

# A peculiar climbing Megalonychidae from the Pleistocene of Peru and its implication for sloth history

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The Xenarthra, particularly the Tardigrada, are with the Notoungulata and Marsupialia among the most diversified South American mammals. Lujanian South American Land Mammal Age localities from the coastal Piedra Escrita site and Andean Casa del Diablo Cave, Peru, have yielded three specimens of the Megalonychidae ***Diabolotherium nordenskiöldi* gen. nov.** This singular fossil sloth exhibits a peculiar mosaic of cranial and postcranial characters. Some are considered convergent with those of other sloths (e.g. 5/4 quadrangular teeth, characteristic of Megatheriidae), whereas others clearly indicate climbing capabilities distinct from the suspensory mode of extant sloths. The arboreal mode of life of *D. nordenskiöldi* is suggested by considerable mobility of the elbow, hip, and ankle joints, a posteriorly convex ulna with an olecranon shorter than in fossorial taxa, a radial notch that faces more anteriorly than in other fossil sloths and forms an obtuse angle with the coronoid process (which increases the range of pronation–supination), a proximodistally compressed scaphoid, and a wide range of digital flexion. *D. nordenskiöldi* underscores the great adaptability of Tardigrada: an arboreally adapted form is now added to the already known terrestrial, subarboreal, and aquatic (marine and freshwater) fossil sloths. A preliminary phylogenetic analysis of the Tardigrada confirmed the monophyly of Megatherioidea, Nothrotheriidae, Megatheriidae, and Megalonychidae, in which *Diabolotherium* is strongly nested. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 149, 179–235.

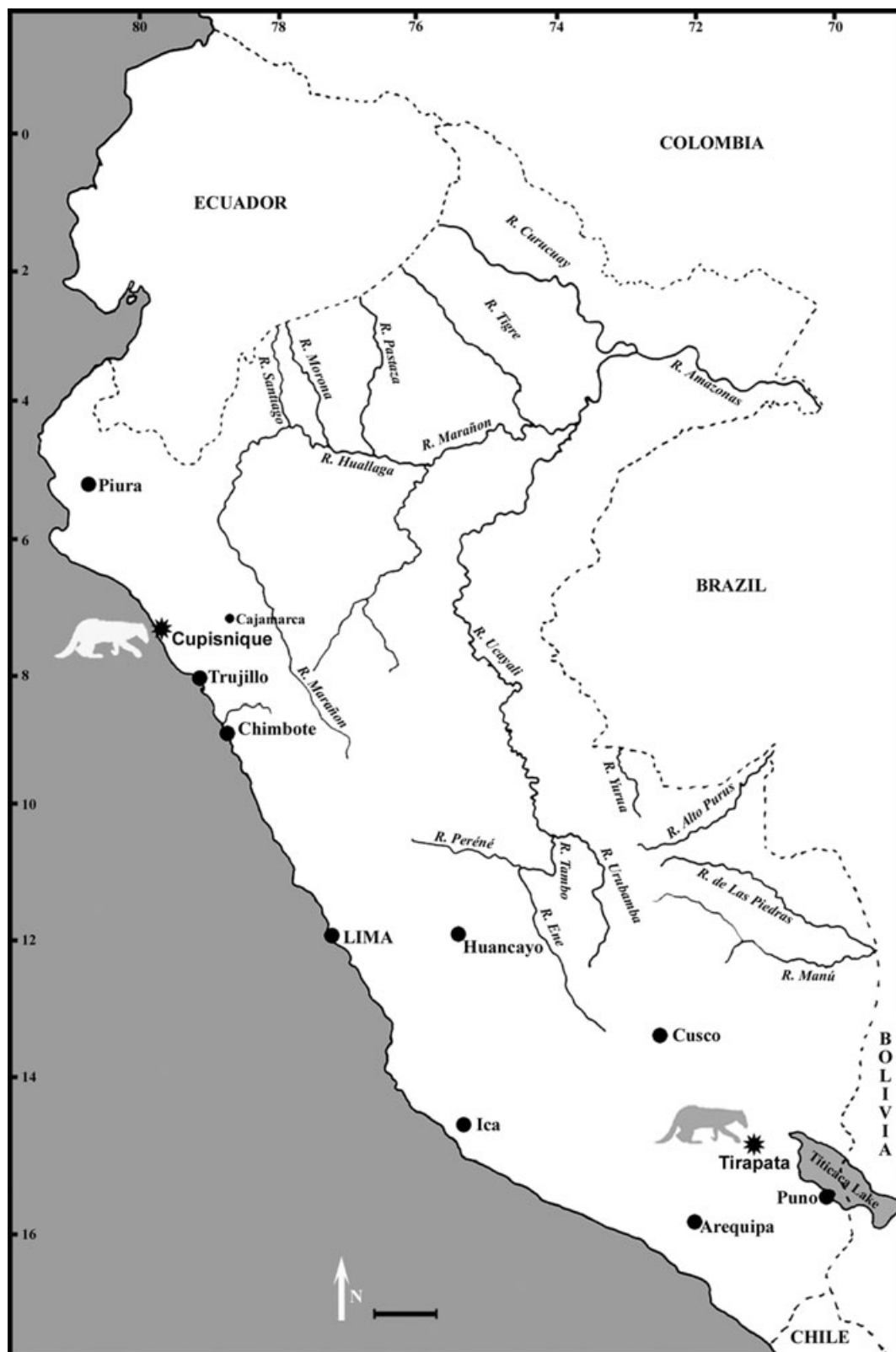
**ADDITIONAL KEYWORDS:** climbing sloth – *Diabolotherium* gen. nov. – functional anatomy – phylogeny – systematics.

## INTRODUCTION

At the beginning of the 20th century, the Swedish explorer Erland Nordenskiöld visited South America and collected Pleistocene mammals from several Peruvian and Bolivian localities (Nordenskiöld, 1905). Those from Casa del Diablo cave, near the town of Tirapata (Lake Titicaca; Nordenskiöld, 1908) are par-

ticularly relevant for the present paper (Fig. 1). Nordenskiöld also recovered remains of *Onhippidion* sp., *Lama* sp., *Canis* sp., *Furcifer?* sp., *Charitoceros* sp., *Scelidotherium* (probably *Scelidodon chiliensis*), *Megatherium* sp. (under study), and a humerus of a small-sized sloth (Nordenskiöld, 1908: figs 2, 3). Nordenskiöld believed that the humerus represented a new fossil sloth, but refrained from creating a new taxon on the basis of this isolated bone. Based on the description and figures in Nordenskiöld's publication, the Argentinean palaeontologist Lucas Kraglievich

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**Figure 1.** Map showing the location of the Pleistocene Peruvian sites Casa del Diablo cave (near the town of Tirapata) and Piedra Escrita (Cupisnique Desert), from which the specimens of *Diabolotherium nordenskiöldi* gen. nov. were discovered. Scale bar = 100 km.

assigned this humerus to a new species of *Nothropus* Burmeister, 1882, *N. nordenskiöldi* Kraglievich, 1926 and confirmed its status 5 years later (Kraglievich, 1926, 1931).

During a French palaeontological exploration in 1975 in the Cupisnique Desert of the Peruvian coast (Fig. 2; 80 km north of the city of Trujillo), Robert Hoffstetter (Muséum National d'Histoire Naturelle, Paris, France; MNHN) and Claude Chauchat (Institut de Préhistoire et de Géologie du Quaternaire, Bordeaux, France; IPGQ) discovered the partial skeleton (MNHN CPN 9–1) of a small fossil sloth in the site of Piedra Escrita [site number PV22-9 according to Chauchat (1998)]. The humerus of this specimen is markedly similar to the one figured by Nordenskiöld (1908). The bones were found on the surface and had suffered eolian erosion. Marshall *et al.* (1984) identified the small fossil sloth MNHN CPN 9–1 as cf. *Nothropus*. A hand-written note by R. Hoffstetter associated with the specimen (Fig. 2) indicates that it belongs to a single individual of a new nothotheriine sloth. A field mission in March 2001 in the Cupisnique Desert organized by the senior author (F.P., based on the directions of C. Chauchat) rediscovered the site that yielded MNHN CPN 9–1 (7°27'53.6"S 79°20'11.3"W).

The Cupisnique Desert bears several archaeological (Chauchat, 1998) and palaeontological localities (Collina-Girard, Guadelli & Usselman, 1992; Falguères *et al.*, 1994; Chauchat, 1998; Pujos, 2000; Pujos & Salas, 2004b), but these sites have not yet been correlated. Pleistocene mammals are common in the Cupisnique Desert and the fauna mainly includes *Stegomastodon* (= *Haplomastodon*) sp. (Gomphotheriidae: Anancinae), *Neochoerus* sp. (Rodentia: Hydro-

choeridae), *Palaeolama* sp. (Artiodactyla: Camelidae), *Equus* (*Amerhippus*) *santaeelenae* (Equidae: Equinae), *Odocoileus* sp. (Artiodactyla: Cervidae), *Pseudalopex* (= *Dusicyon*) sp. (Canidae: Caninae), *Scelidodon chiliensis* (Pilosa: Scelidotheriinae), *Eremotherium laurillardii* (Xenarthra: Megatheriinae), and *Holmesina* cf. *paulacoutoi* (Cingulata: Pamphathiinae) (F.P., personal identification) associated with several freshwater tortoise remains (Marshall *et al.*, 1984; Pujos & Salas, 2004b). Palaeontological sites of the Cupisnique Desert are Lujanian in age (Ur/Tr radiometric dating of *Stegomastodon*, *Amerhippus*, and *Scelidodon* remains give an age between 25 and 15 kypb; Falguères *et al.*, 1994).

In 1993, during a visit to the Swedish Museum of Natural History (Stockholm, Sweden; NRM), G. De Iuliis identified in the Nordenskiöld collections a partial dentary from Casa del Diablo (NRM-PZ M4287) cave, similar to the MNHN specimen from Piedra Escrita. This specimen is referred here to *Diabolothe-rium nordenskiöldi* (see above).

In summary, the elements attributed to this new Pleistocene Peruvian sloth are:

from Casa del Diablo (Andean cave near Lake Titicaca):

the humerus NRM-PZ M4286 described by Nordenskiöld (1908),

the dentary NRM-PZ M4287 collected by Nordenskiöld together with the humerus;

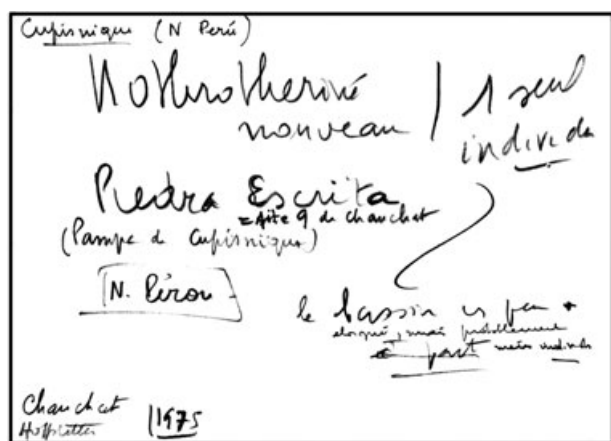
from Piedra Escrita (Cupisnique Desert near the city of Trujillo):

the partial skeleton MNHN CPN 9–1 collected in 1975 by the Hoffstetter–Chauchat mission.

The aim of this work is to describe a peculiar Lujanian Megalonychidae from coastal and Andean areas of Peru (see below), previously noted by Pujos (2002), Argot & Pujos (2003), and Pujos *et al.* (2004). The skull and postcranial elements of this taxon are described in detail and compared with various well-known species of the four Megatherioidea clades. Diagnostic characters and a preliminary morphofunctional and phylogenetic analysis are proposed.

## OVERVIEW OF XENARTHROAN HISTORY

During most of the Cenozoic, South America was isolated from other continents. Vertebrates and especially mammals evolved and diversified endemically. Xenarthra is one of the most representative groups of this peculiar endemic fauna and includes the Pilosa (Tardigrada and Vermilingua) and Cingulata (armoured Xenarthra). Tardigrada (= Phyllophaga; see Fariña, Vizcaíno & Storch, 2003) include fossil and extant sloths. Modern sloths live in New World tropical forests and are represented by four species of



**Figure 2.** Note written by the French palaeontologist R. Hoffstetter explaining the conditions and the locality from which the remains of *Diabolothe-rium nordenskiöldi* gen. nov. MNHN CPN 9–1 were discovered in 1975.

*Bradypus* (*B. variegatus*, *B. tridactylus*, *B. torquatus*, and *B. pygmaeus*; see Anderson & Handley, 2001) and two species of *Choloepus* (*C. hoffmanni* and *C. didactylus*; see Eisenberg, 1989). Extant sloths are characterized by a highly specialized arboreal suspensory locomotor mode associated with anatomical transformations, such as the elongation of long bones, highly mobile joints, the fusion of carpal and tarsal bones, hook-shaped claws, and various astragalar modifications (Mendel, 1985a, b).

The systematic position of Xenarthra among placental mammals is unclear. Following McKenna (1975), morphologists (e.g. Engelmann, 1978; Novacek & Wyss, 1986; Novacek, 1992; McKenna & Bell, 1997) have generally recognized Xenarthra as a sister group to the remaining eutherian mammals, the latter grouped as the Epitheria. Phylogenetic analyses by Madsen *et al.* (2001) and Murphy *et al.* (2001a) based on molecular evidence identified four major placental clades: (I) Xenarthra, (II) Afrotheria (elephants, manatees, hyraxes, tenrecs, aardvarks, and elephant shrews), (III) Laurasiatheria (cetartiodactyls, perissodactyls, carnivores, pangolins, bats, and eulipotyphlans), and (IV) Euarchontoglires, including Glires (rodents and lagomorphs) and Euarchonta (flying lemurs, tree shrews, and primates). Further molecular phylogenetic analyses (e.g. Delsuc *et al.*, 2002; Amrine-Madsen *et al.*, 2003; Reyes *et al.*, 2004) have supported this basic fourfold subdivision among placentals. Madsen *et al.* (2001) further suggested the strong possibility that Afrotheria and Xenarthra have Gondwanan origins. Murphy *et al.* (2001b) suggested that Xenarthra are sister taxon to the Boreoeutheria, a superclade comprising Laurasiatheria and Euarchontoglires (the northern hemisphere group of mammals). They estimated that the Xenarthra–Boreoeutheria split occurred 103 mya, which corresponds to the vicariance event that separated Africa and South America.

Fossil sloths are known since the early Eocene of Antarctica (Vizcaíno & Scillato-Yané, 1995). Sloths are first recorded in South America from the Early Oligocene [Tinguirirican South American Land Mammal Age (SALMA); Wyss *et al.*, 1993] and had become abundant by the end of the Oligocene (Deseadan SALMA; Hoffstetter, 1956; Engelmann, 1987). An Oligocene radiation resulted in two groups: orophodontoids (not recognized in post-Oligocene faunas; Hoffstetter, 1982; Engelmann, 1987; but see below) and Megatherioidea. A phylogenetic analysis of Tardigrada by Gaudin (2004) accommodated orophodontoids (i.e. *Octodontotherium*) among mylodontoids, contra McKenna & Bell (1997). Although the systematics of these taxa is beyond the scope of this paper, the study of new Bolivian orophodontoids performed by Pujos & De Iuliis (2007) corroborates Gaudin's

view. The Megatherioidea are represented by the four clades traditionally recognized as families: Megatheriidae, Megalonychidae, Mylodontidae, and Nothrotheriidae (Gaudin & De Iuliis, 1999; Gaudin, 2004). The systematics of nothrotheres *sensu* Hoffstetter (1954a) is unsettled and the group has been considered as a family (Gaudin & De Iuliis, 1999; Gaudin, 2004; de Muizon *et al.*, 2004a; Pujos & Salas, 2004b), a megatheriid subfamily (Paula Couto, 1971; Patterson & Pascual, 1972; Hirschfeld, 1985; Patterson *et al.*, 1992; St-André, 1996), or a megalonychid subfamily (Kraglievich, 1925, 1931; Simpson, 1945, 1948; Hoffstetter, 1954a; Cartelle & Fonseca, 1983; de Muizon & McDonald, 1995; McDonald & de Muizon, 2002; de Muizon *et al.*, 2003), depending on the taxa considered. Moreover, the relationships among well-known Megatherioidea families and some Santacrucian sloths (e.g. *Hapalops*, *Eucholoeps*, and *Planops*) are in debate. The craniodental study performed by Gaudin (2004) suggested *Planops* as a Megatheriinae and *Hapalops* as a sister taxon of (*Analcimorphus* + (Megatheriinae + Nothrotheriidae) + Megalonychida).

Several recent studies described Pleistocene sloths from Peru and assigned them to Mylodontidae (Mylodontinae and Scelidotheriinae), Megatheriidae (*Megatherium* and *Eremotherium*) and Nothrotheriidae (Pujos & Salas, 2004b). They are abundant along the coast (Marshall *et al.*, 1984; Pujos, 2000; Pujos & Salas, 2004a, b; Pujos *et al.*, 2004) and in the Andes (Marshall *et al.*, 1984; Hoffstetter, 1986; Pujos, 2001b; Pujos, Salas & Mattos, 2002; Pujos & Salas, 2004a).

Until the 1990s, fossil sloths were generally considered graviportal mammals (= Gravigrada; Hoffstetter, 1982). Recent work (e.g. White, 1989, 1993, 1997; de Muizon & McDonald, 1995; Aramayo & Manera De Bianco, 1996; Casinos, 1996; de Toledo, 1996; Pujos *et al.*, 2002; Argot & Pujos, 2003; Bargo, 2003; Blanco & Czerwonogora, 2003; Tito & De Iuliis, 2003) emphasized the diversity of locomotor modes that evolved among fossil Tardigrada. White (1993) in particular viewed *Hapalops* and some West Indian megalonychids as semiarboreal taxa. Moreover, de Muizon & McDonald (1995), McDonald & de Muizon (2002), and de Muizon *et al.* (2003; 2004a), described *Thalassocnus*, a lineage of five Mio-Pliocene species from the Pisco Formation of Peru, and considered them as aquatic or semiaquatic forms. The functional peculiarities of the singular new Pleistocene Tardigrada from Casa del Diablo Cave and Cupisnique Desert are discussed below.

#### ABBREVIATIONS

##### *Palaeontological and phylogenetic abbreviations*

BNL, basonasal length, measured from the posterior edge of the occipital condyles to the anterior edge of



the nasal bone (following Gaudin, 2004); C and c, upper and lower caniniform teeth, respectively; L, left; M., muscle; M and m, upper and lower molariform teeth, respectively; Mc, metacarpal; MCC, metacarpal–carpal complex; MEC, mesocuneiform–entocuneiform complex; Mt, metatarsal; N<sup>x</sup>, number of characters used in the phylogenetic analysis and state of the character considered; P(1–2), fused first and second phalanges; R, right.

#### *Institutional abbreviations*

AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; IFEA, Institut Français d'Etudes Andines, Lima, Peru; INC, Instituto Nacional de la Cultura del Perú, Lima, Peru; IPGQ, Institut de Préhistoire et de Géologie du Quaternaire, Bordeaux, France; LACM, Los Angeles County Museum, Los Angeles, USA; MAE, Ministère des Affaires Étrangères, Paris, France; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MUSM, Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima, Peru; NHM, Natural History Museum, London, UK (casts of *Planops martini* Hoffstetter, 1961 are housed at MNHN); NRM, Swedish Museum of Natural History, Stockholm, Sweden; ROM, Royal Ontario Museum, Toronto, Canada; UCMP, Museum of Paleontology, University of California, Berkeley, USA; UF, Florida Museum of Natural History, University of Florida, Gainesville, USA; UZM, Universitat Zoologisk Museum, Copenhagen, Denmark.

### SYSTEMATIC PALAEONTOLOGY

XENARTHRA Cope, 1889

TARDIGRADA Latham & Davies in Forster, 1795

MEGATHERIOIDEA Gray, 1821

MEGALONYCHIDAE Gervais, 1855

#### ***Diabolotherium* gen. nov.**

Type species: *D. nordenskioldi* (Kraglievich, 1926)

(Figs 3–9, 10A–D, 11–14, 15G, N, 16H, 17, Appendix 1)

*Synonymy*: *Nothropus nordenskioldi* Kraglievich, 1926 and 1931. cf. *Nothropus* Marshall *et al.*, 1984.

*Holotype*: NRM-PZ M4286, L humerus (Fig. 10A, B).

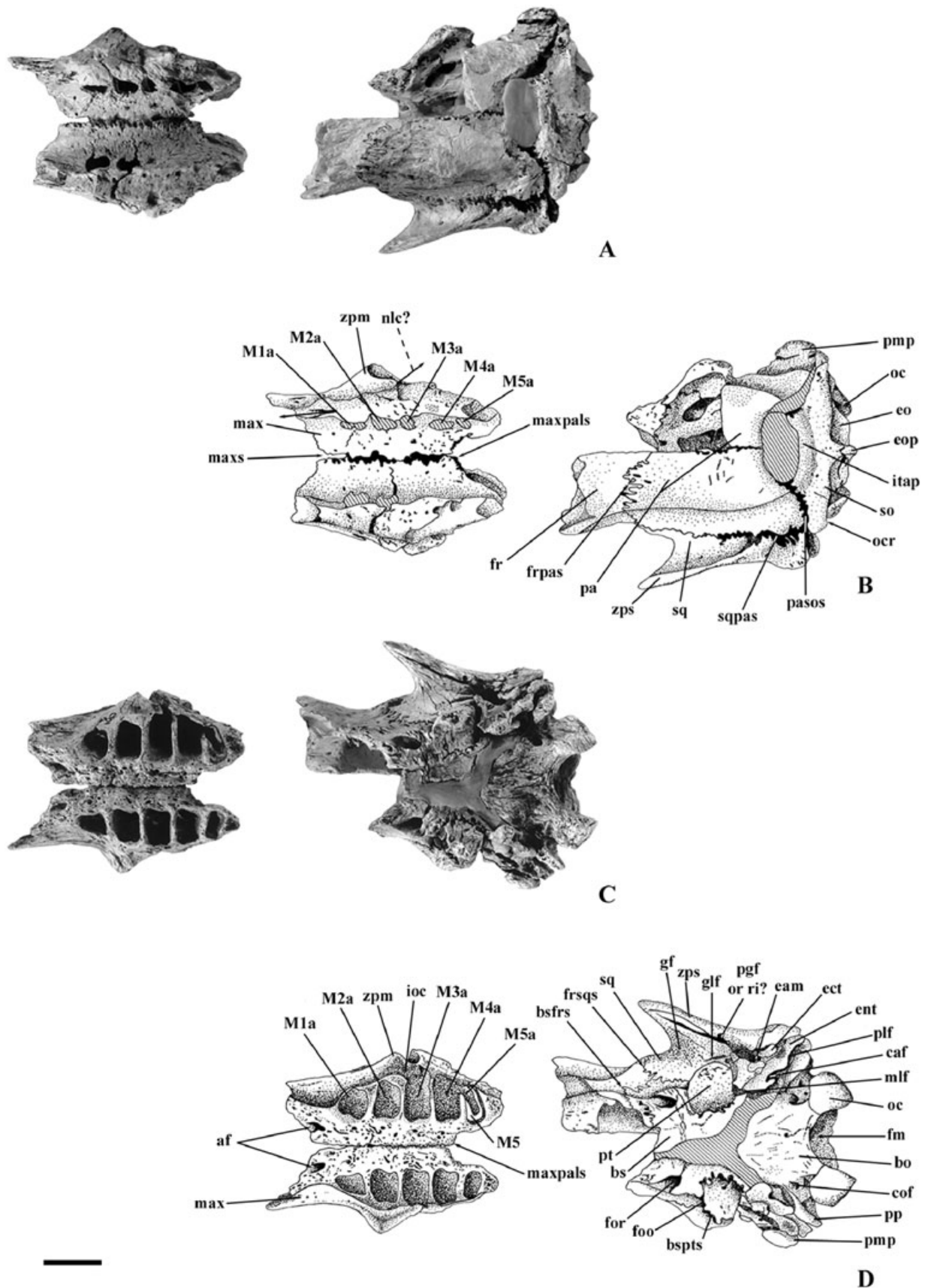
*Paratype*: An edentulous R dentary (NRM-PZ M4287; Fig. 6A, B).

*Species diagnosis*: Small-sized fossil sloth (half the size of the North American Megalonychidae *Pliometanastes prostitus* and similar to the West Indies form *Parocnus browni*); dentition: 5/4 quadrangular molariform teeth; first anterior molariform tooth (M1) slightly triangular with a mesial longitudinal groove

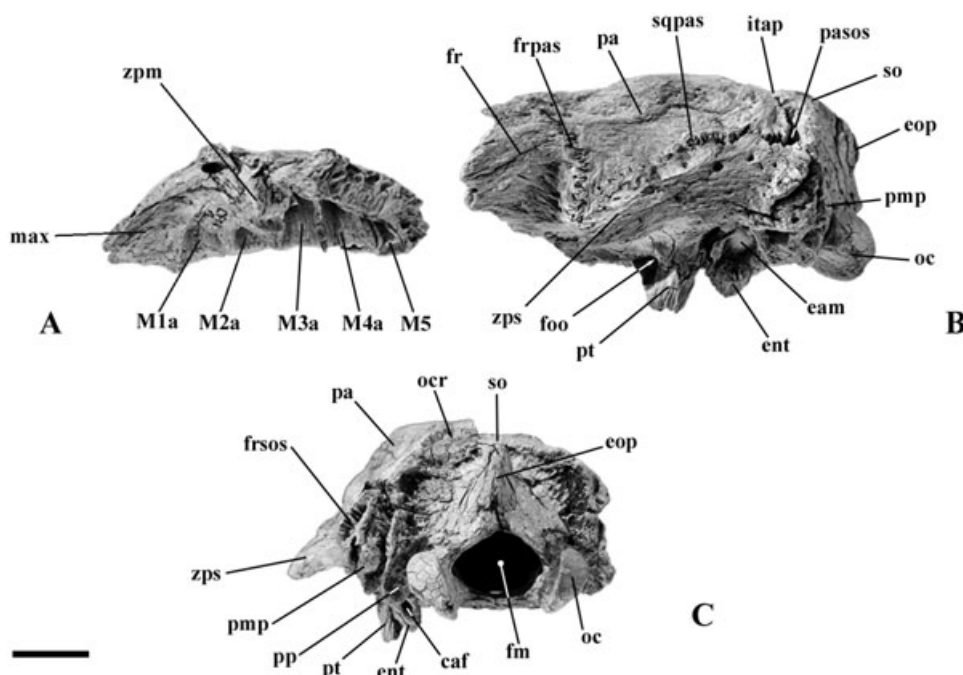
(not caniniform as in other Megalonychidae); M2–M4 rectangular (as in Plio-Pleistocene Nothrotheriidae, probably by convergence, and not oval as in West Indies Megalocninae and Choloepodinae, North and Central American Megalonychidae), and anteroposteriorly compressed with lateral and mesial longitudinal grooves; M5 reduced, rectangular, and without longitudinal grooves; m1–m4 with longitudinal grooves on labial and lingual margins of m2–m4; stylohyal fossa lateroventrally inclined and anteroposteriorly extended; mandible with thin and prominent angular process well separated from condyloid process; slender humerus without entepicondylar foramen and with reduced deltopectoral crest; medial and lateral epicondyle and epicondylar crest less developed than in other Megalonychidae; ulnar trochlear notch proximolaterally to distomedially extended; radial notch markedly anterior and nearly in the same plane as the trochlear notch; ulnar diaphysis slightly sigmoid in lateral view (as in *Hapalops*); ulnar styloid process distomedially long and spatulate as in modern tree sloths; radial diaphysis medially concave in anterior view; scaphoid proximodistally compressed; Mc II–IV subequal in length, shortness, and robustness; ilium subparallel to sacral vertebrae (similar to *Hapalops*); shallow acetabular fossa; undifferentiated odontoid and discoid facets of astragalus; in distal view the angle between the astragalar odontoid and discoid facets is 160°; astragalar head medial to odontoid process; ectal facet L-shaped; sustentacular facet constituted by two parts arranged at right angles; calcaneum wing-shaped, dorsoplantarly flattened, with a dorsoplantar foramen on the anterior portion of its lateral margin; Mt III anteroposteriorly compressed and medial articular facet (for the Mt II?) posteromedial and plantarly inclined; lateral wing of Mt V extremely reduced.

*Type locality*: Casa del Diablo cave from the Peruvian Andes near Tirapata (Puno Department; Fig. 1).

*Referred material*: MNHN CPN 9–1 partial skeleton of a subadult specimen (Figs 3–5, 6C–H, 7–9, 10C, D, 11–14, 15G, N, S, 16H, 17, and Appendix 1) from Piedra Escrita preserving portions of the skull and R edentulous dentary; atlas and three other cervical vertebrae; approximately ten dorsals and ten caudals partially preserved, a haemal arch, portions of the sacrum fused with partial innominate, R scapula, R and L humeri, R ulna, R radius, R and L scaphoids, L lunar, distal half of R and L cuneiforms, dorsal two-thirds of L unciform, R and L Mc III, L Mc II (medial side damaged), R Mc IV (lateral side damaged) and lateral portion of L Mc IV, six ungual phalanges (with the R manual third phalanx), several undetermined phalanges (manual and pedal), R and L astragali,



**Figure 3.** Drawings and photographs of the skull of *Diabolotherium nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen) in dorsal (A, B) and ventral (C, D) views. af, alveolar foramina; bo, basioccipital; bs, basisphenoid; bsfrs, basisphenoid–frontal suture; bspts, basisphenoid–pterygoid suture; caf, carotidian foramen; cof, condylar foramen; eam, external auditory meatus; ect, ectotympanic; ent, entotympanic; eo, exoccipital; eop, external occipital protuberance; fm, foramen magnum; foo, foramen ovale; for, foramen rotundum; fr, frontal; frpas, frontoparietal suture; frsq, frontosquamosal suture; gf, glenoid fossa; glf, Glaserian fissure; ioc, infraorbital canal; itap, interparietal process; max, maxilla; maxpals, maxillopalatine suture; maxs, suture between the maxillae; mlf, medial lacerate foramen; M1a–M5a, alveolae of the five upper molariform teeth; M5, fifth upper molariform tooth; nlc?, possible nasolacrimal canal; oc, occipital condyle; ocr, occipital crest; pa, parietal; pasos, parietosupraoccipital suture; pgf?, possible postglenoid foramen; plf, posterior lacerate foramen; pmp, pars mastoidea of the periotic; pp, paroccipital process; pt, pterygoid; ri?, possible passage for the inferior ramus of the stapedia artery and the chorda tympani; so, supraoccipital; sq, squamosal; sqpas, squamosoparietal suture; zpm, zygomatic process of the maxilla, zps, zygomatic process of the squamosal. Scale bar = 2 cm.



