx; pterygoid hollowed out medially, perhaps for soft-walled pterygoid bulla; parietal without anteroventral process, does not contact alisphenoid; stylohyoid fossa circular; mastoid process (= paroccipital process of Wible and Gaudin 2004) compressed mediolaterally; anterior edge of symphyseal spout with straight profile in lateral view; lesser tubercle of humerus larger than greater; humeral supinator ridge nearly vertically oriented; gracile ulna with strongly anteriorly projecting anconeal process; magnum has proximolateral contact with cuneiform; distally positioned greater trochanter of femur; medial condyle of femur abuts against patellar trochlea; patella short and wide.

Description

Skull. Measurements for the skull and mandible are provided in Table 1. The right premaxilla has been prepared separately from the remainder of the skull (Text-fig. 1). The bone is Y-shaped as is typical for 'nothrotheres' (see below; De Iuliis 1994). Its anterior process does not extend as far forward as that in *Hapalops* (Scott 1903, 1904) or *Nothrotherium* (Cartelle and Bohórquez 1986), although it is very similar in its proportions to the premaxillae of *Nothrotheriops* (Lull 1929; also LACM 192/15145). The premaxilla has a well-developed lateral ramus. Some of the lateral ramus is missing posteriorly. The facial process of the maxilla bears an articular fossa anteroventrally that received the lateral ramus of the premaxilla (Text-figs 2, 3). The shape of this fossa suggests that the missing portion of the lateral ramus was substantially deeper than the portion that is preserved. The medial ramus of the premaxilla tapers posteriorly to a thin wedge that inserted into a depression ventral to the vomer in the anterior floor of the nasal cavity. The notch for the incisive foramen between the medial and lateral rami is keyhole shaped (Text-figs 1A, 3). However, it is likely that only the rounded anterior portion of this notch was exposed ventrally when the premaxilla was articulated with the maxilla, as in *Nothrotherium* (Cartelle and Bohórquez 1986).

The facial portion of the maxilla is bounded by the nasal dorsally and the frontal, lacrimal, and jugal posteriorly (Text-fig. 2). It contains a well-developed buccinator fossa that extends from the lateral edge of the palate ventrally to a dorsal border just

**TABLE 1.** Measurements of cranial elements of *Mionothropus cartellei* gen. et sp. nov.

Skull and mandible	
Length, premaxillae to occipital condyles	274*
Length, maxillae to condyles	249*
Length, premaxillae	25*
Length, C1 to occipital condyles	214*
Length, C1 to M4	70.0
Length, M1 to M4	47.2
Length, diastema between C1 and M1	17.0
Width, between lateral margins of maxillae at M1	41.9
Width, preorbital fossa, measured dorsally	40.3
Width, postorbital constriction	69*
Width, between postorbital processes (determined by doubling width between R postorbital process and midline)	80.7
Width, between mastoid processes (determined by doubling width between R mastoid process and midline)	87.4
Minimal palatal width, measured at midpoint of C1/M1diastema	30.7
Maximal length of palate at midline (excluding premaxilla)	105.6
Length, mesial margin of C1 to anterior margin of maxilla	40.1
Maximal palatal width anterior to C1	39.5
Width of palate between lingual margins of M1	20.7
Width of palate between lingual margins of M4	26.6
C1, vestibulolingual width/mesiodistal length	5.0/6.0
M1, vestibulolingual width/mesiodistal length	10.9/11.0
M2, vestibulolingual width/mesiodistal length	13.4/11.4
M3, vestibulolingual width/mesiodistal length	13.9/10.4
M4, vestibulolingual width/mesiodistal length	12.3/5.7
Mandible	
Length, mandibular spout to mandibular condyle (anteriormost portion of spout missing)	205*
Length, mandibular spout to angular process (anteriormost portion of spout missing)	213*
Length, c1 to angular process	152.9
Length, c1 to m3	53.1
Length, m1 to m3	36.8
Length, mandibular spout, from mesial margin of c1 (anteriormost portion of spout missing)	61*
Width, mandibular condyle	18.5
Maximal height of ramus, at m2	45.6
c1, vestibulolingual/mesiodistal	5.8/6.7
m1, vestibulolingual/mesiodistal	14.3/10.3
m2, vestibulolingual/mesiodistal	13.8/9.5
m3, vestibulolingual/mesiodistal	13.8/11.4

Measurement in mm.
*Estimated measurement.

below the zygomatic process of the maxilla. As noted by Frailey (1986), the fossa is bounded anteriorly by the root of C1 and extends posteriorly to the mesial margin of M2. It forms a dis-

TEXT-FIG. 1. Right premaxilla of *Mionothropus cartellei* gen. et sp. nov. A, ventral view. B, dorsal view. C, lateral view. Abbreviations: if, incisive foramen; lr, lateral ramus; mr, medial ramus. Scale bar represents 1 cm.
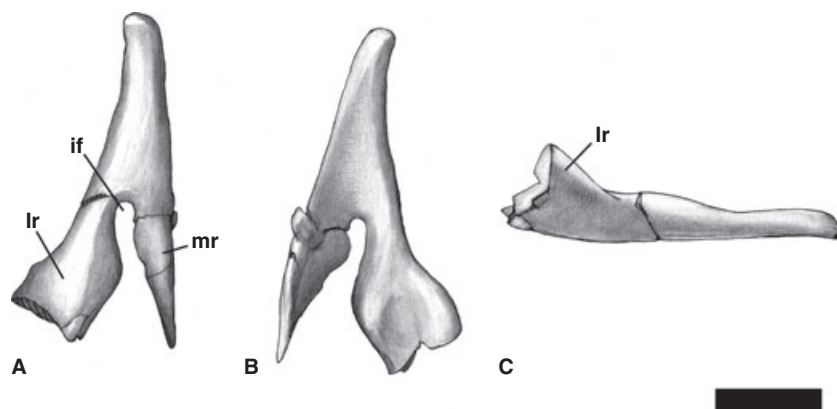
tinct indentation in the lateral edge of the palate. The palatal process of the maxilla (Text-fig. 3) is very similar to that of *Nothrotheriops* (Stock 1925). It is relatively flat anterior to C1 and becomes increasingly more convex transversely as it extends posteriorly towards the maxillopalatine suture. The anterior portion of the palatal process bears two anterior palatal foramina that open into distinct groves that extend forward almost to the maxillopremaxillary suture. These anterior palatal foramina and their accompanying grooves are widely distributed among sloths and anteaters (Gaudin 2004). The frontal, palatine, and jugal border the orbital portion of the maxilla posterodorsally (Text-fig. 2). This orbital portion of the maxilla is marked laterally by a shallow depression posterior to the root of M4 and forms a boss behind the crown of M4. Because of this enlarged boss, the maxilla closely approaches the posterior margin of the palate. The infraorbital canal perforates the zygomatic process of the maxilla. The length of the infraorbital canal is 12.9 mm, 5 per cent of BNL (BNL = basonasal length, measured from anterior tip of the nasal to posterior edge of the occipital condyle), which is comparable in relative length to that of *Nothrotheriops* (LACMHC 1800-3 – 16.2 mm, 4.9 per cent BNL) and *Pronothrotherium* (FMNH P14467 – 11.1 mm, 5 per cent BNL). In contrast to *Nothrotherium* (Paula Couto 1959, fig. 3; Cartelle and Bohórquez 1986), the maxillary foramen may have jugal participation in its dorsal margin as in *Nothrotheriops* (Stock 1925); however, the sutures here are somewhat hard to interpret.

The maxillopalatine suture lies between the second and third molariforms at its anterior extremity (Text-fig. 3), slightly in advance of the position in *Nothrotheriops*, which Stock (1925, pp. 43–44) described as lying 'between or behind the posterior ends of the third upper cheek tooth.' The anterior portion of the suture is transversely oriented and fairly wide. The palatine of *Mionothropus* lacks the well-developed posterior palatine shelf that is present in *Nothrotheriops* (Stock 1925) and *Nothrotherium* (Cartelle and Fonseca 1983) and is elongated in *Pronothrotherium* (FMNH P14467). The posterior palatine notch is thus broader than in the latter three taxa. Three small posterior palatine foramina are found in the posterior palatine area on the right, and two more are present on the left. Following Wible and Gaudin (2004), these are likely the minor palatine foramina for the minor palatine vessels and nerves. These small multiple foramina resemble the condition in *Pronothrotherium typicum*

Ameghino, 1907 (FMNH P14467), in contrast to the large, single foramen found in *Nothrotheriops* (Stock 1925) on both sides of the skull (Text-fig. 2).

The nasopharynx of *Mionothropus* is broadly open ventrally because of the lack of a posterior palatine shelf. A large palatine exposure is visible in the anterior half of the lateral wall of the nasopharynx. The extent of exposure of the palatine in the roof of the nasopharynx is unknown because of the presence of matrix covering this area (Text-fig. 3).

The orbital process of the palatine has a quadrangular, diamond-like shape (Text-fig. 2). It is bounded by the maxilla anteroventrally and the frontal anterodorsally. The alisphenoid and pterygoid abut the palatine's orbital process posteriorly. The extent of the contact between palatine, alisphenoid, and pterygoid is unclear because we are unable to determine the position of the alisphenopterygoid suture. The bone here is extremely thin and there is some breakage in the area, as well as some matrix that could not be removed because of the delicacy of the bone. The orbital process of the palatine contains two foramina located within a common fossa (Text-fig. 2). The sphenopalatine foramen lies in the dorsal portion of the fossa, whereas the caudal palatine foramen is situated ventrally.

The nasal contacts the maxilla laterally and the frontal posteriorly (Text-fig. 2). It is strongly convex transversely in its anterior half, but less so posteriorly. *Mionothropus* lacks the concavity found at the midline nasal suture in *Nothrotheriops* (Stock 1925). The nasal narrows in the middle in dorsal view and is strongly flared posteriorly at the nasofrontal suture (Text-fig. 4). The nasal is narrower transversely than that of *Nothrotheriops*. The ratio of maximum nasal length to nasal width measured at the midpoint is 5.2 for *Mionothropus* and 1.9 for *Nothrotheriops* (based on LACMHC 1800-3). There is a well-preserved lateral process on the right side of the anterior nasal margin. The process is missing on the left. This process is narrower than that of *Nothrotheriops* (Stock 1925) with a rounded anterior margin like that present in *Hapalops* (Scott 1903, 1904). The medial nasal process is damaged on both sides. The nasal slopes anteroventrally in lateral view. The slope is particularly steep in the posterior one-third of the nasal. As a result, the snout is strongly depressed relative to the braincase. The nasofrontal suture is V-shaped. This suture is narrower and deeper than that of *Nothrotheriops* (Stock 1925) or *Nothrotherium* (Cartelle and Fonseca 1983).

A
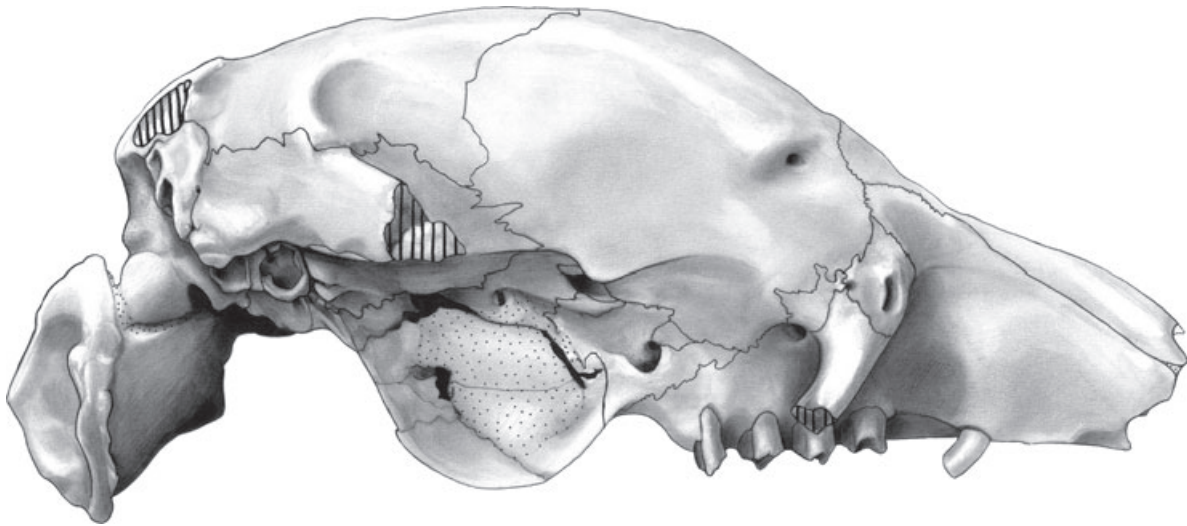
B
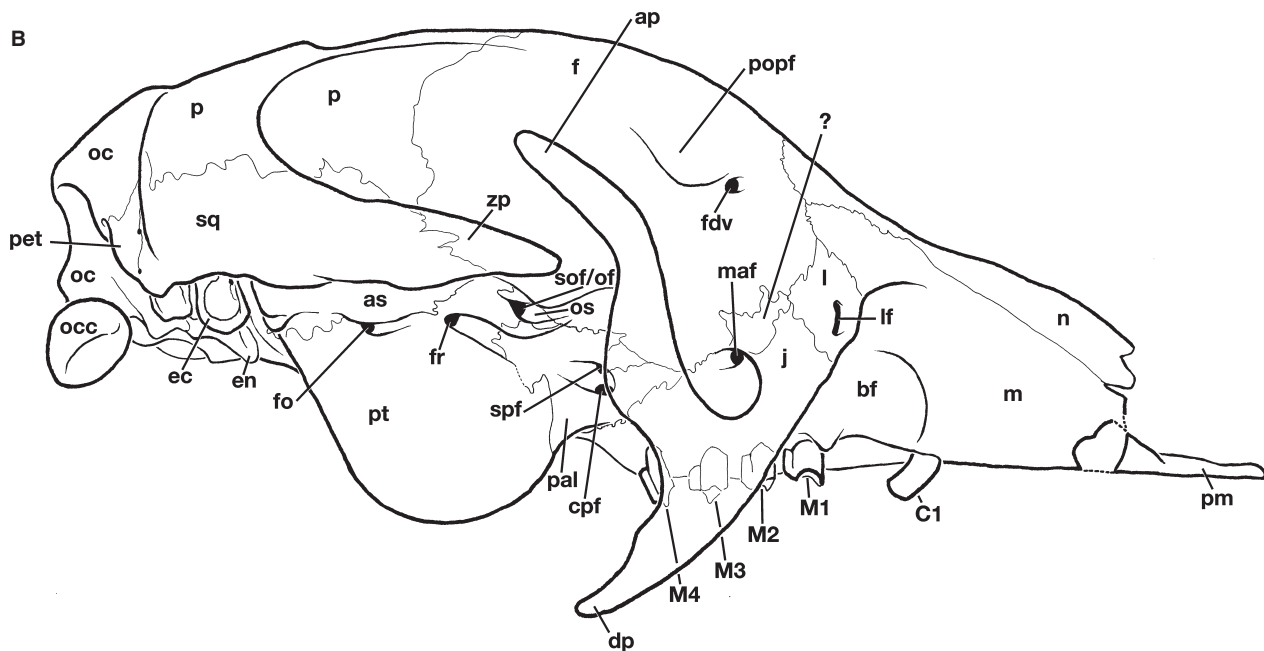
TEXT-FIG. 2. Right lateral view of skull of *Mionothropus cartellei* gen. et sp. nov. A, lateral view of skull and atlas with zygomatic processes of squamosal and jugal mostly removed. B, reconstruction of skull in lateral view. Abbreviations: ap, ascending process of jugal; as, alisphenoid; bf, buccinator fossa; C1, upper caniniform; cpf, caudal palatine foramen; dp, descending process of jugal; ec, ectotympanic; en, entotympanic; f, frontal; fdv, foramen for frontal diploic vein (=supraorbital foramen); fo, foramen ovale; fr, foramen rotundum; j, jugal; l, lacrimal; lf, lacrimal foramen; maf, maxillary foramen; m, maxilla; M1–4, first through fourth upper molariforms; n, nasal; oc, occipital; occ, occipital condyle; os, orbitosphenoid; p, parietal; pal, palatine; pet, petrosal (mastoid exposure); pm, premaxilla; popf, postorbital process of frontal; pt, pterygoid; sof/of, confluent sphenorbital fissure and optic foramen; spf, sphenopalatine foramen; sq, squamosal; zp, zygomatic process of squamosal; ?, unknown region, may be part of frontal or jugal bone. Scale bar represents 5 cm.

The lacrimal on the left side is almost completely destroyed while that on the right side is still intact (Text-fig. 2). The lacrimal is very similar in shape to that of *Nothrotheriops* (Stock 1925) and *Nothrotherium* (Reinhardt 1878; Cartelle and Fonseca 1983) but has a smoother, less rugose surface than that of *Nothrotheriops*. It contacts the frontal posterodorsally, the jugal posteroventrally, and the maxilla anteriorly. The lacrimal foramen is centrally located within the lacrimal on the anterior

TEXT-FIG. 3. Ventral view of skull of *Mionothropus cartellei* gen. et sp. nov. A, ventral view of skull and atlas with zygomatic processes of squamosal and jugal mostly removed. B, reconstruction of skull in ventral view. Abbreviations: ap, ascending process of jugal; apf, anterior palatal foramen; as/egp, entoglenoid process of alisphenoid; bf, buccinator fossa; bo, basioccipital; bot, basioccipital tuber; C1, upper caniniform; dp, descending process of jugal; eam, external auditory meatus; ec, ectotympanic; en, entotympanic; et, opening for Eustachian tube; f, frontal; fm, foramen magnum; gf, glenoid fossa; gfo, groove leading to foramen ovale; gfr, groove leading to foramen rotundum; gsof, groove leading to sphenorbital fissure; hf, hypoglossal foramen; if, incisive foramen; iof, infraorbital foramen; j, jugal; jf, jugular foramen; l, lacrimal; maf, maxillary foramen; m, maxilla; M1–4, first through fourth upper molariforms; occ, occipital condyle; pal, palatine; palf, palatal foramina; pm, premaxilla; pt, pterygoid; ptc, posttemporal canal; ptl, pterygoid lamina; sf, stylohyoid fossa; sof/of, confluent sphenorbital fissure and optic foramen; sq, squamosal; stmf, stylomastoid foramen; v, vomer; zp, zygomatic process of squamosal. Scale bar represents 5 cm.
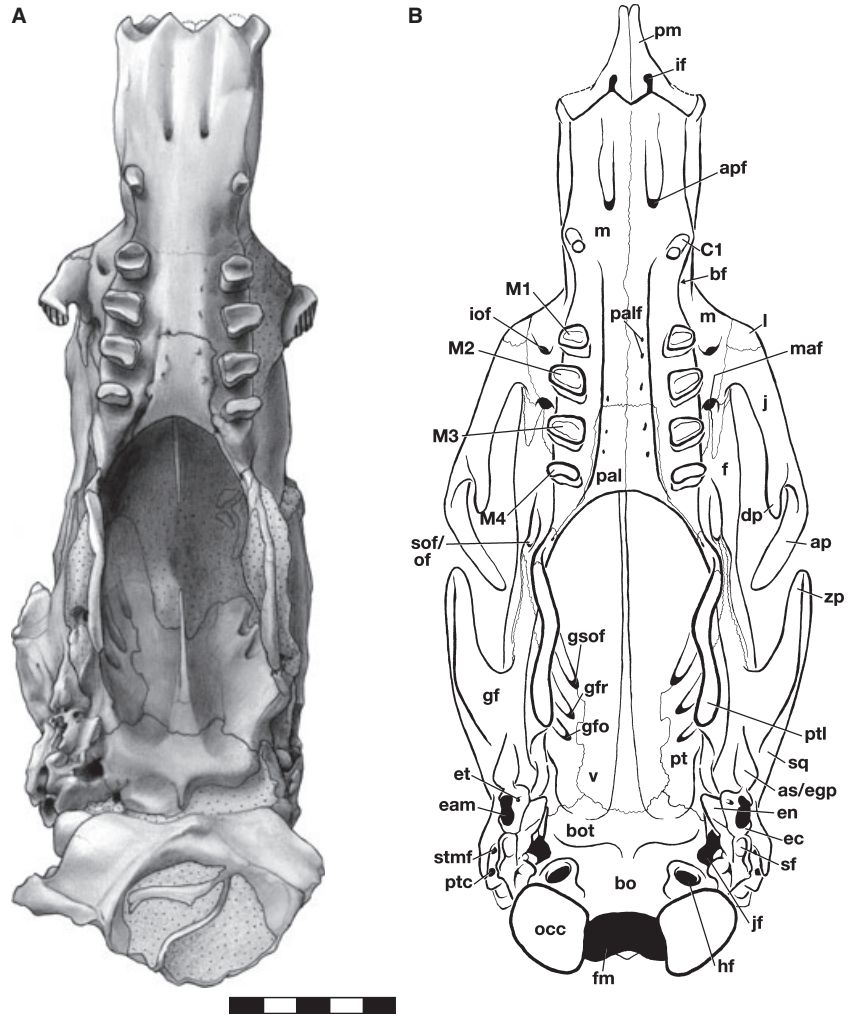

margin of the orbit (Text-fig. 2). The maximum dorsoventral diameter of the lacrimal foramen is small (6.8 mm, 2.6 per cent BNL) compared to that of *Nothrotheriops* (12 mm, 3.6 per cent BNL – LACMHC 1800-3). The lacrimal foramen opens into a ventrally directed groove as in other nothrotheres. There is a weak process (probably the lacrimal tubercle; see Wible and Gaudin 2004) directly behind the lacrimal foramen that is smaller than that found in a corresponding position in *Nothrotheriops* (Stock 1925). There is also a small lacrimal fenestra for the origin of the inferior oblique muscle (Wible and Gaudin 2004) at the posteriormost point of the lacrimal, along its contact with the jugal.