**Figure 4.** Photographs of the skull of *Diabolotherium nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen). A, anterior portion of the skull in lateral view (anterior towards the left), B, C, posterior portion of the skull in lateral and occipital views, respectively. caf, carotidian foramen; eam, external auditory meatus; ent, entotympanic; eop, external occipital protuberance; fm, foramen magnum; foo, foramen ovale; fr, frontal; frpas, frontoparietal suture; itap, interparietal process; max, maxilla; M1a–M4a, alveolae of the anterior four upper molariform teeth; M5, fifth upper molariform tooth; oc, occipital condyle; ocr, occipital crest; pa, parietal; pasos, parietosupraoccipital suture; pmp, pars mastoidea of the periotic; pp, paroccipital process; pt, pterygoid; so, supraoccipital; sqpas, squamosoparietal suture; zpm, zygomatic process of the maxilla, zps, zygomatic process of the squamosal. Scale bar = 2 cm.

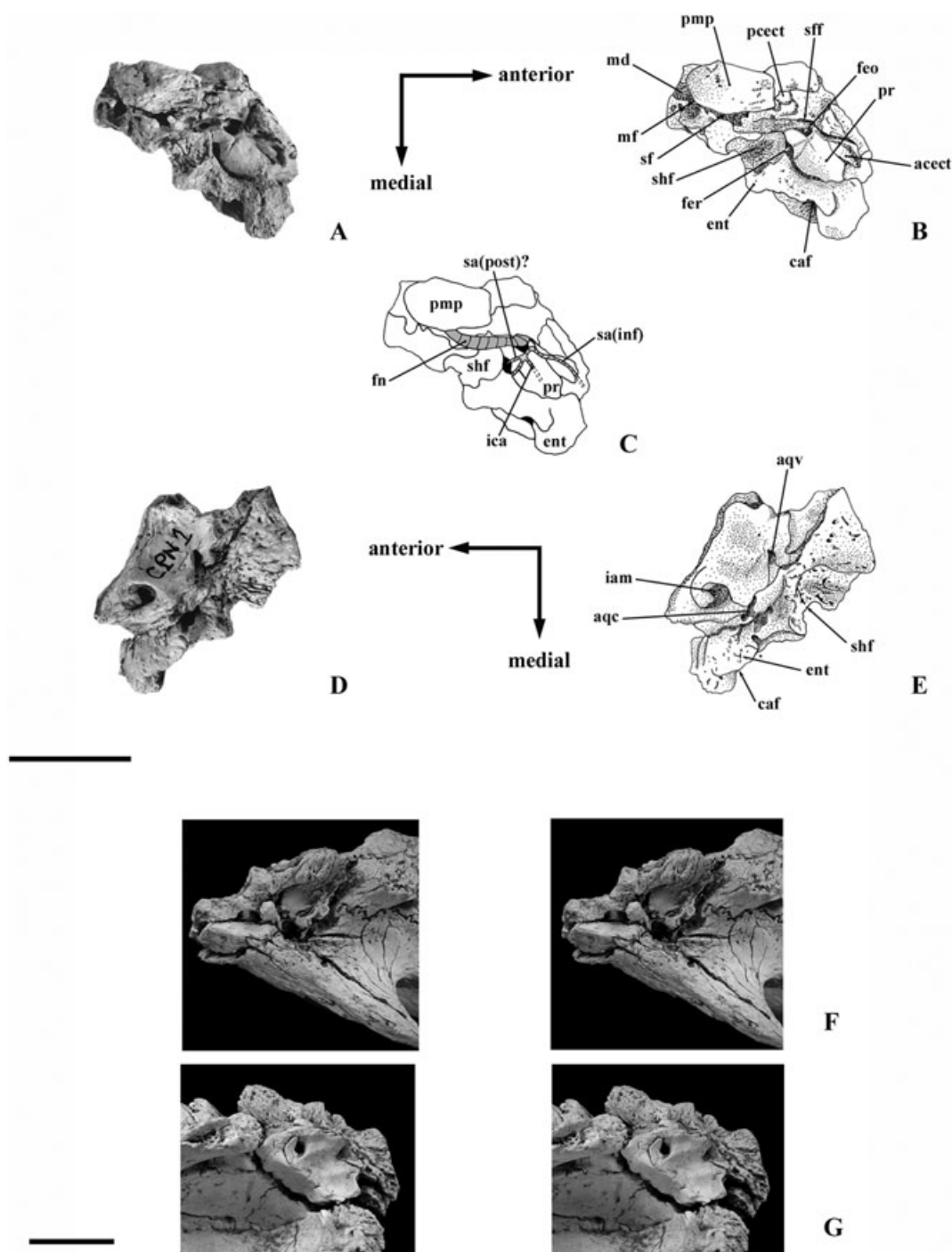
L calcaneum, partial R cuboid, L Mt III, R Mt V, L P1–III, R and L P3–III.

*Etymology of the genus:* ‘Diabolo’, the Latin word for devil, named after Casa del Diablo cave, the type locality where Erland Nordenskiöld found the holotype, and ‘therium’, the Greek word for beast.

*Horizon of the holotype NRM-PZ M4287 and paratype NRM-PZ M4286 (from Casa del Diablo):* Pleistocene deposits in cave.

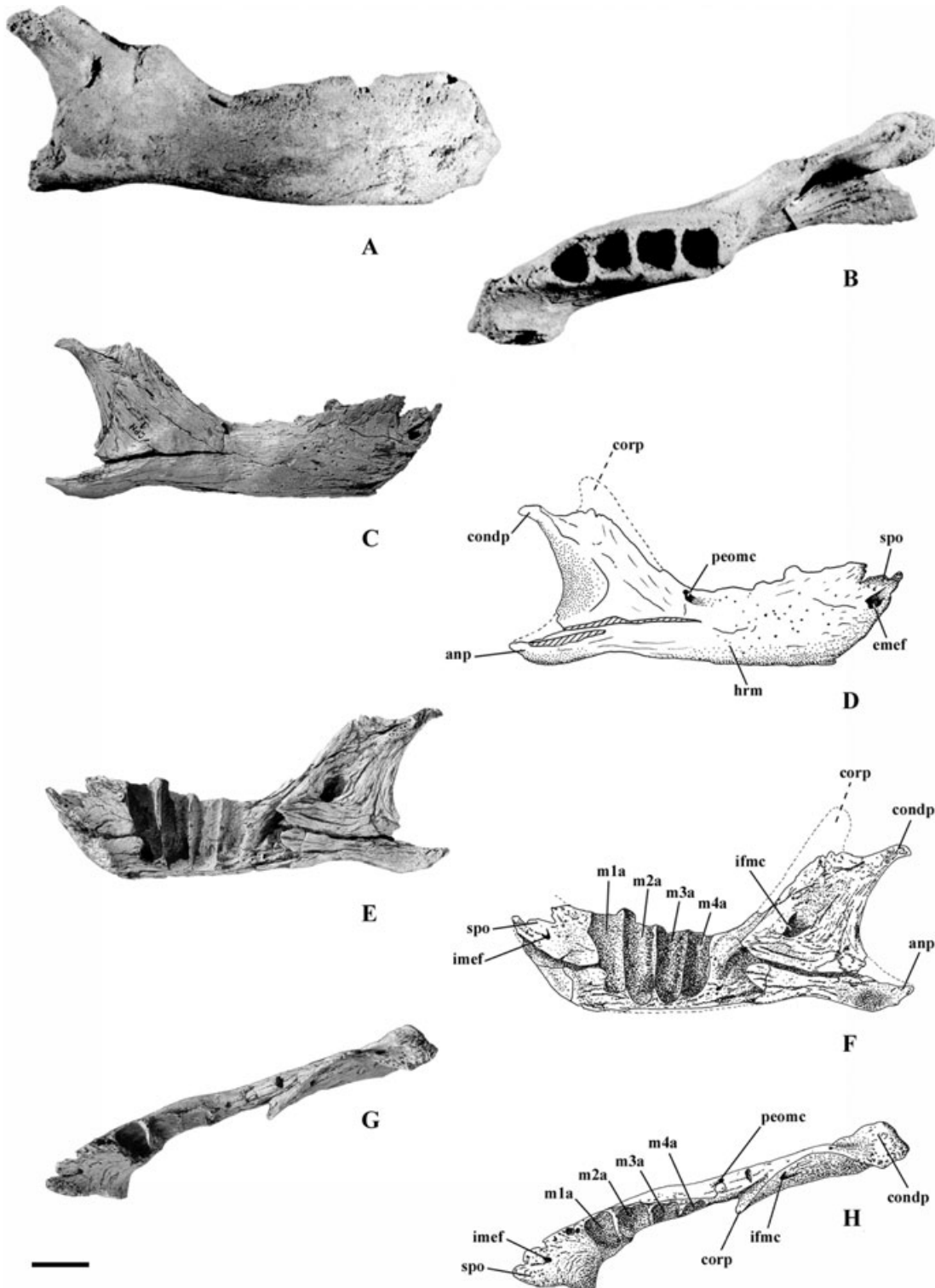
*Horizon and age of referred material (from Piedra Escrita):* Lujanian SALMA deposits of the Cupisnique Desert (between 25 and 15 kybp; Falguères *et al.*, 1994) located at the same geographical position as a Paijanian cut site but not associated with it (C. Chauchat, pers. comm, 1998). Global positioning system position: 7°27'53.6"S, 79°20'11.3"W.

*Geological context of the site of Piedra Escrita:* Archaeological and palaeontological sites [site number PV22-9 from Chauchat (1998)] are located on a fluvial

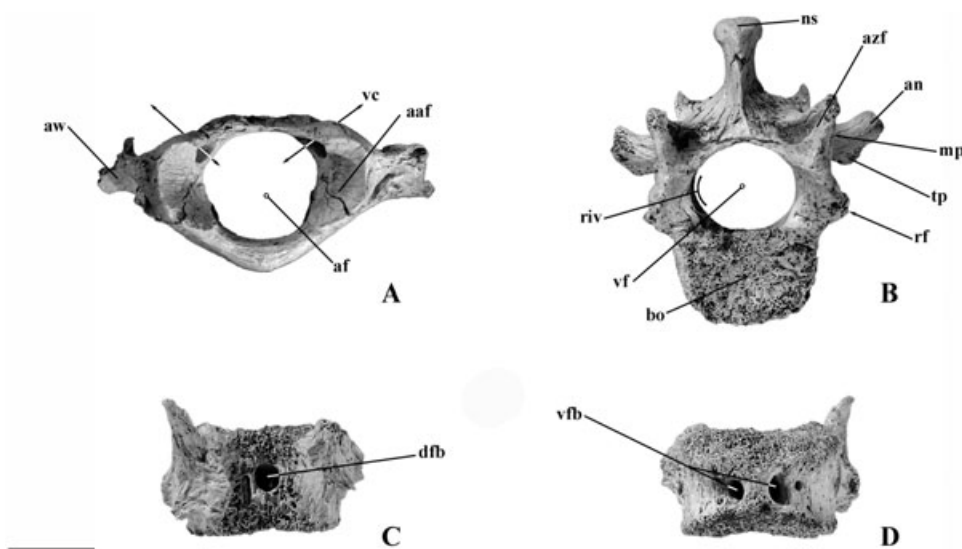


**Figure 5.** Drawings and photographs of the auditory regions of *Diabolotheirus nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen). A–C, right auditory region in lateral view with major arteries and nerves (C). D, E, right auditory region in medial view. F, G, stereo photographs of left auditory region in lateroventral (ventral towards the top, anterior towards the right) and dorsomedial (ventral towards the top, anterior towards the left) views, respectively. acet, anterior crus of the ectotympanic; aqc, aqueductus cochleae; aqv, aqueductus vestibuli; caf, carotidian foramen; ent, entotympanic; feo, fenestra ovalis; fer, fenestra rotundum; fn, facial nerve; iam, internal auditory meatus; ica, internal carotid artery; md, mastoid depression; mf, mastoid foramen; pect, posterior crus of the ectotympanic; pmp, pars mastoidea of the periotic; pr, promontorium (cranial surface of the pars petrosa); sa(inf), inferior ramus of the stapedia artery; sa(post)?, possible posterior ramus of the stapedia artery; sf, stylomastoid foramen; sff, secondary facial foramen; shf, stylohyal fossa. Scale bars = 2 cm.





**Figure 6.** Drawings and photographs of the right dentary of *Diabolotherium nordenskioldi* gen. nov. A, B, NRM-PZ M4287 (paratype) in right lateral and occlusal views, respectively. C–H, MNHN CPN 9–1 (referred specimen) in right lateral (C, D), medial (E, F), and occlusal (G, H) views, respectively. anp, angular process; condp, condyloid process; corp, coronoid process; emef, external mental foramina; hrm, horizontal ramus of the mandibula; ifmc, internal foramen of the mandibular canal; imef, internal mental foramina; m1a–m4a, alveoli of the four lower molariform teeth; peomc, posterior external opening of the mandibular canal; spo, spout. Scale bar = 2 cm.



**Figure 7.** Photographs of the vertebrae of *Diabolotherium nordenskioldi* gen. nov. (MNHN CPN 9-1, referred specimen). A, atlas in anterior view (dorsal towards the top). B, dorsal vertebra in anterior view. C, D, body of a lumbar vertebra in dorsal and ventral views, respectively. aaf, anterior articular facet; af, atlantal foramen; an, anapophysis; aw, atlas wing; azf, anterior zygapophyseal facet; bo, body; dfb, dorsal foramen of the body; mp, metapophysis; ns, neural spine; rf, rib facet; riv, passage of the right intrarachidian vein; tp, transverse process; vc, vertebrarterial canal of the atlas; vf, vertebral foramen; vfb, ventral foramen of the body (passage of vertebral veins). Scale bar = 2 cm.

terrace at the end of the 'Quebrada de Cupisnique'. Pleistocene conglomerated sediments are formed by the erosion of the Río Cupisnique and discharged in the sea.

### DESCRIPTION OF THE SPECIMENS

The study of the cranial and postcranial elements of *D. nordenskioldi* reveals a mosaic of characters unknown in other sloths. This peculiar Megalonychidae shares several features with Santacrucian forms such as *Hapalops*, as well as Megatheriidae, Nothrotheriidae, and modern tree sloths (i.e. the tropical genera *Bradypus* and *Choloepus*). Therefore, *D. nordenskioldi* will be compared below with the modern tree sloths and to all Megatherioidea. This Peruvian taxon does not belong to the genus *Nothropus*, based on a few cranial characters: (1) the upper tooth rows diverge strongly anteriorly in *Nothropus priscus* (Frailey, 1986), whereas they are subparallel in *Diabolotherium*, (2) the upper alveoli are much more compressed anteroposteriorly in *Nothropus* than in *Diabolotherium*, and (3) the occipital condyles are closer in dorsal view in *Diabolotherium* than in *Nothropus*.

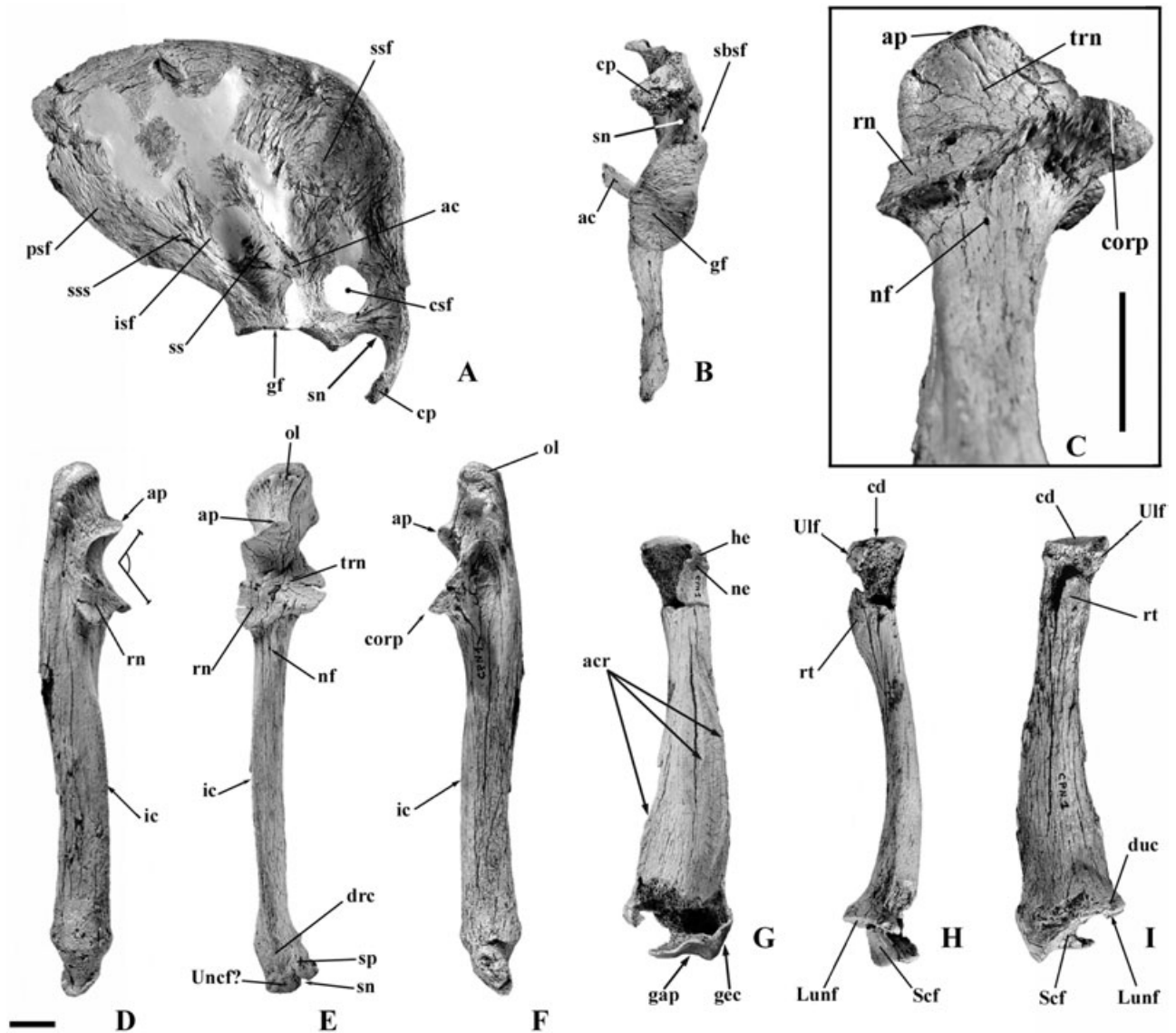
#### SKULL (FIGS 3-5, APPENDIX 1)

The parietal, a small part of the L frontal, the L squamosal, portions of the basisphenoid, posterior portions of the pterygoids, nearly complete occipital bones, and

the ventral portions of the maxillae are preserved (Figs 3-5). R and L auditory regions are partially preserved (Fig. 5). Some of the cranial sutures are incompletely fused (e.g. between the maxillae, frontal/supraoccipital, and frontal/squamosal) and indicate the immature status of the individual (Figs 3, 4).

#### Maxilla

Teeth are absent (except for the basal part of L M5) but the alveolar shapes of the upper molariforms are observable (Fig. 3C, D). *D. nordenskioldi* possesses five upper teeth. The absence of a diastema between the first two teeth and the triangular section of the most mesial tooth indicates a molariform rather than a caniniform. As in Megatheriinae and Nothrotheriidae, the alveoli of M2-M5 are quadrangular. The M1 alveolus is transversely wider distally than mesially and its labial margin is convex. The M2-M4 alveolae are approximately similar in shape, M3 and M4 being wider (Appendix 1). *D. nordenskioldi* and the basal megatheriines *Megathericulus patagonicus* and *Plesiomegatherium halmyronomum* exhibit 5/4 rectangular molariform teeth, instead of the squared molariforms of derived megatheriines, such as *Megatherium (Megatherium) americanum* and *Eremotherium laurillardii* (Cartelle & De Iuliis, 1995; De Iuliis, 1996; Pujos & Salas, 2004a). In Nothrotheriidae (e.g. *Nothrotherium*, Stock, 1917: fig. 3; *Thalassocnus*, de Muizon & McDonald, 1995: fig. 1b) there are only four upper and three lower rectangular molariforms. In the

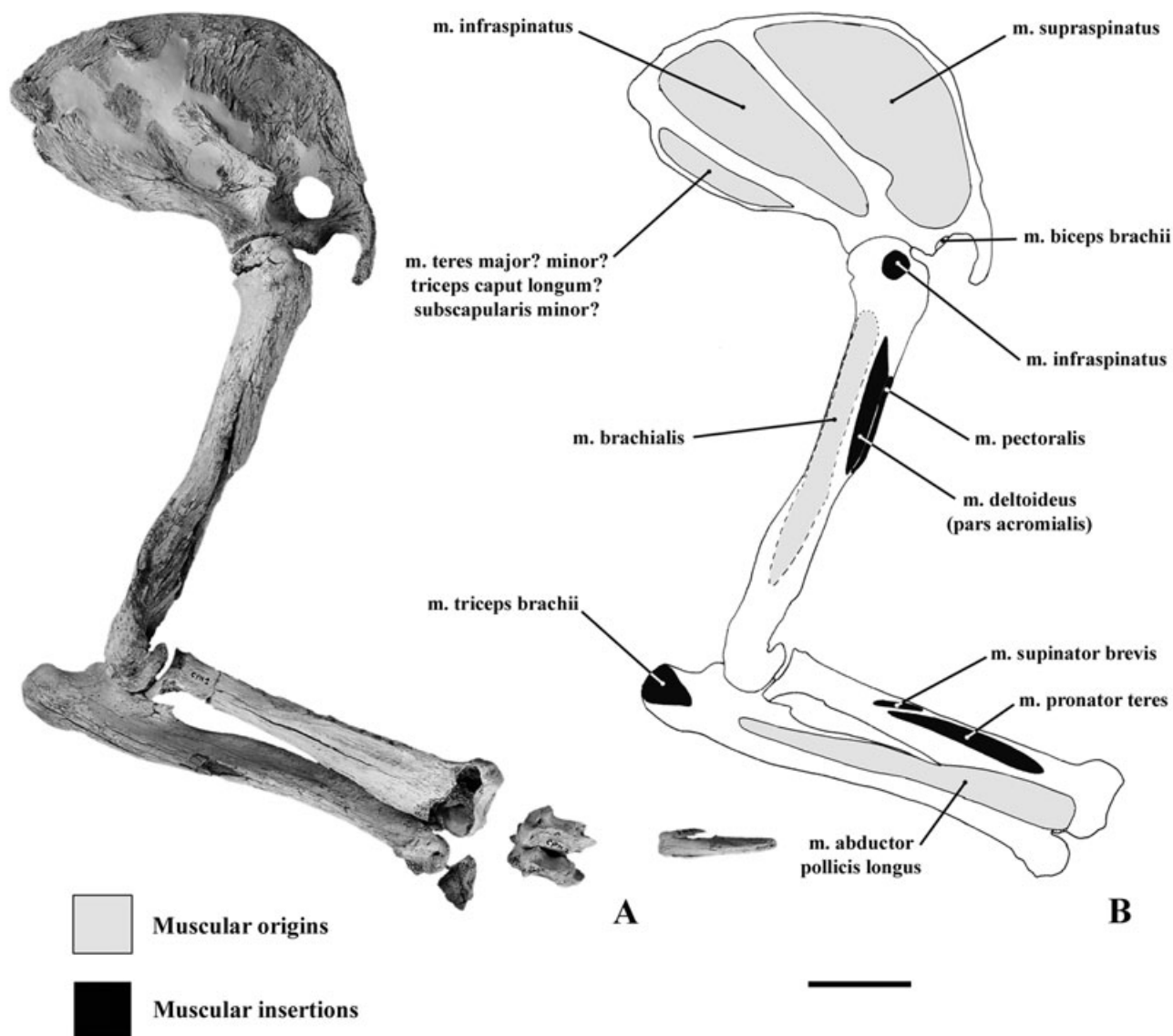


**Figure 8.** Photographs of the pectoral girdle and long bones of the forelimb of *Diabolotherium nordenskioldi* gen. nov. (MNHN CPN 9-1, referred specimen). A, B, right scapula in lateral (dorsal towards the top, posterior towards the left) and anterior (anterior towards the top, lateral towards the left) views, respectively. C, proximal articular facets of the right ulna in anterodistal view, to observe the orientation of the radial notch relative to the coronoid process. D–F, right ulna in lateral, anterior, and medial views, respectively. G–I, right radius in anterior, lateral, and posterior views, respectively. ac, acromion; acr, anterior crests of the radius; ap, anconeal process; cd, capitular depression; corp, coronoid process; cp, coracoid process; csf, coracoscaphular foramen; drc, distal radial contact; duc, distal ulnar contact; gap, groove for tendon of the abductor pollicis longus; gec, groove for the M. extensor carpi radialis; gf, glenoid fossa; he, head; ic, interosseous crest; isf, infraspinous fossa; Lunf, lunar facet; ne, neck; nf, nutrient foramen; ol, olecranon; psf, postscapular fossa; rn, radial notch; rt, radial tuberosity; sbsf, subscapular fossa; Scf, scaphoid facet; sn, styloid notch; sp, styloid process; ssf, supraspinous fossa; ss, scapular spine; sss, secondary scapular spine; trn, trochlear notch; Ulf, ulnar facet; Uncf?, unciform facet. Scale bar = 2 cm.

Santacrucian sloths (e.g. *Hapalops elongatus*, Scott, 1903–04: plate 39–1; *Planops martini*, Hoffstetter, 1961: fig. 2) and West Indies Megalonychidae (e.g. *Megalocnus rodens*, Matthew & Paula Couto, 1959: plate 4; *Acratocnus ye*, MacPhee, White & Woods,

2000b: fig. 4b), the four upper molariforms are oval rather than quadrangular. In *D. nordenskioldi*, the mesiodistal diameter of the upper molariforms decreases from M2 to M5 (Appendix 1). M5 is rectangular, but much smaller than the preceding teeth





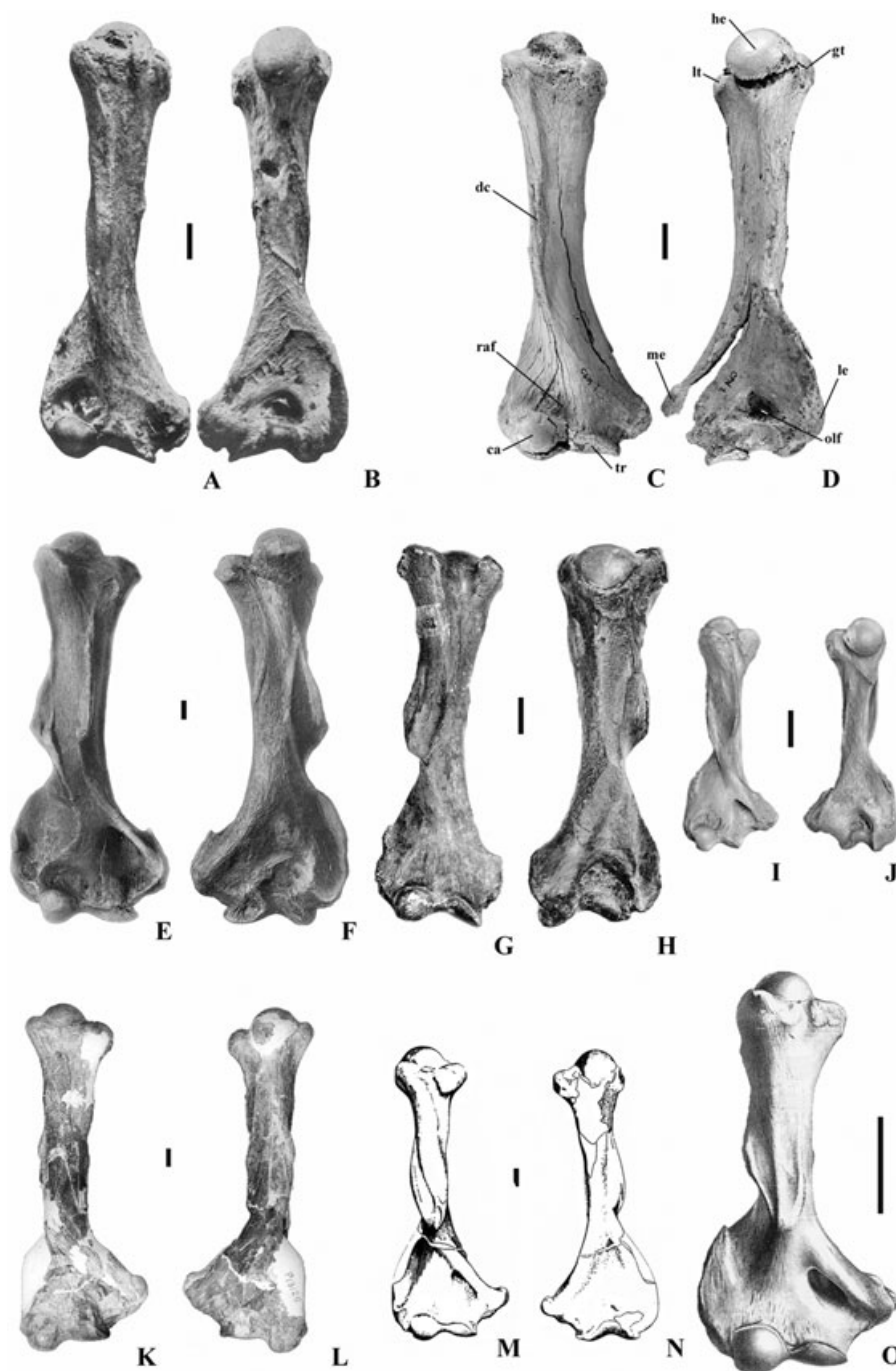
**Figure 9.** Photograph (A) and drawing (B) of the arm (scapula, humerus, ulna, radius, and some elements of the hand) of *Diabolotherium nordenskioldi*, showing areas of musculature origins and insertions. Scale bar = 2 cm.

and mesiodistally compressed as in the Miocene nothrotheriid *Thalassocnus natans* (de Muizon & McDonald, 1995: fig. 1b) and megatheriines. M1–M4 show labial and lingual longitudinal grooves. Similar grooves are present in Megatheriinae and on the M1–M3 of some Nothrotheriidae (e.g. *Nothrotherium*, Pujos, 2001a: fig. 2). M4 bears a faint groove on its posterior distal margin, based on a crest borne by its alveolus. In other Megalonychidae (e.g. *Acratocnus*, Anthony, 1918: fig. 43; *Paulocnus*, Paula Couto, 1967: fig. 26; *Neocnus*, MacPhee *et al.*, 2000b: figs 7–10; *Megalonyx*, Hirschfeld, 1981: fig. 7) longitudinal grooves are not present on the upper and lower molariform teeth. In *D. nordenskioldi*, the tooth rows diverge slightly mesially and distally (at the levels of

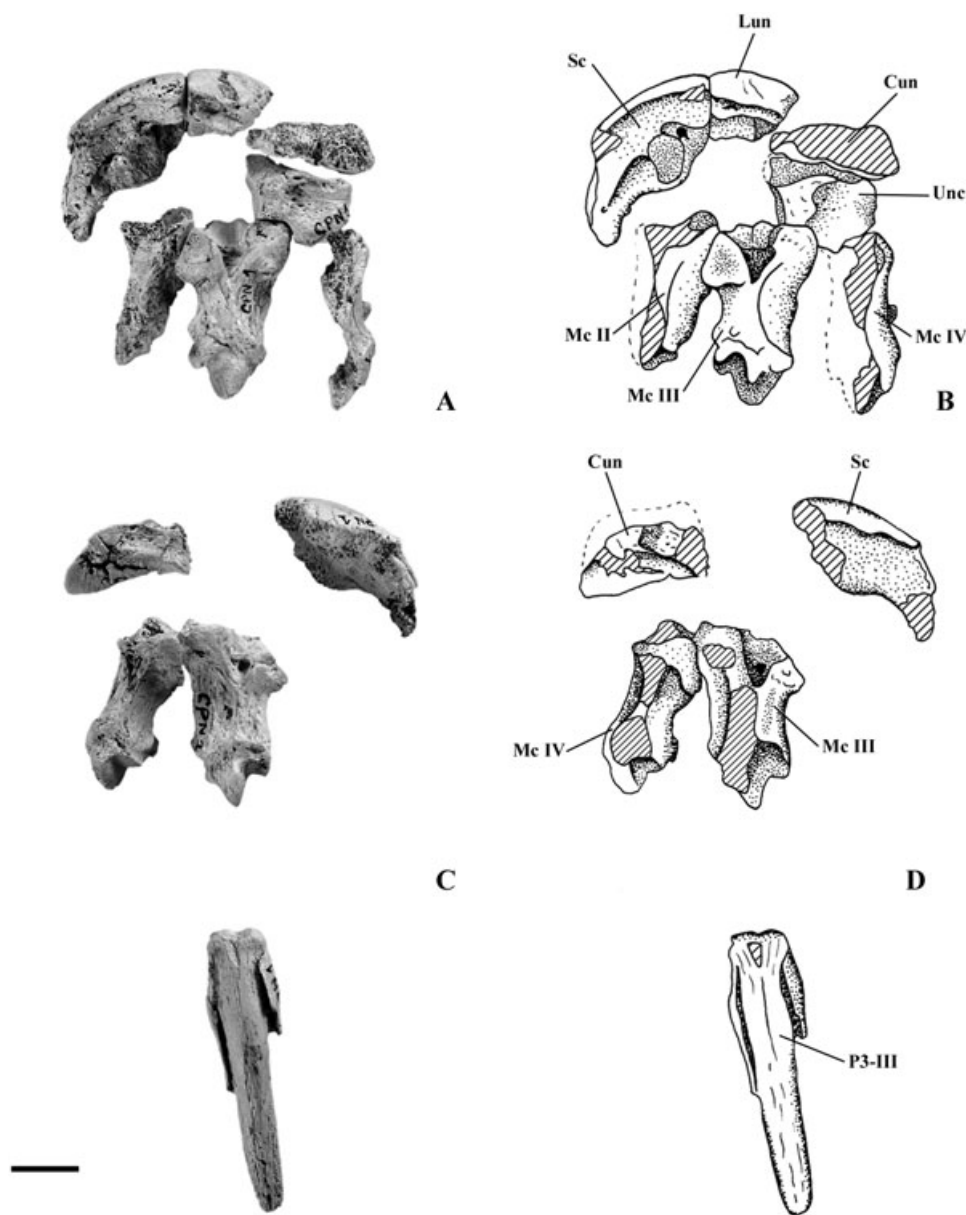
M1 and M5, Fig. 3C, D). A similar morphology occurs in the megatheriine *Eremotherium* (Cartelle, 1992; Cartelle & De Iuliis, 1995; De Iuliis, 1996).

The anterior portions of the maxillae are not preserved (Figs 3, 4) and M1 lies 10 mm posterior to the preserved margin of the maxilla. Several vascular foramina are present on the palate between the tooth rows. Two large foramina are located anteromedially to M1 (Fig. 3C, D). The deep buccinator fossa, which constricts the premolariform region, as in most fossil sloths, is located anterolateral to the tooth row. The zygomatic processes of the maxillae are broken, but located laterally between M2 and M3, as in the Megatheriinae. They lie more anteriorly, at the level of M1, in the Megalonychinae (e.g. *Megalocnus*, Matthew &





**Figure 10.** Photographs (A–H, K–L) and drawings (I, J, M–O) of right humeri in anterior (A, C, E, G, I, K, M, O) and posterior (B, D, F, H, J, L, N) views of: A–D, *Diabolootherium nordenskiöldi* gen. nov. [A, B, holotype NMR-PZ M4286 from Casa del Diablo cave, after Nordenskiöld (1908: fig. 2); C, D, referred material MNHN CPN 9–1 from Piedra Escrita, Cupisnique Desert, reversed from the original]. E, F, *Megalocnus rodens* [AMNH 49969, reversed from the original, modified from Matthew & Paula Couto (1959: fig. 14)]. G, H, *Parocnus browni* [AMNH 49918, modified from Matthew & Paula Couto (1959: figs 32.1, 33.1)]. I, J, *Acratocnus ye* [UF 75528, reversed from the original, modified from MacPhee *et al.* (2000b: fig. 6A, B)]. K–L, *Eucholoeops ingens* (FMNH P13125). M, N, *Pliometanastes propositus* [UCMP 97371, reversed from the original, modified from Hirschfeld (1981: fig. 4)]. O, *Megalonyx jeffersonii* [LACM 21003, reversed from the original, modified from Stock (1925)]. c, capitulum; dc, deltopectoral crest; gt, greater tubercle; he, head; le, lateral epicondyle; lt, lesser tubercle; me, medial epicondyle; olf, olecranon fossa; raf, radial fossa; tr, trochlea. Scale bar = 2 cm for all the humeri except *Megalonyx* (10 cm).



**Figure 11.** Drawings and photographs of the left (A, B) and right (C, D) manus in dorsal view (proximal towards the top) of *Diabolotherium nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen). Cun, cuneiform; Lun, lunar; Mc II–IV, metacarpals 2–4; P3–III, ungual phalanx of the third digit; Sc, scaphoid; Unc, unciform. Scale bar = 2 cm.

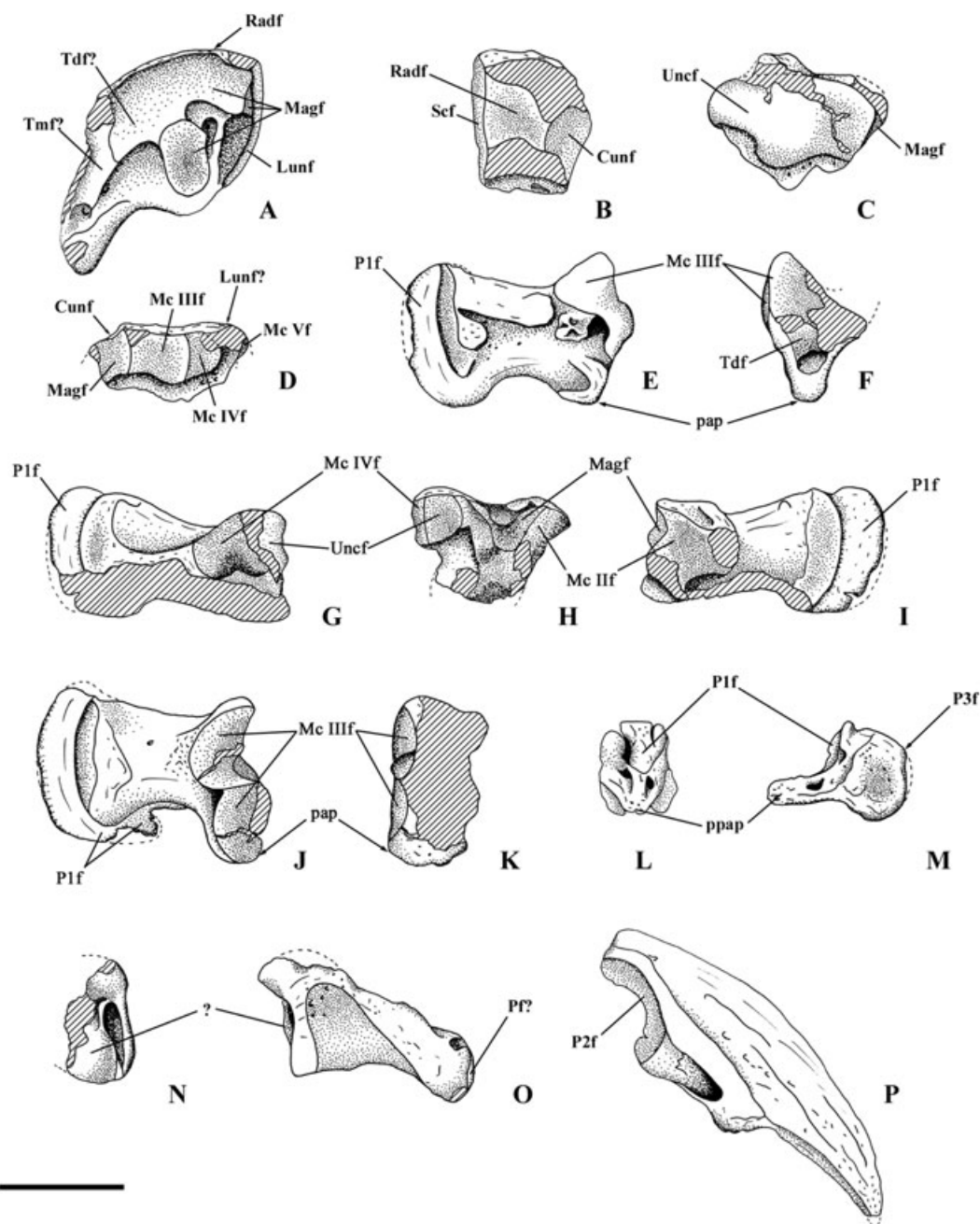
Paula Couto, 1959: plate 4; *Megalonyx*, Hirschfeld & Webb, 1968: fig. 2) and between M1 and M2 in the Santacrucian sloth *Hapalops* (Scott, 1903–04: plate 31). A canal, probably the nasolacrimal canal, passes through the maxilla from the level of M3 (observable thanks to the lack of the lateral wall of the maxilla) and opens in the nasal cavity (Fig. 3A, B). The wide infraorbital canal passes anterolaterally to posteromedially through the ventral portion of the zygomatic process of the maxilla (Fig. 3D). The maxilla–palatine suture is approximately U-shaped and extends anteriorly up to the level of the middle of the M4 (Fig. 3C, D).

#### Frontal

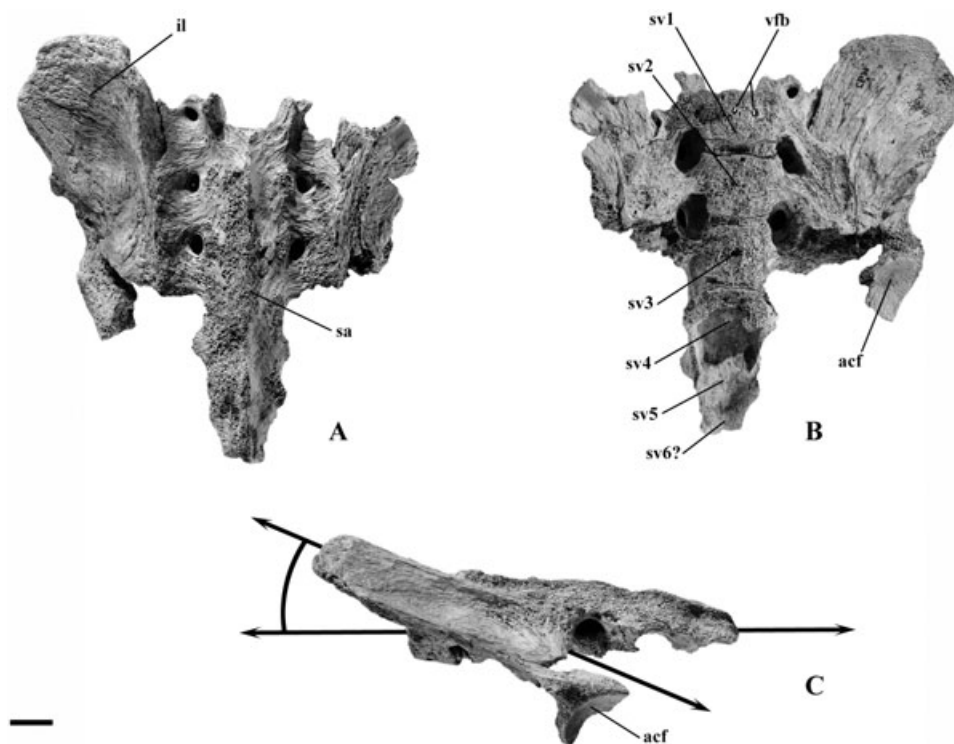
The anterior parts of the frontals are missing (Fig. 3A, B). The frontal contacts the parietal posteriorly, the squamosal lateroventrally, and the basisphenoid ventrally (Figs 3, 4). The dorsoventrally elongated frontal–parietal suture is posteriorly convex and a strong transverse constriction characterizes the skull at the level of this suture (Fig. 3A, B).

#### Parietal

The dorsal profile of the parietals is convex (Fig. 4B). They are slightly inflated laterally (Fig. 3A, B). The



**Figure 12.** Drawings of manus elements of *Diabolootherium nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen). A, left scaphoid in distal view (dorsal towards the top, medial towards the left). B, left lunar in distal view (dorsal towards the top, medial towards the left). C, right cuneiform in distal view (dorsal towards the top, medial towards the right). D, left unciform in distal view (dorsal towards the top, medial towards the left). E, F, left Mc II in lateral (dorsal towards the top, proximal towards the right) and proximal (dorsal towards the top) views, respectively. G–I, left Mc III in lateral (dorsal towards the top, proximal towards the right), proximal (dorsal towards the top), and medial (dorsal towards the top, proximal towards the left) views, respectively. J, K, right Mc IV in medial (dorsal towards the top, proximal towards the right) and proximal (dorsal towards the top) views, respectively. L, M, second manual (or pedal) phalanx in proximal and profile views, respectively (see the strong proximopalmar process ‘ppap’). N, O, phalanx (?) in proximal (?) and profile views, respectively. P, right ungual phalanx of the third anterior digit in lateral view. Cunf, cuneiform facet; Lunf, lunar facet; Magf, magnum facet; Mc II–Vf, metacarpals 2–5 facets; P1–P3f, first to third phalanges facets; Pf?, phalanx facet?; pap, palmar process; ppap, proximopalmar process; Radf, radial facet; Scf, scaphoid facet; Tdf, trapezoid facet; Tmf, trapezium facet; Uncf, unciform facet. Scale bar = 2 cm.



**Figure 13.** Photographs of the innominate of *Diabolotherium nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen), in dorsal (A, anterior towards the top), ventral (B, anterior towards the top), and left lateral (C, anterior towards the left) views. acf, acetabular fossa; il, ilium; sa, sacrum; sv1–sv6(?), first to possible sixth sacral vertebrae; vfb, vertebral foramen of the body (passage of vertebral veins). In (C), the arrows outline the inclination of the ilium relative to the sacrum. Scale bar = 2 cm.

sagittal crest is virtually absent because the individual is a young adult (sutures unfused). Each parietal contacts the frontal anteriorly, the squamosal lateromedially, and the supraoccipital posteriorly (Figs 3, 4). The squamosal–parietal suture is posteromedially to anterolaterally extended. Posterolaterally, the L parietal shows small foramina near the squamosal–parietal suture (Fig. 4B).

#### *Basisphenoid (and alisphenoid?)*

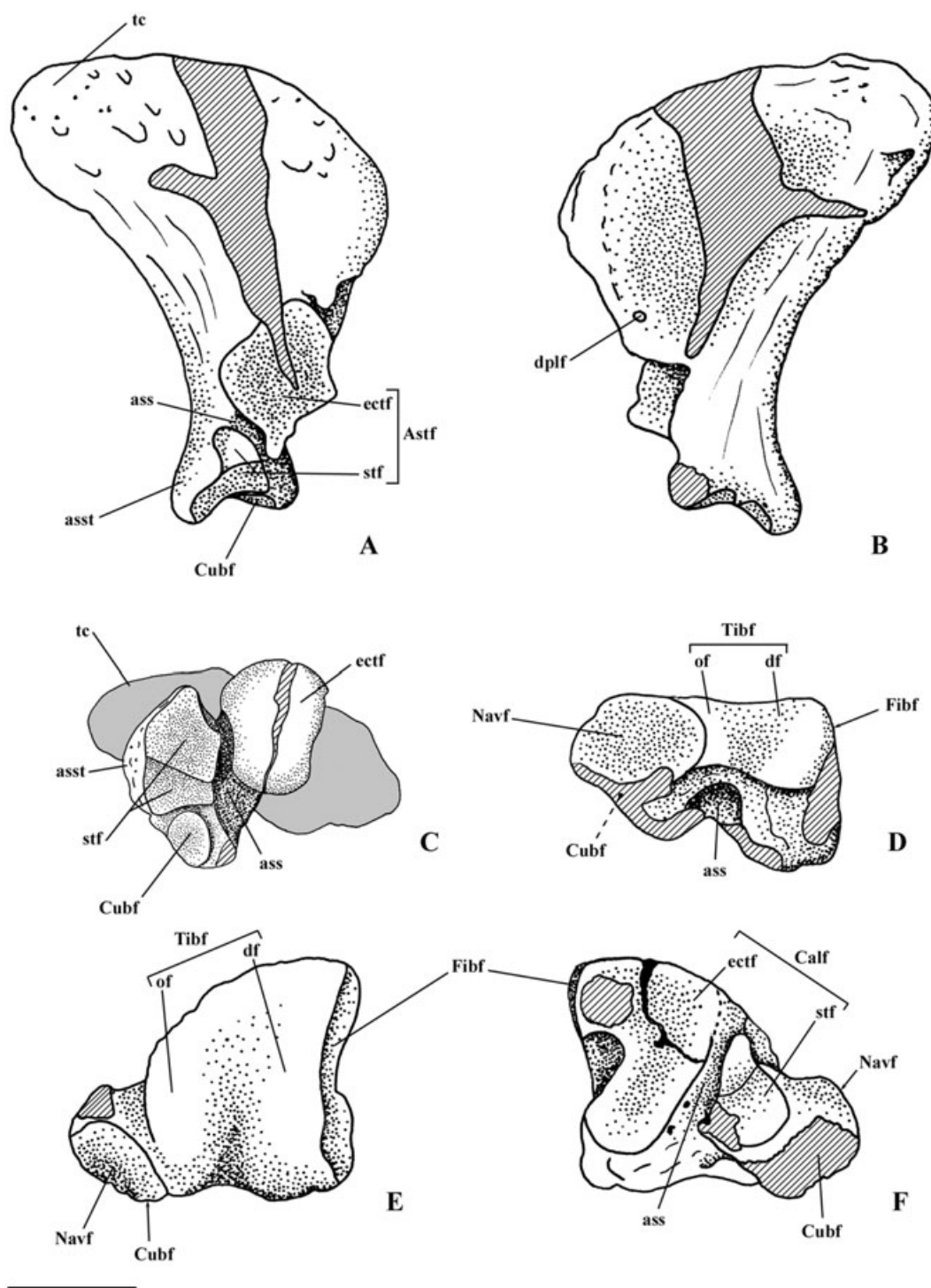
The sphenoid area is partially preserved (Fig. 3C, D). In Tardigrada, the basisphenoid generally contacts the palatine anteriorly, the basioccipital posteriorly, and the pterygoid laterally. In *Thalassocnus natans* (McDonald & de Muizon, 2002: fig. 3), the alisphenoid is located between the squamosal and the pterygoid. Moreover, the foramen ovale is located on the posterior portion of the alisphenoid and the foramen rotundum on the orbitosphenoid–alisphenoid suture. In *D. nordenskioldi*, only the basisphenoid seems to be preserved (Figs 3, 4). It is anterolaterally bordered by the frontal, laterally by the parietal, posteriorly and posteroventrally by the pterygoid, and anteriorly by the palatine. It is perforated by the large foramina

ovale and rotundum (Fig. 3C, D). The foramen rotundum opens anteriorly. Approximately 2 mm posterior to it, the foramen ovale opens lateroventrally (Fig. 3C, D). This foramen contacts the basisphenoid–squamosal suture laterally and the basisphenoid–pterygoid suture posteriorly (and dorsally) (Fig. 3A, B). A wide groove runs laterally along the foramen rotundum and enters in the foramen ovale (Fig. 3C, D). This canal cannot be identified with confidence.

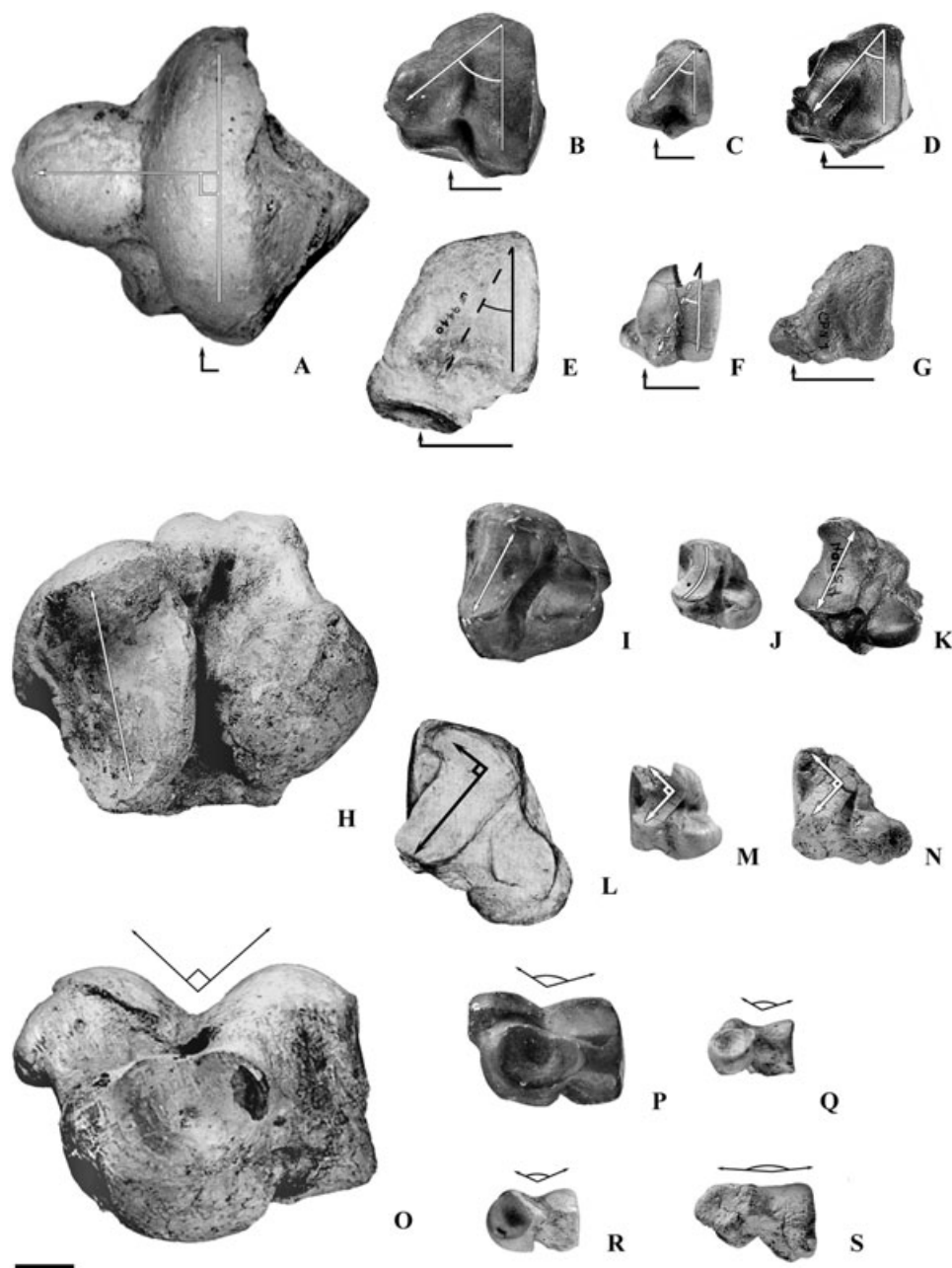
#### *Pterygoid*

Posterior portions of the pterygoids are preserved (Figs 3, 4). The pterygoid is laterally and lateroventrally delimited by the squamosal, and medially (and dorsomedially) by the basisphenoid (Fig. 3C, D). Pterygoids are usually blade-shaped (e.g. nothrottheriid *Thalassocnus natans*, de Muizon & McDonald, 1995; all the Megatheriinae, De Iuliis, 1996; the West Indies Megalonychidae, e.g. *Acratocnus*, Paula Couto, 1967: fig. 14; *Neocnus*, MacPhee *et al.*, 2000b: fig. 7; and the North American Megalonychidae *Megalonyx*, McDonald, 1977: 51, McDonald & Anderson, 1983: fig. 2; *Pliometanastes*, Hirschfeld, 1981: fig. 1), as in *D. nordenskioldi* or inflated with a pneumatic sinus

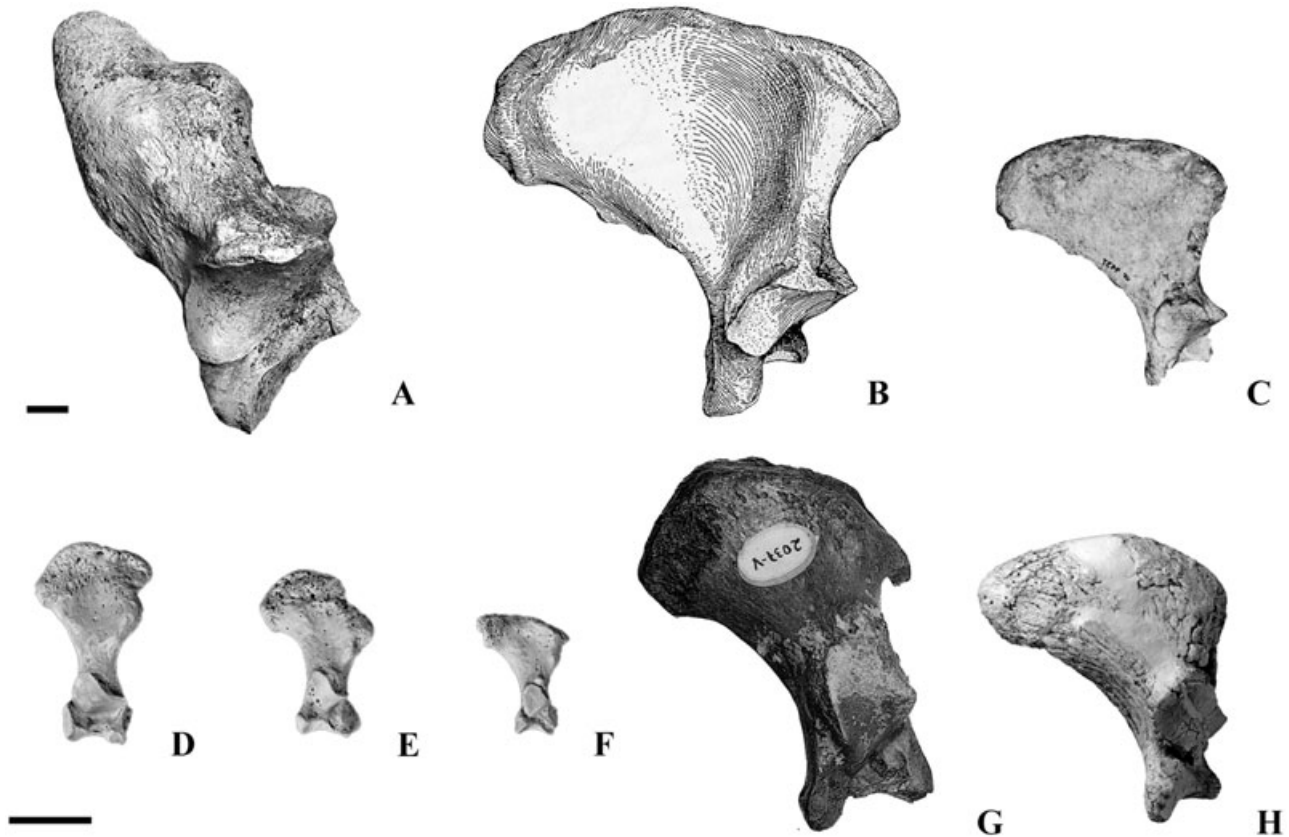




**Figure 14.** Drawings of calcaneum and astragalus of *Diabolotherium nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen). A–C, left calcaneum in dorsal (posterior towards the top, medial towards the left), plantar (posterior towards the top, medial towards the right), and anterior (dorsal towards the top, medial towards the left) views, respectively. D–F, left astragalus in anterior (dorsal towards the top, medial towards the left), dorsal (posterior towards the top, medial towards the left), and plantar (posterior towards the top, medial towards the right) views, respectively. ass, astragalar sulcus; asst, astragalar sustentaculum; Astf, astragalar facets; Calf, calcaneal facets; Cubf, cuboid facet; df, dis-coid facet; dplf, dorsoplantar foramen; ectf, ectal facet; Fibf, fibular facet; Navf, navicular facet; of, odontoid facet; stf, sustentacular facet; tc, tuber calcanei; Tibf, tibial facets (astragalar trochlea). Scale bar = 2 cm.