The right jugal was initially attached to the skull (Frailey, 1986). It has now been broken through its base and prepared free of the skull. As described by Frailey (1986), the jugal does not contact the zygomatic process of the squamosal (Text-fig. 2). The ascending process closely resembles that present in the early Miocene genus *Hapalops* (Scott 1903, 1904). It is elongate and slender and extends posterodorsally well above the level of the zygomatic process of the squamosal. A very weak postorbital process is discernable on its anterior edge. The descending process of the jugal resembles that of *Nothrotheriops* (Stock

1925) rather than *Hapalops* (Scott 1903, 1904). It is roughly triangular and hooked posteriorly with a convex anterior border and a concave posterior border. The middle process of the jugal is short and blunt with a flat 'blocked off' posterior edge. The jugal is firmly attached at its base to the maxilla and the lacrimal. In other nothrotheriids, there is a large orbital wing of the jugal that precludes maxillolacrimal contact within the orbit (Gaudin 2004). It is unclear whether this orbital wing is present in *Mionothropus*. There is an area surrounded by two superficial lines, either one of which could represent the posterior border of the jugal. Depending on which is the actual suture, this area might pertain to the jugal or to the frontal or maxilla.

The frontal and parietal have been badly damaged on the left side. However, on the right side, they are well preserved (Text-fig. 2). As noted by Frailey (1986), the blunt postorbital process of the frontal is positioned above M3. A large supraorbital foramen (= foramen for frontal diploic vein in Wible and Gaudin 2004) lies immediately anterior to the postorbital process. The frontal is strongly convex transversely in its posterior half, but flattens out anteriorly. In dorsal view, it narrows as it extends towards the frontoparietal suture. There is a large orbital wing of the frontal that extends ventrally to the level of the maxillary
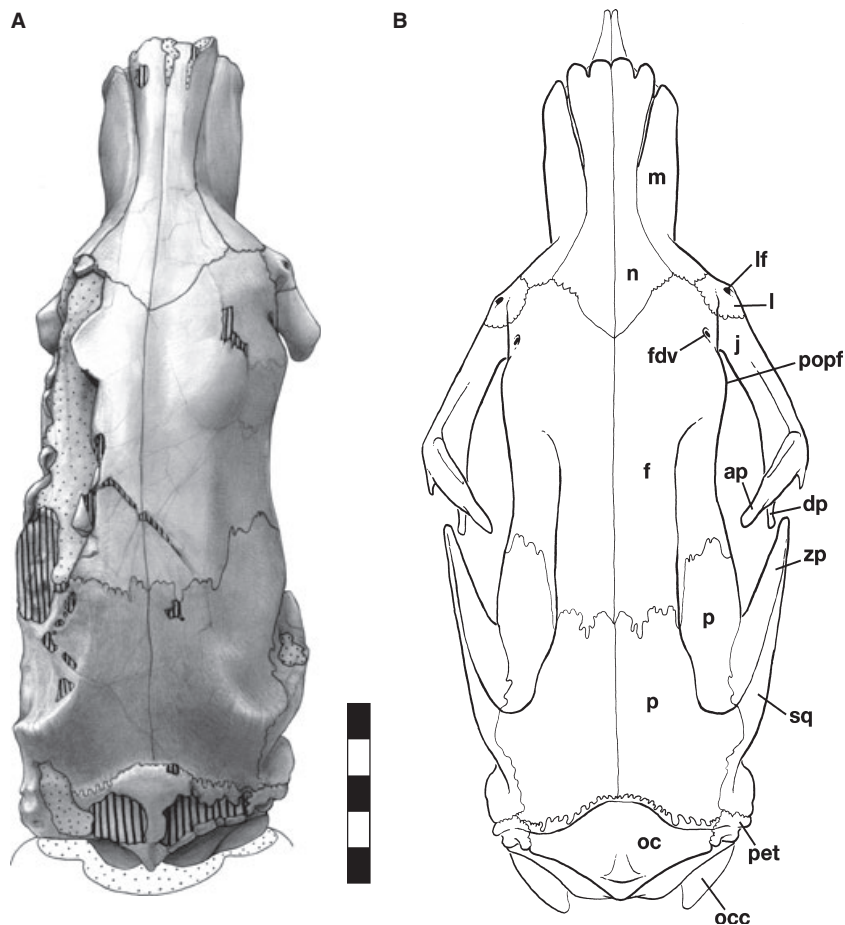
TEXT-FIG. 4. Dorsal view of skull of *Mionothropus cartellei* gen. et sp. nov. A, dorsal view of skull and atlas with premaxilla, zygomatic processes of squamosal, and jugal mostly removed. B, reconstruction of skull in dorsal view. Abbreviations: ap, ascending process of jugal; dp, descending process of jugal; f, frontal; fdv, foramen for frontal diploic vein (= supraorbital foramen); j, jugal; l, lacrimal; lf, lacrimal foramen; m, maxilla; n, nasal; oc, occipital; occ, occipital condyle; p, parietal; pet, petrosal (mastoid exposure); popf, postorbital process of frontal; sq, squamosal; zp, zygomatic process of squamosal. Scale bar represents 5 cm.

and sphenopalatine foramina. It bears a large orbital process that lies dorsolateral to the combined sphenorbital fissure/optic foramen. This process, which is likely a site of origin for extrinsic eye muscles, is continuous posteriorly with a low infratemporal crest that crosses the alisphenoid and squamosal to connect with the anterior edge of the glenoid fossa. The frontal also forms the anterior half of a groove leading out of the combined sphenorbital fissure/optic foramen anteriorly.

The parietal contacts the frontal via an irregularly shaped suture (Text-figs 2, 4). *Mionothropus* has no sagittal crest. The temporal lines are similar to those of *Nothrotheriops* (Stock 1925) and *Nothrotherium* (Reinhardt 1878). The temporal line extends posteriorly from the postorbital process of the frontal across the dorsal surface of the frontal and parietal. It then turns ventrally across the lateral surface of the parietal well in advance of the nuchal crest, becoming continuous ventrally with the dorsal edge of the zygomatic process of the squamosal. This stands in contrast to the condition in *Pronothrotherium* (FMNH P14467) where the temporal lines contact the nuchal crest posterior to the zygomatic process of the squamosal. There is a short anteroventral process of the parietal, but there is no alisphenoid/parietal contact, unlike the condition in *Pronothrotherium* (FMNH P14467), *Nothrotherium* (Reinhardt 1878; Paula Couto 1959), and some *Nothrotheriops* (Stock 1925).

The zygomatic process of the squamosal is preserved only on the right side of the skull (Text-figs 2, 3). This process is not as long (37.8 mm, 14.8 BNL) as that of *Nothrotheriops* (Stock 1925; LACMHC 1300 – 68 mm, 20.6 per cent BNL). It is more similar in size to the zygomatic process of *Pronothrotherium* (FMNH P14467 – 39 mm, 18 per cent BNL). However, the process tapers distally in lateral view, a condition not seen in *Pronothrotherium* (FMNH P14467), *Nothrotherium* (Reinhardt 1878; Cartelle and Fonseca 1983), or *Nothrotheriops* (Stock 1925). As in *Nothrotheriops* (Stock 1925), the zygomatic process is oriented parallel to the long axis of the skull (Frailey 1986) (Text-figs 3, 4). This is a derived condition found in other Plio–Pleistocene nothrotheres (Gaudin 1995, 2004).

The squamosal contacts the parietal dorsally, the frontal anterodorsally, and the alisphenoid anteroventrally (Text-fig. 2). It appears to contact the pterygoid posterior to the foramen ovale. The squamosal forms the dorsal rim of this opening externally, whereas the foramen ovale lies within the alisphenoid internally as in many other sloths (Gaudin *et al.* 1996; Gaudin 2004). The glenoid fossa is present on the right side but missing on the left. It is U-shaped, widening anteriorly. It is gently concave anteroposteriorly and mediolaterally. As noted by Gaudin (1995), the postglenoid region of *Nothrotheriops* (Stock 1925) is characterized by longitudinal grooves and ridges. These are also present in *Mionothropus*. The postglenoid area also contains a small postglenoid foramen. A greatly enlarged entoglenoid process is present posteromedial to the glenoid and anterior to the tympanic (Text-fig. 5B).

The pterygoid is largely intact on both sides of the skull. Its orbital portion is sutured to the palatine anteriorly, and the alisphenoid and the squamosal dorsally. It also contacts the entotympanic posteriorly (Text-fig. 2). The orbital portion forms at least the posteroventral margin of the foramen ovale externally, as in many other sloths (Gaudin *et al.* 1996). There is a large pterygoid exposure in the lateral wall of the nasopharynx. The pterygoid contacts the vomer medially and the basisphenoid posteriorly in the roof of the nasopharynx. The descending lamina of the pterygoid is large and very thin. The descending lamina is shaped like those of *Hapalops* (Scott 1903), *Planops* Ameghino, 1887 and other Santacrucian 'nothrotheres' (Scott 1903, 1904). It is deep with a rounded semicircular ventral edge. In *Nothrotheriops* (Stock 1925) and *Nothrotherium* (Cartelle and Fonseca 1983), the descending lamina is shallower and anteroposteriorly elongated. On the posterior edge of the descending lamina of the pterygoid, there is a deep groove for the tensor veli palatini muscle. This grove is known to be present in a number of other sloth taxa (Patterson *et al.* 1992; Gaudin 1995). The pterygoids of *Nothrotherium* (Reinhardt 1878; Cartelle and Fonseca 1983) and *Nothrotheriops* (Stock 1925) feature a bony bulla. This bulla is unknown in all other sloths except *Choloepus* Illiger, 1811, where it displays a somewhat different construction (Patterson *et al.* 1992; Wetzel 1985). *Mionothropus*, however, possesses a deep medial excavation at the base of the pterygoid descending lamina (Text-figs 3, 5). This excavation was part of a large sinus, as indicated by the presence of a fossa on the roof of the nasopharynx that extends medially to the mid-vomerine ridge and posteriorly onto the surface of the basisphenoid. These depressions suggest the existence of an extensive pterygoid bulla walled by soft tissue. Such a soft-walled bulla could have been the precursor to the bony bullae found in *Nothrotherium* (Reinhardt 1878; Cartelle and Fonseca 1983) and *Nothrotheriops* (Stock 1925).

The portion of the pterygoid exposed in the roof of the nasopharynx is crossed by three open grooves present on each side of the skull. These grooves begin near the vomeropterygoid suture and pass anterolaterally towards the orbital foramina, perforating the descending lamina of the pterygoid to open in the medial wall of the orbit. The anteriormost groove emerges laterally as the combined sphenorbital fissure/optic foramen, the middle as the foramen rotundum, and the posterior groove as the foramen ovale. Such grooves have not been reported in other sloths.

The vomer of *Mionothropus* is the element that unambiguously identifies this skull as pertaining to Nothrotheriinae. The vomer is greatly expanded posteriorly to form the bulk of the central roof of the nasopharynx, likely covering anterior portions of the basisphenoid (Text-fig. 3). It bears a thin, straight, flat-sided, ventrally elongated crest. The crest lies on the midline of the skull posteriorly and extends anteriorly to a position just to the right of the midline as it enters the choanae. All nothrotheriines are characterized by a posteriorly expanded vomer that is broadly exposed in the nasopharyngeal roof and bears the same remarkable, asymmetrical longitudinal crest (Patterson *et al.* 1992; Gaudin 2004). In *Nothrotheriops*, the crest is low with a sigmoid longitudinal curvature (Lull 1929; Patterson *et al.* 1992). It shows a similar condition in *Nothrotherium* (Paula Couto

1980). In *Pronothrotherium* (FMNH P14467), the crest is straight but offset to the left anteriorly. It recurves towards the left along its ventral edge and bears a bulbous expansion at its posterior end (FMNH P14467; see illustration in Patterson *et al.* 1992). In *Mionothropus*, as described above, the crest is straighter, flatter, and much deeper than in *Nothrotheriops, Nothrotherium,* or *Pronothrotherium*. Its depth near the choanae is at least 29 mm (11 per cent BNL). The amount of matrix at its base makes its maximum height hard to determine precisely.

The alisphenoid is preserved almost in its entirety on the right side (Text-figs 2, 3) but is heavily damaged and/or covered by matrix on the left. It is located anteroventral to the squamosal, posterior to the palatine, posteroventral to the frontal, and dorsal to the pterygoid. As noted above, it surrounds the foramen ovale interiorly and forms at least the posterior rim of the foramen rotundum. It clearly forms the posterior wall for the combined sphenorbital fissure/optic foramen. The extent of its participation in the rim of the foramen rotundum and the foramen ovale is difficult to determine because, as noted above, we are unable to determine the position of the alisphenopterygoid suture.

The orbitosphenoid of *Mionothropus* is preserved on the right side of the skull. Its exposure in the medial wall of the orbit is small (Text-figs 2, 3). The orbitosphenoid forms the floor and the medial wall of the groove emerging anteriorly from the combined sphenorbital fissure/optic foramen.

The basisphenoid lies directly posterior to the vomer and pterygoid and medial to the entotympanic (Text-fig. 3). The basioccipitobasisphenoid suture is fused so that we are unable to precisely determine the posterior extent of the basisphenoid. The basicranial surface bears prominent tuberosities anteriorly and is marked by well-developed fossae for the rectus capitis muscles. The basicranial surface is wide and short as in other nothrotheres (Stock 1925; Reinhardt 1878; Cartelle and Fonseca, 1983; Patterson *et al.* 1992; Gaudin 1995).

The occiput is oriented vertically (Text-fig. 2). The left side is poorly preserved while the right side is largely intact. As in other nothrotheres, it has a well-developed supraoccipital exposure on the skull roof (Reinhardt 1878; Stock 1925; Cartelle and Fonseca 1983). Although much of the surface of this supraoccipital exposure has been worn away in *Mionothropus*, the preserved portion appears relatively smooth, in contrast to the moderately rugose surface found on *Pronothrotherium* (FMNH P14467) and the very rugose surface in *Nothrotheriops* (Stock 1925). The supraoccipital exposure bears a strong midline crest in *Nothrotheriops* (Stock 1925). In *Pronothrotherium* (FMNH P14467), the crest is also present but short and weakly developed. Such a midline crest is not observable in *Mionothropus*, though a short crest like that of *Pronothrotherium* may be present. The nuchal crest of *Mionothropus* is prominent, as in *Pronothrotherium* (FMNH P14467) and in contrast to *Nothrotheriops* (Stock 1925). However, as in both *Pronothrotherium* (FMNH P14467) and *Nothrotheriops* (Stock 1925), *Mionothropus* possesses a strong, transverse crest that lies posterior to the nuchal crest for most of its length but is continuous with the nuchal crest laterally. This is likely equivalent to the ventral nuchal crest of dogs (Evans 1993) that serves as the site of attachment for rectus capitis dorsalis muscles. There are distinct excavations immediately ventral

to this ventral nuchal crest, although they are not as deep as those found on *Nothrotheriops* (Stock 1925) or *Pronothrotherium* (FMNH P14467). The external occipital protuberance lies at the midpoint of the ventral nuchal crest. It is damaged but appears to be rather weakly developed in *Mionothropus*, as is the case in *Nothrotheriops* (Stock 1925). In *Pronothrotherium* (FMNH P14467), the external occipital protuberance is quite prominent. There is a distinct external occipital crest in *Mionothropus* extending ventrally from the external occipital protuberance nearly to the dorsal rim of the foramen magnum, as in other nothrotheres (Reinhardt 1878; Stock 1925; Cartelle and Fonseca 1983). The dorsal rim of the foramen magnum is indented dorsally in the midline and flanked by two posteriorly projecting lappets with rounded edges. Again, this is similar to the condition in other nothrotheres (Reinhardt 1878; Stock 1925; Cartelle and Fonseca 1983).

The atlas remains attached to the skull by matrix, covering most of the occipital condyles and the foramen magnum. The condyles are reconstructed in Text-figure 2B based on the morphology in *Nothrotheriops* (Stock 1925).

The ear region is very well preserved on the right side of the skull (Text-figs 3, 5). Much of the lateral surface is badly eroded on the left side of the skull, although at least the medial portions of the ectotympanic ring were preserved. This left ectotympanic was removed from the skull to expose the ventral surface of the petrosal, which we were unable to access on the right side without damaging the underlying ectotympanic and entotympanic.

The ectotympanic is a horseshoe-shaped element, somewhat elongated dorsoventrally as in other xenarthrans (Patterson *et al.* 1989, 1992; Gaudin 1995). It is inclined slightly dorsolaterally to ventromedially, but its long axis in ventral view is essentially parallel to the long axis of the skull as in *Nothrotherium* (Cartelle and Fonseca 1983), *Pronothrotherium, Nothrotheriops*, and many other sloths (Gaudin 1995). The ventral portion of the ring is expanded medially to roughly the same degree as seen in *Pronothrotherium* (Patterson *et al.* 1992) and *Nothrotherium* (Cartelle and Fonseca 1983) – more so than in *Hapalops* but much less than in *Nothrotheriops* (Patterson *et al.* 1992; Gaudin 1995; Gaudin unpubl. data). The recessus meatus appears even shorter than that of *Pronothrotherium* (Patterson *et al.* 1992), with little or no lateral extension of the ectotympanic. There is a strong styliform process ventrally, lying immediately lateral and anterior to the opening for the Eustachian tube. This process is much stronger than that present in *Pronothrotherium* or *Nothrotheriops* (Patterson *et al.* 1992; Gaudin unpubl. data). In further contradistinction to the latter two taxa, the opening for the Eustachian tube is completely enclosed within the ventromedial edge of the ectotympanic. Virtually the entire posterior crus of the ectotympanic is missing on the right side, and on the left, the dorsal half of the anterior and posterior crura was damaged during preparation. However, based on those portions that are preserved, it would appear that the anterior crus is somewhat larger than the posterior (Text-fig. 5A). The anterior crus has a broad but apparently rather loose attachment to the squamosal extending from the Glaserian fissure to the superficies meatus. The anterior crus also appears to have had an extensive medial abutment with the processus crista facialis of the petrosal, a fea-

ture it shares with *Nothrotheriops* (Gaudin unpubl. data) but not with *Pronothrotherium* (Patterson *et al.* 1992). The posterior crus appears to broadly overlap the tympanohyoid posteriorly, although it too is loosely attached to the superficies meatus of the squamosal at its dorsal extremity. The posteroventral surface of the ectotympanic forms the anterior border of the stylohyoid fossa, as in *Pronothrotherium* (Patterson *et al.* 1992).

The entotympanic is well preserved on both the right and left sides of the skull. As in other sloths, it takes the form of an elongated, anteromedially directed ridge suturally attached to the promontorium of the petrosal along its dorsal margin. At its anterior extremity, it forms a triangular dorsal process that extends between the promontorium and pterygoid as in other sloths (Patterson *et al.* 1992; Gaudin 1995). However, in *Mionothropus*, this process extends so far dorsally and laterally that it contacts the medial edge of the processus crista facialis of the petrosal. Posteriorly, the dorsal entotympanic is marked by a deep lateral fossa as in *Pronothrotherium, Nothrotheriops* and mylodontid sloths (Patterson *et al.* 1992; Gaudin 1995), meaning that the entotympanic forms a substantial part of the floor of the tympanic cavity (Text-fig. 5). The entotympanic attaches to the ventral edge of the ectotympanic along its lateral edge, forming a completely ossified auditory bulla. However, as in *Pronothrotherium* (Patterson *et al.* 1992), the entotympanic extends well ventral to the ectotympanic along its entire length. Anteriorly, it is drawn into an elongate, rounded anteroventral process. The anteroventral process of the entotympanic is a characteristic feature of megatherioid sloths (Gaudin 2004). In *Mionothropus*, the anterior margin of the process bears a deep lateral groove that must have accommodated the Eustachian tube. On its medial side, the anteroventral process of the entotympanic abuts the pterygoid. It is unclear whether or not the entotympanic contacts the basisphenoid as well. There is a gap between the entotympanic and the lateral wall of the basicranium that becomes progressively broader posteriorly. The anterior half of this gap is roofed by a medial shelf of the entotympanic. This shelf has a weak ridge along its medial edge, forming a sulcus for the internal carotid artery. The internal carotid presumably enters the braincase via the carotid foramen, the latter hidden from view by matrix and by the contact between the entotympanic and the pterygoid. The anatomy of the internal carotid sulcus in *Mionothropus* is very much like that in *Pronothrotherium* (Patterson *et al.* 1992), whereas in *Nothrotheriops*, the groove for the internal carotid is much deeper, with a raised medial wall (Patterson *et al.* 1992). Behind the internal carotid sulcus of the entotympanic is the very large jugular foramen. The posterior portion of the entotympanic has sutural contacts laterally with the tympanohyoid, and posteriorly with the paracondylar process of the exoccipital. This portion of the entotympanic forms the medial wall of the stylohyoid fossa.

The promontorium of the petrosal resembles that of most other sloths (Patterson *et al.* 1992; Gaudin 1995). It is globose posteriorly and somewhat elongated anteroventrally, this latter portion with a flat lateral surface. The fenestra vestibuli is unusually large, and the rim for the attachment of the annular ligament of the stapes, although covered by matrix, was apparently quite deeply recessed. The fenestra vestibuli is separated posteriorly by a bar of bone from the fenestra cochleae, which is

TEXT-FIG. 5. Close-up of ear region of *Mionothropus cartellei* gen. et sp. nov. A, right lateral view. B, ventral view. Abbreviations: ac, anterior crus of ectotympanic; as, alisphenoid; as/egp, entoglenoid process of alisphenoid; at, atlas; bo, basioccipital; bot, basioccipital tuber; cf, carotid foramen; ec, ectotympanic; en, entotympanic; eo, exoccipital; et, opening for Eustachian tube; fc, fenestra cochleae; fo, foramen ovale; fv, fenestra vestibuli (=f. ovalis); gf, glenoid fossa; glf, Glaserian fissure; gmtvp, groove for m. tensor veli palatini; hf, hypoglossal foramen; ics, sulcus for the internal carotid artery; jf, jugular foramen; nc, nuchal crest; np, nasopharynx; oc, occipital; occ, occipital condyle; p, parietal; pc, posterior crus of ectotympanic; pcp, paracondylar process; pet, petrosal (promontorium); pgf, postglenoid foramen; pop, paroccipital process (=mastoid process); pt, pterygoid; ptc, posttemporal canal; ptl, pterygoid lamina; sf, stylohyoid fossa; sq, squamosal; stmf, stylomastoid foramen; stym, sulcus tympanicus; th, tympanohyoid; zp, zygomatic process of squamosal. Scale bar represents 1 cm.
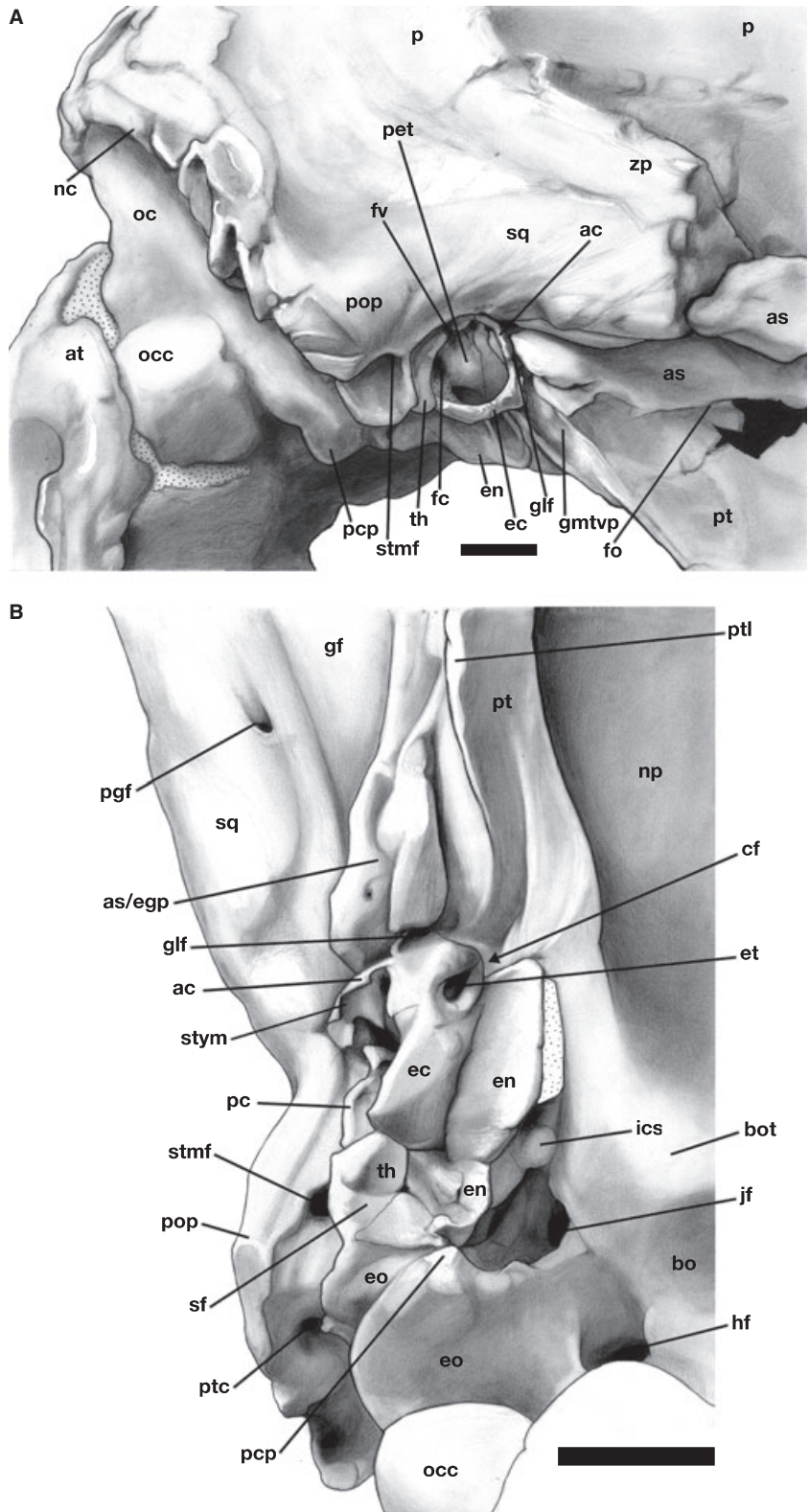
also quite large. As in other sloths (Patterson *et al.* 1992; Gaudin 1995), the fenestra cochleae faces posteriorly and slightly ventro-laterally and is connected medially to a groove that traverses the posterior edge of the promontorium at least as far as its contact with the dorsal edge of the entotympanic. At its anterolateral extremity, the petrosal is developed into a roughly horizontal
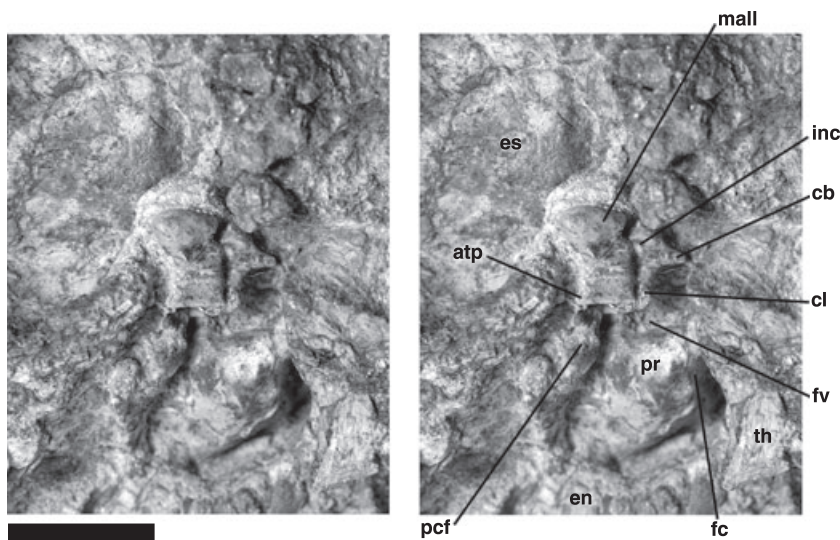
TEXT-FIG. 6. Stereophotographs of the left malleus and incus of *Mionothropus cartellei* gen. et sp. nov. Abbreviations: atp, anterior process of the malleus; cb, crus brevis of the incus; cl, crus longum of the incus; en, entotympanic; es, epitympanic sinus; fc, fenestra cochleae; fv, fenestra vestibuli (=f. ovalis); inc, incus; mall, malleus; pcf, processus crista facialis; pr, promontorium of petrosal; th, tympanohyoid. Scale bar represents 1 cm.

platform, the processus crista facialis (Patterson *et al.* 1989, 1992). The processus in *Mionothropus* is large and rugose, as in *Pronothrotherium* (Gaudin 1995), though not quite as large as that of *Nothrotheriops*, which is exposed on the external surface of the auditory bulla (Gaudin 1995). The posterior edge of the processus hides the primary facial foramen from view laterally. The facial sulcus remains largely obscured by matrix, but at its far posterior end, the crista parotica is attached to a large tympanohyoid element. The tympanohyoid is cylindrical, elongated in a ventral and slightly posterior direction. At its distal extremity, it forms a flat, circular, ventrally and somewhat posteromedially oriented surface that constitutes roughly the anterior and lateral third of the stylohyoid fossa. The medial portion of the fossa incudis is exposed on the ventrolateral edge of the crista parotica on the left side of the skull. The fossa incudis is not fully prepared on the right side, but based on the anatomy of the exposed area on the right, it is clear that the fossa incudis traverses virtually the entire posterior wall of the epitympanic recess, as in other nonmylodontid sloths (Gaudin 1995).

On the left side of the skull, the lateral surface of the squamosal has been eroded away. This allowed us to prepare out a circular cavity connected to the cavum tympani, the epitympanic sinus. There are no clear sutures in the preserved medial wall of the cavity, so that the relative contributions of petrosal and squamosal to the walls of the chamber are not clear. The cavity is relatively smooth walled like that of *Pronothrotherium* (FMNH P14467), although a few small processes like those present in *Bradypus* Linnaeus, 1758 and *Eremotherium* Spillmann, 1948 (Patterson *et al.* 1992) can be seen along what little is preserved of the roof of the cavity. *Nothrotherium*, *Pronothrotherium*, and *Nothrotheriops* all have a distinct lateral bulge in the squamosal, lying at the root of the zygoma, to accommodate the epitympanic sinus (Reinhardt 1878; Patterson *et al.* 1992; Gaudin 1995). *Mionothropus* lacks such a bulge.

Two ossicles were discovered in the space connecting the epitympanic sinus to the cavum tympani on the left side of skull – an articulated malleus and incus preserved in life position

(Text-fig. 6). The malleus is either incompletely preserved or was damaged in preparation. The manubrium and the anterior tip of the anterior process are missing. There is a large transverse crack through the lamina, and a small preserved proximal portion of the neck was lost in preparation. The form of the malleus is much like that described for *Bradypus* in Patterson *et al.* (1992). It has an elongate head with subequal upper and lower incudal facets, the upper facet inclined somewhat ventrally as well as posteromedially. The head of the malleus of *Mionothropus* is much more elongate than that of *Nothrotheriops* (Patterson *et al.* 1992), although in this respect *Mionothropus* resembles the general sloth condition (Patterson *et al.* 1992). The incus appears to be preserved intact, although it is partly obscured anterolaterally by the overlying malleus. Its morphology is like that of other fossil sloths, as described by Patterson *et al.* (1992). It has a squat rectangular body, and the short and long processes are bluntly rounded at their tips and nearly equal in length.

The mastoid is suturally distinct from the squamosal anterolaterally and the occipital posteromedially, except on the large mastoid process (= paroccipital process of Wible and Gaudin 2004), where the squamosomastoid suture is fused (Text-figs 2, 5). The mastoid process is well developed in *Mionothropus*, as it is in all nothrotheriids (Reinhardt 1878; Stock 1925; Cartelle and Fonseca 1983; Patterson *et al.* 1992), although it is somewhat more mediolaterally compressed than is the case in *Pronothrotherium* (Patterson *et al.* 1992) and *Nothrotheriops* (Stock 1925, Gaudin unpubl. data), where the mastoid process is bulbous. As in all sloths (Gaudin 1995), there is a large mastoid exposure on the posterolateral surface of the skull, lying in a depression between the nuchal crest and a vertical crest on the exoccipital (the latter crest extends from the nuchal crest dorsally to the paracondylar process ventrally and is called the 'exoccipital crest' by Gaudin 1995). The mastoid depression is deep, like that of *Nothrotheriops* and in contrast to the condition in *Pronothrotherium* (FMNH P14467), although its surface is not as rugose as that of *Nothrotheriops*. Near the top of this depression is a large ventral process, just below the confluence of the nuchal and exoccipital crests and

likely carried on the exoccipital rather than the mastoid. This process is found in no other nothrotheriid, but presumably served as an additional site of insertion for muscles of the sternocleidomastoid complex (see Windle and Parsons 1899).

The mastoid forms the bulk of the circular stylohyoid fossa (Text-figs 3, 5). Gaudin (1995) notes that the stylohyoid fossa is oval, elongated anteroposteriorly, in *Pronothrotherium* and *Nothrotheriops*. The shape of the stylohyoid articular surface in *Mionothropus* resembles the general condition among sloths. The medial wall of the stylohyoid fossa is formed by the entotympanic, which participates only to a slight degree in the anteromedial portion of the articular surface. The remainder of the articulation is formed by the tympanohyoid and the mastoid region of the petrosal. The paracondylar process of the exoccipital (=paroccipital process of Patterson *et al.* (1992); Gaudin (1995)) is larger than that of *Pronothrotherium* (Patterson *et al.* 1992), comparable in its degree of development to that of *Nothrotheriops* (Gaudin 1995). However, unlike the latter taxon, the paracondylar process of *Mionothropus* does not participate in the stylohyoid fossa.

The internal carotid artery travelled in a wide groove between the entotympanic and basicranium (Text-fig. 5). As noted previously, this groove is roofed anteriorly by the medial shelf of the entotympanic. The internal carotid passed through a carotid canal lying between the medial shelf of the entotympanic, the anteroventral process of the entotympanic, and the lateral surface of the pterygoid. It almost certainly passed into the braincase via the carotid foramen, which is hidden ventrally by the contact of the anteroventral process of the entotympanic with the pterygoid. The Glaserian fissure is a discrete foramen lying between the anterior crus of the entotympanic posteromedially and the entoglenoid process of the squamosal anterolaterally. In *Nothrotheriops*, the Glaserian fissure is also medial to the entoglenoid process (Gaudin, 1995), whereas in *Pronothrotherium* (contra Gaudin 1995), the Glaserian fissure appears to bisect the entoglenoid process, traversing its ventral surface in a condition much like that illustrated in *Thalassocnus natans* Muizon and McDonald, 1995 (see McDonald and Muizon 2002, fig. 4A). The stylomastoid foramen emerges into a posteroventrolaterally directed groove in the mastoid, immediately behind a bridge of bone connecting the anterior crest of the mastoid process to the base of the tympanohyoid. The posterior crus of the ectotympanic is excluded from the margins of the stylomastoid foramen, as in *Nothrotheriops* (Gaudin unpubl. data) and *Nothrotherium* (Cartelle and Fonseca 1983), but in contrast to the condition in *Pronothrotherium* (Patterson *et al.* 1992). As in *Pronothrotherium* and *Nothrotheriops* (Gaudin 1995), there is a dorsally directed groove for the occipital artery immediately behind the stylomastoid groove. The former groove terminates at the entrance to a canal that perforates the mastoid process, leading to two foramina on the lateral surface of the skull, posterodorsal to the mastoid process and just anterior to the nuchal crest. These latter foramina are evidently unique to Nothrotheriidae (Gaudin 1995). The posttemporal foramen for the arteria diploetica magna (*sensu* Rougier *et al.* 1992) presumably opens internally within the canal for the occipital artery. As in other nothrotheriids (Cartelle and Fonseca 1983; Patterson *et al.* 1992), the jugular foramen is large and broadly confluent anteriorly with the internal carotid sulcus.

Its ventral margins are formed by the exoccipital posteriorly, the entotympanic anteriorly and laterally, and the basioccipital medially. There is a single, large hypoglossal foramen posteromedial to the jugular foramen, and separated from it by a wide bar of bone. In *Pronothrotherium*, the hypoglossal foramen is ventral to the ventral margin of the jugular foramen. The hypoglossal foramen is somewhat recessed dorsally in *Mionothropus*. It is even more recessed in *Nothrotheriops* (Gaudin unpubl. data).