**Figure 15.** Left astragali in dorsal (A–G, posterior towards the top, medial towards the left), plantar (H–N, posterior towards the top, medial towards the right), and distal (O–S, dorsal towards the top, medial towards the left) views of: A, H, O, *Megatherium urbinai* (MUSM 15) from the Pleistocene of Sacaco, Peru (Pujos & Salas, 2004a); B, I, P, *Planops martini* (cast of BMNH M-9214) from the lower Miocene of Cap Fairweather, Patagonia, Argentina (Hoffstetter, 1961: 61); C, J, Q, *Hapalops* sp. (MNHN SCZ 168, unpublished astragalus) from the Santacrucian (Early Middle Miocene) of Río Coyle, Patagonia, Argentina; D, K, *Megalocnus rodens* [AMNH 49984, from Matthew & Paula Couto (1959) reversed from the original] from the Pleistocene of Cuba; E, L, *Pliometanastes protistus* [UF 9440, from Hirschfeld & Webb (1968)] from the Early Amphillian (Middle Pliocene) of Florida, USA; F, M, R, *Xyophorus villarroeli* (MNHN ACH 15, reversed from the original) from the Huayquerian (Late Miocene) of Achiri, Bolivian Altiplano (St-André, 1996: fig. 8); G, N, S, *Diabolotherium nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen) from the Lujanian (Late Pleistocene) of Piedra Escrita site, Cupisnique Desert, Peru. The arrows underline the transformation of the astragalar morphology: A–G, the angle between the principal axis of the discoid and odontoid processes and the position of the ‘stud’ relative to the principal axis of the discoid facet; H–N, extension(s) of the ectal facet; O–S, the angle between the surfaces of the discoid and odontoid facets. Scale bar = 2 cm.



**Figure 16.** Photographs (A, C–H) and a drawing (B) of the left calcaneum in dorsal view (posterior towards the top, medial towards the left) of: A, *Megatherium urbinai* (MUSM 15, reversed from the original) from the Pleistocene of Sacaco, Peru (Pujos & Salas, 2004a); B, *Megalonyx jeffersonii* [LACM 20095, modified from Stock (1925)] from the Quaternary of North America; C, *Pliomastanotus protistus* [UF 9437, from Hirschfeld & Webb (1968) reversed from the original] from the Early Hemphillian (Middle Pliocene) of Florida, USA; D, *Acratocnus ye* [UF 170269, modified from MacPhee *et al.* (2000b) reversed from the original] from the Late Quaternary of Haiti; E, *Neocnus dousman* [UF 170291, modified from MacPhee *et al.* (2000b) reversed from the original] from the Late Quaternary of Haiti; F, *Neocnus toupiti* [UF 170443, modified from MacPhee *et al.* (2000b) reversed from the original] from the Late Quaternary of Haiti; G, *Megalocnus rodens* [AMNH 16876, modified from Matthew & Paula Couto (1959)] from the Quaternary of Cuba; H, *Diabolootherium nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen) from the Lujanian (Late Pleistocene) of Piedra Escrita site, Cupisnique Desert, Peru. Scale bar = 2 cm.

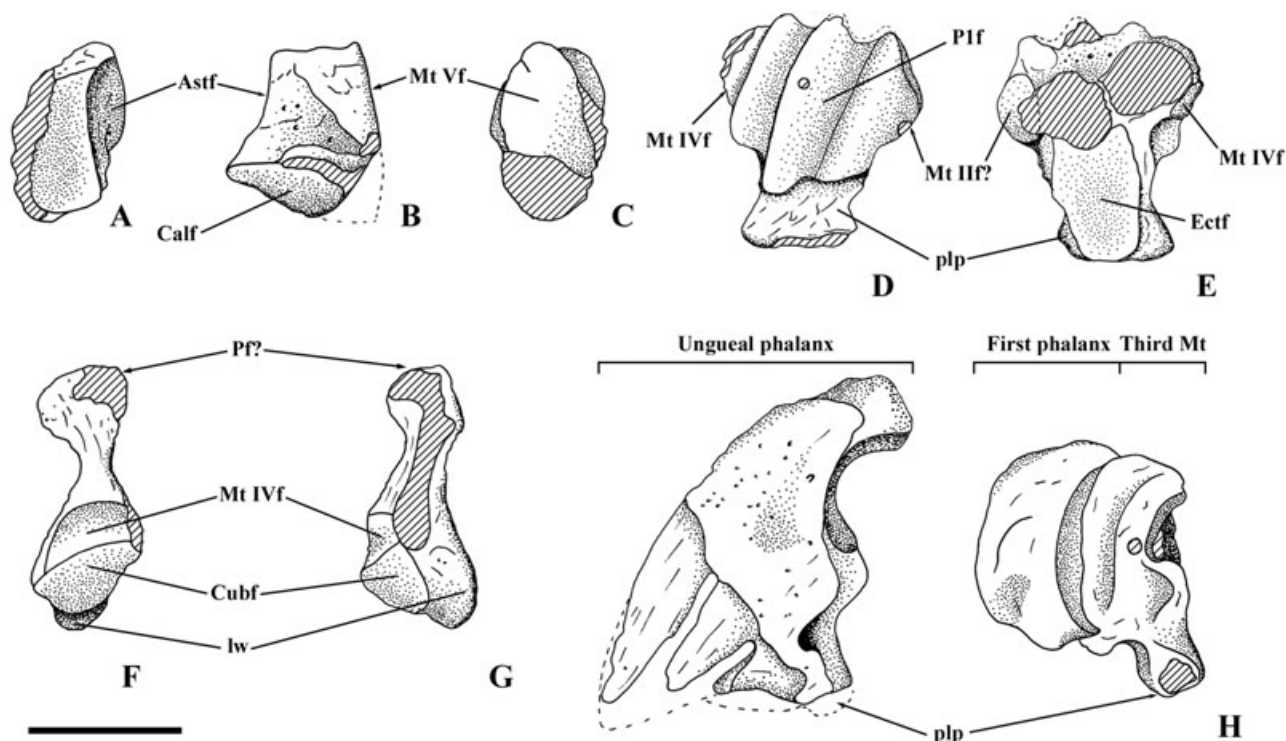
(e.g. nothrotheriids such as *Nothrotherium*, Reinhardt, 1878; *Nothrotheriops*, Stock, 1917; the modern tree sloth *Choloepus*). In *D. nordenskioldi*, the posterior portion of attachment of the pterygoid to the basisphenoid and the squamosal is a medially flattened column that extends anteriorly as a thin lateral blade covering the foramen ovale (Fig. 3C, D).

#### Squamosal

The L squamosal is complete (Figs 3, 4). It is delimited anteriorly by the frontal, dorsomedially by the parietal, posteriorly by the exoccipital, anteroventrally by the basisphenoid, medioventrally by the pterygoid, and posteroventrally by the auditory region. The zygomatic process of the squamosal is extremely short, strongly tapered, directed laterally, and is at an angle

of 25° with the anteroposterior axis of the skull (Fig. 3). The zygomatic process is slightly eroded and must have been faintly longer. This peculiar morphology of the zygomatic process is typically megalonychid [and is also present in the Santacrucian sloth *Eucholoeops*, considered by Gaudin (2004) as a Megalonychidae]. In Megatheriidae and Nothrotheriidae, the zygomatic process is anterolaterally extended and transversely flattened. Laterally, the zygomatic process is slightly inclined ventrally (Fig. 4A). The glenoid fossa is shallow. A small foramen is located at the level of the posterior portion of the pterygoid, near the lateral margin of the squamosal. It might represent the postglenoid foramen, but if so its position would be unique among Tardigrada. In fossil sloths, the postglenoid foramen is generally more medial and located





**Figure 17.** Drawings of the cuboid and posterior digits of *Diabolotherium nordenskioldi* gen. nov. (MNHN CPN 9–1, referred specimen). A–C, right cuboid in posterior (dorsal towards the top, lateral towards the right), lateral (dorsal towards the top, posterior towards the left), and anterior (dorsal towards the top, lateral towards the left) views, respectively. D, E, left Mt III in anterior (dorsal towards the top, medial towards the left) and posterior (dorsal towards the top, lateral towards the left) views, respectively. F, G, right Mt V in medial (anterior towards the top, plantar towards the left) and dorsal (anterior towards the top, medial towards the left) views, respectively. H, left third posterior digit in lateral view (dorsal towards the top, anterior towards the left) with from left to right P3–[P2 missing]–P1–Mt III. Astf, astragalus facet; Calf, calcaneum facet; Cubf, cuboid facet; Ectf, ectocuneiform facet; lw, lateral wing; Mt II–Vf, metatarsals 2–5 facets; plp, plantar process; P1f, first phalanx facet; Pf?, phalanx facet? Scale bar = 2 cm.

posteriorly to the glenoid fossa. This foramen has been regarded by McDonald & de Muizon (2002) as a possible passage for the ramus inferior of the stapedial artery and the chorda tympani. A deep, elongated groove, located posteriorly to the glenoid fossa, extends along the lateral margin of the pterygoid (Fig. 3C, D). It probably corresponds to the Glaserian fissure or less probably to the Eustachian groove (e.g. *Megalonyx mathisi*, Hirschfeld & Webb, 1968: fig. 8). Several vascular foramina are present on the lateral and dorsolateral margins of the squamosal (Fig. 4B). The squamosal of *D. nordenskioldi* borders the external auditory meatus anterolaterally, laterally, and posterolaterally.

#### Auditory region

The description of the auditory region of *D. nordenskioldi* is based on comparisons with the descriptions by van der Klaauw (1930, 1931), Guth (1956, 1961), MacPhee (1981), Patterson *et al.* (1992), Gaudin (1995, 2004), Gaudin *et al.* (1996), Wible

(1984), Wible *et al.* (2001), McDonald & de Muizon (2002), and Pujos (2002; 2006).

Dorsal extremities of the ectotympanics are preserved. In sloths, the ectotympanic is semicircular (e.g. *Scelidotherium leptcephalum*, Guth, 1956; *Thalassocnus natans*, McDonald & de Muizon, 2002) or a ring (e.g. *Eremotherium laurillardii*, Cartelle, 1992) and its ventral portion is extended medially. It delimits the external acoustic meatus and holds the tympanic membrane. The anterior crus of the ectotympanic shows a deep sulcus possibly representing the passage of the inferior ramus of the stapedial artery (Fig. 5A–C). In mammals (e.g. *Solenodon paradoxus*, Wible *et al.*, 2001: fig. 4D), except marsupials (where it is lost in adults), the stapedial artery divides anteriorly into inferior and superior rami. The passage for the superior ramus is not observable in *D. nordenskioldi*, but the inferior ramus probably passed between the anterior crus of the ectotympanic and the squamosal. Both crura are fused to the entotympanic but unfused to the squamosal, probably due



to the immaturity of the individual (Fig. 5A, B, F, G). The posterior crus extends along the anterior margin of the stylomastoid foramen (Fig. 5A, B). The stylomastoid and mastoid foramina are closely situated, lateroventrally open, and located in a deep groove that is extended anteroposteriorly. The facial nerve (VII) leaves the skull by the stylomastoid foramen (MacPhee, 1981) and enters the skull by the secondary facial foramen (Fig. 5C). The pars mastoidea of the periotic forms the lateral and dorsal walls of the mastoid and stylomastoid foramina (Fig. 5A–C, F) and contacts posteromedially the paroccipital process of the exoccipital (Fig. 3C, D). The mastoid depression extends posteriorly from the groove for the facial nerve. This groove borders the stylohyal fossa dorso-posteriorly. This fossa is inclined lateroventrally and extended anteroposteriorly (Fig. 3A–C). An oval-shaped stylohyal fossa is also present in the Megalonychinae *Acratocnus*, Pleistocene Nothrotheriidae *Pronothrotherium* and *Nothrotheriops*, the Scelidotheriinae *Catonyx* and *Scelidotherium*, and *Octodontherium* (Gaudin, 1995; character 54<sup>1</sup>). In other sloths (e.g. Megatheriidae, Pujos, 2002, in press a; the Mio-Pliocene nothrotheriid *Thalassocnus*, McDonald & de Muizon, 2002; the Megalonychidae *Megalonyx mathisi*, Hirschfeld & Webb, 1968: fig. 8), the stylohyal fossa is circular. A stylohyal fossa is absent in the modern tree sloth *Bradypus* (Naples, 1982: fig. 3A).

The stylohyal fossa limits the posteroventral portion of the promontorium. In placental mammals, the promontorium is a rounded prominence within the middle ear (MacPhee, 1981) and laterally bears two large foramina. The most dorsal opening is the fenestra ovalis (= fenestra vestibuli). The L stapes is preserved *in situ*, articulated to the fenestra ovalis (Fig. 5F). It is triangular, perforated by a small stapedial foramen (as in all extinct xenarthrans; Gaudin *et al.*, 1996), and bears a long shaft. It is more triangular than in Mylodontidae (e.g. *Glossotherium harlani*; Patterson *et al.*, 1992: fig. 22B) and the shaft is more elongated and less massive than in *Eucholoeops ingens* (Patterson *et al.*, 1992: fig. 23B). The fenestra ovalis is bordered laterally by the groove for the facial nerve. Anterior to it is the secondary facial foramen through which the facial nerve leaves the cranial cavity (Fig. 5A–C). The fenestra ovalis overhangs the fenestra rotundum (= fenestra cochleae), which opens more ventrally than the fenestra ovalis and is limited ventrally by the stylohyal fossa. Several grooves mark the lateral wall of the promontorium (Fig. 5A, B). As they have not been previously described (or rarely preserved) in Xenarthra, they are interpreted on the basis of those of early Cretaceous mammals, as described by Wible *et al.* (2001). The main groove of the promontorium is dorsoventrally orientated. It begins at the anterior extremity of the fenestra rotundum, turns

anteriorly at the dorsal margin of the promontorium and extends to the ectotympanic (Fig. 5A–C). This groove shows two extensions. The anteroventral extension passes towards the anteroventral corner of the promontorium, but does not reach it. It probably corresponds to the passage for the promontory artery, a branch of the internal carotid artery. The second, posteroventral extension of the main groove corresponds to the posterior ramus of the stapedial artery (Fig. 5C).

The entotympanic is limited anteriorly by the median lacerate foramen and separated anteroposteriorly in two parts by an oblique crest (Fig. 3C, D), as in most sloths (e.g. the nothrotheriid *Thalassocnus*, McDonald & de Muizon, 2002: fig. 4). The anteromedial portion of the entotympanic bears a deep fossa that is perforated by two foramina. The carotidian foramen (for the entrance of the internal carotid artery into the skull) is the most anterior (Figs 3C, D, 5). It is large and circular. The second foramen lies posterior to it and is considerably more compressed transversely, but of uncertain function. The anterior portion of the entotympanic is expanded into a large tuberosity. The entotympanic is anteromedially to posterolaterally orientated, anterolaterally bordered by the oval foramen, and posteriorly bordered by the posterior lacerate foramen for the glossopharyngeal, vagus, and spinal cranial nerves (cranial nerves IX, X, and XI, respectively). The posterior lacerate foramen, although damaged, is anterolaterally and laterally delimited by the entotympanic and posterolaterally by the paroccipital process of the exoccipital (Fig. 3C, D). A deep condylar foramen is located between the posterior lacerate foramen and the anteromedial corner of the occipital condyle.

The cerebral surface of the auditory region of fossil Xenarthra has never been described in detail in the literature [partially by Patterson *et al.* (1992)]. The opening of the internal auditory meatus, for the facial and vestibulocochlear nerves (cranial nerves VII and VIII), is spiral-shaped (Fig. 5D, E, G). It is delimited dorsoposteriorly by a large and very shallow depression and posteriorly by the aqueductus cochleae. The aqueductus cochleae, involved in the perilymphatic circulation, constitute a 90° angle with the internal auditory meatus and the large depression previously described (Fig. 5G). A transversely compressed foramen lies on the posterior margin of the depression. It represents the aqueductus vestibuli involved in the endolymphatic circulation.

#### Occipital bones

The bones of the occipital area are fused together and the limits between them are not discernible (Fig. 4B). The occipital morphology of the immature specimen of *D. nordenskioldi* (MNHN CPN 9–1) suggests that the elements of the occipital area are among the first to fuse

in Tardigrada (see Cartelle & De Iuliis, 2006). In dorsal view (Fig. 3A, B), the supraoccipital develops a strong interparietal process. In posterior view, the occipital area is rectangular, wider than high (Fig. 4B). The lateral margins are concave and the dorsal margin is gently convex dorsally. In lateral view, the external occipital protuberance is prominent and rounded (Fig. 4A). The prominent paroccipital process of the exoccipital is ventrally extended. The occipital condyles are posteroventrally inclined and not separated in lateral view from the occiput, as also occurs in the Megalonychidae *Acratocnus* (MacPhee *et al.*, 2000b: fig. 12A), *Megalocnus* (Matthew & Paula Couto, 1959: plate 2), and *Neocnus* (MacPhee *et al.*, 2000b: fig. 7C), in contrast to *Parocnus* [= *Mesocnus* (according to White & MacPhee, 2001); Paula Couto, 1967: figs 9, 10].

#### MANDIBLE (FIG. 6, APPENDIX 1)

The R dentary (paratype, NRM-PZ M4287, Fig. 6A, B) from Casa del Diablo Cave is 10% larger in linear dimensions, but morphologically identical to the R dentary (MNHN CPN 9–1, Fig. 6C–H) from Piedra Escrita. The lower molariform alveoli are complete in NRM-PZ M4287, but not in MNHN CPN 9–1. On the other hand, the anterior and posterior extremities of the latter are slightly better preserved than in the paratype. In both specimens, the posterior portion of the spout is preserved, but its total length is difficult to estimate (Fig. 6). A large lateral mental foramen lies at the base of the spout of MNHN CPN 9–1 (Fig. 6C, D). In fossil sloths that exhibit a similar dental formula (Megatheriinae, 5/4 quadrangular molariform teeth) or different dentition (other Megalonychidae, 1/1C-4/3 oval molariform teeth), the lateral mental foramen is approximately in the same position as in *D. nordenskioldi*. On the medial margin of the spout, a large internal mental foramen lies 14 mm anterior to the m1 alveolus (Fig. 6E–H).

The m1 is rather triangular and the m2–m4 are squared in section (Fig. 6), unlike the rectangular upper molariforms (Fig. 3C, D). The form of the lower molariforms resembles that in Megatheriinae, whereas they are oval in section in the other Megalonychidae (e.g. *Megalocnus rodens*, Matthew & Paula Couto, 1959: plate 8; MacPhee *et al.*, 2000b: fig. 5) and rectangular Pleistocene Nothrotheriidae (e.g. *Nothrotherium*, Pujos, 2001a). Labiolingual width increases from m1 to m2, but m3 and m4 are nearly square in *D. nordenskioldi*. Labial longitudinal grooves are present on m2–m4. The maximum depth of the horizontal ramus occurs between m1 and m2 (Fig. 6A). In occlusal view, the lateral margin of the tooth row is convex and the medial margin is rectilinear. The dentary is strongly compressed transversely posterior to m4 (Fig. 6B).

The dorsal extremity of the coronoid process is incomplete in both specimens. The base of the process is strongly inclined posteriorly and the angle with the occlusal plane is approximately 50/60° in both specimens (Fig. 6). The angular process is prominent and extended more posteriorly in MNHN CPN 9–1 (Fig. 6C–F). A distinct notch separates the lower margin of the angular process and the ramus. The base of the angular process is slightly inclined medially. The condyloid process is anteroposteriorly short and wide, and elevated markedly above the alveolar plane. The posterior margin of the horizontal ramus forms a wide and shallow notch.

The condyloid and angular processes are well separated (approximately 45 mm in MNHN CPN 9–1), a condition possibly related to the high degree of hypsodonty in *Diabolotheium*. In the other Megalonychidae, the angular process is generally strong and less distinct from the condyloid process (e.g. *Megalocnus*, Matthew & Paula Couto, 1959: plate 2; *Acratocnus*, Paula Couto, 1967: figs 18, 19; *Neocnus*, MacPhee *et al.*, 2000b: fig. 8; and *Pliometanastes*, Hirschfeld, 1981: fig. 2). In Nothrotheriidae, the angular process is thin, but closer to the condyloid process than in *Diabolotheium* (e.g. *Thalassocnus*, McDonald & de Muizon, 2002; de Muizon *et al.*, 2003, 2004a). In Megatheriinae, the robustness of the angular process is intermediate between that in *Diabolotheium* and other Megalonychidae (i.e. North American and West Indies forms), but the condyloid process is dorsal, which might also be related to a high degree of hypsodonty. The internal foramen of the mandibular canal is located on the medial side of the coronoid process just above the occlusal plane (Fig. 6E, F). The posterior external opening of the mandibular canal is located dorsolaterally and close to the base of the coronoid process, as in most sloths (Fig. 6G, H), but in contrast to the position in Megatheriidae.

#### VERTEBRAE AND RIBS (FIG. 7, APPENDIX 1)

Two cervical, approximately ten thoracic, and ten caudal vertebrae are partially preserved. The posterior surface of the atlas has suffered erosion. The atlas is anteroposteriorly compressed. The three facets of the atlantoaxial joint are in contact. The two articular facets for the occipital condyles are highly concave and dorsoventrally elongated (Fig. 7A). They face medially and are posterodorsally limited by the vertebral arterial canal.

The posterior thoracic vertebrae exhibit typical xenarthry, i.e. anapophyses with articular facets that allow supplementary intervertebral articulations (Fig. 7B, Grassé, 1955; Hoffstetter, 1958). The presence of these facets is considered among the most important synapomorphies of the order Xenarthra (Gaudin,

1999). Each anapophysis articulates ventrally with a metapophysis or between a metapophysis and the transverse process of the succeeding vertebrae (Rose & Emry, 1993) (Fig. 7B). The anapophyses are extremely reduced in modern tree sloths (Gaudin, 1999). They are generally present in the last thoracic and all the lumbar vertebrae. In *D. nordenskiöldi*, the neural spines of the few thoracic vertebrae are higher than in modern sloths. A similar morphology is also present in Nothrotheriidae (e.g. *Nothrotherium*, Reinhardt, 1878; Cartelle & Fonseca, 1983; *Nothrotheriops*, Lull, 1929), West Indies Megalonychidae (e.g. *Megalocnus rodens*, Matthew & Paula Couto, 1959: plate 26), and *Hapalops longipes* (Scott, 1903–04: plate 30).

The vertebral foramen is slightly asymmetrical in lumbar and nearly all thoracic vertebrae (Fig. 7B). The foramen probably corresponds to the passage of one of the intrarachidian veins located between the medulla and the wall of the vertebrae, as suggested by De Burlet (1922), Hoffstetter (1959), and Pujos (2002; in press a) for some ground sloths (i.e. *Scelidotherium*, *Glossotherium*, *Myiodon*, and *Megatherium*). In the suspensory tree sloths *Choloepus* and *Bradypus*, two longitudinal veins run along the rachidian canal and the L vein is reduced in both genera (Hochstetter, 1898; De Burlet, 1922). This intrarachidian circulation is also indicated by dorsoventral perforations of the bodies of the last thoracic vertebrae for the passage of the vertebral veins (Fig. 7C, D). There is a pair of foramina on the ventral side of the body (Fig. 7D). The two veins join and exit from a single orifice on the dorsal margin of the body (Fig. 7C). Similar perforations are present at least in the Miocene forms *Nematherium* (Scott, 1903–04: 348) and *Planops martini* (Hoffstetter, 1961) and the Plio-Pleistocene forms *Megatherium* (Pujos, 2002) and *Thalassocnus natans* (F. Pujos, pers. observ.).

The tail is incomplete and approximately ten highly damaged caudal vertebrae are preserved. Transverse processes are more slender dorsoventrally and more elongated transversely than in Megatheriinae (Pujos & Salas, 2004a; Pujos, in press a) and *Scelidotherium leptcephalum* (McDonald, 1987). One haemal arch is complete. It is extremely similar to the first haemal arch of *Nothrotherium* located between the eighth and ninth caudal vertebrae (Cartelle & Fonseca, 1983: fig. 9).

Several ribs are preserved, but extremely damaged. *D. nordenskiöldi* has ossified sternal ribs, a condition that is synapomorphic for Xenarthra (Hoffstetter, 1982: 402–403; McDonald, 2003: 10).

#### SCAPULA (FIGS 8A, B, 9, APPENDIX 1)

The scapula is approximately triangular in lateral view (Fig. 8A), in contrast to the quadrangular scap-

ula of the West Indies Megalocninae *Megalocnus rodens* (Matthew & Paula Couto, 1959: plate 13). The lateral side bears two dorsoventrally orientated spines. The scapular spine separates the supra- and infraspinous fossae (Fig. 8A). The supraspinous fossa is broader than the infraspinous fossa, but narrower than in the megalocnine *Megalocnus rodens* (Matthew & Paula Couto, 1959). The secondary scapular spine runs along the posterior border between the posterolateral margin of the glenoid fossa and the posterior angle of the scapula.

A secondary scapular spine is present in all sloths (Stock, 1925; Tito & De Iuliis, 2001; McDonald, 2003), but is not unique to Xenarthra. This spine separates the infraspinous and postscapular fossae. In modern tree sloths, the postscapular fossa is absent and the secondary scapular spine merges with the ventral margin of the scapula (e.g. Rose & Emry, 1993: fig. 7.5, in *Choloepus*). The scapular notch of *D. nordenskiöldi* is strongly concave, as in all sloths, and the ventral margin of the scapula is convex. The glenoid fossa is oval in outline, longer than wide, and anteroposteriorly concave (Fig. 8B). The dorsal margin is gently convex and rises anteriorly near the coracoid process, in contrast to the strongly concave dorsal margin in Megatheriinae. The coracoid process of *Diabolothe-rium* is anteroventrally extended and laterally prominent to connect with the acromion (Fig. 8B). This acromial arch (Stock, 1925) is not preserved in *D. nordenskiöldi*. In contrast to fossil sloths, the coracoid process of *Bradypus* protrudes medially.

As in all Tardigrada, the scapula of *D. nordenskiöldi* is perforated by the coracoscapular foramen (Fig. 8A). This foramen is circular, located between the acromion and the coracoid process, and medial to the acromial arch. The subscapular fossa forms the whole medial face of the element. It bears prominent crests for the insertion of the M. subscapularis.

#### HUMERUS (FIGS 9, 10A–D, APPENDIX 1)

The three known humeri of *D. nordenskiöldi* include the holotype (NRM-PZ M4286, Fig. 10A, B), figured by Nordenskiöld (1908: fig. 2), and the two humeri of MNHN CPN 9–1 (Figs 9, 10C, D). The humeri from the two specimens are nearly identical in length and morphology. The humerus from Casa del Diablo belongs to an adult, whereas the specimen from Piedra Escrita belongs to an immature specimen, the proximal epiphysis being only partially fused to the diaphysis (see Fig. 10D).

The humerus is extremely slender compared with that of most other fossil sloths. The diaphysis is sub-oval in cross-section, anteroposteriorly compressed (Fig. 9). The head is subcircular, slightly longer anteroposteriorly than transversely wide, and posteri-



only inclined (Fig. 9, 10B, D). As in *Hapalops* (MNHN SCZ 162, 163, and 164), the North American Megalonychidae *Pliometanastes prostratus* (Fig. 10J, K), and the Patagonian taxon *Eucholoeops ingens* (FMNH P13125, Fig. 10K, L), the greater tubercle of *Diabolotheirus* extends more proximally than the lesser tubercle, in contrast to *Planops martini* (BMNH M.9207), in which both tubercles reach the same level. In *D. nordenskioldi*, the greater tubercle is well developed and bears two insertion areas. The anterior area, where the *M. supraspinatus* inserts, bears few scar lines and insertion crests (Fig. 9). The second area, for *M. infraspinatus*, is broader, rounded, and medio-posteriorly orientated (Fig. 9). The Megatheriidae, Nothrotheriidae, and Mylodontidae have a narrower insertion for the *M. infraspinatus*. The lesser tubercle, where the *M. subscapularis* inserts, is bulky, antero-posteriorly extended, and shows a central, anteroposterior groove (Figs 9, 10A, B).