Mandible. The horizontal ramus of the mandible is shallow dorsoventrally (Text-fig. 7), whereas the horizontal ramus in *Nothropus* is quite robust (Burmeister 1882; Ameghino 1907). The coronoid process, largely missing on the left, fully intact on the right, is sloped posterodorsally. This process is low, barely rising above the condyle. In this sense, it resembles *Nothropus tarijensis* (Ameghino 1907) more than *N. priscus* (Burmeister 1882). It is pointed at its distal extremity and broad anteroposteriorly at its base, as in *Nothrotherium* (Cartelle and Fonseca 1983) but in contrast to the coronoid in at least some *Nothrotheriops* (Gaudin, 2004), in which the coronoid is narrow anteroposteriorly (but see, e.g. Stock 1917, fig. 6, or Wilson 1942, fig. 1, where the coronoid process is much broader). There is a strong ridge extending along the anterior edge of the coronoid on its medial face. This ridge is not present in other nothrotheriids, although it is found in other sloths (Gaudin 2004). The angular process is elongated, shallow, and bulges ventrally. The angular process is much deeper than that illustrated for *Nothrotheriops* by Stock (1925) but is similar in depth to the angular process of *Nothrotherium* (Reinhardt 1878; Cartelle and Fonseca 1983) and of other specimens of *Nothrotheriops* described in the literature (Stock 1917; Lull 1929; Naples 1990). There is a deep fossa on the medial side of the angular process, as is typical for sloths (Gaudin 2004). This fossa presumably serves as the site of origin for the medial pterygoid muscle (Naples 1987; Evans 1993). The ridge that forms the ventral boundary to this fossa becomes lower anteriorly but curves anteriorly and then dorsally to connect with the medial ridge on the anterior edge of the coronoid. The mandibular foramen lies roughly 9 mm behind the confluence of these two crests, slightly dorsal to the level of the tooth row. The condylar process is thin transversely, relatively short and thick dorsoventrally with a prominent lateral ridge distally. The condyle, preserved only on the right, is damaged medially but nevertheless clearly bears a medial hook-shaped extension. The condyle as a whole is irregularly ovoid with its long axis oriented transversely in dorsal view. The articular surface faces slightly posteriorly and is strongly convex mediolaterally. The lateral half of the articular surface faces dorsolaterally, whereas the medial portion faces almost directly mediad. It would appear that this medial portion is somewhat elongated anteroposteriorly, whereas the lateral portion is elongated transversely in dorsal view. The posteroexternal opening of the mandibular canal opens lateral to the ascending ramus, in a position very similar to that of *Nothropus priscus* (Burmeister 1882). The symphysis takes the form of an elongate mandibular spout, as in other nothrotheriids. In *Mionothropus,* the spout has a straight ventral edge in lateral view, in contrast to the somewhat ventrally concave spout of *Nothrotherium* (Cartelle and Fonseca 1983) and the strongly concave ventral mar-
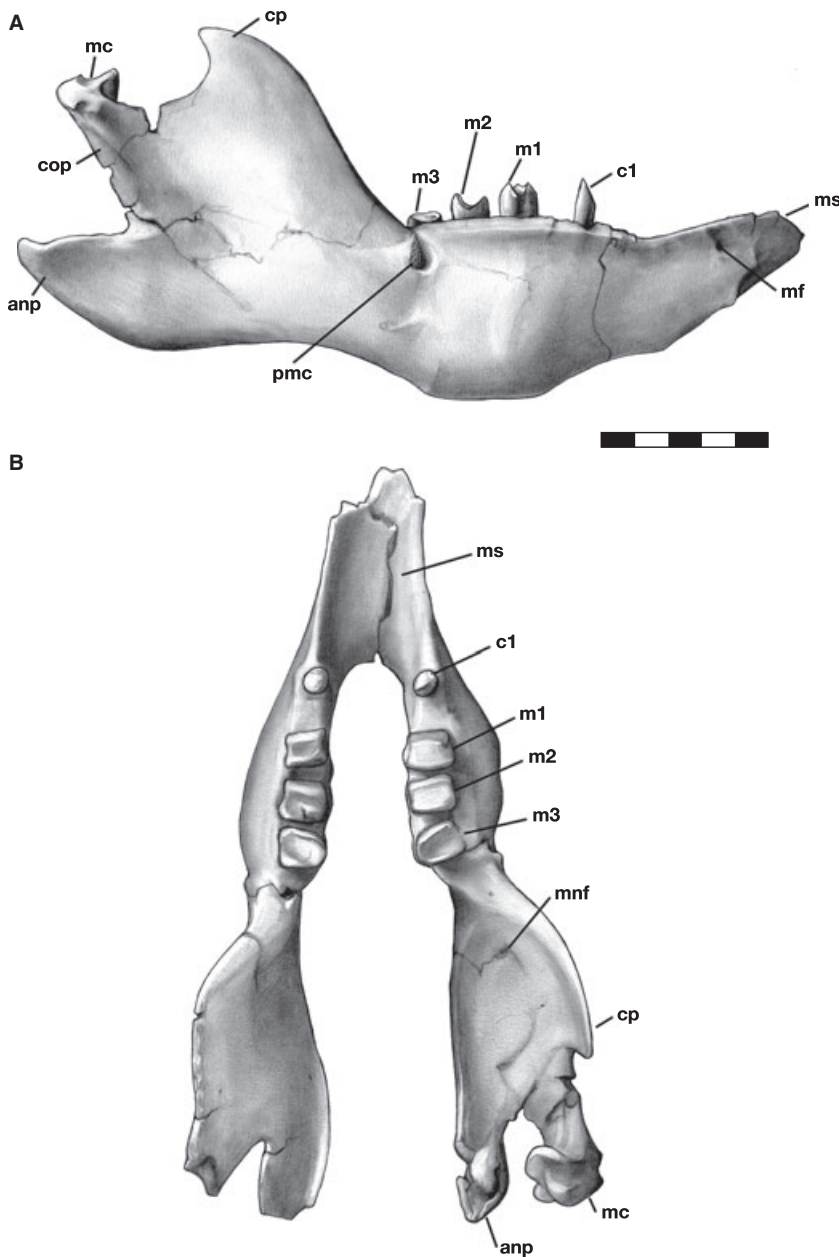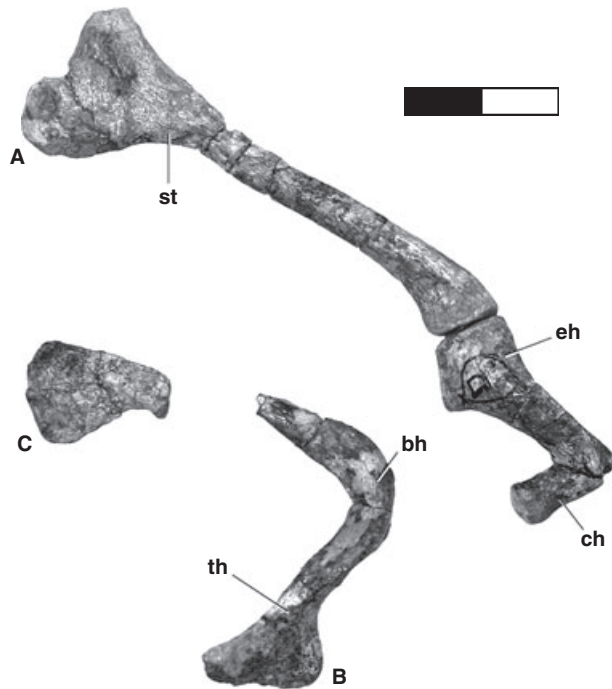
TEXT-FIG. 7. Mandible of *Mionothropus cartellei* gen. et sp. nov. A, right lateral view. B, occlusal (dorsal) view. Abbreviations: anp, angular process; c1, lower caniniform; cop, condyloid process; cp, coronoid process; m1–3, first through third lower molariforms; mc, mandibular condyle; mf, mental foramen; mnf, mandibular foramen; ms, mandibular spout/symphysis; pmc, posteroexternal opening of the mandibular canal. Scale bar represents 5 cm.

gin of the spout in *Nothrotheriops* (Stock 1925). There is a small caniniform. It is oval in section and strongly worn obliquely with the wear facet facing anteriorly. It is followed by a diastema. The upper and lower teeth of *Mionothropus* have been thoroughly described by Frailey (1986), and the reader is referred to that work for further details.

Hyoid apparatus. The elements of the hyoid apparatus of *Mionothropus cartellei* (Text-fig. 8) are preserved but were not recovered *in situ*. The stylohyoid is a long slender element, more so than that of *Paramylodon harlani* (Owen, 1839) (Stock 1925, pl. 27, fig. 2) and resembling more that of *Megatherium americanum* Cuvier, 1796 (MNHN PAM 297) in this respect. Proximally, however, the element is much less rugose than in the latter species. The proximal protuberance articulating with the

stylohyoid fossa is blunt. The muscular angle is a large and thin flange, concave both laterally and, more deeply so, medially. The body is a slender, mediolaterally compressed and gently sinuous rod, with a nearly flattened medial surface and slightly convex lateral surface, the reverse of the condition described by Stock (1925) for *Nothrotheriops*. Distally, the stylohyoid expands slightly and bears an oval surface, oriented obliquely to the long axis, for articulation with the epihyoid. The latter is a stockier and shorter element, deeper proximally than distally. The presumed right epihyoid, based on its articular relationship with the right stylohyoid, has a ventrolaterally directed flange just ventral to the articular surface for the stylohyoid. The distal end bears a surface, oriented obliquely to the long axis, for the ceratohyoid, a small nearly cylindrical element, the proximal facet of which, for the epihyoid, is also set on a strongly oblique

TABLE 2. Measurements of postcranial elements of *Mionothropus cartellei* gen. et sp. nov.

Humerus	
Maximal length	327
Maximal proximal width, between tubercles	77
Maximal distal width, between epicondyles	119
Head, anteroposterior depth	48
Head, transverse width	42
Anteroposterior depth, at maximal anterior projection of deltopectoral shelf	43*
Maximal width, distal articular surface	69
Radius	
Maximal length	309
Head, anteroposterior depth	31
Head, transverse width	37
Minimal width, neck	28
Diaphyseal width, at pronator ridge	43
Minimal diaphyseal width, distal to pronator ridge	41
Anteroposterior depth at midshaft	17
Maximal distal transverse width	55
Maximal distal anteroposterior depth	38
Ulna	
Maximal length	338
Olecranon length	128
Maximal olecranon width	31
Anteroposterior depth at anconeal process	48
Anteroposterior depth at coronoid process	67
Transverse width, proximal articular surface	54
Transverse width at midshaft	21
Anteroposterior depth at midshaft	31
Maximal distal transverse width	26
Maximal distal anteroposterior depth	23
Transverse width, distal articular surface	22
Femur	
Maximal length (head to lateral articular condyle)	333
Head, anteroposterior depth	60
Head, transverse width	57
Proximal width, head to greater trochanter	131
Distal width, across epicondyles	122
Midshaft width	93
Anteroposterior depth at midshaft	36
Width, patellar trochlea	49

Measurements in mm.
*Estimated measurement.

TEXT-FIG. 8. Hyoid apparatus of *Mionothropus cartellei* gen. et sp. nov. A, articulated right stylohyoid (sh), epihyoid (eh), and ceratohyoid (ch) in dorsal to ventral order in lateral view. B, V-shaped bone, including basihyoid (bh) and thyrohyoid (th) in dorsal view. C, scrap of bone possibly representing remnant of ossified thyroid cartilage. Scale bar represents 2 cm.

surface so that an acute angle is formed between these hyoid elements and the ceratohyoid is oriented posteroventrally. The presumed right ceratohyoid is preserved completely but the left is missing its distal end. The distal end of the ceratohyoid contacts the basihyoid, which as in sloths generally is fused to the thyrohyoids to form a V-shaped element (Stock 1925). The proximal half of the thyrohyoid is a slender rod but its distal end (preserved only for the right thyrohyoid) expands markedly, resembling *M. americanum* (MNHN PAM 297). A scrap of bone (Text-fig. 8C) recovered from the matrix in the pharyngeal region may represent the distal left thyrohyoid based on its overall shape but may also represent a remnant of ossified thyroid cartilage, as occurs in *P. harlani* (Stock 1925). See Perez *et al.* (2010) for a morphofunctional analysis of the hyoid apparatus of *Mionothropus* and other xenarthrans.

Humerus. Measurements for postcranial elements are provided in Table 2. The right humerus is nearly complete (Text-fig. 9). Only small portions are missing from the margins of the deltoid crest and proximal part of the supinator plate. Of the left humerus, only the proximal half (missing most of its anterior surface, head, and greater trochanter) and the distolateral third, including the entepicondylar foramen and trochlea, are preserved.

The humerus of *Mionothropus* has a proximal, subcylindrical proximal portion that widens markedly into a flattened distal portion, as is the case in nearly all sloths except mylodonts. The head is oval in proximal view, with its major axis oriented ante-

roposteriorly, as in *Nothrotherium*, rather than mediolaterally as in *Nothrotheriops* (Stock 1925, pl. 8, 2a). It is as 'exposed' between the tubercles in anterior view as in *Hapalops elongatus* Ameghino, 1891 and *Nothrotherium*; it is less evident in anterior view in *Nothrotheriops*. The tubercles are widely separated, with the lesser tubercle larger than the greater tubercle, as in *Hapalops* (Scott 1904, pl. 41). The tubercles are subequal in *Nothrotheriops* (Stock 1925, pl. 8; McDonald 1985) and *Nothrotherium* (Reinhardt 1878; pers. obs.). In *Mionothropus* and *Hapalops,* the lesser tubercle projects farther proximally than the greater tubercle, whereas in *Nothrotheriops,* the tubercles project to approxi-

TEXT-FIG. 9. Right humerus of *Mionothropus cartellei* gen. et sp. nov. A, anterior view. B, posterior view. Scale bar represents 10 cm.

mately the same level and in *Nothrotherium,* the greater tubercle extends farther proximally. The bicipital groove is broad and shallow in all genera. A groove crosses obliquely over the anterior surface of the lesser tuberosity. A similar groove is present in *Nothrotherium* and *Nothrotheriops* but is apparently shallower in *Hapalops*.

The deltopectoral shelf is a raised, flattened, distally tapered structure on the central third of the anterior diaphyseal surface (Text-fig. 9A). It is defined medially by the pectoral ridge and laterally by the deltoid ridge. The latter begins on the lateral diaphyseal surface, just distal to the greater tubercle. The pectoral ridge begins just distal to the head about midway between the tubercles. The ridges become more pronounced distally and converge to form a strongly raised triangular eminence. A third, short, and pronounced ridge (probably for the cephalohumeralis muscle) lies between the pectoral and deltoid ridges as they converge distally. The deltopectoral shelf is strongly developed and prominently raised in *Hapalops* (Scott 1903, pl. 30), in which both the deltoid and pectoral ridges are strongly raised into crests and flared, although the deltoid projects more laterally than the pectoral does medially. In *Mionothropus,* the shelf is raised but not to the same degree as in *Hapalops*. Both ridges are also less prominently developed and flared, although for the deltoid ridge this may be an artefact because of breakage along its margin. The shelf is considerably less prominent in *Nothrotherium* and *Nothrotheriops shastensis*, in large part because of a weaker pectoral ridge, and the shelf is essentially reduced to a triangular eminence on the diaphyseal surface. In contrast is the

condition in *Nothrotheriops texanus* (Hay, 1916) (McDonald 1985, fig. 2, 1), in which the deltoid ridge is particularly prominent and laterally projecting, although the pectoral ridge remains little developed and the shelf little raised (i.e. resembling *N. shastensis*).

The deltoid ridge and the supinator ridge define the musculo-spiral grove (McDonald 1985), which forms a rounded notch on the lateral surface of the humerus (Text-fig. 9). This notch is more strongly defined in *N. texanus* than in *Hapalops*. The groove is considerably less well defined, in anterior view, in *Nothrotherium, Mionothropus,* and *Nothrotheriops shastensis*, and a notch is not present.

The ectepicondyle and entepicondyle are robust, as in *Nothrotherium, Nothrotheriops,* and *Hapalops*. In *Mionothropus* and *Hapalops,* the supinator ridge is nearly vertical as it extends proximally from the ectepicondyle, so the supinator plate appears large and squared. In *Nothrotherium* and *Nothrotheriops,* the supinator ridge gently slopes proximomedially, so the supinator plate appears smaller and triangular. The trochlea, for articulation with the ulna, is more prominent anteroposteriorly in *Mionothropus* and *Hapalops* than in *Nothrotheriops* and mediolaterally wider relative to the capitulum in *Mionothropus* and *Hapalops* compared to *Nothrotherium* and *Nothrotheriops*. The entepicondyle is drawn proximomedially into a strong protuberance in *Mionothropus,* but not in *Nothrotherium* and *Nothrotheriops*. In *Hapalops,* it is more strongly developed than in *Mionothropus* and forms a hook-like process.

Radius. The right radius is nearly complete (Text-fig. 10A, B), whereas the left preserves only the distal half, lacking the epiphysis. The radius of *Mionothropus* is gracile and relatively elongated, resembling the condition in *Nothrotheriops* (Stock 1925) and *Nothrotherium* (MCL 1020/39), rather than that in *Hapalops* (Scott 1903, 1904). In medial or lateral view, the radius is nearly rectilinear along its longitudinal axis in *Hapalops, Mionothropus,* and *Nothrotheriops*, whereas in *Nothrotherium*, it is markedly bowed anteriorly. The head and the concave capitular facet it bears proximally are oval, with the major axis oriented mediolaterally. In *Mionothropus,* the head and capitular facet are inclined, so that they project farther proximally laterally than medially, resulting in a peaked lateral margin. The inclination and angle of the lateral portion of the head seem more marked in *Hapalops,* but less so in *Nothrotherium* and, particularly, *Nothrotheriops*. The articular circumference is centred on the lateral surface, just distal to and contiguous with the capitular facet. It is expansive, extending onto the anterior and posterior surfaces of the head.

The neck is constricted, similarly to that of *Nothrotheriops* and *Hapalops*, and more so than that of *Nothrotherium*. The bicipital tuberosity is well developed in *Hapalops* and *Mionothropus* and larger than in *Nothrotheriops* and *Nothrotherium*. In the last three genera, the bicipital tuberosity is on the posterolateral surface and projects mainly posteriorly, whereas in *Hapalops,* it lies more towards the lateral surface and projects laterally in anterior view.

Distal to the tuberosity, the diaphysis curves medially to about one-third the length of the diaphysis in *Mionothropus, Nothrotherium,* and *Nothrotheriops*. From this point, at which the

TEXT-FIG. 10. Right forelimb elements of *Mionothropus cartellei* gen. et sp. nov. Radius in A, posterior and B, lateral views; ulna in C, lateral, D, anterior and E, medial views. Scale bar represents 10 cm.

diaphysis is at its widest, the diaphysis extends distally along a nearly proximodistal course. This configuration produces a bend in the radius, so that the distal end is offset medially with respect to the proximal end, as occurs in many other sloths, including megatheriines. At the level of the bend, the diaphysis bears a prominent medial muscular scar, probably for the insertion of the pronator teres. Distally from this scar, the lateral and medial surfaces in *Mionothropus* are nearly parallel and curved slightly so that the medial margin is concave and the lateral margin is convex (apparently because of a well-developed interosseus crest). In *Nothrotheriops* and *Nothrotherium,* the medial and lateral margins are shallowly concave. In *Hapalops,* both margins are slightly concave.

The radius of *Hapalops* differs in several regards from the conditions just described. The bend in the diaphysis, for example, is more pronounced in *Hapalops*, producing a greater degree of offset between the proximal and distal ends of the bone. Also, the position of the bend occurs relatively more distally, so that the portion of the diaphysis distal to it seems less elongated and gracile. This portion of the diaphysis also appears to widen slightly distally. Lastly, the scar for the pronator teres is more prominent. These features together position the scar at the midlength of the radius.

In all the genera, the radius widens at its distal epiphysis. The distal articular surface bears the large, concave, and mediolaterally elongated surface for articulation with the lunar and scaphoid of the carpus.

Ulna. The right ulna is nearly complete, missing only small portions of its posterior surface and the lateral margin of the trochlear notch (Text-fig. 10C–E). The olecranon process is long and robust in *Mionothropus* and *Hapalops* (Scott 1903, pl. 32, fig. 4; 1904, pl. 42, fig. 5), shorter in *Nothrotheriops* (Stock 1925, pl. 9, fig. 1) and *Nothrotherium* (MCL 1020/38). The medial part of the trochlear notch, for articulation with the humeral

capitulum, is semicircular in medial view. The coronoid process projects moderately anteriorly, approximately to the same degree as in *Nothrotherium* and more so than in *Hapalops*. In contrast, it projects markedly in *Nothrotheriops*. The anconeal process largely reverses this trend. It is about equally prominent in *Mionothropus* and *Hapalops*, in which it overhangs the articular surface. In the latter, with the relatively weak coronoid process, the anconeal and coronoid processes project anteriorly to about the same level. The anconeal is weaker in *Nothrotherium* and weakest in *Nothrotheriops*. The ulna of *Mionothropus* is gracile compared with that of *Nothrotheriops* and *Nothrotherium* in that the diaphysis gradually narrows distally in lateral or medial view. There is a very slight expansion of the anterior surface just before the diaphysis narrows abruptly into the lateral styloid process. In *Hapalops,* the ulna is less elongated but resembles that of *Mionothropus* in tapering slightly distally. In *Nothrotheriops* and *Nothrotherium,* the stout diaphysis retains its anteroposterior thickness throughout almost its entire length. Its very distal portion narrows and supports articular facets for the radius and cuneiform. In *Nothrotherium,* the diaphysis constricts somewhat in its central portion and expands slightly distally before constricting again. In *Nothrotherium* and *Nothrotheriops,* both the anterior and posterior surfaces converge distally. In *Mionothropus,* the posterior surface remains essentially linear; narrowing of the distal end is because of the slope of the anterior surface. The posterior surface of the ulna is lightly convex in *Mionothropus* and *Nothrotheriops*, and more strongly so in *Hapalops*. In *Nothrotherium,* it is slightly concave.
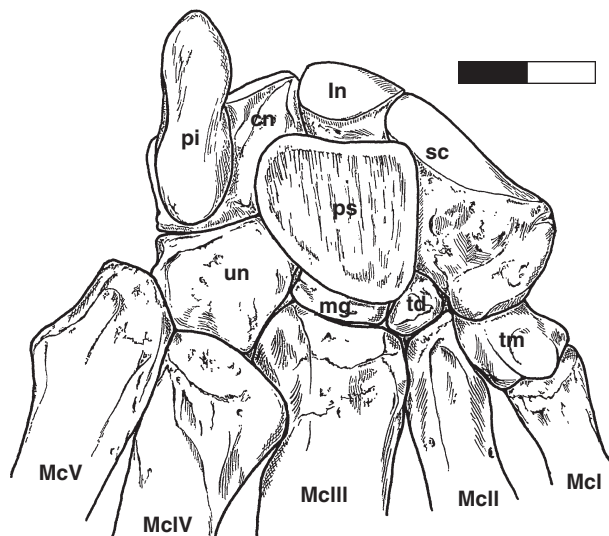
Carpals. The manus includes seven carpals (Text-fig. 11). The proximal row includes, in medial to lateral order, scaphoid, lunar, and cuneiform; the distal row the trapezium, trapezoid, magnum, and unciform. As described by Cartelle and Fonseca (1983) for *Nothrotherium*, large ossifications associated with the
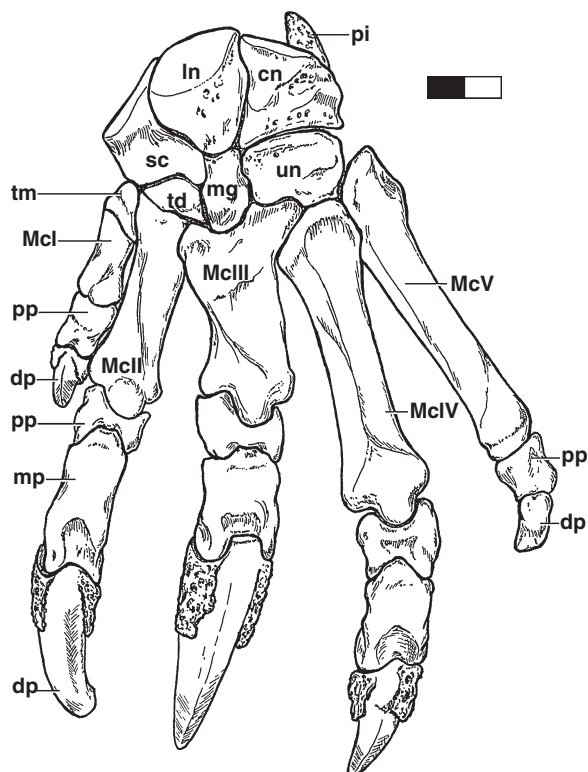
TEXT-FIG. 11. Left manus of *Mionothropus cartellei* gen. et sp. nov. in dorsal view. Abbreviations: cn, cuneiform; dp, distal phalanx; ln, lunar; Mc I, metacarpal I; Mc II, metacarpal II; Mc III, metacarpal III; Mc IV, metacarpal IV; Mc V, metacarpal V; mg, magnum; mp, middle phalanx; pi, pisiform; pp, proximal phalanx; sc, scaphoid; td, trapezoid; tm, trapezium; un, unciform. Scale bar represents 2 cm.

TEXT-FIG. 12. Left carpus of *Mionothropus cartellei* gen. et sp. nov. in palmar view. Abbreviations: cn, cuneiform; ln, lunar; Mc I, metacarpal I; Mc II, metacarpal II; Mc III, metacarpal III; Mc IV, metacarpal IV; Mc V, metacarpal V; mg, magnum; pi, pisiform; ps, palmar sesamoid; sc, scaphoid; td, trapezoid; tm, trapezium; un, unciform. Scale bar represents 2 cm.

carpus are the pisiform and palmar sesamoid (Text-fig. 12). In this genus, fusion occurs between the trapezoid and magnum (Cartelle and Fonseca 1983), but fusion does not occur among carpals in *Mionothropus*, *Nothrotheriops*, and *Hapalops*.

Cuneiform. The proximal surface of the cuneiform is almost entirely covered by the nearly flat and rectangular articular facet for the ulna (Text-fig. 13A–C). A small palmolateral portion of the facet's margin is contiguous with the small facet for the pisiform, which occupies a small portion of the cuneiform's palmar surface. The medial surface is nearly entirely articular, with all but a narrow distal strip given over to the large facet for the lunar. It conforms in shape to that of the lunar's cuneiform facet, described below, except that it is strongly convex. The narrow distal strip contacts the magnum. Distally, the cuneiform articulates with the unciform via a large triangular facet, with base oriented medially and apex laterally. The cuneiform is proximodistally deeper in *Mionothropus*, *Nothrotherium* (Cartelle and Fonseca 1983, fig. 10), and *Nothrotheriops* (ROM 44928; Paula Couto 1974, figs 1, 2) than in *Hapalops* (Scott 1903, pl. 33, fig. 2). In the latter, it is also more nearly triangular, tapering laterally. In the other three genera the lateral surface is deeper, giving the cuneiform a blockier, almost rectangular shape.

Lunar. The medial surface of the lunar bears the facet for the scaphoid, which corresponds in shape to that of the scaphoid for the lunar (Text-fig. 13). Proximally, the facet for the radius forms a dorsopalmarly elongated and markedly convex surface. Distally, the lunar bears an oval, dorsopalmarly elongated, and markedly dorsopalmarly concave facet mainly for the magnum. A small dorsomedial strip of this surface contacts the wedge-shaped projection of the scaphoid (see below). On the lateral surface is the large irregularly shaped and deeply dorsopalmarly concave facet for the cuneiform. Its distal margin is extensively contiguous with that for the magnum. In dorsal view, the contact between the lunar and magnum is most extensive in *Hapalops* (Scott 1903, pl. 33, fig. 2), followed by *Nothrotheriops* (ROM 44928; Paula Couto 1974, figs 1, 2) and then *Nothrotherium*. In the latter, the magnum and lunar appear not to make contact, mainly because of the size of the proximolateral part of the scaphoid, in the specimen described by Cartelle and Fonseca (1983, fig. 10). The magnum is not preserved in the specimen illustrated by Winge (1915: pl. 24, left image), but the magnum probably contacted the lunar, approximately as in *Nothrotheriops*, judging from the space between the proximal ends of the cuneiform and scaphoid.

Scaphoid. Viewed proximally or distally, the scaphoid (Text-fig. 13G–I) comprises, as is usual among sloths, a large lateral half and a tapered medial half. The proximal surface bears a large, nearly triangular, and gently undulating articular surface for the radius. The tapered medial part of the scaphoid extends nearly posteromedially. The lateral surface of the scaphoid bears an extensive surface for articulation with the lunar and magnum. Much of this surface, articulating with the lunar, extends dorsopalmarly along the proximal half of the lateral surface and has a
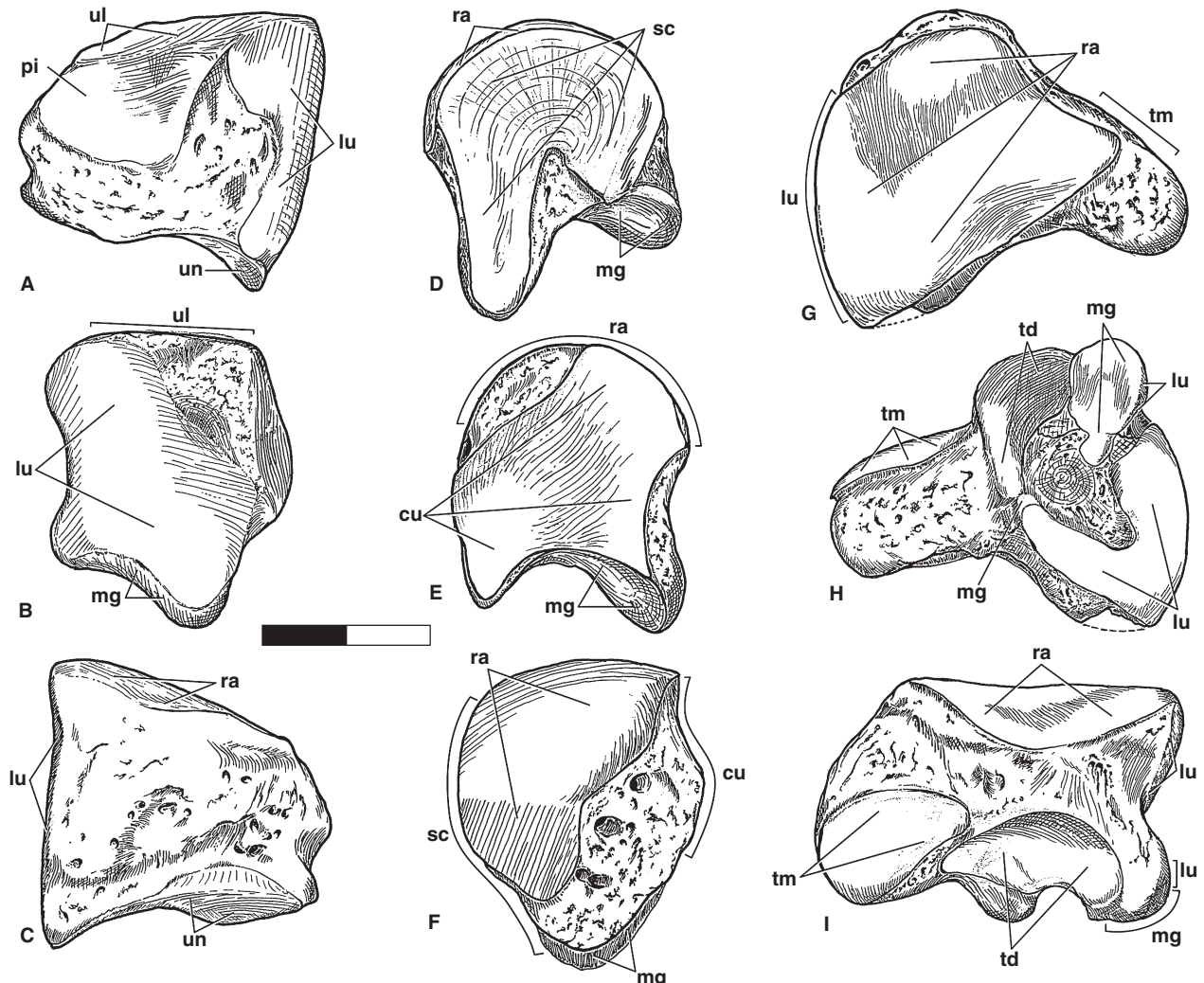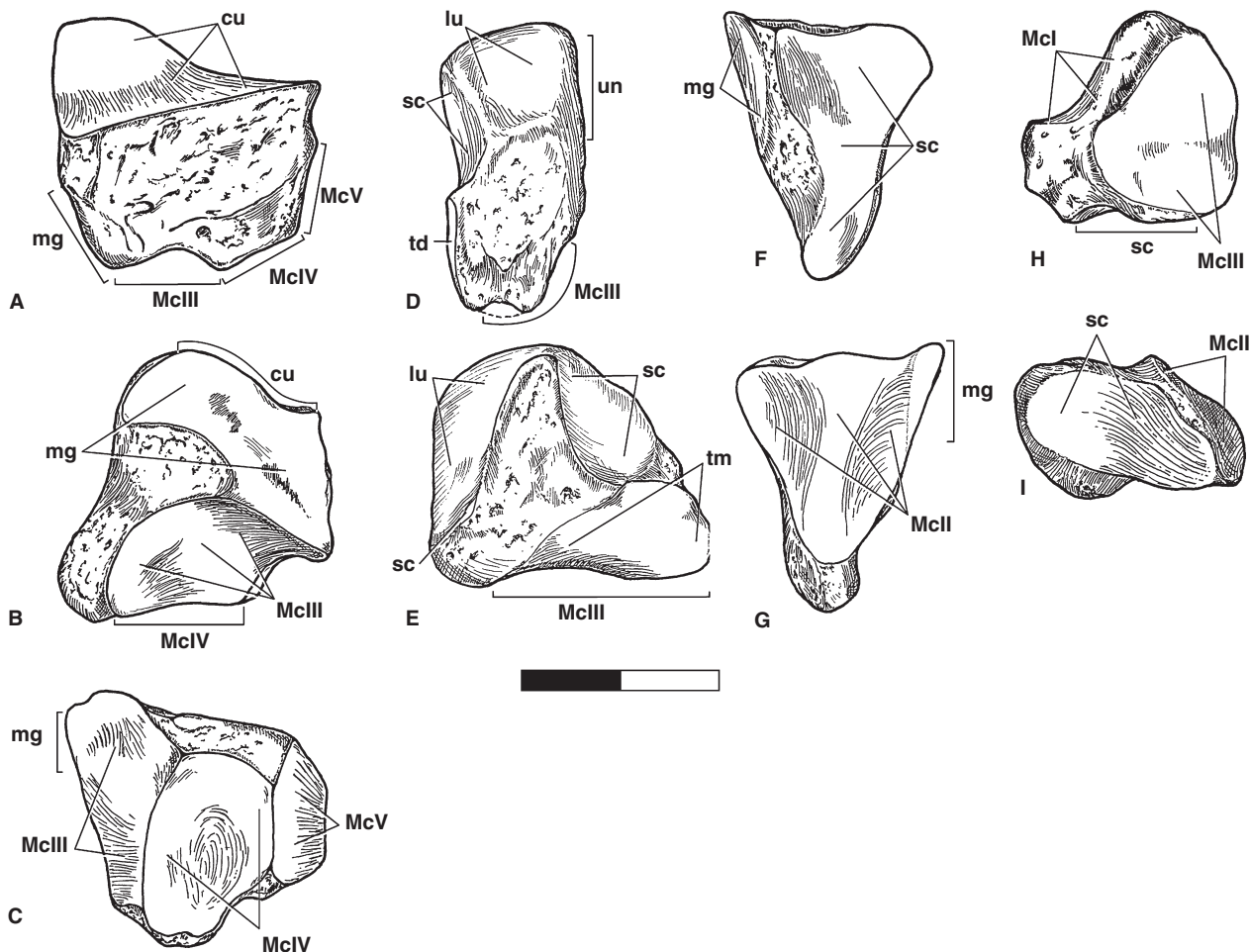
TEXT-FIG. 13. Left proximal carpals of *Mionothropus cartellei* gen. et sp. nov. A–C, cuneiform in palmar (proximal towards top, lateral towards left), medial (proximal towards top, palmar towards left), and dorsal (proximal towards top, medial towards left) views, respectively. D–F, lunar in medial (proximal towards top, palmar towards left), lateral (proximal towards top, palmar towards right), and palmar (proximal towards top, lateral towards right) views, respectively. G–I, scaphoid in proximal (dorsal towards top, lateral towards left), distal (dorsal towards top, lateral towards right), and dorsal (proximal towards top, lateral towards right) views, respectively. Abbreviations: cn, cuneiform; lu, lunar; mg, magnum; pi, pisiform; ra, radius; sc, scaphoid; td, trapezoid; tm, trapezium; ul, ulna; un, unciform. Scale bar represents 2 cm.

narrow elongated extension palmarly. The surface for the lunar continues onto the lateral surface of the blocky extension of the scaphoid that extends between the proximal halves of the trapezoid and magnum. The distal end of the extension bears the small, approximately oval and distopalmarly facing facet for the magnum. The facet for the trapezoid occupies approximately the central third of the distal surface of the scaphoid. The facet is wider dorsally than palmarly. A portion of the facet lies on the medial surface of the scaphoid's blocky extension. Medially, next to the trapezoidal facet is the facet for the trapezium, which is a markedly convex, elongated, and oval surface. The extension is much smaller and wedge shaped in *Hapalops* (Scott 1903, pl. 33, fig. 2). It is blocky and larger in *Nothrotheriops* (ROM 44928; Paula Couto 1974, figs 1, 2) and particularly *Nothro-*

therium (Cartelle and Fonseca 1983, fig. 10). In these last two genera, the lateral end of the process is squared. In the *Nothrotherium* specimen described by Cartelle and Fonseca (1983, fig. 10), it extends laterally to the level of the articulation between the lunar and cuneiform, but in the specimen illustrated by Stock (1925, fig. 28), the projection is approximately as is *Nothrotheriops*. The condition of this projection is partly reflected in the shape of the magnum, as discussed below.

Unciform. The unciform is oddly shaped (Text-fig. 14A–C). Its proximal surface has a blunt medial projection partly surrounded by a flattened surface, which together bear the approximately triangular facet for the cuneiform. Medially, the unciform articulates with the magnum. The distal surface of the

TEXT-FIG. 14. Left distal carpals of *Mionothropus cartellei* gen. et sp. nov. A–C, unciform in dorsal (proximal towards top, medial towards left), medial (proximal towards top, palmar towards right), and distal (dorsal towards top, medial towards left) views, respectively. D, E, magnum in dorsal (proximal towards top, medial towards left) and medial (proximal towards top, palmar towards left) views, respectively. F, G trapezoid in dorsal (dorsal towards top, lateral towards left) and distal (dorsal towards top, medial towards left) views, respectively. H, I trapezium in distal (dorsal towards top, medial towards left) and palmar (dorsal towards top, medial towards left) views, respectively. Abbreviations: cn, cuneiform; lu, lunar; Mc I, metacarpal I; Mc II, metacarpal II; Mc III, metacarpal III; Mc IV, metacarpal IV; Mc V, metacarpal V; mg, magnum; sc, scaphoid; td, trapezoid; tm, trapezium; un, unciform. Scale bar represents 2 cm.

unciform articulates with Mc III medially and Mc IV laterally. The facets for these elements, broadly contiguous, face distomedially and distolaterally, respectively. The facet for Mc V, contiguous with that for Mc IV, lies on the lateral surface of the unciform and faces almost entirely laterally.

Magnum. The magnum is a narrow, irregularly shaped bone (Text-fig. 14D, E). Its dorsal end, proximodistally elongated, is more extensive than its palmar portion. It articulates proximally almost entirely with the lunar but does make a narrow proximolateral contact with the cuneiform, which is apparent in dorsal view, but in *Hapalops* (Scott 1903, pl. 33, fig. 2), *Nothrotherium* (Cartelle and Fonseca 1983, fig. 10), and *Nothrotheriops* (ROM 44928; Paula Couto 1974, figs 1, 2), this contact is not present. Nonetheless, the proximal end of the magnum is transversely broadest in *Hapalops*, in which the magnum is wider proximally

than distally. In *Mionothropus*, the proximal end of the magnum, though broad, is not as wide as in *Hapalops*, and the proximal and distal ends are almost the same width. In *Nothrotherium* and *Nothrotheriops*, the proximal end of the magnum tapers proximally, so the distal end is considerably wider than the proximal end. This narrowing is more pronounced in the *Nothrotherium* specimen described by Cartelle and Fonseca (1983), in which the proximal end of the magnum ends in a sharp point that, in dorsal view, is excluded from contact with the lunar. However, in the specimen illustrated by Stock (1925, fig. 28), in which the magnum is not preserved, the form of the proximal ends of the cuneiform and scaphoid suggest that the magnum resembled that in *Nothrotheriops*. The medial surface of the magnum articulates with the scaphoid proximally and the trapezoid distally. The lateral surface is given over mainly for articulation with the unciform along its proximal and dorsal margins. The

distal surface of the magnum, dorsopalmarly convex, fits into most of the notched surface on the proximal surface of Mc III.