The deltopectoral crest extends distally from the greater tubercle along the anterior surface of the diaphysis (Fig. 10A, C). It is slender, weak along its proximal third, more prominent at the midshaft, and fades distally. The anterior margin of the deltopectoral crest corresponds to the insertion of the *M. pectoralis*, the *M. deltoideus* inserting more laterally (Fig. 9). The morphology of the deltopectoral crest is variable within the sloth families, and members of a family or subfamily may have distinct deltopectoral crest morphologies. As suggested by De Iuliis (2003), the function and homology of the ridges running along the anterior and lateral surfaces are unclear in ground sloths. The deltopectoral crest is generally well developed in all the other Megalonychidae, West Indies forms [Megalocninae and Choloepodinae, according to White & MacPhee (2001), Fig. 10E–L], *Eucholoeops* (Fig. 10K, L), and North American forms (*Pliometanastes* and *Megalonyx*: Fig. 10M–O).

In *Hapalops*, one of the better known primitive Megatherioidea, the deltopectoral crest is reduced, but extends distally in an entepicondylar crest that delimits the entepicondylar foramen. *D. nordenskioldi* lacks an entepicondylar crest and foramen, in contrast to *Planops* (BMNH M.9207), which also has a strong deltopectoral crest. A strong deltopectoral crest associated with an entepicondylar foramen is present in the two Megalonychidae from North America (*Megalonyx*, Fig. 10O; *Pliometanastes*, Fig. 10M) and all the West Indies forms (Fig. 10E, F, I–L) except *Parocnus* (Fig. 10G, H). In Megatheriidae (see De Iuliis, 2003) and Nothrotheriidae (e.g. *Nothrotherium*, Reinhardt, 1878: fig. 3-1), the deltopectoral crest is generally reduced. An entepicondylar foramen is absent in all Megatheriinae, but present in nothrotheriids *Nothrotheriops* (McDonald, 1985) and *Nothrotherium* (Reinhardt, 1878). In Mylodontidae, the deltopectoral

crest is prominent and the presence of the entepicondylar foramen is variable. It is present in the scelidotheriine *Scelidodon chiliensis* (Pujos, 2000) and the mylodontiine *Pseudoprepotherium confusum* (Hirschfeld, 1985), absent in the scelidotheriine *Catonyx cuvieri* (Guérin *et al.*, 1993) and in the mylodontine *Thinobadistes* (Webb, 1989).

The medial surface of the diaphysis of the humerus of *D. nordenskioldi* is concave. A small tuberosity, probably for insertion of the *M. teres major*, lies at the middle of the medial margin of the shaft (Figs 9, 10A, C). This scar is reduced, which is not consistent with a well-developed muscle, but could be related to the young age of the specimen.

The posterior diaphyseal surface of the R humerus of MNHN CPN 9-1 exhibits two proximodistally orientated crests, running along two-thirds of the length of the shaft (Fig. 10B, D). The most medial one may represent the origin of *M. triceps caput mediale*, and the most lateral one (more rugose), the origin of *M. brachialis* (Fig. 9).

The medial epicondyle is strong, short, and bears a rounded muscular insertion (slightly raised anteriorly) for the flexors of the digits. This epicondyle is less developed in *Diabolotheirus* than in the other Megalonychidae, particularly *Parocnus* (Fig. 10G, H) and *Eucholoeops* (Fig. 10K, L). The lateral epicondyle is also more reduced than in all other fossil Megalonychidae. The lateral epicondylar crest, preserved only in the holotype, is convex, slender, and extends along one-third of the humeral length (Fig. 10A, B). The capitulum is rounded, anteriorly prominent, and distally separated from the trochlea by a deep groove. The radial fossa is deep (Fig. 10A, C). Posteriorly, the olecranon fossa is shallow (Fig. 10B–D), similar to those of *Hapalops* (MNHN SCZ 162), *Acratocnus* (Fig. 10J), and *Eucholoeops* (Fig. 10L) and deeper than those of *Megalonyx* (Leidy, 1855: plate 9) and *Pliometanastes* (Fig. 10N).

The holotype differs slightly from MNHN CPN 9-1 in exhibiting a more prominent deltopectoral crest, a deeper coronoid fossa, and a larger medial epicondyle (Fig. 9C, D). These differences may be attributed to the younger age of MNHN CPN 9-1.

#### ULNA (FIGS 8C–F, 9, APPENDIX 1)

The ulna is long and slender. The olecranon is massive and slightly compressed anteroposteriorly (Figs 8D, F, 9) compared with the other Megalonychidae. The olecranon of *Diabolotheirus* is relatively short compared with Mylodontidae and similar in this respect to those of *Hapalops* (Scott, 1903–04: plate 32-4), *Planops* (BMNH M.9208), and *Acratocnus* (Anthony, 1918: fig. 48A–C). By contrast, the olecranon is markedly shorter in the suspensory modern taxa and larger fos-



sil sloths, such as Nothrotheriidae (e.g. *Nothrotherium*, Reinhardt, 1878: plate 3.3), Megatheriidae (De Iuliis, 1996), and the Megalonychidae *Megalonyx* (Leidy, 1855: plate 9). In Mylodontidae, the ulna is shorter than in nothrotheres and megatheres, more massive, and the olecranon is very long (e.g. Sefve, 1915: plate 11; Cuenca-Anaya, 1995: 120–121; Vizcaíno *et al.*, 2001 on *Scelidotherium*). In *D. nordenskioldi*, an anteroposterior groove, limited by two tuberosities (proximal and distal), lies on the medial margin of the olecranon (Fig. 8F) and possibly marks the insertion of the M. epitrochleo-anconeus or M. triceps brachii caput mediale (Fig. 9).

The anconeal process, similar to the condition in *Pliomatanastes* (Hirschfeld & Webb, 1968: fig. 17A, B), is much more prominent than in *Megalonyx* (Leidy, 1855: plate 9) and the West Indies Choloepodinae *Acratocnus* (Anthony, 1918: fig. 48D). The coronoid process is distally bent and the opening of the trochlear notch is approximately 105° (Fig. 8D, F). The coronoid process is concave laterally and extended medially. The trochlear notch exhibits the same morphology and position as in *Hapalops* (Scott, 1903–04). A wide opening of the trochlear notch usually occurs in arboreal mammals (de Muizon, 1998; Argot, 2001). The radial notch is rounded and orientated more anteriorly than laterally. In anterodistal view, the angle between the coronoid process and the radial notch is widely open (120°, see Fig. 8C), in contrast to the condition in all other fossil sloths.

In lateral view, the posterior edge of the diaphysis is sigmoid, as in *Hapalops* (Scott, 1903–04: plate 32.4) (Fig. 8D, F). The ulnar diaphysis is rectilinear in Megatheriinae (De Iuliis, 1996) and the mylodontid *Thinobadistes* (Webb, 1989). In the other Megalonychidae, the diaphysis may be nearly rectilinear (*Megalonyx*, Leidy, 1855: plate 9; proximal medial half of *Pliomatanastes*, Hirschfeld & Webb, 1968: fig. 17B) or regularly convex (West Indies form *Acratocnus*; Anthony, 1918: fig. 48D). In arboreal didelphimorphs (Marsupialia), the ulna presents a proximal posterior convexity opposite to the insertions of the M. biceps brachii and brachialis (Argot, 2001: 65) in contrast to terrestrial taxa.

The lateral surface of the ulnar shaft bears a shallow fossa for the origin of the M. abductor pollicis longus (Fig. 9). This fossa begins at the level of the trochlear notch and ends at the distal two-thirds of the diaphysis (Fig. 8D). The deep medial fossa located at the level of the trochlear notch corresponds to the origin of the M. flexor digitorum profundus (Fig. 9). The anterior margin of the diaphysis bears a long and prominent interosseous crest (Figs 8D–F, 9).

On the distal epiphysis, the styloid process projects distomedially (Fig. 8E). It projects further posteriorly than anteriorly and is spatulate (Fig. 8D–F). This pecu-

liar morphology, unique among fossil Tardigrada, and the presence of a large, flat surface on the styloid process, possibly indicate a broad articular contact with the cuneiform, as occurs in the modern sloths *Bradypus* and *Choloepus*. However, the poor preservation of the styloid process and the absence of complete cuneiforms do not allow confirmation of this hypothesis. A large and deep proximodistal groove extends along the flat area of the styloid process (Fig. 8E) and possibly corresponds to the passage for the tendon of the M. flexor carpi ulnaris. The contact with the radius is unclear.

#### RADIUS (FIGS 8G–I, 9, APPENDIX 1)

The radius is short and massive. The proximolateral and distal parts of its anterior surface and the proximal part of its posterior surface are not preserved. In proximal view, the head is circular. The fovea that articulates with the humeral capitulum is concave in *Diabolotherium*, as in most fossil sloths. A small portion of the articular circumference is preserved immediately distal to the fovea, proximolateral to the radial tuberosity.

The diaphysis is anteroposteriorly compressed and anteriorly convex in lateral view (Fig. 8H). Its width regularly increases distally (Fig. 8G, I). In anterior view, the diaphysis of *Diabolotherium* is medially convex, as in *Bradypus*. The radius (like the ulna, see above) of Mylodontidae is shorter and more robust than that of Megalonychidae. The distal two-thirds of the diaphysis are much more compressed transversely in Nothrotheriidae and Megatheriidae than in *Diabolotherium*.

The development of the bicapital tuberosity is similar to that in *Planops* (BMNH M.9209), less extended than that in *Hapalops* (MNHN SCZ167), and stronger than that in *Nothrotheriops* (McDonald, 1985: fig. 2-2) and West Indies Megalonychidae (e.g. *Megalocnus*, Matthew & Paula Couto, 1959: plate 15). The medial half of the anterior diaphyseal surface bears three crests, orientated proximolaterally to distomedially, that contact the medial diaphyseal margin (Fig. 8G). These crests define two muscle insertion areas for M. supinator brevis and pronator teres (Fig. 9).

The anterior margin of the distal epiphysis exhibits central and anteromedial grooves (the lateral portion is not preserved) (Fig. 8G). The anteromedial groove probably corresponds to the passage of the tendon of the abductor pollicis longus and the central one for the passage of the M. extensor carpi radialis (Fig. 8G). These grooves are similar in *Diabolotherium* and the Choloepodinae *Acratocnus* (Anthony, 1918: fig. 48E).

The distal epiphysis is poorly preserved. The lateral half of the distal articular surface received the lunar and the medial half the scaphoid, as typically occurred in fossil sloths.

## MANUS (FIGS 9, 11, 12, APPENDIX 1)

*Proximal carpal row*

*Scaphoid*: R and L scaphoids are present, but poorly preserved (Figs 9, 11, 12A). The R scaphoid lacks its proximopalmar part and the L element is eroded. The facet articulating with the radius occupies the whole proximal surface, which is dorsopalmarly and transversely convex. The lateral surface bears the crescentic and dorsopalmarly elongated facet for the lunar (Fig. 12A). Distally, the dorsal part of the lunar facet overhangs a small facet that probably articulates with the magnum. The lunar facet is limited distally by a deep pit. The scaphoid develops a medial process that is extended mediopalmarly (Figs 11A, B, 12A).

The dorsal part of the scaphoid distal surface bears a facet that extends from the dorsal margin of the lunar facet to the middle of the medial process. This large facet is dorsopalmarly and transversely concave. Its medial half probably articulates with the trapezium and the trapezoid, and the lateral half probably with the magnum. This facet represents the principal, rectangular facet for the magnum. It is inclined distally, extended and slightly concave dorsopalmarly, and reaches the palmar margin of the bone (Fig. 12A). The facet is medially and laterally limited by two deep pits. The proximal and distal surfaces of the scaphoid converge and join dorsally (Fig. 11). The morphology of the distal surface of the scaphoid suggests the absence of an isolated trapezium (and thus its incorporation into an MCC), as occurs in the megatheriines *Megatherium* and *Eremotherium* (De Iuliis & Cartelle, 1993), the nothrotheriids *Nothrotheriops* (Stock, 1925; Paula Couto, 1976: 72) and *Nothrotherium* (Pujos, 2001a), some mylodontids such as *Scelidodon* (Pujos, 2000) and *Thinobadistes* (Webb, 1989), and the megalonychid *Megalocnus rodens* (Matthew & Paula Couto, 1959: plate 16), but in contrast to the condition in *Hapalops* (Scott, 1903–04) and *Eucholoeops* (FMNH P13125). The scaphoid of *Diabolotherium* is clearly distinct from those of other fossil sloths, due to its proximodistal compression and dorsal junction of the proximal and distal surfaces.

*Lunar*: The lunar is dorsopalmarly extended and rectangular in distal view (Fig. 12B). The facet for the radius occupies the proximal side and extends dorsally (Fig. 11A, B), as in *Hapalops* (Scott, 1903–04: 193), but much more than in *Nothrotheriops*. This facet is strongly convex dorsopalmarly and slightly convex transversely. The scaphoid facet occupies the entire medial surface. Although the distal surface of the L lunar is not well preserved (Fig. 12B), two partial facets, dorsopalmarly and transversely concave, can be observed. The magnum facet contacts medially the scaphoid facet and laterally the cuneiform facet. The cuneiform facet is inclined laterodistally and occupies

at least the palmar two-thirds of the laterodistal surface (Fig. 12B). An articular contact between the lunar and unciform, present in most fossil sloths, is not preserved. The lunar does not provide diagnostic characters for *D. nordenskioldi*.

*Cuneiform*: The distal half of the R cuneiform (Figs 9, 11C, D, 12C) is better preserved than the L element (Fig. 11A, B). The distal surface bears the large unciform facet (Fig. 12C). Its medial half, nearly flat along the medial margin, extends distally. Its lateral half is dorsopalmarly convex and extends dorsally. The dorsopalmar diameter of this facet decreases laterally. The medial surface of the cuneiform bears the triangular magnum facet (Fig. 12C), which distally contacts the unciform facet. Its proximodistal diameter decreases palmarly. The magnum facet is orientated palmarly and is slightly concave in all directions. The dorsal margin of the cuneiform is wide and shows several nutrient foramina, but this carpal is too damaged for comparison and for revealing the presence of a contact with the styloid process of the ulna.

*Distal carpal row*

*Unciform*: The dorsal half of the L unciform is preserved (Figs 9, 12D). The unciform is massive, transversely extended, and rectangular in dorsal view, as in *Hapalops* (Scott, 1903–04: 194). The unciform distal half of *Diabolotherium* bears at least five articular facets (Fig. 12D). A large, transversely extended facet lies on its proximal surface. Facets for the cuneiform and lunar, present in other sloths, are not preserved. The Mc V facet is located distolaterally, orientated palmarly, and separated from the Mc IV facet by a deep dorsopalmar groove. The Mc IV facet is reduced and medially contacts the Mc III facet, which is deep, transversely concave, and medially contacts the magnum facet. The latter is slightly concave, rectangular, and extends proximodistally. These facets occupy the dorsal half of the distal surface of the unciform. A similar unciform morphology is present in *Hapalops* (Scott, 1903–04), but with deeper facets for the metacarpals. A similar organization of the facets is also present in *Nothrotheriops* (Paula Couto, 1976), in which the facets are shallower than in *D. nordenskioldi*. In the North American Megalonychidae *Pliometanastes prostritus* (Hirschfeld, 1981: fig. 6A), the unciform differs in bearing a long process extending distally from the centre of the bone.

*Metacarpals*: *Diabolotherium* had at least three anterior functional digits (II–IV, Figs 9, 11). L Mc III is complete (Fig. 12G–I), whereas Mc II and IV are damaged (Fig. 12E, F, J, K). Mc II–IV have the same length and robustness (Fig. 11), which never occurs in other

fossil sloths. In Nothrotheriidae (e.g. *Nothrotheriops shastense*, Paula Couto, 1976) and Megatheriidae (e.g. *Megatherium urbinai*, Pujos & Salas, 2004a), Mc IV is longer than Mc III and Mc III is longer than Mc II. In the Megalocninae *Megalocnus rodens* (Matthew & Paula Couto, 1959: plate 16), Mc III is longer than Mc IV and Mc IV and Mc II are subequal in length. In *Hapalops*, Mc IV is longer than Mc III and Mc III is longer than Mc II (Scott, 1903–04). Finally, in *Eucholoeops* (FMNH P13125), Mc IV is longer than Mc III.

The medial margin of Mc II is lacking (Fig. 12E, F). The dorsal two-thirds of the lateral surface of the proximal epiphysis articulate with Mc III (Fig. 12E). This facet is proximopalmarly to distodorsally concave and overhangs a deep fossa. At the middle of the proximal side, a small portion of the concave trapezoid facet is preserved (Fig. 12F). A strong palmar process is located at the root of the proximal epiphysis. The distal keel is convex and well developed palmarly. The Mc II of *D. nordenskioldi* is similar to that of *Pliometanastes prostitus* (Hirschfeld & Webb, 1968: fig. 18A, B), but is shorter and more robust.

Mc III is the most massive metacarpal. It is Y-shaped in dorsal view (Fig. 11). The proximomedial branch of Mc III is shorter than the proximolateral branch. In proximal view, Mc III is approximately triangular and bears four articular facets (Fig. 12G–I). The medial surface (Fig. 12I) bears the Mc II facet (see Mc II description). The Mc IV facet (Fig. 12G), occupies the dorsal half of the proximal epiphysis, in contrast to *Pliometanastes prostitus*, in which it extends much more palmarly (Hirschfeld & Webb, 1968: fig. 18D). In *D. nordenskioldi*, the Mc IV facet is dorsopalmarly convex, slightly proximodistally concave, and it contacts proximally the unciform facet that occupies the dorsolateral corner of the proximal surface (see the description of the unciform). The magnum facet occupies the centre of the proximal surface of Mc III. This facet is laterodorsally limited by the unciform facet, lateroplantarly by a deep fossa, and medially by the Mc II facet. The magnum facet is complex and can be divided into three parts (Fig. 12H). The dorsal portion is V-shaped and extremely deep. The central portion is flat and quadrangular. The palmar portion is a deep dorsopalmar notch. It appears that the magnum had a small and complex articulation with the Mc III. A large pit is located beside the palmar and lateral margins of the magnum facet. The diaphysis of Mc III is short and bulky (Fig. 12G, I) and the distal epiphysis medially concave (Fig. 11). The distal articular facet for the proximal phalanx is strongly keeled. The dorsal portion of the keel extends further distally than the palmar portion. The articular facet extends medially, but not laterally, a condition that indicates that the third digit was medially curved as in Megatheriinae (Pujos & Salas, 2004a),

Nothrotheriidae (e.g. *Nothrotheriops*, Paula Couto, 1976) and probably more than in *Hapalops* (Scott, 1903–04) and the Cuban Megalocninae *Megalocnus* (Matthew & Paula Couto, 1959: plate 16). Like Mc II, the Mc III is shorter and much more robust in *Diabolotherium* than in *Pliometanastes prostitus* (Hirschfeld & Webb, 1968: fig. 18C, D).

The R Mc IV of *D. nordenskioldi* is preserved (Fig. 12J, K), but its lateral side is missing. The medial portion of the proximal epiphysis bears the Mc III facet, which is composed of two parts. The dorsal part is dorsopalmarly concave with a distal convex margin (Fig. 12J). The palmar part, slightly more proximal, is concave in all directions. The proximal epiphysis presents a very strong palmar process that contacted the ground like the other Mc. As in Mc II–III, the Mc IV diaphysis is short, massive, similar to that of *Megalocnus rodens* (Matthew & Paula Couto, 1959: plate 16) and clearly distinct from the elongated and slender Mc IV of *Pliometanastes prostitus* (Hirschfeld & Webb, 1968: fig. 18E–G). The keel of the distal epiphysis is inclined medially (Fig. 11), as in *Megalocnus*, and not extended distally, as in *Pliometanastes*. The keel of Mc IV of *D. nordenskioldi* reaches palmarly the middle of the diaphysis (Fig. 12J). This morphology indicates the great range of flexion of the fourth anterior digit of *D. nordenskioldi* in contrast to the other Megalonychidae (e.g. *Pliometanastes prostitus*; Hirschfeld & Webb, 1968: fig. 18A, G).

**Phalanges:** Several phalanges are known but poorly preserved. It is difficult to determine the identity of most of them. Two correspond to the third posterior pedal digit and are described below. Approximately 20 other phalanges, of which eight are ungual phalanges, are known and described below. The proximal phalanges are short and massive. Almost all the intermediate phalanges are slender, transversely compressed, and as long as in *Megalonyx* (Leidy, 1855: plate 10). All the ungual phalanges known were clawed, indicating a probable primitive condition in *D. nordenskioldi* (i.e. five anterior claws), as in *Hapalops* (Scott, 1903–04: plate 33), or at least four anterior claws (II–V), as in the Cuban Megalocninae *Megalocnus rodens* (Matthew & Paula Couto, 1959: plate 16). In a resting posture, the claws of *Diabolotherium* protrude, almost at right angles to the palmar plane (Fig. 12P), in contrast to most small-sized fossil sloths (see White, 1997). Tree sloths have extremely long and curved claws, adapted to suspensory arboreal habits (Mendel, 1981b, 1985a, b) and completely distinct from those of *D. nordenskioldi* (Fig. 12P).

**Uncertain metapodials and/or phalanges:** Two elements are unique (Fig. 12L–O). The first one is probably a second phalanx (Fig. 12L, M). It is short, massive, and distally bears a deep, pulley-like groove.



It is also characterized by a proximally projecting palmar process (Fig. 12M). The latter might be pathological, or result from a fracture or represent the fusion of sesamoid(s) with the proximopalmar portion of the phalanx. All fossil sloths possess a large palmar sesamoid in the palm of the manus. A recently recovered *Thalassocnus* specimen (Megatherioidea: Nothrotheriidae) from Mio-Pliocene levels of the Pisco Formation (Peru) possesses a large palmar sesamoid and several small sesamoids located palmarly at the metacarpal-phalangeal joints (F. Pujos, pers. observ., 2001). Similar sesamoids might have been present in *D. nordenskioldi*.

The second unique element is probably a phalanx, although with an unusual shape (Fig. 12N, O). In profile, it is ventrally curved (Fig. 12O). It exhibits one or two articular facets. The proximal facet is flat but incomplete. The nearly complete but poorly preserved distal facet is small, rounded, and convex. This facet probably contacted a vestigial ungual phalanx. This element belongs to the first manual or pedal digit, and more probably represents the Mc I fused with one or two phalanges or the MCC, i.e. a part or the entire first anterior manual digit fused with a carpal element. The main point of discussion remains the ventral curvature, as no fossil sloth possesses a ventrally curved MCC or metapodial. The curvature is possibly related to the climbing capacities of *D. nordenskioldi*, as in 'arboreal hominids' (see Susman, Stern & Jungers, 1984) and lemurs (see Godinot & Beard, 1993) characterized by curved phalanges.

#### INNOMINATE (FIG. 13, APPENDIX 1)

The innominate includes the L ilium, a small portion of the R ilium, and a fragment of the L acetabular fossa (Fig. 8). Most of the sacral vertebrae are preserved. The vertebrae are imperfectly fused, a condition that confirms the immaturity (old adolescent or young adult; Fig. 7B) of the MNHN CPN 9–1 skeleton. At least five sacral vertebrae are apparently preserved. The presence of an intrarachidian vein, as in the innominate of *Planops* (Hoffstetter, 1961: 72–73), is indicated by the two large foramina (for the passage of the two afferent veins) located ventrally to the first sacral vertebra (Fig. 13B). The bases of the neural spines are fused together, as in all fossil sloths (Fig. 13A). The innominate of *D. nordenskioldi* is extremely similar to that of *Hapalops ruetimeyeri* (Scott, 1903–04: fig. 21) and differs from that of *Bradypus* (Rose & Emry, 1993: fig. 7.4) only by the extreme posterior position of the first sacral vertebra.

The ilia are compressed transversely and extended anteriorly as in *Hapalops* (Scott, 1903–04: fig. 21), *Planops* (Hoffstetter, 1961: fig. 9), and the modern tree

sloth *Bradypus* (Rose & Emry, 1993: fig. 7.4), and not extended transversely as in Megatheriinae (De Iuliis, 1996), Mylodontidae (McDonald, 1987; Esteban, 1996), Nothrotheriidae (e.g. Cartelle & Fonseca, 1983: fig. 12, for *Nothrotherium*; Lull, 1929: plate 8, for *Nothrotheriops*), and others Megalonychidae (e.g. Matthew & Paula Couto, 1959: plates 18, 19, for *Megalocnus rodens*). In lateral view, the ilia of *D. nordenskioldi* are nearly horizontal and the angle between them and the sacral bone is 20–25° (Fig. 13C), a condition similar to that of *Hapalops* (Scott, 1903–04: fig. 21). In Mylodontidae, Pliopleistocene Nothrotheriidae, West Indies and North American Megalonychidae, and particularly Megatheriinae, this angle is much higher and the anterior portions of the ilia protrude dorsally (e.g. Paula Couto, 1967: fig. 3, on *Megalocnus*).

The anterior portion of the L acetabular fossa is partially preserved (Fig. 13B, C). It is located at the level of the limit between the third and fourth sacral vertebrae. The fossa is extremely shallow and seems to be deeper in the sloths previously cited.

#### PES (FIGS 14, 15G, N, S, 16H, 17, APPENDIX 1)

##### *Astragalus*

The astragalus is a postcranial element highly diagnostic in Tardigrada (Figs 14, 15). In sloths, the astragalar trochlea is composed of the medial odontoid facet and the lateral discoid facet. In *D. nordenskioldi* (Fig. 15G), the facets are contiguous and the odontoid facet is not a peg-like process, as in *Xyophorus villarroeli* (MNHN ACH 15, Fig. 15; St-André, 1996). In *Hapalops* (MNHN SCZ 168, Fig. 15C), usually considered as one of the most primitive Megatherioidea, in the Hemphillian North American Land Mammal Age (NALMA) (middle Pliocene) North American megalonychid sloth *Pliometanastes* (Fig. 15E), and in the West Indies Megalocninae *Megalocnus rodens* (Fig. 15D), the odontoid facet is slightly separated from the discoid facet anteriorly by a small notch. In Megatheriinae (e.g. *Megatherium urbinai*, Fig. 15A), most of Nothrotheriidae (e.g. *Nothrotheriops*; Stock, 1925: fig. 31), and Mylodontidae (Scelidotheriinae, McDonald, 1987; Mylodontinae, Esteban, 1996), the odontoid process is distinct (transversely extended) and the angle between the odontoid and the discoid facets is approximately 90° in Pleistocene Megatheriinae (Fig. 15A, O) and Nothrotheriidae. Consequently, the astragalar head, which supports the navicular and cuboid facets, protrudes medially (see arrows: Fig. 15A–G, O–S). In *Hapalops* sp. (Fig. 15C, Q), *Xyophorus villarroeli* (Fig. 15F, M), and *Megalocnus rodens* (Fig. 15D), the astragalar head is medial and located at the extremity of the odontoid process. In the Nothrotheriidae

*Thalassocnus littoralis* (MNHN SAS 163), the astragalar head is located between the odontoid and discoid processes, as in *Megatherium* (Fig. 15O). In *D. nordenskioldi*, the astragalar head, which is slightly damaged plantarly (Fig. 14D–F), is located on the medial margin of the odontoid process (Fig. 15G, N, S). In anterior view (Fig. 15O–S), the angle between the odontoid and the discoid facets is 160° in *Diabolootherium* (Fig. 15S), 90–115° in Megatheriinae (De Iuliis, 1996; Pujos, 2002, e.g. *Megatherium urbinai*; Fig. 15O) and in the nothrotheriid *Thalassocnus*, 130–140° in Mylodontidae (in *Glossotherium* MNHN PAM 141 and *Scelidootherium* MNHN PAM 204, respectively), 130° in *Planops* (Fig. 15P, BMNH M.9214), and 150° in *Hapalops longipes* (Fig. 15Q) and *Xyophorus villarroeli* (Fig. 15R).

The astragalar head is stud-shaped to receive the navicular and cuboid (Fig. 14D). A small part of the cuboid facet is preserved on its plantar margin. The cuboid facet is located more medioplantarly (see description of calcaneum) in *Diabolootherium* than in Megatheriidae and Nothrotheriidae, but its position is similar to the condition observed in *Hapalops longipes* and *Xyophorus villarroeli*. The astragalar plantar surface shows facets for the calcaneum (Fig. 14F). The ectal facet is L-shaped (Figs 14F, 15N), extended anterolaterally to posteromedially, and is concave, as in *Xyophorus villarroeli* (Fig. 15M), although less L-shaped than in *Pliometanastes prostitus* (Fig. 15L). In other fossil sloths, except Mylodontidae, the ectal facet is usually rectangular, for example *Megatherium* (Fig. 15H) and the West Indies Megalonychidae *Megalocnus* (Fig. 15K). In the mylodontine *Glossotherium* (MNHN PAM 141), this facet is fused to the sustentacular facet. In the scelidothereine *Scelidootherium* (MNHN PAM 204), the ectal facet is extremely reduced. The sustentacular facet of *D. nordenskioldi* is medioplantarly elongated and subdivided into two facets that meet at a right angle (Fig. 14F). No other fossil sloth exhibits a sustentacular facet divided into two parts and with a similar medial inclination. The astragalar sulcus of *D. nordenskioldi* is parallel to the main axis of the ectal facet (Figs 14F, 15N). The transverse diameter of the astragalar sulcus decreases posteriorly and the facets of the calcaneum are nearly in contact posteriorly.

The fibular facet occupies the entire lateral surface of the astragalus (Fig. 14E), as in *Hapalops* (MNHN SCZ 168), *Xyophorus* (MNHN ACH 15; St-André, 1996: fig. 8A), Nothrotheriidae (e.g. *Thalassocnus littoralis*, MNHN SAS 163), *Planops* (BMNH M.9214), and the other Megalonychidae *Megalonyx* (Leidy, 1855: plate 12) and *Megalocnus* (Matthew & Paula Couto, 1959: plate 22-3). In large fossil sloths, such as Megatheriidae and Mylodontidae, the fibular facet occupies only the dorsal portion of the lateral

astragalar surface. The fibular facet of *Diabolootherium* is semicircular and laterally contacts the discoid facet. Plantarly, the fibular facet contacts the anterior and posterior portions of the ectal facet. The central part of the plantar margin of the fibular facet is separated from the ectal facet by a deep fossa.

#### Calcaneum

The calcaneum is dorsopalmarly compressed. It is wing-shaped and the tuber calcanei is posteromedially extended (Figs 14A, B, 16H). The morphology of the posterior epiphysis suggests that the muscular insertions of the gastrocnemii are mainly located at the posteromedial angle of the calcaneum (Fig. 14A, B). The posterior epiphysis of the tuber calcanei is imperfectly fused, attesting to the immaturity of the MNHN specimen. The posterior and posterolateral margins of the calcaneum are convex and the medial margin of the diaphysis is concave from the tuber calcanei to the astragalar sustentaculum. A foramen is located on the lateral margin of the diaphysis posterior to the ectal facet (Fig. 14B). The foramen is larger on the L than on the R calcaneum. This asymmetry suggests that it was used for the passage of a nerve or a vein rather than a muscle or a tendon. This foramen is absent in other sloths. The tuber calcanei and the diaphysis are transversely convex. In plantar view (Fig. 14B), the calcaneum shows a deep, anteroposteriorly and transversely concave fossa.

In large fossil sloths, such as Megatheriinae (De Iuliis, 1996: figs 117–121; Fig. 16A), Mylodontidae (e.g. *Scelidootherium*, Hoffstetter, 1954b: fig. 2), and some Nothrotheriidae (e.g. *Thalassocnus*, MNHN SAS 1606), the tuber calcanei is massive. In the other fossil sloths, the calcaneum is not tuberosus and more dorsopalmarly compressed, as in *Hapalops* (MNHN SCZ 169), Megalonychinae from the West Indies (Fig. 16D–G) and North America (Fig. 16B, C), some Nothrotheriidae (e.g. *Nothrotherium*, Reinhardt, 1878; Winge, 1915; Cartelle & Fonseca, 1983; *Nothrotheriops*, Paula Couto, 1971), the undetermined nothrotheriid from La Venta (UCMP 39949; Hirschfeld, 1985: fig. 32D), and particularly *Valgipes deformis* (doubtful family; Gervais, 1874: plate 5, figs 4–7). Similarities exist between the nothrotheriid from the Miocene of Colombia and *Diabolootherium*, but the calcaneum is more anteroposteriorly elongated in the Colombian taxon. *Diabolootherium* had a true heel and the calcaneum contacted the ground along its posterior and posterolateral margins.

Anteriorly the calcaneum bears the articular facets for the astragalus (see astragalus description) and cuboid (Fig. 14C). In anterior view, the ectal facet is central and the sustentacular and cuboid facets are supported medially by the astragalar sustentaculum.

The sustentacular facet overhangs the small, oval, and flat facet for the cuboid. A transverse sinus separates these facets. This configuration is similar to that of other fossil sloths. In *Hapalops* (MNHN PAM CS2169), the ectal facet is angled, the sustentacular facet is undivided, and the cuboid facet is broader than in *Diabolotherium*.

#### Cuboid

Part of the R cuboid is preserved and bears at least three articular facets (Fig. 17A–C). The astragalar facet, occupying the entire posterior surface (Fig. 17A), is rectangular and transversely and dorsoplantarly concave. The calcaneal facet, extended anteroposteriorly, lies on the posteroplantar side of the cuboid (Fig. 17B). It is convex transversely and slightly inclined laterally. A deep anteroposterior sulcus divides the lateral surface (Fig. 17B). The medial surface of the cuboid is poorly preserved. The plantar half of the distal side is lacking. The facet with the astragalus represents the whole articular area on the anterior surface (Fig. 17C). The facet for the metatarsal(s) is slightly transversely convex. At least Mt V occupies the distal cuboid margin. Mt IV probably articulated with the cuboid. The cuboid of *D. nordenskioldi* shows the same morphology as the cuboid of the plantigrade Santacrucian sloth *Hapalops* (Scott, 1903–04: fig. 33), which has five functional pedal digits.

#### Metatarsals

Mt III and V of *D. nordenskioldi* are partially preserved (Fig. 17D–G). The posterior surface of Mt III is extremely damaged (Fig. 17E). Mt III is anteroposteriorly compressed and shows a prominent plantar process (Fig. 17D, E, H). A prominent plantar process is present in most fossil sloths, but the compression observed in *Diabolotherium* is unique among sloths. In Megatheriinae (e.g. *Megatherium urbinai*; Pujos & Salas, 2004a) and especially Plio-Pleistocene Nothrotheriidae (e.g. *Nothrotherium*; Pujos, 2001a), *Hapalops* (Scott, 1903–04: fig. 33), and the West Indies Megalonychidae *Megalocnus* (Matthew & Paula Couto, 1959: plate 24), Mt III is rectangular or square, but never anteroposteriorly compressed, as in *D. nordenskioldi*. The distal keel of Mt III is flat in *Diabolotherium*, convex in *Hapalops*, and concave in *Megatherium*. Mt III articulates posteriorly with the ectocuneiform, medially with Mt IV, and probably posterolaterally with Mt II (Fig. 17E). In fossil sloths that had five functional pedal digits (e.g. *Hapalops*, Scott, 1903–04: fig. 33), Mt III articulates medially with Mt II. In fossil sloths that have undergone digit reduction, such as Megatheriinae (see De Iuliis, 1996),

Mt III articulates medially with the MEC, which corresponds to the fusion of the two internal cuneiforms, and digits I–II. In *D. nordenskioldi*, the carpals and metacarpals are relatively similar to those of *Hapalops* and suggest the same primitive condition, namely the absence of the MEC. This implies that Mt III articulated medially with Mt II. The medial facet of Mt III of *Nothrotherium* (UZM 720), *Megatherium* (MUSM 15), *Hapalops* (e.g. *Hapalops*, Scott, 1903–04: fig. 33), and *Megalocnus* (Matthew & Paula Couto, 1959: plate 24) is orientated medially, whereas it is orientated posteromedially and plantarly in *Diabolotherium*. The facet of Mt V that articulates with Mt IV in *D. nordenskioldi* is reduced and also inclined plantarly. Mt III is slightly inclined laterally and suggests a weak torsion of the foot.

Mt V is extremely poorly preserved (Fig. 17F, G) and only the posterior epiphysis is informative. The lateral margin of Mt V is laterally convex. Mt V bears two articular facets. The dorsal extremity of the posterior facet for the cuboid is inclined anteriorly (Fig. 17F). The medial margin of this facet is rectilinear and extends dorsoplantarly. The facet is flat and antero-medially limited by the Mt IV facet (Fig. 17F, G). It is too poorly preserved to allow description. Mt V of some sloths exhibits a 'lateral wing' (e.g. the North American Megalonychidae *Megalonyx*; Leidy, 1855: plate 13). This lateral protuberance indicates a peculiar contact, probably heavy, between the pes and the ground: in large Gravigrada, such as Mylodontidae (Stock, 1917; McDonald, 1987; Esteban, 1996), Mt V reflects the graviportal stance and a strong lateral contact with the ground occurs. In Nothrotheriidae (e.g. *Nothrotherium*; Cartelle & Fonseca, 1983: fig. 15) the 'lateral wing' is well developed laterally. This difference between the Nothrotheriidae and the Megatheriidae and Mylodontidae may be related to the lighter body masses of the members of the first family.

#### Phalanges

P1–III is the only pedal phalanx that may be identified, as it articulates with Mt III (Fig. 17H). P1 is not diagnostic in *D. nordenskioldi*. It bears a posterior dorsoplantar carina and an anterior double pulley for P2, and lacks a plantar process. The clawed ungual phalanx, P3 (Fig. 17H) is short, poorly extended transversely, and bears a strong plantar process. This phalanx is weakly inclined laterally, like Mt III.

## DISCUSSION ON THE ANATOMY OF *DIABOLOTHERIUM*

### TEETH

The combination of the dental formula and the morphology of the teeth is highly peculiar. The typical den-



tal formula of fossil sloths is 5/4, which was considered as the primitive condition by Engelmann (1987), who considered the C1/c1–M4/m3 dental formula of Santacrucian taxa such as *Hapalops*, the most plesiomorphic arrangement. The orophodontoid sloths (Hoffstetter, 1956, 1982) have extremely primitive teeth, similar to those of armadillos (extreme bilophodonty of posterior teeth), clearly distinct from the teeth of Mio-Pliocene families (i.e. Megatheriidae, Nothrotheriidae, and Megalonychidae).

According to Hoffstetter (1982), the orophodontoid sloths [included in the Mylodontidae by Gaudin (2004)] did not survive the Oligocene. The alveoli of the Mylodontidae exhibit a distinct morphology compared with those of *Diabolotherium* in having a distinctly bilobed last molariform. From the *Hapalops* state [C1/c1 (oval)–M4/m3 (oval)], the condition of megalonychid, megatheriid, and nothrotheriid may have evolved independently, but none of them shows the bilobate condition or the increased complexity of the posterior molariform teeth of orophodontid sloths.

In Nothrotheriidae, the caniniform tooth disappears progressively during the Plio-Pleistocene. It is present in the late Miocene nothrotheriid specimen assigned to *Nothropus* by Frailey (1986), but absent in the Pleistocene genera *Nothrotherium* and *Nothrotheriops*. The molariforms are rectangular with, generally, labial and lingual longitudinal (apicobasal) grooves.

In all Megatheriidae (Mio-Pleistocene forms), a squared bilophodont molariform takes the place of the caniniform tooth, at least from the lower Miocene. *Megathericulus* is the only Megatheriinae that possesses rectangular molariforms. All the Megatheriidae are large except *Planops*, from the Santacrucian (Middle Miocene) of Patagonia, considered by most authors as a member of this family (De Iuliis, 1994; Gaudin, 1995, 2004).

All of the Megalonychidae except *Diabolotherium* have retained the dental arrangement considered as primitive in Megatherioidea (i.e. C1/c1–M4/m3). When present, the caniniform, located at the anterior extremity of the maxilla, is prominent and the molariform teeth are approximately oval (several morphologies exist), but never quadrangular. *D. nordenskioldi* has the same dental formula as Megatheriinae (quadrangular 5M/4m) but M2–M5 are rectangular rather than square in outline, as in some Plio-Pleistocene nothrotheriids (e.g. *Nothrotherium maquinensis*; Pujos, 2001a) and *Megathericulus* (see De Iuliis, 1996). However, the lower molariforms of *D. nordenskioldi* are squared, as in Megatheriinae (but rectangular in *Megathericulus* and *Plesiomegatherium halmyronomum*; De Iuliis, Ré & Vizcaíno, 2004), rather than rectangular, as in Nothrotheriidae, or oval, as in other Megalonychidae.

## CRANIAL BONES

The auditory region of Xenarthra exhibits several diagnostic characters (Patterson *et al.*, 1992; Gaudin, 1995). The phylogenetic analysis performed by Gaudin (1995, 2004) corroborates the monophyly of the Megalonychidae [including the three-toed sloth *Choloepus* (Gaudin, 1995, 2004) and the Santacrucian genus *Eucholoeops* (Gaudin, 2004)]. Gaudin's (1995) phylogenetic analysis based on the auditory region of sloths supports the monophyly of the Megalonychidae (i.e. *Choloepus*, *Acratocnus*, *Megalocnus*, and *Megalonyx*) on the basis of seven synapomorphies. The auditory region of *D. nordenskioldi* is damaged, but three of these characters can be observed (Figs 3–5): a ventral edge of the entotympanic extended into an anteroventral process (Gaudin, 1995: character 21<sup>1</sup>); a glenoid cavity ventral to superficies meatus (Gaudin, 1995: character 75<sup>1</sup>); and a root of the zygomatic process directed laterally (85<sup>2</sup>; see the description of the squamosal above). These three synapomorphies strongly suggest that *D. nordenskioldi* is a megalonychid. However, *Diabolotherium* exhibits only two of the 20 unequivocal synapomorphies of the family Megalonychidae suggested by the craniodental phylogenetic analysis of Gaudin (2004): absence of the supraoccipital exposure on the cranial roof (Fig. 4A) and a small condyloid foramen (maximal diameter < 2% of BNL; Fig. 3C, D). Among the 18 remaining characters, 11 relate directly to the caniniform tooth (13<sup>1</sup>, 14<sup>1</sup>, 20<sup>0</sup>, 24<sup>1</sup>, 25<sup>1</sup>, 29<sup>1</sup>, and 30<sup>1</sup>), four relate indirectly to the caniniform tooth (4<sup>1</sup>, 23<sup>1</sup>, 76<sup>2</sup>, and 122<sup>3</sup>), and six are not observable on the specimens described here (86<sup>2</sup>, 106<sup>2</sup>, 142<sup>1</sup>, 156<sup>2</sup>, E30<sup>0</sup>, and E38<sup>1</sup>) because the skull and mandibles are damaged or incomplete (Figs 3–6). The Oligocene Orophodontoidea and Megatherioidea share an anterior upper and lower caniniform tooth and four upper and three lower molariform teeth. It may be hypothesized that the first anterior tooth of *Diabolotherium* developed from a posterior migration and modification of a more anterior caniniform tooth, which has occurred several times in xenarthran evolution. *Diabolotherium* is the only Megalonychidae that has this peculiar dental formula associated with quadrangular molariform teeth. The similarities between *Diabolotherium* and the families Megatheriidae and Nothrotheriidae are probably convergent.

The pterygoids of *D. nordenskioldi* are poorly preserved, but informative. In nearly all sloths, including *D. nordenskioldi* (except *Nothrotherium* and *Nothrotheriops*), the pterygoids are blade-shaped. In *Diabolotherium*, the posterior part of the pterygoid is extremely robust and forms a column, as in some West Indies Megalonychidae (e.g. the Megalocninae *Megalocnus*; Matthew & Paula Couto, 1959).

## VERTEBRAE

Most vertebrae are known, but poorly preserved. The dorsal vertebrae confirm the existence of an intrarachidian circulation, as occurs in most fossil sloths (Hoffstetter, 1959) (Fig. 7B–D).

## FORELIMB

The scapula of *Diabolootherium*, resembling that of *Hapalops* and modern tree sloths by its triangular shape, is clearly distinct from those of Megatheriidae, Nothrotheriidae, Mylodontidae, and all other Megalonychidae from the West Indies and North America (Fig. 8A, B). The major difference between *Hapalops* (Scott, 1903–04) and *Diabolootherium* is the broad postscapular fossa in the Peruvian taxon, absent in *Hapalops* as well as in recent sloths (Rose & Emry, 1993). The scapula of *Planops martini* (Hoffstetter, 1961) is fragmentary, but resembles that of *D. nordenskioldi* in its anteroposterior extension and dimensions of the postscapular fossa (Fig. 8A). The postscapular fossa represents the origin of the M. teres major, a powerful adductor of the arm [according to Rose & Emry (1993: 89, fig. 7.5), in *Tamandua* and *Euphractus*], or of the M. teres minor [according to McDonald (2003)], a protractor and external rotator of the arm, or of the caput longum of the M. triceps brachii, an extensor of the arm and retractor of the scapula (Fig. 9). Another interpretation is that the caput longum of the triceps brachii originated along the secondary spine and ahead of the M. subscapularis minor on the postscapular fossa, as occurs in bears (Davis, 1949: 302, fig. 77). In relation to the scar and the position of the insertion of the teres major (see humerus description below), it is very likely that the M. teres major was less developed in *Diabolootherium* than in fossorial ground sloths.

The humeral morphology is more informative in Xenarthra relative to performed movements (and so, function) than to phylogenetic affinities (Rose & Emry, 1993: 91; De Iuliis, 2003). The humeri of *Diabolootherium* (Fig. 10), other Megalonychidae (e.g. Matthew & Paula Couto, 1959: plate 34; on *Parocnus torrei*), and *Hapalops* and *Planops* are more slender and elongated than in Megatheriidae, Nothrotheriidae, and especially Mylodontidae (i.e. large to gigantic terrestrial or fossorial taxa). The humerus of *D. nordenskioldi* is characterized in particular by a long but not prominent deltopectoral crest and the absence of the entepicondylar crest (Fig. 10A, C). In Megalonychidae, *Diabolootherium* and the megalonychiine *Parocnus* (Fig. 10G, H) are also characterized by the absence of an entepicondylar foramen. The deltopectoral crest, however, is more developed in *Parocnus*. The extreme reduction in *D. nordenskioldi* of the deltopectoral

crest, in comparison with all other fossil Tardigrada, may indicate a weaker development of the M. deltoideus and pectoralis than in large to gigantic terrestrial or fossorial taxa (Fig. 9). The humeral head suggests a very mobile shoulder joint, a characteristic of all sloths.

Like the humerus, the ulna of *Diabolootherium* closely resembles that of *Hapalops*, but not that of other Megalonychidae. The olecranon process is informative with respect to posture and locomotory habits of mammals, as shown, for example, by Rose (1993) for primates and Argot (2001) for didelphids. In Xenarthra, the olecranon is extremely short in suspensory forms (*Bradypus* and *Choloepus*; Mendel, 1981a, 1985a) and elongated in fossils with digging abilities, such as mylodontids. Several Xenarthra, including modern and fossil armadillos (e.g. Vizcaíno & Fariña, 1997; Vizcaíno, Fariña & Mazzetta, 1999; Bargo *et al.*, 2000; Vizcaíno & Milne, 2002; Vizcaíno, Milne & Bargo, 2003) and some fossil ground sloths (e.g. *Scelidotherium*, *Glossotherium*, and *Lestodon*; Zárate *et al.*, 1998; Vizcaíno *et al.*, 2001) are or were powerful diggers. For example, Vizcaíno *et al.* (1999, 2001) hypothesized that *Scelidotherium*, *Glossotherium*, and *Lestodon* probably produced several large Pleistocene burrows in the Mar del Plata area of Argentina. The olecranon of *D. nordenskioldi*, although quite long relative to the ulnar length (Fig. 8D–F), does not reach the relative length observed in digging Xenarthra. However, it is as long as that of *Hapalops* and *Planops*, considered to be semiarboreal (White, 1993), and its length is compatible with a well-developed M. triceps.

The trochlear notch is widely open in *D. nordenskioldi* (approximately 105°), which reduces the stability of the elbow joint (Fig. 8D). The radial notch faces more anteriorly in this sloth than in the other fossil sloths, and forms an obtuse angle with the lateral border of the coronoid process in anterodistal view (Fig. 8C). As for arboreal marsupials (de Muizon, 1998; Argot, 2001), this condition, together with the circular radial head, probably increased the range of pronation–supination movements in *Diabolootherium*. White (1993) gave an index of dorsal olecranon projection, corresponding to the ratio between the anteroposterior diameter of the proximal epiphysis (at the middle of the trochlear notch) and the proximodistal diameter of the trochlear notch (between the anconeal and coronoid processes). In *Diabolootherium*, this ratio is 0.78, which indicates, according to White (1993), a high degree of arboreal capacity, intermediate between those of the Santacrucian fossil sloth *Pelecynodon arcuatus* and the West Indies fossil Megalonychidae *Neocnus gliriformis* (White, 1993: 234).

In fossil sloths, distinct categories are used to describe the locomotory modes that evolved within the group, such as climbing (*Hapalops*), digging (armadil-

los and some large ground sloths), bipedalism and/or quadrupedalism (e.g. megatheriine sloths; Pujos *et al.*, 2002), swimming (e.g. the nothrotheriid sloth *Thalassocnus*; de Muizon & McDonald, 1995; McDonald & de Muizon, 2002; de Muizon *et al.*, 2003, 2004a). These categories are usually reflected by the morphology of the ulna. The posteriorly convex ulnar diaphysis with a proximal posterior convexity (with maximum convexity distal to the coronoid process) that characterizes *Diabolotherium* and *Hapalops* probably indicates climbing habits (as in marsupials; de Muizon, 1998; Argot, 2001). The medial and lateral ulnar fossae suggest well-developed Mm. abductor pollicis longus and flexor digitorum profundus, consistent with a non-reduced pollex and a wide range of digital flexion.

Distally the styloid process is extremely peculiar (Fig. 8D–F). It is spatulate and well extended distomedially (Fig. 9E). The flat anterodistal portion of the styloid process probably corresponds to a large carpal contact (probably with the unciform). The only xenarthrans that exhibit this peculiar morphology are the modern tree sloths *Bradypus* and *Choloepus*. However, the poor preservation of the styloid process and the absence of complete cuneiforms preclude interpretation of this morphology for *Diabolotherium*.

Contrary to most small-sized fossil sloths, the proximal third of the radial diaphysis of *Diabolotherium* is not sharply angled, but is regularly convex (Fig. 8G, I). As in all Tardigrada, the head of the radius of *Diabolotherium* is circular, a morphology that increases pronation and supination capabilities. On the radial shaft, the anterior surface bears three crests, orientated proximolaterally to distomedially, that define two muscle insertion areas (Fig. 8G). The more proximal area is narrower and probably corresponds to the insertion of the M. supinator brevis. The most distal area is broader and corresponds to the insertion of the M. pronator teres (Fig. 9B). In *D. nordenskioldi*, the large insertion for the M. pronator teres, broader and more rugose than in *Hapalops* (MNHN SCZ167) and *Planops* (BMNH M.9209), suggests a powerful muscle and a great range of rotation of the manus, reflecting the ability of the animal to grasp supports.

Several skeletal elements of the limbs tend to fuse in each sloth lineage. Fusion may occur in the manus (medial carpals and digits), pes (medial tarsals and digits), and tibia and fibula. These fusions appear independently in the various sloth families. In the manus, the first digit is usually reduced or absent. One of the best examples of digit reduction occurs in large Megatheriidae. For example, the Pleistocene genera *Megatherium* and *Eremotherium* are distinct by the number of functional digits. Both genera exhibit a MCC [according to De Iuliis & Cartelle (1993)], but this complex includes distinct carpal and metacarpal elements. *Eremotherium* has five

(*E. eomigrans*; De Iuliis & Cartelle, 1999) or three functional digits (*E. laurillardii*; Cartelle, 1992; De Iuliis, 1996), in contrast to the four functional digits of *Megatherium* (Owen, 1858). De Iuliis & Cartelle (1999) have shown that the digit reduction appeared independently in these two genera. Fusions of bones are apparently less frequent in families that have retained supposed 'primitive conditions' and a relatively small size (e.g. most of the Megalonychidae, except *Megalonyx*). During tardigrade evolution, the trapezium is the first carpal bone to fuse with digit 1. The trapezium is an independent element in the earlier variant of *Eremotherium eomigrans* and is fused to Mc I in the later variant of the same species (De Iuliis & Cartelle, 1999).

The Santacrucian sloth *Hapalops longipes* has an independent trapezium (Scott, 1903–04: 193) and the scaphoid does not exhibit a distomedial process, in contrast to *Diabolotherium* (Fig. 12A). The presence of this process in *D. nordenskioldi* suggests a fused trapezium and Mc I, as in Nothrotheriidae or Megatheriidae. However, except for the presence of a distomedial process, the scaphoid of *Diabolotherium* is morphologically similar, but more specialized than that of Santacrucian sloths. It is strongly compressed proximodistally, which suggests a great range of dorsoflexion of the manus (as observed in an arboreal borhyaenoid marsupial, *Prothylacinus patagonicus* compared with the more terrestrial *Borhyaena tuberosa*; Argot, 2004), and therefore a probable palmigrade resting posture (Fig. 11). The scaphoid of the Santacrucian (e.g. *Hapalops* and *Eucholoeps*) sloths is proximodistally more compressed than in the large ground sloths (*Glossotherium* or *Megatherium*), but never as much as in *Diabolotherium*. Many fossil sloths possess a large palmar sesamoid, which corresponds to an ossification of the tendon for the flexor digitorum profundus, as suggested for Megatheriinae by Cabrera (1929). This element has not been recovered in *D. nordenskioldi*.

*Diabolotherium* had at least three anterior functional digits (II–IV). The first and fifth digits are not preserved (Figs 9, 11, 12). The metacarpals are morphologically similar to those of *Hapalops*, *Eucholoeps*, and some Megalonychidae from the West Indies (e.g. *Megalocnus rodens*; Matthew & Paula Couto, 1959: plate 16), although much shorter. In *D. nordenskioldi*, Mc II–IV are equal in length, which is not the case in the other small-sized fossil sloths. The subequal length of the metacarpals of *Diabolotherium* indicates relatively longer lateral digits, which improved the grasping ability of the manus. The presence of strong palmar processes at the root of the proximal epiphysis of the metacarpals indicates an important contact with the ground (or boughs) during locomotion (Fig. 12E–K), a feature also indicative of a



palmigrade posture. In Megatheriidae, weight was supported during quadrupedal walking on the lateral portions of the fourth and fifth manual digits and the lateral margins of the calcaneum and fifth pedal digit (Pujos & Salas, 2004a; Pujos *et al.*, 2004). By contrast, *Diabolotherium* does not exhibit any character suggesting a lateral loading. The metacarpal keels are well extended dorsopalmarly. The wide range of digital flexion allowed *Diabolotherium* to grasp food or branches. All the ungual phalanges discovered bore claws in life. The claw of the third manual digit of *Diabolotherium* is slender and projects strongly palmarly in a resting posture (Fig. 12P), so that the digit appears to be hook-like, which facilitated the grasping of any support.

#### HIND LIMB

The innominate of sloths exhibits two distinct shapes. In taxa that are generally considered terrestrial [large ground sloths, such as Megatheriinae (not including *Planops*), Mylodontidae, Nothrotheriidae, and the North American Megalonychidae *Megalonyx*], the wings of the ilia protrude laterally and dorsally. In small terrestrial and possibly climbing sloths (*Hapalops* and some Megalonychidae from the West Indies; see White, 1993, 1997), the ilia are subparallel to the sacral vertebrae and less prominent laterally. In modern tree sloths, the iliac wings are also compressed transversely and parallel to the sacral vertebrae. The innominate of *D. nordenskioldi* (Fig. 13) is similar to that of modern tree sloths and subarboreal fossil sloths (e.g. *Hapalops*): weakly developed laterally, with ilia subparallel to the sacral vertebrae. A peculiar feature is the shallowness of the acetabular fossa. It is generally deep in all sloths. This peculiar morphology of the acetabular fossa suggests a mobile hip joint poorly stabilized in *Diabolotherium*.

The astragalus provides important information on locomotory mode and phylogenetic relationships among Xenarthra (Rose & Emry, 1993). Hoffstetter (1958: 594) noted that, in Tardigrada, among the postcranial elements 'c'est surtout l'astragale qui présente des modifications remarquables, probablement corrélatives d'une torsion du pied vers l'intérieur...'. Several authors have used the astragalus to establish phylogenetic relationships among Gravigrada families (Hoffstetter, 1958; Engelmann, 1985; De Iuliis, 1994). The dental formula and teeth, auditory region, humerus, femur, and astragalus provide the most informative characters for reconstructing the phylogeny of Tardigrada.

In *Diabolotherium*, *Xyophorus*, and to a lesser extent *Pliometanastes*, the odontoid process is not peg-shaped (Fig. 15E–G), the tibial articulation is nearly flat (Fig. 15R, S), and the ectal facet is L-shaped (Fig. 15L–

N). These three genera differ especially in the position of the astragalus head (it lies much more medially in *Diabolotherium*) and in the morphology of the sustentacular facet. The morphology of the astragalus of these three genera is similar to the condition found in the Santacrucian sloth *Hapalops* (Fig. 15C, J, Q). A similar locomotory mode in all these small sloths possibly explains the similarities of their astragali.

Based on astragalus morphology, we suggest some characters that could indicate a special locomotory mode.

The arboreal/climber (*D. nordenskioldi*, *Xyophorus villarroeli*?) or semiarboreal (*Hapalops*, medium-sized North American Megalonychidae *Pliometanastes*) fossil sloths were small or medium-sized and show (Fig. 15C, E–G, J, L–N, Q–S):

- an odontoid process that is incipient (*Hapalops*, *Pliometanastes*; Fig. 15C, E) or not individualized from the discoid facet (*Xyophorus villarroeli* and especially *D. nordenskioldi*; Fig. 15F, G);
- an obtuse angle between the discoid and the odontoid facets (this angle reaches a maximum of approximately 160° in *D. nordenskioldi*; Fig. 15S);
- an extremely medial astragalus head (especially in *D. nordenskioldi*; Fig. 15G);
- and a fibular facet that occupies the entire lateral surface of the astragalus (Fig. 15E–G).

Generally, the largest fossil sloths (the true 'ground sloths'), such as Megatheriidae, Mylodontidae, and the Megalonychidae *Megalonyx*, are quadrupedal and sometimes bipedal. Their astragalus exhibits (Fig. 15A, H, O):

- a well-defined odontoid process that extends medially (Fig. 15A);
- an acute angle between the discoid and the odontoid facets (seen in anterior view; Fig. 15O);
- an astragalus head located in the middle of the anterior surface and sometimes orientated slightly laterally (Fig. 15A);
- and a relatively small fibular facet (Fig. 15A).

The other forms, such as *Planops martini* [Megatheriidae according to Gaudin (2004)] and the West Indies Megalonychidae *Megalocnus* (Fig. 15D, K) are intermediate.