Trapezoid. The trapezoid outlines an isosceles triangle in proximal and distal views, with base dorsal and an elongated palmar apex portion (Text-fig. 14F, G). In dorsal view, the trapezoid is also triangular, but its distal base is wide and its height relatively low. The distal surface articulates mainly with Mc II, with a small lateral portion of the distal surface articulating with Mc III. The proximomedial surface and most of the proximolateral surfaces of the trapezoid articulate with the scaphoid, with the distolateral surface destined for the magnum. Contact between the trapezoid and trapezium is prevented by a proximal wedge-like extension of the proximomedial surface of Mc II. A similar condition exists in *Nothrotherium* (Cartelle and Fonseca 1983) and *Hapalops* (Scott 1903), but in *Nothrotheriops,* the two carpals do articulate with one another (Stock 1925; Lull 1929).

Trapezium. The trapezium is a small element, about the same size as the trapezoid (Text-fig. 14H, I). It is proximomedially thicker laterally than medially. In proximal view, it is roughly rhomboidal in outline, with long axis oriented mediopalmarly, oblique to the main transverse axis of the carpals. The trapezium articulates proximally with the scaphoid via an elongated and concave facet. The dorsolateral surface bears a nearly triangular facet, with apex distally, for Mc II. The surface of the facet faces obliquely to the long axis of the trapezium. The distal surface bears a saddle-shaped facet for Mc I. The form of the surface suggests little if any movement was possible at this joint. As may be surmised from this description, the trapezoid is not fused with Mc I, as also occurs in *Hapalops* (Scott 1903; Stock 1925). In *Nothrotherium,* these two elements are fused (Cartelle and Fonseca, 1983). Fusion between the elements is common in *Nothrotheriops* (Paula Couto 1979), although they may exist as separate elements (Stock 1925; Lull 1929; Paula Couto 1979).

Digits. Metacarpals I–V are present (Text-figs 11, 15). Cartelle and Fonseca (1983) noted that in the manus of *Nothrotherium,* the metacarpals are markedly divergent, producing widely open interdigital spaces. Based on Lull's (1929, 1930) illustrations, the digits seem less divergent in *Nothrotheriops shastensis*, but based on ROM 44928 and Paula Couto's (1974, figs. 1–3) illustrations, *Nothrotheriops* strongly resembles *Nothrotherium* in this feature, and this same impression seems to hold for *Mionothropus* and *Hapalops*, but in the latter two, Mc V seems more divergent. In *Mionothropus,* Mc I is positioned very close to Mc II and slightly palmar to the plane of the remaining digits; i.e. less divergent than in the other genera.

The pattern in length among the metacarpals holds across all genera discussed here. Mc III is about equal to Mc II and notably shorter than Mc IV and Mc V, which are about equal in length. Mc I is about half the length of Mc II. Mc III is the most robust metacarpal in all genera. In *Hapalops,* Mc II is nearly as robust as Mc III, followed by Mc IV, then Mc V. In *Mionothropus,* Mc IV is slightly more robust than Mc II, followed by Mc V. In *Nothrotheriops,* Mc IV is almost as robust as Mc III, notably more so than Mc II and Mc V, which are nearly equal in this

respect. In *Nothrotherium,* Mc II and Mc IV are about equally robust, but Mc V is very slender, more so, in the main portion of its diaphysis at least, than Mc I.

Digits I–IV of *Mionothropus* ended in claws, as indicated by well-preserved ungual phalanges. The fifth digit, however, did not bear a claw, as in *Nothrotherium* and *Nothrotheriops* but in contrast to *Hapalops*, in which digit V has an ungual phalanx (Scott 1903). Mc V bears two small, reduced phalanges, the most distal of which clearly lacks a distal articular facet. This is also true of *Nothrotherium maquinense*. There is some confusion with regard to the condition in *Nothrotheriops*. From the descriptions and illustrations of Stock (1925) and Paula Couto (1974), it is apparent that *Nothrotheriops* followed the pattern of *Mionothropus* and *Nothrotherium* in this respect. Lull (1929, 1930) claimed the presence of a complete digit V in the left manus of YPM 13198, recovered from New Mexico, north of El Paso, Texas. Lull (1929, p. 13) noted that in the right manus, the ungual phalanx of digit V had been lost during life and only the distal half of the (supposed) middle phalanx was preserved, the proximal portion of which was 'rounded off distally.' The condition in the manus of *Nothrotheriops*, however, is precisely that observed in *Nothrotherium* and *Mionothropus*, with Mc V bearing two small nodular phalanges, as suggested by Paula Couto (1979) and as evident in Lull's (1929, pl. 5B) illustrations. The two phalanges at the end of Mc V of the left manus illustrated by Lull (1929, pl. 4C) are more probably those of digit I (which Lull noted were removed by a spectator), incorrectly restored to digit V.

Digit I. Mc I is a short, relatively slender element. Proximally, it articulates with the trapezium and makes no contact with Mc II, as occurs in the other genera discussed here. As noted above, Mc I is not fused with the trapezium. Its bluntly rounded distal keel supports the proximal phalanx, which resembles a fused, smaller version of the proximal and middle phalanges of digits II–IV. Whereas little or no movement apparently occurred at the metacarpal–phalangeal joint, the trochleated distal end of the proximal phalanx allowed limited flexion and extension of the distal or ungual phalanx. The latter has a relatively short and laterally compressed ungual core that bore a small claw.

Digit II. Mc II is relatively slender, though about equal in length to Mc III. It articulates with the trapezium medially, the trapezoid proximally, and Mc III laterally. A proximomedial wedge of Mc II prevents contact between the trapezoid and trapezium (see above). Its distal surface bears a large, rounded keel. Three phalanges are present. The proximal phalanx is short, with a deeply concave surface that receives the keel of Mc II. This joint apparently allowed little mediolateral or flexion–extension movements. Distally, the proximal phalanx is trochleated for the middle phalanx, but little movement appears to have been possible at this joint. The ungual phalanx is large. It was capable of extensive flexion. Although the distal tips are broken, the bony ungual cores of digits II and III are apparently subequal, whereas in *Nothrotheriops,* that of digit II is notably longer. The bony core in *Mionothropus* is low, wide, and dorsally rounded, in contrast to the condition of the remaining ungual phalanges, in which the core is high, laterally compressed, and triangular in

section. Also, the core of digit II is nearly of constant width, whereas it tapers distally in the other digits.

Digit III. Mc III is the most robust metacarpal, and its phalanges maintain this distinction over the remaining digits. Mc III articulates proximally with five elements into a tightly interlocking carpal–metacarpal structure. Proximomedially, it articulates with Mc II. The proximal surface of Mc III articulates with three carpals. A lateral part of the trapezoid covers a small triangular part of this surface. Much of the central part of the proximal surface, deeply notched, receives the magnum, whereas the unciform articulates more laterally with a proximolaterally facing surface. The lateral surface articulates with Mc IV along a distolaterally facing facet.

Distally, Mc III bears a robust keel for articulation with the short proximal phalanx, which in turn bears a distal trochleated surface for the middle phalanx. The latter is shorter and more robust than that of digit II. The ungual phalanx is the most robust of the manus, though it may not be the longest. It is considerably larger than the ungual of Digit IV, in contrast with *Nothrotheriops*, in which these unguals are subequal.

Digit IV. Mc IV articulates proximally with Mc III, Mc V, and the unciform. The articular surface for Mc III, facing proximomedially, is the largest and is slightly concave. The unciform facet is a narrow, slightly concave surface facing proximally. The nearly flat facet for Mc V faces laterally. Distally, Mc IV bears the familiar pattern of short proximal, elongated middle, and robust ungual phalanges. As with digits II and III, little movement was apparently possible except at the distal interphalangeal joint. The middle phalanx is subequal in length to but more gracile than that of digit III.

Digit V. Mc V is more slender than that of Mc IV. It articulates proximally with Mc IV and the unciform. The phalanges of digit V, comprising small proximal and distal nodular elements, were discussed above.

Sesamoids. As noted above, the palmar sesamoid is a large, dorsopalmarly compressed element. Its placement in Text-figure 12 is based on its *in situ* position in the right manus. Approximately centrally located on the palmar surface of the carpus, it nearly outlines a quarter circle in dorsal and palmar views. Its medial and proximal margins are nearly rectilinear and meet at a right angle, with its curved margin laterodistal. The palmar surface is shallowly concave, whereas the dorsal surface is flattened. Cartelle and Fonseca (1983, fig. 11) described a similarly shaped palmar sesamoid (or falciform) in *Nothrotherium*, but its illustrated position is just distal to the proximal ends of Mc III and Mc IV, rather than in the carpal region as in *Mionothropus*. Winge (1915, pl. 24, left image) also figured a palmar sesamoid for *Nothrotherium*. Paula Couto (1974) described a palmar sesamoid in *Nothrotheriops*.

Several other sesamoids, some notable in size, were recovered from the matrix during preparation (Text-fig. 15). Small, nodular sesamoids are typically associated with phalangeal joints or present in tendons of digital flexors of mammals. In several cases, the recovered elements were near their anatomical posi-
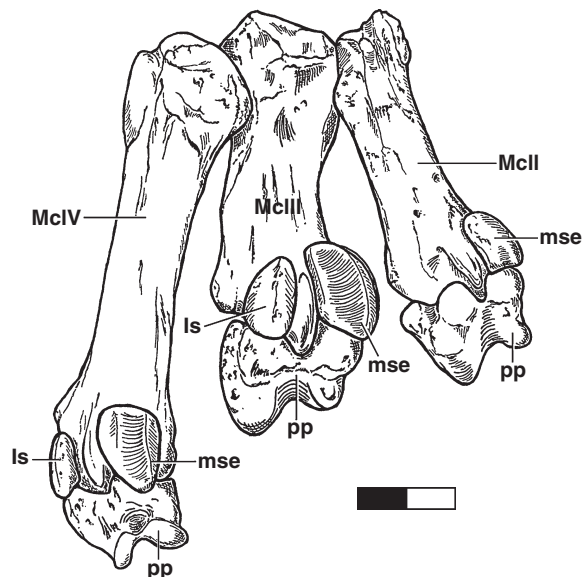
TEXT-FIG. 15. Left metacarpal region and digital sesamoids of *Mionothropus cartellei* gen. et sp. nov. in palmar view. Abbreviations: Mc II, metacarpal II; Mc III, metacarpal III; Mc IV, metacarpal IV; ls, lateral sesamoid; mse, medial sesamoid; pp, proximal phalanx. Scale bar represents 2 cm.

tions. For those that bear easily identifiable articular surfaces, their positions could be deciphered, but not for several of the smaller, approximately oval nodular elements.

Two of the larger elements are associated with digit III and lie between Mc III and the proximal phalanx (Text-fig. 14). The larger medial sesamoid bears a well-developed palmar groove, probably for passage of the medial tendon of the interosseus muscle that extended between Mc II and the proximal phalanx, with a high medial flange forming the medial wall of the groove. The main contact with Mc III occurs through a large, shallowly concave facet on its dorsal surface. The facet is contiguous with a much smaller facet on the sesamoid's lateral surface, which makes a minor contact with Mc III. A small oval facet on the distal surface contacts the proximal phalanx. The lateral sesamoid is approximately triangular in palmar view with tapered end proximal and does not bear the marked groove present on the medial sesamoid. Presumably, the sesamoid lay within the lateral tendon of the interosseus muscle. Its dorsal and lateral surfaces, bearing large and small facets, respectively, articulate with Mc III. A small facet on its distal surface contacts the proximal phalanx.

The medial sesamoid between Mc IV and its proximal phalanx resembles the medial sesamoid for digit III, but it is slightly smaller, lacks the high flange forming the medial wall of the grooved palmar surface, and its dorsal surface is more strongly concave. Its distal surface bears a very faintly demarcated surface for articulation with the proximal phalanx. The lateral sesamoid for this digit is considerably smaller. It forms a proximodistally elongated wedge, with base bearing a well-defined facet for articulation with Mc IV. A small facet lies distally for contact with the proximal phalanx. As with the lateral sesamoid of digit III, the palmar surface is not grooved.

TEXT-FIG. 16. Femur of *Mionothropus cartellei* gen. et sp. nov. A, B, right and left femora in anterior view. C, left femur in medial view. Scale bar represents 10 cm.

The medial sesamoid between Mc II and its proximal phalanx is approximately intermediate in size between the medial and lateral sesamoids of digit IV. It is nearly triangular, with proximal apex, and bears facets dorsally for Mc II and distally for the proximal phalanx. Its palmar surface bears a shallow groove. Presumably, a lateral sesamoid was also present at this joint.

The pattern of sesamoid morphology appears to be that the medial sesamoid is grooved, either deeply, as in digits III and IV, or shallowly, as in digit II, whereas the lateral sesamoid is not. This suggests that the medial tendon of the interosseus muscle for these digits was more prominently developed than the lateral tendon. This may be related to the posture of the manus during locomotion, which has been traditionally viewed as inturned so that weight was supported by its dorsolateral surface.

Femur. Right and left femora are nearly complete (Text-fig. 16A–C). The medial tibial condyle and a small portion of the lesser trochanter are missing in the right femur. Most of the lateral tibial condyle and portions of the lateral margin are missing in the left femur. The femur of *Mionothropus* is wide and flattened, as occurs generally in ground sloths. It resembles that of *Hapalops* in being mediolaterally narrower distally than proximally (Scott 1903, 1904), whereas in *Nothrotheriops* and *Nothrotherium,* the reverse is true (Reinhardt 1878; Stock 1925; Paula Couto 1971; MCL 1020/48). However, it is about as robust as that of *Nothrotherium,* rather than the more gracile femur of *Hapalops* and the stout femur of *Nothrotheriops.*

The head is approximately spherical and relatively small, similar to that of *Hapalops* and in contrast to the prominent head in *Nothrotheriops* and *Nothrotherium.* The fovea ligamentum teres is a deep and prominent depression on the posteromedial part of the articular surface of the head, as occurs also in *Nothrotherium, Nothrotheriops,* and *Hapalops.* The greater trochanter is prominent but is displaced distally relative to that in the other genera, so the crest of bone between the head and greater trochanter slopes laterodistally. In contrast, the greater trochanter is very prominent and projects proximally, reaching about the same level as the head in *Hapalops,* so that the bony crest is notably concave. In *Nothrotherium,* the greater trochanter projects slightly proximally, and the crest is less strongly concave than in *Hapalops.* In *Nothrotheriops,* the greater trochanter does not project proximally, but it is neither as distal as in *Mionothropus,* so that the crest of bone is nearly linear and square with the long axis of the femoral diaphysis.

The lesser trochanter in *Mionothropus* is prominent, forming a triangular protuberance projecting from the medial surface of the femur, as occurs also in *Hapalops* and *Nothrotherium*. It resembles more that of the latter in being less proximally developed. The lesser trochanter is strongly reduced to a rugose protuberance on the diaphysis in *Nothrotheriops*.

The third trochanter is prominent, as in *Hapalops*, and lies at about the midlength of the femur, though more of it extends proximally. The third trochanter may be somewhat more prominent in *Mionothropus* in that it seems to extend farther proximally, to just below the greater trochanter, but we suspect this is because of the more distal placement of the greater trochanter in this genus. In *Mionothropus,* it extends along the central third of the lateral margin of the diaphysis, from just distal to the diaphyseal midlength proximally to just below the greater trochanter. In *Nothrotherium,* the third trochanter lies just distal to the midlength of the femur. It is about as prominent as in *Mionothropus*, although its base is less extensive proximodistally. In *Nothrotheriops,* the trochanter forms a rugose region on the diaphysis, rather than a flange-like projection and lies distal to the femoral midlength.

A curved spike of bone is fused to the posteromedial surface of the left (but not right) femur of *Mionothropus*, just dorsal to the medial condyle (Text-fig. 16C). This almost certainly represents the medial fabella (Evans 1993) fused to an extended ossification of the tendon (i.e. the spiked end) of the medial part of the gastrocnemius muscle. Although the cyamella or cyamofabella, a sesamoid element articulating with the posterior part of the proximolateral articular facet of the tibia, has been described for fossil sloths (see Salas *et al.* 2005; Pearson and Davin 1921), sesamoids of the gastrocnemius on the posterior surface of the femur have not been noted previously, although Scott (1903, p. 199) reported facets for these fabellae (termed flabellae by this author) for a femur of *Hapalops*.

The patellar trochlea of *Mionothropus* is more strongly concave mediolaterally than in *Nothrotheriops* and *Nothrotherium*. In distal view, the femur of *Mionothropus* (Text-fig. 17) resembles more that of *Nothrotheriops* than *Nothrotherium* in that the ectepicondyle is relatively smaller and does not project markedly anteriorly. Also, the position of the medial margin of the lateral condyle is similar in *Mionothropus* and *Nothrotheriops*, reaching the lateral third of the patellar trochlea's width, whereas it reaches just medial to the lateral margin of the trochlea in *Nothrotherium*. However, the medial condyle extends more laterally in *Mionothropus* and *Nothrotherium*, resulting in closer proximity of the lateral and medial condyles in *Mionothropus*, so that the intercondyloid fossa appears narrower.

The anterior margin of the medial condyle is extended towards the patellar trochlea in *Nothrotheriops* and *Nothrotherium*. This extension is marked in *Mionothropus*, so that an isthmus of bone extends between the condyle and the distomedial margin of the trochlea (Text-fig. 16). These articular surfaces butt against each other but are not contiguous as is clearly indicated by the raised margin of the trochlea. In *Hapalops* and *Thalassocnus* (Muizon *et al.* 2003), the lateral and medial condyles are contiguous with the patellar trochlea, but they are separate from the trochlea in *Nothrotheriops*, *Nothrotherium*, and *Pronothrotherium*.
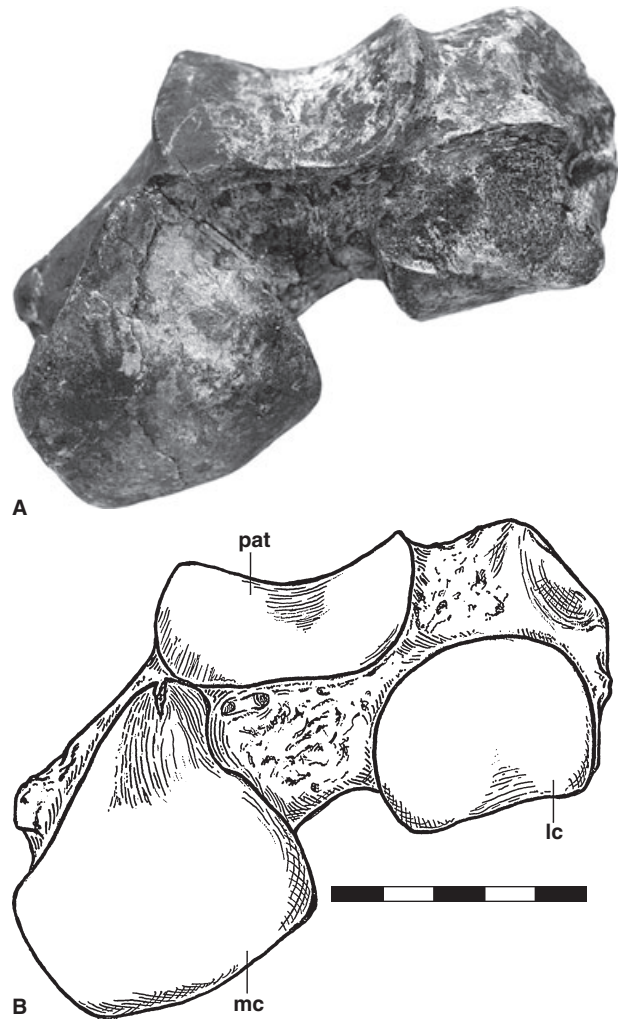
TEXT-FIG. 17. Left femur of *Mionothropus cartellei* gen. et sp. nov. in distal view. A, photograph. B, drawing of A, with lateral condyle reconstructed from right femur. Abbreviations: lc, lateral condyle; mc, medial condyle; pat, patellar trochlea. Scale bar represents 10 cm.