The calcaneum is wing-shaped (Figs 14A, B, 16H), as in most Megalonychidae and Santacrucian SALMA sloths (e.g. *Hapalops*). The calcaneum of *Diabolotherium* is similar to the small nothrothere from the Miocene of La Venta described by Hirschfeld (1985), to *Valgipes deformis* (Gervais, 1874) from Brazil, and to a lesser extent to the North American Megalonychidae *Pliometanastes prostitus* (Fig. 16C; Hirschfeld & Webb, 1968). However, the astragalus of the La Venta nothrothere is much more specialized than in *Diabo-*

*lothorium*: 'it is narrow, elongate, with the internal condyle convex, displaying incipient development of an odontoid process' (Hirschfeld, 1985: 44). The calcaneal morphology of *Diabolotherium* suggests a posterior and posterolateral contact with the ground (through the entire posterolateral margin of the tuber calcanei), probably as in *Pliometanastes* (Fig. 16C). Contrary to the terrestrial and graviportal ground sloths, such as Mylodontidae and Megatheriinae (Fig. 16A), which show a pedolateral rotation, the calcaneum of *Diabolotherium* (and of small sloths, such as *Hapalops* and *Pliometanastes*) indicates the existence of a true heel and a plantigrade pes. A tuberosus calcaneum (Fig. 16A) is associated with an astragalus typical of graviportal sloths and is characteristic of the Megatheriidae, Mylodontidae, and Nothrotheriidae (except the astragalus of *Xyophorus*). A gracile, wing-shaped, and dorsopalmarly compressed calcaneum (Fig. 16B, C) is generally associated with arboreal or semiarboreal fossil sloths and most Megalonychidae (except the large North American *Megalonyx*; Fig. 16B), the Santacrucian sloths (e.g. *Hapalops* and *Eucholoeops*), the poorly known *Valgipes*, and the Miocene nothrothere from La Venta.

The metatarsal morphology is peculiar in *Diabolotherium*. Mt III is anteroposteriorly compressed, the medial facet is posteromedial and inclined plantarly, and the distal keel is flat (Fig. 17D, E, H). The lateral wing of Mt V is poorly developed (Fig. 17G), in contrast to the condition in the other Megalonychinae. Mt III and the third phalanx of the same digit are slightly sloped laterally and bear strong plantar processes that probably contacted the ground.

Appendix 2 summarizes the functional features discussed below. It emphasizes the characteristics of *Diabolotherium* relative to other Tardigrada:

- a scapula with a posteriorly extended caudal angle, and a postscapular fossa;
- a long deltopectoral crest, but less prominent than in fossorial taxa;
- an olecranon of the ulna shorter than in fossorial taxa;
- a posterior border of the ulna more convex than in other sloths, except those considered as semiarboreal, such as *Hapalops*;
- a radial notch that faces more anteriorly than in other fossil sloths and forms an obtuse angle with the coronoid process;
- a radius regularly convex anteriorly and widened distally;
- a proximodistally compressed scaphoid;
- well-developed digits, all clawed and with median digits of the same size.

*Diabolotherium* was a relatively small sloth, with long and slender bones (compared with graviportal and fos-

sorial sloths) and highly mobile elbow, hip, and ankle joints. The shape and orientation of the iliac blades could be related to the small size of the animal and the reduced weight of internal organs. The forelimb characters mentioned above suggest arboreal capabilities for this taxon; it is noteworthy that Pujos (2002) interpreted the depositional environment of the Piedra Escriba site as representing an oasis. Adaptations similar to those described here for *D. nordenskioldi* have been noted by White (1989, 1993, 1997) for some Megalonychidae from the West Indies. Unfortunately, the relatively poor knowledge of the megalonychid family (see below) does not allow a more complete understanding of the evolutionary history of these features. Moreover, two peculiar features are still unresolved functionally: the shape of the styloid process of the ulna and the wing-shaped tuber calcanei. A better understanding of the functional anatomy of *Diabolotherium* would require the discovery of more megalonychid fossils in Peru (or Bolivia), and more complete remains of *D. nordenskioldi*.

## TARDIGRADA PHYLOGENY

### MATERIAL AND METHODS

Several authors have analysed the phylogeny of various Megatherioidea subfamilies. De Iuliis (1996) and Pujos (in press a) each presented a phylogenetic analysis of the Megatheriinae. The former author's analysis included 12 cranial and postcranial characters distributed among six genera and nine species, whereas Pujos' (in press a) work included 32 discrete and unordered cranial and postcranial characters distributed among 14 megatheriine species (included in the same six genera). Engelmann (1978) performed a phylogenetic analysis of Xenarthra, with special emphasis on Cingulata, using 130 cranial and postcranial characters distributed among 22 genera. St-André (1994) and Esteban (1996) each realized a phylogeny of Mylodontinae (25 and 50 cranial and postcranial characters distributed among 15 and 12 genera, respectively) and McDonald & Perea (2002) of Scelidotheriinae (27 characters distributed among four genera). Perea (1999), McDonald & de Muizon (2002), and de Muizon *et al.* (2003) performed nothrotheriine phylogeny using 11, 29, and 33 cranial and postcranial characters distributed among five genera. Recently, Carlini & Scillato-Yané (2004) analysed the phylogeny of Tardigrada based on 17 characters of the mandible. All of these phylogenetic analyses of sloth clades corroborated the monophyly of each group.

Gaudin's (1995, 2004) phylogenetic analyses of Tardigrada included 21 and 33 genera and were based on 85 ear region and 286 osteological characteristics of the skull, lower jaw, dentition, and hyoid arch.

In Gaudin's first analysis (Gaudin, 1995), *Bradypus* fell out as the sister taxon of all other sloths. The monophyly of Megatheriidae, Mylodontidae, and Megalonychidae (including *Choloepus*) was proposed, and Nothrotheriinae was considered as a possible paraphyletic assemblage. *Planops* was included with (*Megatherium*, *Eremotherium*) in the Megatheriidae and *Hapalops* with *Euchloeops* constituted a weakly supported clade.

In the second, more comprehensive, analysis, Gaudin (2004) recognized a more 'conventional' topology that was nearly in accordance with Hoffstetter's (1958, 1982) views. *Euchloeops* was linked to Megalonychidae (and constitutes the oldest well-known member of this family), *Planops* remained with (*Megatherium*, *Eremotherium*) in the megatheriid clade, *Bradypus* fell out as the sister taxon of all other sloths, and *Hapalops* was at the base of the Megatherioidea. According to Gaudin (2004), Nothrotheriidae and Megatheriidae are closely related and Megalonychidae are closer to [Nothrotheriidae + Megatheriidae] than Mylodontidae.

A preliminary phylogenetic analysis based on 42 cranial and postcranial characters is provided in order to assess the relationships between *D. nordenskioldi* and other fossil sloths, as well as the extant tree sloths. In this analysis, 16 genera belonging to the four well-known Tardigrada clades (Megatheriidae, Nothrotheriidae, Mylodontidae, and Megalonychidae) were used, as well as some taxa of uncertain affinities, such as *Hapalops longipes* [a basal Megatherioidea according to Gaudin (2004)], *Planops martini* [a megatheriid according to Gaudin (2004)], and the extant sloths *Choloepus hoffmanni* [a megalonychid according to most authors, such as Gaudin (2004) and Carlini & Scillato-Yané (2004)], and *Bradypus variegatus* [the sister genus of all other sloths according to Gaudin (2004)]. The taxa used were considered to be the best representatives of each family and are sufficiently well known to be coded.

The following primary literature sources were consulted in addition to specimens observed in palaeontological institutions (FMNH, MACN, MLP, MNHN, ROM, and UZM). *Megatherium americanum*: Owen (1851, 1855, 1856, 1858, 1860); De Iuliis (1994, 1996). *Eremotherium laurillardii*: Cartelle & Bohórquez (1982, 1986); Cartelle (1992); Cartelle & De Iuliis (1995); De Iuliis (1996); Pujos & Salas (2004b). *Nothrotherium maquinense*: Reinhardt (1878); Paula Couto (1979); Cartelle & Fonseca (1983); Cartelle & Bohórquez (1986); Pujos (2001a). *Nothrotheriops shastense*: Stock (1925); Paula Couto (1976); Naples (1987); Perea (1999). *Scelidodon chiliensis*: Lydekker (1886); McDonald (1987); Pujos (2000); Pujos & Salas (2004a). *Myodon darwini*: Stock (1925); Kraglievich (1928); Esteban (1996). *Planops martini*: Hoffstetter (1961);

De Iuliis (1994). *Hapalops longipes*: Scott (1903–04); De Iuliis (1994). *Euchloeops ingens*: Scott (1903–04). *Megalocnus rodens*: Paula Couto (1956, 1967); Matthew & Paula Couto (1959); Fischer (1971); MacPhee et al. (2000b). *Acratocnus odontotrigonus*: Anthony (1916, 1918); Matthew & Paula Couto (1959); Paula Couto (1967); MacPhee et al. (2000b). *Megalonyx jeffersonii*: Leidy (1855); Sinclair (1905); Stock (1925); McDonald (1977); McDonald & Anderson (1983). *Pliometanastes propositus*: Hirschfeld & Webb (1968); Hirschfeld (1981). *Choloepus hoffmanni*: Mendel (1981a, b); Naples (1982); Webb (1985); Eisenberg (1989); Redford & Eisenberg (1992); Eisenberg & Redford (1999); and MUSM specimens (MUSM 17728, 6111). *Bradypus variegatus*: Naples (1982); Mendel (1985a); Webb (1985); Eisenberg (1989); Redford & Eisenberg (1992); Eisenberg & Redford (1999); Anderson & Handley (2001); and MUSM specimens (MUSM 8301, 8302, and 13363).

*Propalaeohoplophorus australis* (Cingulata: Glyptodontoidea) from the Miocene of Patagonia (Scott, 1903–04) and the modern armadillo *Dasypus novemcinctus* (Eisenberg, 1989; Redford & Eisenberg, 1992; Eisenberg & Redford, 1999; MUSM 6113) were used as outgroups. Vermilingua are generally considered as the sister group of Tardigrada; together, these taxa form the clade Pilosa (Tardigrada, Vermilingua), which is the sister group of the Cingulata or armoured Xenarthra. As Vermilingua are highly derived (because of their specialized diet and the absence of teeth), most of the cranial characters were not applicable. For this reason, Vermilingua were excluded as a possible outgroup and armoured Xenarthrans were chosen.

Comments are included in the list given below, when relevant.

## CHARACTERS USED IN THE CLADISTIC ANALYSIS

### CRANIAL

1. Dental formula (Pujos, 2002: character 1): (0) > 5/4; (1) 5/4; (2) 4/3.

The oldest sloths from the Tinguirirican SALMA of Chile (Eocene–Oligocene boundary, *Pseudoglyptodon* sp.; Wyss et al., 1993) and the Deseadan SALMA of Argentina (*Orophodon* and *Octodontotherium*; Hoffstetter, 1954c, 1956) and Bolivia (*Pseudoglyptodon*, Engelmann, 1987; *Orophodontoid* and *Megalonychoid* sloths; F. Pujos & G. De Iuliis, unpubl. data) exhibit 5/4 teeth. This arrangement is considered as the primitive condition in sloths (Engelmann, 1987). Cingulata are the oldest Xenarthra (Late Palaeocene, Itaboraia SALMA of Brazil) and exhibit a dental formula greater than 5/4 (e.g. 8/8 in *Propalaeohoplophorus*



*australis*; Scott, 1903–04). Vermilingua have secondarily lost the teeth and most Nothrotheriids have lost the most mesial tooth (e.g. *Thalassocnus*, *Nothrotherium*, and *Nothrotheriops*; de Muizon *et al.*, 2003).

2. Presence of a caniniform tooth (McDonald & de Muizon, 2002; de Muizon *et al.*, 2003: character 1 modified; Pujos, 2002: character 2 modified): (0) no; (1) yes. In some sloths (e.g. most megalonychids and mylodontids), the most mesial tooth is peg-shaped, circular or oval in section, curved along its longitudinal axis, obliquely worn, and quite often separated by a diastema from the remaining cheek teeth; in other words, caniniform. Deseadan sloths may present a true caniniform tooth (e.g. the Megalonychidae *Deseadognathus riggsi*; Carlini & Scillato-Yané, 2004) or a caniniform not separated by a diastema from the second cheek tooth (as in the orophodontoid form *Octodontotherium*; Hoffstetter, 1956; F. Pujos & G. De Iuliis, unpubl. data). The homology between these caniniform teeth is unclear. The disappearance of the caniniform or the modification of a caniniform to a molariform tooth appears to occur independently in distinct sloth lineages. The absence of a caniniform characterizes all the megatheriines, in which the most mesial tooth is molariform, most of the Nothrotheriidae (e.g. *Nothrotheriops*, *Nothrotherium*, and *Thalassocnus*; de Muizon *et al.*, 2003), and Scelidotheriinae, in which the most mesial tooth is lost. Santacrucian sloths, such as *Schismotherium* (see Scott, 1903–04), reveal that the presence of a true caniniform tooth is not always accompanied by the existence of a diastema.

3. Size of the most mesial upper tooth (Gaudin, 2004: character 13 modified): (0) smallest tooth; (1) greatly enlarged; (2) neither the smallest nor enlarged. Gaudin (2004) considered the most mesial upper tooth as a caniniform in all sloths that retain the primitive dental formula (5/4). We only consider the size and proportion of the first upper mesial tooth (C or M) relative to those distal to it. In Megatheriinae, the last upper cheek tooth (M5) is the smallest of the tooth row. The Nothrotheriidae, considered here (e.g. *Nothrotheriops*), have lost the most mesial tooth, so that this character is not applicable. In Megalonychidae, the most mesial upper tooth is greatly enlarged (including *Diabolotherium*). In Mylodontidae, the most mesial tooth is reduced in Mylodontinae and well developed in Scelidotheriinae. The same consideration applies to the next character. The only important fact is the morphology of the alveolus of the most mesial lower tooth of *Diabolotherium* (greatly enlarged).

4. Size of the most mesial lower tooth (Gaudin, 2004: character 14 modified): (0) smallest tooth; (1) greatly enlarged; (2) neither the smallest nor enlarged.

The shape of the m1 alveolus of *Diabolotherium* is similar in every respect to that of the Megatheriinae.

5. Left and right tooth rows (Gaudin, 2004: character 4; Carlini & Scillato-Yané, 2004: character 10): (0) parallel in occlusal view; (1) anteriorly divergent.

In Cingulata, tooth rows are always parallel. In Tardigrada, the tooth rows are consistently parallel posteriorly and sometimes divergent anteriorly. The latter morphology is often accompanied by the presence of a prominent caniniform and marked diastema, as in the mylodontid *Mylodon* and most Megalonychidae (e.g. *Megalonyx*). Gaudin (2004) suggested that *Hapalops* presents both tooth row patterns.

6. Diastema (Gaudin, 2004: character 6): (0) absent or rudimentary; (1) elongated.

The caniniform tooth often precedes a marked diastema in most sloths, except in most Mylodontoidea (e.g. *Mylodon*) and some Santacrucian sloths, such as *Schismotherium*. As the oldest Xenarthra (Dasypodidae) lack a diastema, the absence of a diastema is probably the primitive condition in sloths (as in the Tinguirirican and Deseadan form *Pseudoglyptodon*). This character is not applicable for Nothrotheriidae that have lost the most mesial tooth (e.g. *Nothrotheriops*).

7. Shape and morphology of the molariform teeth in occlusal view (Pujos, 2002: character 3 modified; McDonald & de Muizon, 2002: character 2 modified): (0) all the teeth are oval with a transversal crest (Dasypodid pattern) or the anterior molariform teeth are oval with a transversal crest and the last upper and lower teeth multilobed (Glyptodontoid pattern); (1) all the molariform teeth are oval with a raised peripheral margin; (2) upper molariform teeth are rectangular and lower squared with mesial and distal crests; (3) upper and lower molariform teeth are squared (with transverse and parallel mesial and distal crests).

According to Engelmann (1985), the primitive dental morphology in sloths is (5/4) multilobed, particularly flat, molariform teeth (e.g. Mylodontidae). A similar morphology is present in Glyptodontoidea. Santacrucian sloths, such as *Hapalops* and *Planops*, the modern tree sloth *Bradypus*, and Megalonychinae possess oval teeth with a raised peripheral margin. In Megatheriidae (not including *Planops*) and Nothrotheriidae, molariform teeth are quadrangular and bilophodont. *Planops* possibly represent the intermediate form between the oval molariform teeth of *Hapalops* and the specialized quadrangular teeth of Megatheriinae and Nothrotheriidae, although clearly distinct from the two latter clades. According to Hoffstetter (1961), the occlusal pattern of *Planops* (as well as *Hapalops*) is more closely related to Megalony-

chidae than Mylodontidae, Megatheriidae, and Nothrotheriidae. The alveoli of *Diabolotherium* more closely resemble those of Nothrotheriidae than Megatheriidae.

8. Length and form of premaxilla (McDonald & de Muizon, 2002: character 4 modified; Pujos, 2002: character 5 modified): (0) short and rounded; (1) long and V-shaped; (2) very long and Y-shaped.

As observed by De Iuliis (1994), two typical morphologies exist for sloth premaxillae. In Megalonychidae and *Bradypus*, the premaxillae are extremely short and rounded, a morphology that Engelmann (1985) suggested as a synapomorphy of the Megalonychidae. In *Hapalops*, Mylodontinae, Nothrotheriidae, and most Megatheriidae (e.g. *Eremotherium*), the premaxillae are long and V-shaped. However, in the temperate megatheriine genus *Megatherium*, the premaxillae are extremely elongated (especially in *M. americanum* in which it is Y-shaped). In *Myodon* and *Bradypus*, the premaxillae are short and rounded, apparently by convergence with Megalonychidae. In Scelidotheriinae (e.g. *Scelidodon*), the premaxillae are more anteroposteriorly elongated, perhaps in relation to the extension of the skull in this Mylodontidae clade.

9. Length of the predental region of the dentary as measured along the ramus plane (Carlini & Scillato-Yané, 2004: character 13): (0) longer than the length of the molariform series; (1) equal or slightly shorter; (2) much shorter.

In sloths, the anterior portion of the rostrum and the predental region of the dentary can sometimes be more or less extended, probably in relation to feeding habits, as in *Thalassocnus* lineage (see de Muizon *et al.*, 2004b). It is extremely reduced in orophodontoids, some Megalonychidae, and *Bradypus*. In relation to the morphology and eventually extension of the premaxillary, the sloths exhibit an elongated 'spout'.

10. Relative lengths of ascending and descending processes of the jugal (Gaudin, 2004: character 151): (0) ascending process less than or equal to descending process; (1) ascending process longer.

In sloths, jugals (Webb, 1985) are constituted by an ascending and a descending process. The ascending process is longer in Megalonychidae than in Megatheriidae, Mylodontidae, and *Nothrotheriops*. This character is not applicable in Cingulata.

11. Pterygoid inflation (Pujos, 2002: character 7 modified; Gaudin, 2004: character 137): (0) uninflated; (1) inflated only at base; (2) large sinus present.

In most Xenarthra, the pterygoids are blade-like, and uninflated or inflated only at their base. In the nothrotheriids *Nothrotheriops* and *Nothrotherium*, the extant tree sloth *Choloepus*, and some West Indies megalonychids (*Megalocnus* and *Parocnus*; Gaudin,

2004) the pterygoids are inflated with a large pneumatic sinus.

12. Stylohyal fossa (Pujos, 2002: character 8; Gaudin, 1995: characters 53, 54): (0) absent; (1) circular; (2) oval.

The stylohyal fossa is missing in most Cingulata and present in most Tardigrada (Gaudin, 1995, 2004). In sloths, this fossa is circular in Megatheriinae, most Megalonychidae, and in the Santacrucian sloths *Hapalops* and *Planops*. The stylohyal fossa is oval in *Scelidodon*, Nothrotheriidae, *Diabolotherium*, and some specimens of *Choloepus* (Gaudin, 1995). In Megalonychidae, the stylohyal fossa may be circular (e.g. *Megalocnus* and *Pliometanastes*) or oval (e.g. *Acratocnus* and *Diabolotherium*).

13. Ventral edge of the entotympanic (Gaudin, 1995: character 21; Pujos, 2002: character 9): (0) flat in lateral view; (1) extended into an anteroventral process. In lateral view, the ventral edge of the entotympanic is flat in *Bradypus*, *Acratocnus*, and Mylodontidae [which was considered to be the primitive condition by Gaudin (1995)]. It forms an anteroventral process in Megatheriidae, Nothrotheriidae, most Megalonychidae, and the Santacrucian sloths *Hapalops* and *Planops*.

14. Position of glenoid fossa relative to superficial meatus (Gaudin, 1995: character 75; Pujos, 2002: character 10): (0) glenoid fossa at or above the meatus; (1) glenoid fossa ventral to the meatus.

The glenoid fossa may be located at the same level as the external auditory meatus [which was considered to be the primitive condition by Gaudin (1995)], as in *Bradypus*, Santacrucian sloths, Megatheriidae, Nothrotheriidae, Mylodontidae, and *Eucholoeops*. In the other sloths, the fossa is more ventral than the meatus.

15. Direction of the root of the zygoma (Gaudin, 1995: character 85; Pujos, 2002: character 11): (0) anterior; (1) anterolateral; (2) lateral.

According to Gaudin (1995), an anteriorly directed zygomatic root is the plesiomorphic condition, as occurs in Megatheriidae, Nothrotheriidae, and *Bradypus*. The root of the zygoma protrudes laterally in the Glyptodontidae and in Megalonychidae (except *Eucholoeops*). An intermediate state occurs in the Santacrucian sloths *Planops*, *Hapalops*, and *Eucholoeops*.

16. Length of the zygomatic process of the squamosal (Gaudin, 2004: character 168 modified): (0) moderate, length > 5%; (1) elongated, length 10–15% of BNL; (2) greatly elongated, length > 15% of BNL.

17. Shape of glenoid fossa (Gaudin, 1995: character 76; Pujos, 2002: character 12): (0) elongated anteroposteriorly; (1) hemispherical; (2) widened transversely.

According to Gaudin (1995), the plesiomorphic condition in *Xenarthra* is an anteroposteriorly elongated glenoid fossa (as in *Nothrotheriidae*). The glenoid fossa may also be hemispherical, as in *Megatheriidae*, or clearly widened transversely, as in most *Megalonychinae* (*Megalocnus* and *Megalonyx*), but unfortunately poorly preserved and unobservable in *Diabolotherium*.

18. Supraoccipital exposure on cranial roof (Gaudin, 2004: character 94): (0) absent; (1) small; (2) large. The supraoccipital exposure on the cranial roof is absent in *Cingulata*, Quaternary *Nothrotheriidae*, and *Megalonychidae* (polymorphic character in *Acratocnus*). It is reduced in the Quaternary *Megatheriidae* and *Mylodontidae*.

19. Anteorbital or buccinator fossa of maxilla (Gaudin, 2004: character 106): (0) absent; (1) weak; (2) well developed.

The absence of the buccinator fossa is probably the plesiomorphic state. This fossa is absent in *Bradypus*, *Megatheriidae*, and *Nothrotheriidae*. Most *Megalonychidae* exhibit a very large and deep buccinator fossa.

20. Condylloid foramen size (Gaudin, 2004: character 187 modified): (0) small, maximal diameter < 2% of BNL or moderate, diameter 2–3% of BNL; (1) enlarged, diameter ≥ 3% of BNL.

The condylloid foramen is clearly more enlarged in *Tardigrada* than in *Cingulata*.

21. Basicranial/basifacial angle (Gaudin, 2004: character 90 modified): (0) parallel, cranial base approximately horizontal; (1) reflexed (Webb, 1985).

The basicranial/basifacial angle is reflexed in the *Megalonychidae* and *Cingulata* used in this phylogenetic analysis.

22. Shape of the angular process (Gaudin, 2004: character 48): (0) short and deep, ratio of maximal length to depth measured at midlength < 1.0; (1) intermediate development, ratio of length to depth 1.0–1.25; (2) elongated and narrow, ratio of length to depth ≥ 1.5.

23. Posterior external opening of the mandibular canal anteromedial on the medial surface of the ascending ramus (Pujos, 2002: character 15 modified; Gaudin, 2004: character 75 modified): (0) no; (1) yes.

The mandibular canal exhibits a posterior external opening in all sloths (Gaudin, 2004: character 74) in contrast with *Cingulata* and *Vermilingua*. The position of the opening has been suggested as diagnostic, distinguishing sloth clades (e.g. *Megatheriidae*) by several authors (Engelmann, 1985; De Iuliis, 1994; Pujos, 2002). The posterior external opening of the mandibular canal is anteromedial on the medial surface of the ascending ramus in *Megatheriidae*.

24. Shape of the coronoid process (Gaudin, 2004: character 47 modified): (0) elongate and narrow, ratio of

maximal height to anteroposterior length measured at midheight > 1.25; (1) intermediate development, ratio of height to length 1.0–1.25; (2), short and broad, ratio of height to length ≤ 1.0 (Scott, 1903–04).

25. The lower margin of the horizontal ramus is relatively straight (Engelmann, 1985; St-André, 1994): (0) yes; (1) no.

This character has been considered by Engelmann (1985) as characteristic of the *mylodontid* sloths.

#### POSTCRANIAL

26. Development of the deltopectoral crest of the humerus (Pujos, 2002: character 19): (0) prominent; (1) weak or practically absent.

The anterior portion of the deltopectoral crest corresponds to the attachment of the *M. pectoralis* and *M. deltoideus*. The deltopectoral crest is strong in some *Megalonychidae* (e.g. *Megalocnus*), *Planops*, *Hapalops*, *Mylodontidae*, and in *Cingulata*. It is extremely robust in the large *mylodontine* *Myodon*. On the other hand, it may be reduced in large (*Megatheriidae*) or medium-sized (*Nothrotheriidae*) terrestrial sloths and practically absent in extant tree sloths (*Bradypus* and *Choloepus*) and weak in *Diabolotherium*.

27. Entepicondylar foramen of the humerus (Pujos, 2002: character 20): (0) present; (1) absent.

In *Scelidotheriinae*, it is present in *Scelidodon chiliensis* and absent in *Catonyx cuvieri* (Pujos, 2000). It is absent in some *Megalonychidae* (e.g. *Acratocnus*, *Eucholoeops*), *Megatheriidae*, and *Bradypus*, but present in *Choloepus* and Quaternary *Nothrotheriidae*.

28. Spatulate styloid process (Pujos, 2002: character 23): (0) absent; (1) present.

The ulna of *Diabolotherium* bears a spatulate styloid process. Extant tree sloths show the same peculiar morphology of the distal extremity of the ulna, although less prominently developed than in *Diabolotherium*. This peculiar morphology is unknown in the other *Tardigrada*.

29. Fusion of the proximal and second phalanges of digit III of the manus (McDonald & de Muizon, 2002: character 25; Pujos, 2002: character 24): (0) absent; (1) present.

McDonald & de Muizon (2002) used this character in their *nothrotheriine* phylogeny. In *Nothrotheriidae*, this fusion is present only in the *Thalassocnus* lineage. It also occurs frequently in the Pleistocene *Megatheriidae* (i.e. *Megatherium* and *Eremotherium*) and is absent in the other sloths. The fusion of two phalanges clearly represents the derived condition.

30. Dorsoventral compression of the ungual phalanx of the manus (de Muizon *et al.*, 2003: character 30



modified): (0) all the ungual phalanges are flattened; (1) only the ungual phalanx of digit II of the manus is flattened; (2) none is flattened.

The phalanges are all flattened in Cingulata and in Scelidotheriine sloths, which possess adaptations for digging. In Nothrotheriidae, only the ungual phalanx of digit II is flattened, but its significance is not clear. All the known phalanges of *Diaboloherium*, *Megalocnus*, and *Acratocnus* are unflattened.

31. Third trochanter of the femur (McDonald & de Muizon, 2002: character 29 modified; Pujos, 2002: character 25 modified): (0) isolated; (1) extended towards the lateral condyle; (2) extended towards the greater trochanter.

In Cingulata, the nothrotheres *Pronothrotherium* and *Nothropus* (McDonald & de Muizon, 2002), *Megalonyx*, *Acratocnus*, and Santacrucian sloths *Hapalops* and *Planops*, the third trochanter of the femur is isolated at the midshaft of the diaphysis. It is extended towards the lateral condyle, as in Megatheriidae, the Pleistocene Nothrotheriidae *Nothrotherium* and *Nothrotheriops*, and Mylodontidae. Finally, it may be connected to the greater trochanter (e.g. *Megalocnus*). Unfortunately, the femur is unknown in *Pliometanastes* and *Diaboloherium* and this character is not applicable in extant sloths (in which the third trochanter is missing). Continuity of the third trochanter with the lateral condyle is apparently associated with a graviportal stance (except *Megalonyx*).

32. Femoral trochlea (McDonald & de Muizon, 2002: character 23 modified; Pujos, 2002: character 26): (0) contiguous with both condylar surfaces; (1) separated from the medial condyle; (2) separated from both condylar surfaces.

In large Megatheriidae, perhaps in relation to an extreme graviportal stance, the femoral trochlea does not contact the medial condyle. It is separated from both condylar surfaces in Pleistocene Nothrotheriidae (i.e. *Nothrotheriops* and *Nothrotherium*) and in *Megalonyx*. In other sloths, the femoral trochlea is contiguous with both condyles.

33. Shape of the femur: (0) poorly anteroposteriorly compressed (the ratio length/width at the centre of the diaphysis is  $> 3.7$ ); (1) moderately compressed (length/width 3–3.7); (2) strongly compressed (length/width  $< 3$ ).

The femur is extremely wide (or anteroposteriorly compressed) in large Megatheriinae and relatively narrow in West Indies Megalonychidae and *Pliometanastes*. This character is not applicable in modern arboreal sloths in relation to the lengthening of the limbs.

34. Tibia–fibula ankylosis: (0) proximal and distal; (1) proximal; (2) none.

Ankylosis between the tibia and fibula is frequent in Cingulata and Megatheriidae.