Patella. The right patella is nearly complete, missing only its very distal portion (Text-fig. 18A, B). Although incomplete, it is clear that the patella of *Mionothropus* resembles that of *Hapalops* (Scott 1903, pl. 32, figs 6, 6a) in being triangular, with a strongly tapered distal end. The patella of *Nothrotheriops* is relatively elongated proximodistally with a more prominent and less pointed distal portion (Stock 1925; Paula Couto 1971), whereas that of *Nothrotherium* (Reinhardt 1878; Paula Couto 1971) and *Pronothrotherium* is also elongated but with an even more prominent and squared, rather than tapered, distal portion. The proximal surface in *Mionothropus* and *Hapalops* bears a large lateral groove and a smaller medial groove. This is less evident in *Nothrotheriops*, in which the medial half of the proximal surface extends farther proximally than the medial surface. In *Pronothrotherium,* the proximal surface bears a very deep median groove. The articular surface is approximately oval in *Mionothropus*, and

TEXT-FIG. 18. Patella, tibia and fibula of *Mionothropus cartellei* gen. et sp. nov. A, B, anterior and posterior views of patella. C, proximal portion of left tibia in anterior view. D, proximal portion of left fibula in anterior view. Scale bar represents 5 cm.
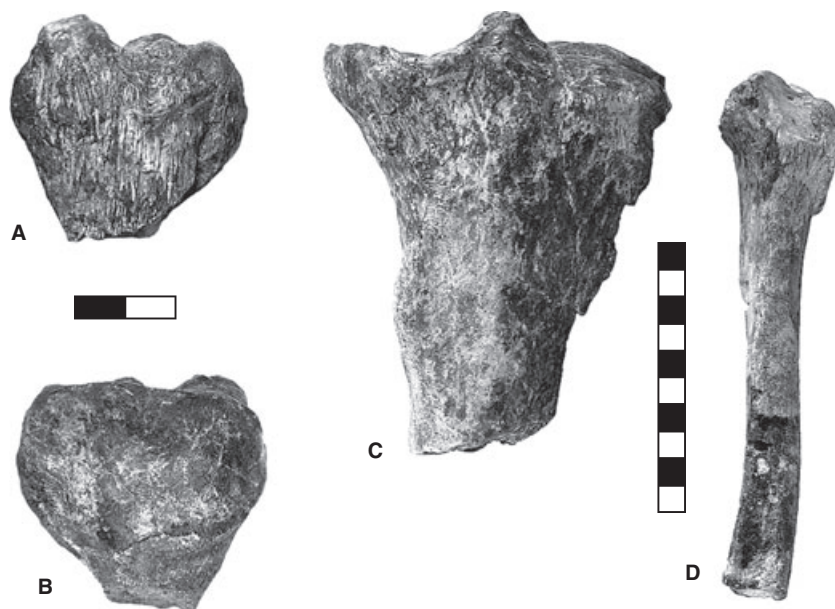
wider than high. It resembles more that of *Hapalops* than the rhomboidal form of *Nothrotheriops* or the triangular, proximo-distally elongated form of *Nothrotherium*.

Tibia. The proximal portion of the left tibia is preserved, but most of its lateral condyle, including the articular facet for the fibula, is missing (Text-fig. 18C). Few distinguishing features are therefore discernable. As is typical of nothrotheres, the cnemial crest forms a low, gently rounded projection. Just distal to the concave medial articular surface, the anterior surface of the diaphysis bears a muscular scar, probably for the semimembranosus muscle. The scar extends distomedially and ends distally as a tuberosity projecting medially from the shaft. This also occurs in *Hapalops*, although the tuberosity apparently lies relatively more distally. A medially projecting tuberosity is absent in *Nothrotherium* and *Nothrotheriops*, although in the latter, the medial margin of the tibia bears rugose scars along its entire length (Stock 1925).

Fibula. Nearly the proximal half of the fibula is preserved (Text-fig. 18D). Its proximal portion is expanded, with a large tibial facet, which is approximately oval, anteroposteriorly longer than high, and faces proximomedially. A small crescentic facet for the cyamella is contiguous with the posterolateral portion of the tibial facet. A large protuberance lies on the proximolateral surface of the fibula, directly lateral to the tibial facet, serving presumably for the attachment of the lateral collateral ligament and peroneus longus muscle. The posterior end of the protuberance is extended distally as a strongly raised tapering ridge, perhaps for the attachment of digital flexor musculature.

DISCUSSION

As noted by Gaudin (2004), the term nothrothere has traditionally been used to designate two groups of sloths:

one including early–middle Miocene genera such as *Hapalops*, *Pelecyodon* Ameghino, 1891, and *Schismotherium* Ameghino, 1887, among others (i.e. mainly those recognized as Schismotheriinae by McKenna and Bell 1997); and the other including late Miocene to Pleistocene genera such as *Pronothrotherium*, *Nothrotherium*, *Nothropus*, and *Nothrotheriops* (i.e. the Plio–Pleistocene nothrotheres and their close relatives, which is essentially equivalent to Nothrotheriinae *sensu stricto* of Hoffstetter 1958, and several genera erected since; see Muizon *et al.* 2004*a*). The assemblage has been variably assigned to Megalonychidae (Simpson 1945; Hoffstetter 1958; Muizon and McDonald 1995; McDonald and Muizon 2002) or Megatheriidae (Patterson and Pascual 1972; Paula Couto 1971, 1979; Engelmann 1985; Patterson *et al.* 1992; McKenna and Bell 1997), generally as a subfamily (i.e. Nothrotheriinae).

Two main trends have occurred in nothrothere systematics over the past few decades. One has been to decouple the earlier group from the later group (see De Iuliis 1994; Gaudin 2004). Indeed, Gaudin (2004) suggested restricting the term nothrothere only to the late Miocene to Pleistocene group and referring to the early–late Miocene forms as basal megatherioids, as is done here. The other trend has seen nothrotheres (as just defined) elevated in rank to Nothrotheriidae, based on its clearly independent evolutionary history (Gaudin 1994, 2004; McDonald 1994; Gaudin and De Iuliis 1999; Muizon *et al.* 2004*a*), although McKenna and Bell (1997) view nothrotheres as a subtribe within Megatheriinae and Perea (1999) retains Nothrotheriinae.

Although the general consensus is that the group be raised in rank, we are less concerned about ranking

clades, and will view them as Nothrotheriidae, which conveys the idea that nothrotheres are a main clade of sloths, comparable in terms of evolutionary history and diversity to the clades commonly referred to as Megatheriidae, Megalonychidae, and Mylodontidae. Despite the elevated importance ascribed by most modern researchers to nothrotheres, their phylogenetic relationship to other main sloth clades has not been completely resolved. Gaudin (2004), based on the most recent, inclusive, and exhaustive cladistic analysis of sloths, grouped Nothrotheriidae with Megatheriidae in Megatheria, although he stated that the support for this relationship is not overwhelming. Muizon et al. (2004a), however, considered nothrotheres as more closely related to megalonychids.

Much of the traditional view of nothrothere evolution was outlined by Kraglievich (1925a, b) and may be summarized as follows. The small, Miocene (nearly exclusively Santacrucian) sloths represent a collection of taxa (i.e. the basal megatherioids as noted above) that later led to separate lineages. Among these was the lineage that culminated in the Pleistocene nothrotheres Nothrotheriops and Nothrotherium and that was characterized notably by the reduction and eventual loss of the first upper and lower teeth. These teeth were caniniform and initially relatively small compared to more distal teeth. Nothrotheres representing intermediate stages along this trajectory were Pronothrotherium and Nothropus. Among the earliest representatives of this lineage were a group of species included under the genus Xyophorus Ameghino, 1887.

The more recent recognition of genera such as Chasicobradys Scillato-Yané, Carlini and Vizcaíno, 1987, Amphibradys Scillato-Yané and Carlini, 1998 and Huilabradys Villarroel, 1998 has led to a more complex view of nothrothere history. Scillato-Yané et al. (1987), for example, recognized Chasicobradys and Pronothrotherium as collateral branches, rather than structural precursors of Nothropus, Nothrotheriops, and Nothrotherium. Further, the descriptions of Thalassocnus remains from the Pisco Formation of Peru over the past dozen years by Muizon and McDonald (1995), Muizon et al. (2003, 2004a, b) and McDonald and Muizon (2002) have revealed an aquatically adapted nothrothere lineage.

McKenna and Bell (1997) listed ten nothrothere genera, although at least one other, Huilabradys, has since been referred to this clade by Villarroel (1998). Among these, Xyophorus and Chasicobradys are late Miocene forms. The former genus includes some nine species and Chasicobradys one species, all based essentially on fragmentary cranial or dentary remains. The nature of the material renders objective decisions on the validity of these forms difficult. Scott (1903, 1904), for example, considered Xyophorus a synonym of Hapalops, and Lydekker (1894) of

Hapalops or Pseudhapalops Ameghino, 1891. Although these are older analyses, at least the former remains among the more detailed descriptions of the material. Perea (1999) also included Xyophorus within Hapalops. The validity of Xyophorus has been upheld by various researchers, such as Ameghino (1907), who noted several characters that may eventually prove to be taxonomically important, as well as Kraglievich (1925a, b), Scillato-Yané (1979), Scillato-Yané et al. (1987), and Saint-André (1996).

Size difference exists among the remains on which some Xyophorus species have been based, but there seems little such variation for others. There appears, however, to be little valid morphological variation. Much has been made of characters such as precise outline of the molariforms and the presence or absence of apicobasal grooves on the vestibular or lingual surfaces of the molariforms, for both specific and generic recognition; as has also been done for Chasicobradys. However, both of these characters are known to be variable among the sloth species for which good comparative material exists. Stock (1925) noted that the longitudinal grooves are variable among Nothrotheriops specimens and quoted Scott's (1903, p. 218) observation that in Hapalops elongatus, 'the vertical grooving of these teeth appears to very capriciously present or absent.' Similar comments may be made on the outline of the molariforms, as Stock (1925) has done for Nothrotheriops. Indeed, variation may occur between right and left side molariforms, as occurs in Nothrotheriops (see Stock 1925, pls 2, 4) and in the material presented in this report (see Text-figs 3, 4B). Cartelle (1992, figs 46, 47, 49) has documented considerable variation in this character for the molariforms of Eremotherium laurillardi (Lund, 1842).

Of the authors supporting the validity of Xyophorus, probably Saint-André's (1996) diagnosis provides the clearest character that might distinguish this genus: m1 separated from m2 by a diastema that is shorter than the mesiodistal length of m2. Saint-André (1996) further noted the general tendency towards a more circular outline for m1 (rather than an oval or elliptical outline produced by vestibulolingual compression of m1) as an advanced feature of nothrotheriines along the Xyophorus–Pronothrotherium–Nothropus trajectory (although this lineage has not been documented through phylogenetic analysis and our phylogeny does not support such a lineage). Saint-André quantified this tendency using a ratio of vestibulolingual width to mesiodistal length of m1, arriving at a range of 1.7–1.3 for Xyophorus (although he noted an exception to this tendency in X. simus Ameghino, 1887, which has a circular outline), 1.2 in Pronothrotherium typicum, and 1.1 in Nothropus priscus. With regard to size, Saint-André (1996) indicated the mandibular tooth row as ranging from 32 mm in X. sulcatus to 48 mm in X. crassissimus Ameghino, 1894.

LACM 4609/117533 possibly represents one of these two late Miocene nothrothere genera, but on the basis of the material available for these taxa, there are no objective criteria by which a decision might be reached. Certainly, LACM 4609/117533 is larger than the material for *Xyophorus* and *Chasicobradys*, the diastema is slightly longer than reported for *Xyophorus*, the outlines of the teeth exhibit differences, and the caniniform is not as vestibulo-lingually compressed as in *Xyophorus*, features which taken together would indicate specific differences but are insufficient to rule out an affinity at the generic level. *Huilabradys*, a late–middle Miocene genus, is known from a partial right mandibular ramus. Its tooth bearing portion is relatively much deeper than that of LACM 4609/117533. Further, the teeth of *Huilabradys* are approximately equidistantly separated from each other, in contrast to the long diastema between c1 and m1 in LACM 4609/117533. As LACM 4609/117533 cannot be objectively assigned to one of these or any other nothrothere genus to which comparisons are possible, the best course is to place it in its own genus.

Some other more-notable features of *Mionothropus* are those of the skull and femur, although other elements also signal its distinctness. The skull, in particular, though sharing a large number of similarities with other nothrotheriids, is highly distinctive, exhibiting numerous autapomorphic features. The overall shape of the skull differs strongly from that of other nothrotheriids, with its notably domed braincase and depressed, narrow snout. It has the Y-shaped premaxilla typical of nothrotheriids, but the anterior process is shorter than that of *Nothrotherium*, resembling *Nothrotheriops* in this respect. The hard palate is flat anteriorly and convex transversely as in *Nothrotheriops*, but it lacks the elongated postpalatine shelf of other nothrotheriines, giving it a much broader postpalatine notch like that of *Thalassocnus*. It also has multiple postpalatine foramina, resembling *Pronothrotherium* in this respect and differing from *Nothrotheriops*, which has a single, enlarged postpalatine foramen. The nasal is narrower than in either *Nothrotherium* or *Nothrotheriops*, and the frontonasal suture is deeper. Similarly, the lacrimal surface is smoother and the lacrimal foramen smaller than that of *Nothrotheriops*. The descending process of the jugal is like that of *Nothrotheriops* – triangular and hooked posteriorly. However, the ascending process is elongated and slender, much more like that of *Hapalops* than that of *Nothrotheriops* or *Nothrotherium*, and the middle jugal process is squared off posteriorly, a unique morphology among nothrotheriids. As is typical for nothrotheriids, there is no sagittal crest.

The temporal lines on the frontal and parietal resemble those of *Nothrotherium* and *Nothrotheriops* in that they pass ventrally well in advance of the nuchal crest, in contrast to the condition in *Pronothrotherium*, where they fuse with the nuchal crest posteriorly. There is no anteroventral process of the parietal, and consequently, no parietal/alisphenoid contact, unlike the condition in *Pronothrotherium*, *Nothrotherium*, and many specimens of *Nothrotheriops*. The zygomatic process of the squamosal is similar in length to that of *Pronothrotherium*, both of which are shorter than that of *Nothrotheriops*, but *Mionothropus* differs from both these taxa in that the process tapers anteriorly. As in other nothrotheriines, the zygomatic process extends parallel to the long axis of the skull. The postglenoid surface underneath the zygomatic process is marked by numerous grooves and ridges, resembling *Nothrotheriops* in this respect.

The large descending laminae of the pterygoids are semicircular in outline, similar to the condition in *Hapalops* and differing from the anteroposteriorly elongated form of these laminae in *Nothrotherium* and *Nothrotheriops*. *Mionothropus* lacks the ossified pterygoid bullae that characterize the latter two genera but bears indications that it may have possessed a soft tissue bulla in this area. The pterygoid exposure in the roof of the nasopharynx is marked by open grooves leading to the foramen ovale and foramen rotundum, a feature unique among sloths. *Mionothropus* shares the distinctive morphology of the vomer that is the hallmark of the skulls of Nothrotheriinae. The bone is broadly exposed in the roof of the nasopharynx, expanding posteriorly to cover the presphenoid and much of basisphenoid, and it is marked by a deep, elongated, asymmetrical ventral keel. In *Mionothropus,* this keel is deeper and straighter than that of other nothrotheriines. There is a large supraoccipital exposure on the skull roof as in other nothrotheriids – it has a smooth surface, unlike that of *Pronothrotherium* or *Nothrotheriops*. The nuchal crest of *Mionothropus* is prominent, like that of *Pronothrotherium* but not *Nothrotheriops*. The occipital surface is marked by the very large ventral nuchal crest found in other nothrotheriids, but it lacks the large external occipital protuberance of *Pronothrotherium*.

The ear region of *Mionothropus* shows the same mixture of resemblances to other nothrotheriids and autapomorphic features that characterize the skull as a whole. The ectotympanic is somewhat expanded ventrally as in *Pronothrotherium* and *Nothrotherium*, but not as much as in *Nothrotheriops*. It is unusual in the degree of development of the styliform process. The entotympanic is very similar to that of *Pronothrotherium*, lacking the deep medial sulcus and well-developed medial wall of that sulcus found in *Nothrotheriops*. The petrosal is characterized by a large, rugose processus crista facialis like that of *Pronothrotherium*, which contacts the ectotympanic as in *Nothrotheriops* but is not quite as large as the process in that taxon. Although there is a large epitympanic sinus as in other nothrotheriids, it is not marked by a bulge on the lateral surface of the zygomatic root as it is in these

other nothrotheriid taxa. As is characteristic for Nothrotheriidae, the mastoid process (= paroccipital process of Wible and Gaudin 2004) is well developed and pierced by a dorsally directed branch of the occipital artery that emerges in a foramen on its dorsal side. However, the process is mediolaterally compressed in *Mionothropus*, whereas it is bulbous in shape in *Pronothrotherium* and *Nothrotheriops*. The paracondylar process is large like that of *Nothrotheriops*, but it does not take part in the formation of the stylohyoid fossa as it does in other nothrotheriids. This fossa is circular in *Mionothropus* but is anteroposteriorly elongated in *Pronothrotherium* and *Nothrotheriops*. As in *Nothrotheriops*, the Glaserian fissure of *Mionothropus* opens into a weak groove that lies medial to the large entoglenoid process. In *Pronothrotherium* and *Thalassocnus*, this groove crosses the ventral surface of the entoglenoid process.

As noted above, Rancy (1991) compared the type skull and mandible of *Mionothropus cartellei* (LACM 4609/117533) and those of his new genus and species (UFAC 1284), which he correctly refrained from naming, as his work was part of a doctoral thesis. Rancy (1991, p. 91) noted several differences between these specimens, stating that LACM 4609/117533 possibly represented 'a relatively small, probably female, variant of the new [i.e. his unnamed] genus and species' but that further 'samples may show it to represent a distinct species or even genus.' Although there is no new material to report, the extensive preparation of LACM 4609/117533 has indeed brought to light more pronounced differences between UFAC 1284 and LACM 4609/117533 than Rancy was able to determine; in this sense, his foresight is confirmed, as the differences between the two specimens indicate specific distinction. Among the differences are that the dorsal profile of the skull of LACM 4609/117533 is more prominently domed, as noted by Rancy (1991), and the domed profile reaches farther anteriorly, giving UFAC 1284 the appearance of having a more extensive rostrum. However, the palate seems relatively more elongated in LACM 4609/117533, as the predental palatal region extends farther anteriorly (see below) and the premaxillae are considerably longer anteriorly in LACM 4609/117533. Rancy (1991) noted the lack of a postorbital process in UFAC 1284 and a weak postorbital process in LACM 4609/117533. Also, this author noted the deeper, more ample zygomatic notch of UFAC 1284, but we add here that the lower margin of the notch reaches the alveolar margin in UFAC 1284 but is dorsal to the margin in LACM 4609/117533. The jugal has a very short and blunt zygomatic process in LACM 4609/117533, but a distinct, more elongated process with a rounded posterior margin is present in UFAC 1284, which also has a more robust descending process. The lacrimal and the anterior margin of the zygomatic process of the maxilla are deflected anterolaterally in the latter but are gently posterolaterally directed in LACM 4609/117533, a difference best appreciated in dorsal or ventral views. The palatine notch in LACM 4609/117533 is more broadly U-shaped than in UFAC 1284. Other differences in the skull include the lack of an inflated base to the zygomatic process in the LACM specimen and its presence in the UFAC specimen; a straight upper caniniform in UFAC compared to a recurved caniniform in LACM; and in the UFAC specimen, a more prominent nuchal crest that overhangs the occiput posteriorly; a more prominent lateral ridge and depression on the dorsal surface of the zygomatic process of the squamosal; a more pronounced mastoid process; a deeper median notch anteriorly on the maxilla for the medial process of the premaxilla; a more strongly reflexed basicranial/basifacial axis; and more elongated lateral processes of the nasals. Rancy (1991, Table 7) noted a difference in shape of the pterygoid between these specimens, but our further preparation of the LACM specimen suggests that this difference does not exist. Also, Rancy (1991) noted a difference in position of the supraorbital foramen, but their positions seem to be very similar – over the third molariform tooth and clearly dorsal to the level of the lacrimal foramen. The apparent difference may be caused by the different arrangement of the domed braincase and rostrum.

In the lower jaw, the horizontal ramus is deeper and its ventral margin more convex in UFAC 1284. The posterior portion of the dentary seems dorsally displaced in this specimen compared to LACM 4609/117533, so that the angular process lies almost entirely above the alveolar plane in the former and almost entirely ventral to this plane in the latter. The ascending ramus is more prominent in UFAC 1284 and the coronoid process higher. Rancy (1991) noted the closer position of the condylar process to the coronoid process in UFAC 1284 and the shorter predental symphyseal spout. This shorter spout presumably reflects a shorter predental palatal region noted above. Rancy (1991) stated that the caniniform is worn as a bevel in LACM 4609/117533 but a basin in UFAC 1284. Other differences include that the mandibular condyle is wider transversely and m3 more elongated mesiodistally in the UFAC specimen; and UFAC 1284 overall is more muscular and robust, as indicated by the prominent symphyseal keel and sculpturing on the external surface of the mandibular symphysis, and prominent lateral ridges along the anterior edge of the coronoid process and the lateral surface of the condyloid process.

The pronounced differences noted above strongly suggest that the specimens represent different species. A considerable amount of postcranial material of UFAC 1284 is also preserved but has never been described (A. Ranzi, pers. comm. 2006). Formal treatment of this specimen,

including a description of the postcranial remains, is in progress by R. Negri and A. Ranzi.

As has been noted above, the postcranial elements of *Mionothropus cartellei* have various distinguishing features compared to other nothrotheres. For example, the supinator ridge of the humerus is nearly vertically oriented rather than sloping, the ulna is gracile with a prominent and anteriorly projecting anconeal process, the magnum makes a proximolateral contact with the cuneiform, the greater trochanter of the femur is positioned more distally, and the patella is short and wide. However, the relationship among the distal femoral facets is particularly notable. The isolation of the three distal femoral articular facets has long been considered characteristic of nothrotheres. In discussing the relationships among the trochlea and condyles in sloths, Kraglievich (1923) noted that the apparently primitive condition, present in the Santacrucian sloths, is that in which both condyles are connected to the trochlea. These articular surfaces became discontinuous to varying degrees in various lineages. For example, in megatheriines, the medial condyle is isolated but the lateral condyle maintains a wide connection with the trochlea. In some Megalonychinae, such as the Antillean sloths (e.g. *Megalocnus* Leidy, 1868 – see Matthew and Paula Couto 1959), the three surfaces maintained the primitive condition, whereas in others, such as *Megalonyx* Harlan, 1825 (Leidy 1855), the trochlea is isolated from the condyles. *Pliomorphus* Ameghino, 1885 possessed an apparently intermediate condition, in which the medial condyle was isolated, but the lateral condyle was connected to the trochlea only by a narrow isthmus (Kraglievich 1923). The morphology of *Amphiocnus* Kraglievich, 1922 is similar in some respect to that of *Nothrotheriops*. The former was described by Kraglievich (1922), who viewed it as possibly allied to the Antillean sloths. In *Amphiocnus,* the lateral and medial condyles are each connected to the trochlea by a narrow isthmus. The form of that between the medial condyle and trochlea is very similar to that of *Mionothropus*, except that the articular surfaces are contiguous via the isthmus, whereas in *Mionothropus,* the isthmus butts against the margin of the trochlea. Also, the form of the trochlea of these sloths is strikingly similar in being strongly concave and having a prominently raised medial margin. One difference between them, however, is that medial condyle is relatively more medial in *Amphiocnus*, so that the intertrochlear fossa is wider.

PHYLOGENETIC RELATIONSHIPS

A total of 66 discrete craniodental and postcranial characters were scored via direct observations of the specimens listed in the Appendix S1, or by consultation with the following published descriptions: General sources: Gaudin (1995, 2004), Perea (1999), McDonald and Muizon (2002), Muizon *et al.* (2003), Muizon *et al.* (2004a); *Hapalops*: Scott (1903, 1904); *Thalassocnus*: Muizon and McDonald (1995), McDonald and Muizon (2002), Muizon *et al.*, (2003), Muizon *et al.* (2004a, b); *Nothrotheriops*: Stock (1925), Lull (1929), Paula Couto (1971, 1974), Naples (1987); *Nothrotherium*: Reinhardt (1878), Paula Couto (1959, 1971, 1980), Cartelle and Fonseca (1983), Cartelle and Bohórquez (1986). The characters are described in the Appendix S1. Many of the characters were derived from previous published phylogenetic studies of nothrotheriids (Perea 1999; McDonald and Muizon, 2002; Muizon *et al.* 2003) or of sloths in general (Gaudin 1995, 2004), and these are marked accordingly in the Appendix S1.

The data matrix of 66 characters and six taxa (see Appendix S1) was analysed using the computer program PAUP [version 4.0b10 (Swofford 2002)]. Analyses were conducted using PAUP's 'Exhaustive Search' option, which identifies all possible trees. Characters were optimized using PAUP's DELTRAN option in all analyses (see Gaudin (1995) for justification). Characters were polarized via comparison to a single monophyletic outgroup, *Hapalops*, an early, relatively plesiomorphic megatherioid sloth (following Gaudin 1995, 2004; Perea 1999; McDonald and Muizon 2002; Muizon *et al.* 2003). In those instances in which intraspecific variation was noted for a given character in a given taxon, the taxon was coded for all relevant states and treated as polymorphic in the PAUP analyses. Of the 66 characters, 13 are multistate, and nine of these are ordered along numerical, positional or structural morphoclines. Several characters proved to be parsimony uninformative in the final analyses, but all values reported for consistency index exclude uninformative characters. Following Gaudin (1995), two different weighting schemes were applied to multistate characters to assess their effect on the analysis: (1) all character state changes weighted equally; and (2) character state changes scaled so that all characters are weighted equally regardless of the number of character states. A bootstrap analysis using PAUP's 'branch and bound' algorithm (random-addition sequence, 1000 bootstrap replicates) was also used to evaluate the relative support for various groupings (Hillis and Bull 1993), and Bremer support was calculated for each node following the procedure outlined in Gaudin (2004).

Two different PAUP analyses have been performed – one in which the character state changes are all weighted equally and a second in which character state changes are scaled so that all characters are weighted equally. The two manipulations produce identical results, yielding the single most parsimonious tree illustrated in Text-figure 19
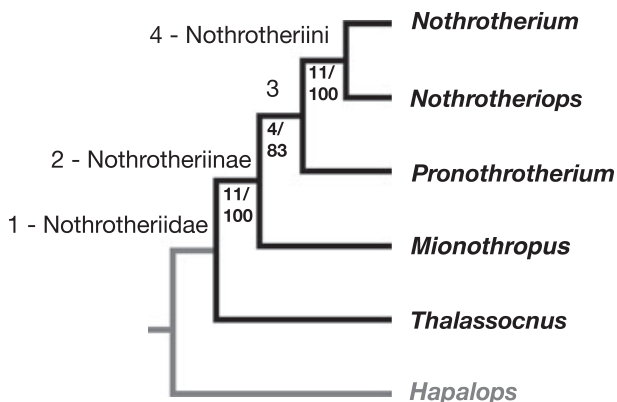
TEXT-FIG. 19. Phylogeny of Nothrotheriidae based on PAUP analysis of 66 osteological characters in five taxa. Characters are polarized via comparison to the basal megatherioid outgroup taxon *Hapalops*. All character state changes are weighted equally in this analysis, which yields a single MPT (TL = 117, CI = 0.737, RI = 0.639). The numbers in bold type at each node represent Bremer support values (given first) and bootstrap values, calculated as described in the text under the heading 'Phylogenetic Relationships.' An apomorphy list for each node is provided in the Appendix S1.

(because the results are identical, tree statistics are provided only for the first analysis – TL = 117, CI = 0.737, RI = 0.639). An apomorphy list for each node is provided in the Appendix S1. Characters are referred to according to their numbers as listed (see Appendix S1).

A monophyletic Nothrotheriidae is recovered (Text-fig. 19), supported by 13 unambiguous synapomorphies, seven of which are unique to this clade (unique characters defined as in Gaudin and Wible 2006). These unique diagnostic traits are molariforms quadrate, rectangular to trapezoidal, transverse width less than twice mesiodistal length (33(1)); molariforms with lingual and labial grooves (34(1)); radial bicipital tuberosity projecting mainly posteriorly (44(1)); pronator teres insertion at proximal one-third of radial diaphyseal length (=relatively elongated distal radial diaphysis) (45(1)); cuneiform proximodistally deep, nearly rectangular in dorsal view (52(1)); ungual process of ungual phalanx of manual digit two semicircular in cross section (55(1)); and, odontoid process of the astragalus present (65(1)).

Within Nothrotheriidae, *Thalassocnus* is the sister taxon to the remaining nothrotheriids, which are allocated to Nothrotheriinae as in Muizon *et al.* (2004*a*). The nothrotheriine node receives strong bootstrap and Bremer support (Text-fig. 19) and is diagnosed by 11 unambiguous synapomorphies, seven of which are unique, and five ambiguous synapomorphies, four of which are unique. The seven unique, unambiguous synapomorphies of this clade are as follows: vomerine exposure in nasopharynx enlarged posteriorly, covers presphenoid and much of

basisphenoid (6(1)); vomer with deep, elongated, asymmetrical ventral keel extending posteriorly into the nasopharynx (7(1)); posterior root of zygoma directed anteriorly (14(1)); ventral nuchal crest hypertrophied (27(1)); coronoid process short and broad, ratio of maximum height to anteroposterior length measured at midheight <1.0 (29(1)); femur flattened anteroposteriorly, transverse width at midshaft much greater than anteroposterior depth (57(1)); and, patellar and lateral articular facets of femur separate (61(1)).

Among Nothrotheriinae, *Mionothropus* is placed as the sister taxon to a clade including the Pliocene taxon *Pronothrotherium* and the Pleistocene taxa *Nothrotheriops* and *Nothrotherium*. In Perea (1999) and Gaudin (2004), *Mionothropus* and *Pronothrotherium* form an unresolved trichotomy with a clade including *Nothrotheriops* and *Nothrotherium*, whereas in McDonald and Muizon (2002) and Muizon *et al.* (2003), *Mionothropus* and *Pronothrotherium* form their own monophyletic clade. Although the analysis identified several derived features shared between the latter taxa (processus crista facialis forms large, rugose bony mass (19(1)); greater trochanter of femur distal to crest between head and greater trochanter, so crest slopes slightly distolaterally (59(3))), the node linking *Pronothrotherium* to the Pleistocene taxa (Node 3, Text-fig. 19), is reasonably well supported. It has a Bremer support of 4, which is the lowest of any node on the tree but is a moderate value compared to those that resulted from the analyses of Gaudin (2004), and the node appears in 83 per cent of the bootstrapped trees. It is diagnosed by 11 unambiguous synapomorphies, seven of which are unique, and two ambiguous synapomorphies, one of which is unique. In contrast, the analysis identified only two derived features shared exclusively between *Mionothropus* and the Pleistocene nothrotheriines (12(1), 49(1)), and two features in which *Mionothropus* appeared to be intermediate between the condition in *Hapalops* and *Pronothrotherium* on the one hand and that of *Nothrotherium* and *Nothrotheriops* on the other (5(1); 38(1)). This arrangement is also consonant with the stratigraphic record, as the oldest nothrotheriine, *Mionothropus* (Huayquerian SALMA, late Miocene), lies at the base of the tree, with the slightly younger *Pronothrotherium* (Huayquerian–Montehermosan SALMA, late Miocene – early Pliocene (Perea 1988)) more closely allied with the even younger Pleistocene taxa *Nothrotherium* and *Nothrotheriops*. The seven unambiguous, unique synapomorphies of Node 3 include the following: presence of a lateral bulge at the base of the zygomatic root for the epitympanic sinus (15(1)); stylohyoid fossa oval, elongate anteroposteriorly (21(1)); lesser tubercle of humerus roughly equal in size to greater tubercle (36(1)); entepicondyle of humerus lacking proximomedially extended protuberance (41(1)); distal width of femoral diaphysis >85 per cent proximal

width (58(1)); patellar and medial tibial articular facets of femur separate (62(2)); and, patella long and narrow, width <65 per cent length (64(1)).

A consensus appears to have emerged among recent investigators of nothrothere phylogeny (Perea 1999; McDonald and Muizon, 2002; Muizon *et al.* 2003; Gaudin 2004) that the Pleistocene nothrotheriines *Nothrotheriops*, from North America, and *Nothrotherium*, from South America, form a monophyletic group. The results of the present study corroborate this clade, which we are herein labelling Nothrotheriini (Node 4, Text-fig. 19). As discussed in Gaudin (2004), the monophyly of the Pleistocene nothrotheriines contradicts earlier claims that *Nothrotheriops* was a direct descendent or close relative of *Nothropus* or *Pronothrotherium* exclusive of *Nothrotherium* (Paula Couto 1971; Frailey 1986). However, node 4 is very strongly supported, with 100 per cent bootstrap support and a Bremer support value of 11. This clade is diagnosed by the longest list of synapomorphies on the tree, including 12 unambiguous synapomorphies, eight of which are unique, and six more ambiguous synapomorphies, three of which are unique (see Appendix S1). The eight unique, unambiguous synapomorphies of this clade are as follows: one pair of greatly enlarged postpalatine foramina (4(1)); osseous pterygoid bulla present (5(2)); little raised deltopectoral shelf with weakly developed pectoral ridge on anterior humeral diaphysis (38(2)); lateral ectepicondylar margin of humerus sloping proximomedially (39(1)); bicipital tuberosity of radius only moderate developed (43(1)); absence of a medially expanded pronator ridge of radius (46(1)); anconeal process of ulna not extended anteriorly to overhang trochlear notch (47(1)); patellar trochlea of femur shallowly concave mediolaterally (63(1)).

CONCLUSIONS

Extensive preparation and redescription of LACM 4609/117533 reveals that it represents an individual of a new genus and species of Nothrotheriidae, *Mionothropus cartellei*, from the late Miocene Huayquerian South American Land Mammal Age. This fossil sloth, from the Río Acre region of western Amazonia, was referred initially to the Pleistocene species *Nothropus priscus* by Frailey (1986). The specimen is well preserved and includes all but the posterior half of the tibia and fibula and the pes. Among nothrotheriids, its distinguishing features include a domed braincase and narrow, depressed rostrum; a straight and very deep vomerine keel, offset slightly to the right anteriorly; open grooves leading to the foramen ovale and foramen rotundum exposed in the roof of the nasopharynx; a medially concave pterygoid; a circular stylohyoid fossa; a mediolaterally compressed

mastoid process; the anterior edge of symphyseal spout with a straight profile in lateral view; the humeral lesser tubercle larger than greater; the humeral supinator ridge nearly vertically oriented; the gracile ulna has a prominent and anteriorly projecting anconeal process; the magnum makes a proximolateral contact with the cuneiform; a more distally positioned greater trochanter of the femur; the medial condyle of the femur abuts against the patellar trochlea; and a short and wide patella.

Rancy (1991) indicated that LACM 4609/117533 was possibly conspecific with a new nothrotheriid species that he described but did not name, as it was included in his unpublished doctoral dissertation. Rancy's (1991) new species was based on UFAC 1284, from the same late Miocene Huayquerian SALMA deposits of the Río Acre region of western Amazonia. This author did leave open the possibility that the specimens were specifically distinct. The current analysis of the skulls of these specimens indicates that this latter conjecture was accurate, and we confirm that they represent distinct species. UFAC 1284, which also includes numerous postcranial elements that Rancy (1991) did not describe, remains unnamed but is under study by A. Ranzi and R. Negri.

Among the differences between these specimens is a more prominently and anteriorly extended domed dorsal skull profile in LACM 4609/117533, so that in UFAC 1284 the rostrum appears elongated. The palate and premaxillae are longer in LACM 4609/117533. The zygomatic notch is deeper and more ample in UFAC 1284, and its lower margin is more ventral. In the jugal, the zygomatic process is more elongated and the descending process more robust in UFAC 1284. The lacrimal and the anterior margin of the zygomatic process of the maxilla are deflected anterolaterally in the latter but are posterolaterally directed in LACM 4609/117533. The upper caniniform is straight in UFAC 1284, but recurved in LACM 4609/117533. The UFAC specimen has a more prominent nuchal crest and mastoid process, a deeper median notch on the maxilla for the medial process of the premaxilla, and a more strongly reflexed basicranial/basifacial axis. The dentary has a deeper horizontal ramus, more convex ventral margin, and shorter symphyseal spout in UFAC 1284; its ascending ramus is more prominent and the coronoid process higher. The caniniform is worn as a bevel in LACM 4609/117533 and a basin in UFAC 1284, in which m3 is more elongated mesiodistally.

Phylogenetic analysis recovered a monophyletic Nothrotheriidae, with *Thalassocnus* the sister taxon to the remaining nothrotheriids, which comprise Nothrotheriinae. Among Nothrotheriinae, *Mionothropus* is the sister taxon to a clade including the Pliocene *Pronothrotherium* and the Pleistocene *Nothrotheriops* and *Nothrotherium*. The proposed relationships among nothrotheriines have

differed in recent analyses, with Perea (1999) and Gaudin (2004) reporting an unresolved trichotomy among *Mionothropus*, *Pronothrotherium* and the clade including *Nothrotheriops* and *Nothrotherium*, whereas *Mionothropus* and *Pronothrotherium* form their own monophyletic clade according to McDonald and Muizon (2002) and Muizon *et al.* (2003). The current analysis, however, provides substantial evidence for the sister group relationship of *Mionothropus* to the remaining nothrotheriines. The present study corroborates the monophyly of a clade including the Pleistocene nothrotheriines *Nothrotheriops* and *Nothrotherium*, termed here Nothrotheriini, as suggested by several recent researchers (Perea 1999; McDonald and Muizon 2002; Muizon *et al.* 2003; Gaudin 2004). The arrangement of Nothrotheriinae presented here also reflects the stratigraphic record, with the oldest nothrotheriine, *Mionothropus* at the base of the tree and the slightly younger *Pronothrotherium* more closely allied with the even younger *Nothrotherium* and *Nothrotheriops*.

Editor. P. David Polly

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Characters and character states for PAUP analysis.

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NOTE ADDED IN PROOF

The generic name *Mionothropus* was inadvertently published in a cladogram by Pérez *et al.* (2010). This name, however, does not conform to Article 13 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999) in that it is not accompanied by a description that differentiates the taxon (Article 13.1.1) and is not accompanied by fixation of a type species (Article 13.3). *Mionothropus* Pérez, Toledo, De Iuliis, Bargo, and Vizcaíno, 2010: 1120: fig. 1 is thus a *nomen nudum*. According to the Code, a *nomen nudum* is not an available name, and therefore the same name may be made available later for the same or a different concept, in which case it would take authorship and date from that act of establishment (i.e. the current publication), rather than its earlier publication as a *nomen nudum* (i.e. Pérez *et al.*, 2010).