35. Peg-shaped odontoid process of the astragalus in dorsolateral view (= anteromedial angle between the principal axis of the odontoid process and the anteroposterior axis of the discoid process) (Pujos, 2002: character 27): (0) odontoid process peg-shaped (angle with the anteroposterior axis of the discoid facet  $> 45^\circ$  and sometimes reaches  $90^\circ$ ); (1) odontoid process poorly peg-shaped (angle included between  $35$  and  $45^\circ$ ); (2) odontoid process not peg-shaped (angle  $< 30^\circ$ ). In Megatheriidae and some Nothrotheriidae (such as *Thalassocnus*) the odontoid process is peg-shaped, perpendicular to the anteroposterior axis of the discoid facet. In *Nothrotherium* and *Nothrotheriops*, the odontoid process is not as well defined (peg-shaped) as in the Pleistocene Megatheriidae (with an angle close to  $70^\circ$ ). The odontoid process is not well defined (anteromedially extended) in *Megalocnus rodens* and *Hapalops longipes* (the angle with the discoid facet is approximately  $40^\circ$ ). Finally, in *D. nordenskioldi* and *Pliometanastes prostratus*, the odontoid process is extended anteriorly and not peg-shaped. The characters related to the astragalus of fossil sloths, because of important modifications at the tarsal bones, are probably correlated to their highly specialized locomotory mode. The characters of the astragalus are not applicable in modern tree sloths.

36. Position of the caput tali in anterior view (Pujos, 2002: character 28 modified): (0) central (at the junction between the odontoid and discoid processes); (1) at the centre of the odontoid process; (2) medial (at the extremity of the odontoid process).

Together with the individualization of the odontoid process, the caput tali seems to migrate medially on the astragalus. It is located at the junction of the odontoid process in anterior view in Cingulata, Megalonychidae (except *Diaboloherium*), and *Hapalops*, whereas it is at the centre of the odontoid process in the Megatheriidae, Nothrotheriidae, *Myodon*, and *Planops*. In *Diaboloherium*, the caput tali is completely medial [as also occurs in *Xyophorus villarroeli* (Nothrotheriidae?); St-André, 1996].

37. Dorsal angle between the odontoid and discoid facets in anterior view (Pujos, 2002: character 29): (0)  $> 140^\circ$ ; (1)  $90$ – $140^\circ$ .

The angle between the odontoid and discoid facets is more or less obtuse. This angle is between  $90$  and  $120^\circ$  in Megatheriidae, *Planops*, and Quaternary Nothrotheriidae;  $130$ – $140^\circ$  in Mylodontidae; and  $> 140^\circ$  in *Megalonyx*, *Hapalops*, and especially *Diaboloherium* (close to  $160^\circ$ ).

38. Ectal and sustentacular facets of the astragalus (Pujos, 2002: character 30): (0) unfused ectal and sus-

tentacular facets and rectangular ectal facet; (1) unfused ectal and sustentacular facets and L-shaped ectal facet; (2) ectal and sustentacular facets in contact. These articular facets, between the calcaneum and the astragalus, are not in contact in most sloths, except in Mylodontidae and the megalonychiine *Megalocnus rodens* and *Megalonyx jeffersonii*. When these facets are unfused, the large ectal facet is rectangular (as in Megatheriidae, *Planops*, and Nothrotheriidae) or L-shaped as in *Pliometanastes*, *Diabolotherium*, and *Xyophorus villarroeli*. *Hapalops longipes* possesses a rectangular, but slightly curved, ectal facet that seems to foreshadow the L-shaped morphology of *Xyophorus* and *Diabolotherium*.

39. Calcaneum (Pujos, 2002: character 31): (0) tuberos, torpedo-shaped, and slightly dorsoplantarly compressed; (1) flat and wing-shaped; (2) tuberos and the diaphysis is relatively gracile.

Calcanei of Megatheriidae, Mylodontidae, and *Planops* are massive. The calcaneum is torpedo-shaped and slightly dorsoplantarly compressed in Megatheriidae and *Planops*. In Mylodontidae, the diaphysis is less massive and the calcaneum shows a characteristic form. In the other sloths studied in this analysis, the calcaneum is strongly compressed dorsoplantarly and generally wing-shaped.

40. Cuneiforms (Pujos, 2002: character 32): (0) three free cuneiforms (meso-, ento-, and ectocuneiform); (1) one free cuneiform (ectocuneiform) and a meso-entocuneiform complex; (2) meso-ento-ectocuneiform complex.

Santacrucian sloths (e.g. *Hapalops longipes*) and *Propalaeohoplophorus* have three free cuneiforms (meso-ento-ecto). During the evolutionary history of sloths, together with a reduction in the number of digits, the cuneiforms show a tendency to fuse together and form a complex. Most sloths (i.e. Megatheriidae, Nothrotheriidae, *Scelidodon*, and fossil Megalonychidae) possess a meso-entocuneiform complex. In *Myloodon darwini*, the three cuneiforms are fused. *Megatherium* displays polymorphism.

41. Fusion of the proximal and second phalanges of digit III of the pes (McDonald & de Muizon, 2002: character 24; Pujos, 2002: character 33): (0) not fused; (1) fused.

As in the manus, the first and second phalanges of the third digit are fused in some sloths (i.e. Megatheriidae, Nothrotheriidae, *Scelidodon chiliensis*, and *Megalonyx jeffersonii*). The other sloths studied in the phylogenetic analysis exhibit the primitive (unfused) condition.

42. Mt V with mediolateral expansion (McDonald & de Muizon, 2002: character 27; Pujos, 2002: character 34): (0) absent; (1) present.

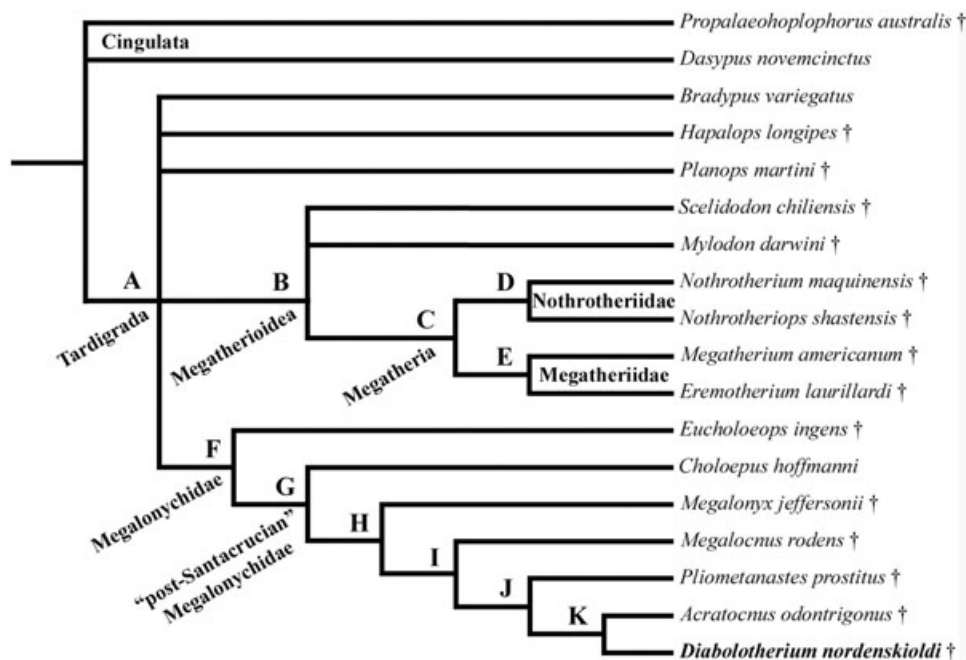
Some terrestrial sloths exhibit a mediolateral expansion of the most lateral pedal digit. The mediolateral expansion may be reduced (i.e. *Diabolotherium* and *Hapalops*) or well developed (i.e. Pleistocene Nothrotheriidae, *Scelidodon*, *Megalocnus*, and *Megalonyx*). This expansion seems to be absent in the largest graviportal Tardigrada (i.e. Megatheriidae) and in outgroups (*Propalaeohoplophorus* and *Dasyus*). Mt V is unknown in *Pliometanastes* and *Eucholoeops* and is absent in extant sloths.

Forty-two discrete and unordered cranial and postcranial characters were coded for the 17 taxa using the computer program NONA 2.0 (Goloboff, 1999) using WINCLADA (Nixon, 2002) (Appendix 3). The default mode was used for character weighting. The exhaustive searches resulted in two most-parsimonious trees (MPTs). Each node of the strict consensus tree (tree length = 157, consistency index = 0.42, retention index = 0.56; Fig. 18) is described in terms of the supported unequivocal and equivocal synapomorphies (Appendix 4). The term equivocal synapomorphy corresponds to a homoplastic character as used by Gaudin (1995, 2004) and Pujos (in press a).

The differences between the two MPTs concern the positions of the three-toed sloth *Bradypus*, the Santacrucian sloths *Hapalops* and *Planops*, and the monophyly of the Mylodontidae. In the first MPT (MPT1), Mylodontidae are monophyletic but not supported by unequivocal synapomorphies and *Bradypus*, *Hapalops*, and *Planops* located at the root of the Megalonychidae [= (*Bradypus* (*Hapalops* (*Planops* (Megalonychidae)))))].

In MPT2, *Planops*, *Myloodon*, and *Scelidodon* are located at the root of the clade (Megatheriidae, Nothrotheriidae) [= clade 1: (*Planops* (*Myloodon* (*Scelidodon* (Megatheriidae, Nothrotheriidae)))))]. Clade 1 is a sister clade to Megalonychidae; the genera *Bradypus* and *Hapalops* are positioned at the base of the clade thus constituted [= (*Bradypus* (*Hapalops* (clade 1, Megalonychidae)))]]. The two MPTs reveal the uncertainty over the position of the Santacrucian sloths *Hapalops* and *Planops*, and the modern tree sloths *Bradypus*, and of the monophyly of the Mylodontidae, one of the most diversified clades of Tardigrada.

The analysis performed by Gaudin (2004), the most complete and detailed Tardigrada phylogenetic analysis (33 sloth genera and 286 osteological characters), confirmed that the mylodontid clade is not strongly supported (five unambiguous synapomorphies) in comparison with other sloth clades. *Bradypus* appears as a sister group to all other sloths (Gaudin, 1999, 2004) and *Hapalops*, as do most Santacrucian sloths (i.e. *Peleciodon*, *Schismotherium*, and *Analcimorphus*; Gaudin, 2004), appears at the base of the Megatherioidea. The uncertainties of the phylogenetic positions



**Figure 18.** Strict consensus tree of two most-parsimonious trees resulting from a heuristic search using the computer program NONA version 2.0 (tree length = 157, consistency index = 0.42, retention index = 0.56) showing the hypothetical phylogenetic relationships of *Diabolootherium nordenskioldi* gen. nov. with other Tardigrada.

of the three-toed sloth and the most well-known Santacrucian sloth (i.e. *Hapalops*) are confirmed in the present analysis (Fig. 18). The most significant difference between Gaudin's (2004) analysis and the present analysis is the relationship of *Planops* to other sloths. *Planops* is commonly recognized as a Megatheriidae (Gaudin, 2004). In the present study, *Planops* is distinct from the other Tardigrada genera. This is also true of *Hapalops*.

#### DESCRIPTION OF THE STRICT CONSENSUS TREE (FIG. 18, APPENDICES 3, 4)

##### Node A [*Tardigrada*]

Ten unequivocal synapomorphies ( $1^1$ ,  $7^1$ ,  $12^1$ ,  $18^2$ ,  $20^1$ ,  $21^0$ ,  $30^2$ ,  $34^2$ ,  $41^0$ ,  $42^1$ ) and one equivocal synapomorphy ( $22^2$ ) support the clade of sloths. This clade is supported by the 5/4 dental formula ( $1^1$ ), commonly recognized as the primitive Tardigrada dental formula; teeth with an oval raised peripheral margin ( $7^1$ ), which is commonly recognized in Megalonychidae genera. The oldest dental remains of Tardigrada from the Deseadan SALMA of South America (Hoffstetter, 1956; Carlini & Scillato-Yané, 2004; F. Pujos & G. De Iuliis, unpubl. data) belong to Megalonychidae and Mylodontidae. One of these two clades could have been secondarily modified in quadrangular teeth as it is present in Nothrotheriidae and Megatheriidae.

Secondary modification of the dentition may have occurred in one of these clades to produce the quadrangular teeth characteristic of Nothrotheriidae and Megatheriidae. Tardigrada are also supported by a circular stylohyal fossa ( $12^1$ ), a large supraoccipital exposure on the cranial roof that is present only in the Santacrucian sloths *Planops* and *Hapalops* and *Bradypus* ( $18^2$ ), and modified in other sloths; an enlarged condyloid foramen ( $20^1$ ) present in all sloths and clearly distinct from the condition in Cingulata; a reflexed basicranial/basifacial angle ( $21^0$ ) closely related to the condition in Cingulata; unflattened phalanges of the manus ( $30^2$ ); the absence of tibia–fibula ankylosis ( $34^2$ ); the fusion of the proximal and second phalanges of digit III of the pes ( $41^0$ ); and Mt V with a mediolateral expansion ( $42^1$ ).

##### *Bradypus*, *Hapalops*, and *Planops*

The affinities of the three-toed sloth *Bradypus* remain uncertain. The phylogenetic relationships among *Bradypus*, *Choloepus*, and the fossil sloths are obscured by the extreme modifications of the postcranial skeleton associated with the peculiar climbing capabilities of modern tree sloths. The skull of *Choloepus* is typically megalonychid (Gaudin, 2004), but the skull of *Bradypus* is clearly distinct from all other Tardigrada (see Gaudin, 2004). Fossils of suspensory



sloths are necessary to resolve the relationships between *Bradypus* and other sloths. Curiously, the phylogenetic position of the Santacrucian sloth *Hapalops*, which is anatomically very well known and used as an outgroup in most phylogenetic analyses of sloth clades (e.g. Nothrotheriinae, de Muizon *et al.*, 2003; Megatheriinae, Pujos, in press a; Megalonychidae, Carlini & Scillato-Yané, 2004), is doubtful. This taxon is often considered as a 'typical primitive sloth' (see De Iuliis, 1994). Except for the Megalonychidae *Euchloeops*, the phylogenetic positions of most sloths from the middle Miocene (e.g. *Hapalops*, *Planops*, *Peleciodon*, *Schismotherium*, and *Analcimorphus*) are not well resolved. These sloths are quite distinct from the Deseadan SALMA sloths (i.e. the Megalonychidae *Deseadognathus* and the Mylodontoid *Octodontothe-rium*, and *Orophodon*), as well as the post-Santacrucian lineages. An analysis of middle and late Miocene sloth material from Bolivia (F. Pujos & G. De Iuliis, unpubl. data) confirms the existence of a sloth fauna that is clearly distinct from the four well-known families and indicates that these sloths share affinities with the Patagonian Santacrucian sloths, which are located at the base of the Megatherioidea in Gaudin (2004) and the present work. The study of this Bolivian material may lead to a better understanding of the phylogenetic position of most of the sloths from the middle and late Miocene.

*Node B [Megatherioidea = ((Megatheriidae, Nothrotheriidae) Mylodontidae)]*

Three unequivocal (10<sup>0</sup>, 11<sup>1</sup>, 31<sup>1</sup>) and five equivocal synapomorphies (7<sup>0</sup>, 18<sup>1</sup>, 33<sup>1</sup>, 34<sup>1</sup>, 35<sup>1</sup>) support this clade. The unequivocal synapomorphies are a jugal with ascending process less elongated or equal in length to the descending process (10<sup>0</sup>); pterygoid inflated only at base (11<sup>1</sup>); and the third trochanter of the femur continuous with the lateral condyle (31<sup>1</sup>). The present study confirms the grouping suggested by Gaudin (2004) of Nothrotheriidae, Megatheriidae, and Mylodontidae in the clade Megatherioidea. *Nothrotherium maquinensis* is the only Megatherioidea that does not have the ascending process less than or equal to the descending process (10<sup>1</sup>).

*Scelidodon, Mylodon*

These two taxa are members of two Mylodontidae clades (i.e. Scelidotheriinae and Mylodontinae). In the strict consensus tree of the present study, no unequivocal synapomorphies support this clade, but in MPT1 both genera were grouped together in the clade Mylodontidae. It is generally the family that is least supported in terms of unequivocal synapomorphies (e.g. Gaudin, 2004). However, the mylodontid sloths are

characterized by a lower margin of the horizontal ramus that is relatively straight (Engelmann, 1985; St-André, 1994) (25<sup>0</sup>), a condition otherwise present only in the outgroup *Dasybus*.

*Node C [Megatheria = (Megatheriidae, Nothrotheriidae)]*

The clade Megatheria is only supported by three equivocal synapomorphies (9<sup>0</sup>, 15<sup>0</sup>, 26<sup>1</sup>). In Megatheria, the length of the predental region of the dentary is longer than the length of the molariform series (9<sup>0</sup>). This character state is convergent in *Planops*. In *Bradypus* and Megatheria, the direction of the root of the zygoma is anterior (15<sup>0</sup>).

*Node D [Nothrotheriidae]*

The loss of the most mesial tooth (1<sup>2</sup>) and the dorsoventral compression of the ungual phalanx of digit II of the manus (de Muizon *et al.*, 2003) (30<sup>1</sup>) are the two unequivocal synapomorphies that support the nothrotheriid clade. Two equivocal synapomorphies (11<sup>2</sup>, 18<sup>0</sup>) are also present at this node. Nothrotheriidae possess rectangular upper and squared lower molariform teeth (with mesial and distal crests) (7<sup>2</sup>). The alveoli of *Diabolotherium* may have influenced Hoffstetter's (see Fig. 2) assignment of the specimen from Piedra Escrita to a 'Nothrotheriinae'.

*Node E [Megatheriidae]*

This is the most strongly supported of the tardigrade clades in the present analysis, with six unequivocal synapomorphies (7<sup>3</sup>, 17<sup>1</sup>, 23<sup>1</sup>, 29<sup>1</sup>, 32<sup>1</sup>, 33<sup>2</sup>) and three equivocal synapomorphies (27<sup>1</sup>, 34<sup>1</sup>, 42<sup>0</sup>). The upper and lower molariform teeth are squared (with parallel mesial and distal transverse crests) (7<sup>3</sup>) in Megatheriidae, a morphology that is clearly distinct from that of *Planops* (7<sup>1</sup>), in which the molariforms are oval with a raised peripheral margin, as in most Santacrucian sloths. The other synapomorphies that support the megatheriid clade are a hemispherical glenoid fossa (17<sup>1</sup>); the posterior external opening of the mandibular canal anteromedial on the medial surface of the ascending ramus (23<sup>1</sup>) (also present in some *Bradypus* specimen); the fusion of the proximal and second phalanges of digit III of the manus (29<sup>1</sup>); a femoral trochlea separated from the medial articular condyle (32<sup>1</sup>); and a femur that is strongly compressed antero-posteriorly (33<sup>2</sup>).

*Node F [Megalonychidae]*

Seven genera are grouped together in this clade, supported by two unequivocal (3<sup>1</sup>, 4<sup>1</sup>) and two equivocal

synapomorphies ( $5^1$ ,  $18^0$ ). The two unequivocal synapomorphies are that the most mesial upper ( $3^1$ ) and lower ( $4^1$ ) teeth are greatly enlarged. The lower most mesial tooth is secondarily modified ( $4^2$ ) in *Diabolothe-rium*. The lower tooth rows are anteriorly divergent in Megalonychidae ( $5^1$ ), but secondarily modified in *Diabolothe-rium* ( $5^0$ ) in relation to the modification of the most mesial lower tooth. The presence of an elongated diastema characterizes the Megalonychidae (but also the Santacrucian sloths *Planops* and *Hapalops*) ( $6^1$ ). A diastema is secondarily absent in *Diabolothe-rium*, also in relation to the modification of the most mesial tooth, which does not have a caniniform morphology in the Peruvian taxon.

*Nodes G–K [(Eucholoeps (Choloepus (Megalonyx (Megalocnus (Pliometanastes (Acratocnus, Diabolothe-rium)))))]*

There are no differences in the MPTs with regard to the relationships among Megalonychidae. Four nodes (G, H, I, K) are supported by equivocal synapomorphies. Node J [(*Pliometanastes (Acratocnus, Diabolothe-rium)*)] is supported by one unequivocal synapomorphy ( $38^1$ ). This character state has been optimized by NONA for *Acratocnus*, for which the state is unknown. Only *Diabolothe-rium* and *Pliometanastes* have astragali with unfused ectal and sustentacular facets and an L-shaped ectal facet ( $38^1$ ). A glenoid fossa ventral to the superficies meatus ( $14^1$ ), a root of the zygoma extended laterally ( $15^2$ ), and a glenoid fossa widened transversely ( $17^2$ ) (not preserved in *Diabolothe-rium*) characterize node G [post-Santacrucian sloths = (*Choloepus (Megalonyx (Megalocnus (Pliometanastes (Acratocnus, Diabolothe-rium))))*)]. We consider these character states diagnostic to this clade because they are not present in other Tardigrada genera included in the analysis and are present in the out-group *Propalaeohoplophorus*. A reflexed basicranial/basifacial angle ( $21^1$ ) characterizes the post-Santacrucian sloths, but also the Megatheriidae (polymorphic state in *Eremotherium laurillardii*).

A detailed study of all megalonychid skeletons is necessary to produce a satisfactorily resolved phylogeny of the North American *Megalonyx* and *Pliometanastes*, the South American *Eucholoeps* and *Diabolothe-rium*, the West Indies *Acratocnus*, *Paulocnus*, *Neocnus*, *Megalocnus*, and *Parocnus*. The inclusion of the modern two-toed tree sloth *Choloepus* is essential for completing the phylogenetic analysis of the West Indies Megalonychidae performed by White & MacPhee (2001) and of the Megatherioidea by Carlini & Scillato-Yané (2004). Our preliminary phylogenetic analysis suggests important differences between *Eucholoeps ingens* and the post-Santacrucian sloths (node G).

## A SHORT OVERVIEW OF MEGALONYCHOID HISTORY

Although the precise systematic position of this peculiar Peruvian sloth may be debatable, this preliminary phylogenetic analysis of the Tardigrada leaves little doubt that *Diabolothe-rium* is a Megalonychidae. The abundant material from two localities, which clearly represents a single taxon, exhibits a mosaic of characters unusual in sloths, but this may be more a consequence of the lack of knowledge of the earlier part of megalonychid history than the singularity of *Diabolothe-rium*.

As explained above, this Lujanian sloth belongs to the family Megalonychidae, based mainly on its cranial morphology [particularly of the temporal region; see the synapomorphies suggested by Gaudin (1995, 2004)] and on the astragalus and calcaneum. The phylogeny performed here corroborates these anatomical observations.

Megalonychidae have been present at least since the Deseadan SALMA in Argentina (Carlini & Scillato-Yané, 2004) and Bolivia (F. Pujos & G. De Iuliis, unpubl. data) and during the Miocene of southern South America by two well-known genera: *Eucholoeps* [according to Hirschfeld & Webb (1968), McKenna & Bell (1997) and Gaudin (2004)] from the early Miocene of the Santa Cruz beds of Patagonia (Argentina) and *Pliomorphus* (Kraglievich, 1923) from the late Miocene/early Pliocene of Entre Ríos and Río Negro Provinces (Argentina; Kraglievich, 1923; Scillato-Yané, Uliana & Pascuala, 1976; Carlini *et al.*, 2000; Cione *et al.*, 2000). Later Megalonychidae are reported mainly from further north in South America, in the Mio-Pliocene of Uruguay with *Pliomorphus* and *Megalonychops* (Mones, 1973) and in the Pleistocene of Brazil with *Megalonychops primigenius* (Paula Couto, 1977) and various taxa of uncertain status.

Megalonychidae are reported in Central America with *Meizonyx* (including two species, *M. salvadorensis* and *M. obtusidens*) in the early to mid-Pleistocene from El Salvador (Webb & Perrigo, 1985). This genus is clearly an intermediate Megalonychidae between the forms from the West Indies and North America (Webb & Perrigo, 1985).

Compared with megatheriids and mylodontids, the Megalonychidae are not abundant or well known in South America. However, they are relatively abundant in North America and, even more so, in the West Indies. The oldest recognized Megalonychidae is from the base of the early Oligocene of the West Indies (i.e. 32 mya; White & MacPhee, 2001). Over a course of more than 30 million years, the Megalonychidae diversified in most West Indies islands (Cuba, Puerto Rico, Hispaniola, La Gonâve, Ile de la Tortue, Curaçao, and Granada; White & MacPhee, 2001). Several authors have

described their remains (e.g. Anthony, 1916, 1918; Matthew, 1931; Hoffstetter, 1955; Paula Couto, 1956, 1967; Matthew & Paula Couto, 1959; Hooijer, 1962, 1964, 1967; Mayo, 1969, 1978a, b, 1980a, b; MacPhee & Iturralde-Vinent, 1994; White, 1996; MacPhee, Singer & Diamond, 2000a; MacPhee *et al.*, 2000b; White & MacPhee, 2001; Rega *et al.*, 2002; MacPhee, Iturralde-Vinent & Gaffney, 2003; Dávalos, 2004). White & MacPhee (2001) recognized five fossil genera distributed in two subfamilies of 'Antillean sloths' [i.e. Megalocninae and Choloepodinae (the latter including the modern tree sloth *Choloepus*)] between the beginning of the Oligocene and the end of the Pleistocene.

Two genera are recognized in North America: *Pliometanastes* and *Megalonyx* (e.g. Cope, 1889; Stock, 1913, 1925; Hirschfeld & Webb, 1968; McDonald, 1977; Hirschfeld, 1981; McDonald & Anderson, 1983). The oldest megalonychid remains from North America is a tooth from the Hemphillian of Nebraska ( $9.3 \pm 0.8$  Myr; Marshall *et al.*, 1979).

The history of the Megalonychidae is particularly incomplete and the origin of *Diabolotherium* is uncertain. Usually a South America origin of the Megalonychidae is accepted. However, the oldest true member of this family is a megalonychid (indeterminate genus) from the Early Oligocene of Porto Rico. In South America, the oldest Megalonychidae is from the late Oligocene of Patagonia (Carlini & Scillato-Yané, 2004) and Bolivia (F. Pujos & G. De Iuliis, unpubl. data). *Eucholoeops*, from the early middle Miocene of Patagonia (Santa Cruz Formation), is the oldest well-preserved member of this clade. A commonly accepted megalonychid origin scenario has the group arising by at least the early middle Oligocene of southern South America, the part of the continent considered as the 'cradle' of sloth evolution (Hoffstetter, 1982). A rapid northern migration along eastern South America may have allowed colonization of the West Indies. The colonization of North America through Central America rather than the West Indies is strongly suggested by the affinities between *Pliometanastes* (from North America) and *Meizonyx*, and marked differences between the West Indies Megalonychidae and *Meizonyx* (Webb & Perrigo, 1985). However, the existence of a singular Lujanian megalonychid on the west coast of South America may require this scenario to be re-evaluated.

Pleistocene Megalonychidae are present in Brazil, Argentina, and Central America (Paula Couto, 1979). It is plausible that during the Quaternary, Megalonychidae migrated from the tropical areas of South America to the Peruvian region. This would have required passing the Andean barrier, but such a passage is not documented by fossils. A Patagonian origin from Santacrucian forms (with *Eucholoeops* as a possible ancestor) seems improbable, based on the lack of

evidence documenting such a migration route, as well as the marked anatomical differences between the two taxa. The other possibility is a 'local origin' for *Diabolotherium*. However, the absence of Oligo-Pliocene continental outcrops on the Pacific coast precludes the testing of this hypothesis. Nearly all the coastal areas of Peru, Chile, and southern Ecuador are Oligo-Pliocene marine strata overlain locally by Pleistocene continental beds (Marshall, Hoffstetter & Pascual, 1983; Marshall *et al.*, 1984; Pujos & Salas, 2004b), and it is among the reasons why earlier representatives of this Peruvian lineage are unknown.

Although it has not been generally acknowledged as a possible centre of sloth evolution, a record of Oligo-Pliocene sloths from the Andean region bordering on Amazonia has accumulated over the past few years. Bolivia, in particular, has emerged as a candidate for a possible radiation of several sloth lineages. This country contains Oligo-Pliocene sites that have yielded early sloths, e.g. Salla with *Pseudoglyptodon sallaensis*, Engelmann, 1987 and Quebrada Honda with *Hapalops angustipalatus*, Frailey, 1988. Several early or earliest Megatheriidae (De Iuliis & St-André, 1997), Mylodontidae (including Orophodontoidea, Hoffstetter *et al.*, 1971; Engelmann, 1987), and Nothrotheriidae (St-André, 1994, 1996) have been reported. Furthermore, an undetermined megalonychoid sloth is also present in the late Oligocene of the Bolivian Altiplano (F. Pujos & G. De Iuliis, unpubl. data).

## CONCLUSIONS

The fossil record of Tardigrada has been considerably enhanced by the discovery of a singular Lujanian Megalonychidae from Peru. *D. nordenskioldi* gen. nov. is from Piedra Escrita (Cupisnique Desert) and Casa del Diablo Cave (Andes). The anatomical study of the three known specimens yielded the following results.

1. *Diabolotherium nordenskioldi* is a small-sized Lujanian megalonychoid sloth, intermediate in size between *Pliometanastes* and *Parocnus*. It is characterized in particular by 5/4 quadrangular and markedly hypsodont molariform teeth (M2–M4 rectangular, m2–m4 squared), a mandible with a thin and prominent angular process well separated from the condyloid process, a triangular scapula with a postscapular fossa, a slender humerus without the entepicondylar foramen, a reduced lateral epicondylar crest and a long but weakly developed deltopectoral crest, a spatulate and distomedially extended ulnar styloid process, a proximodistally compressed scaphoid, Mc II–IV that are subequal in length and robustness, ilia subparallel to the sacral vertebrae, a shallow acetabular fossa, undifferentiated odontoid and discoid astragalar facets, an astragalar head located medial to



the odontoid process, an L-shaped ectal facet, a sustentacular facet constituted by two portions arranged at a right angle, and a wing-shaped calcaneum that is dorsoplantarily flattened and exhibits a dorsoplantar foramen on the anterior portion of its lateral margin.

2. *Diabolotherium nordenskioldi* exhibits a unique mosaic of characters among sloths. Some characters, such as highly mobile elbow, hip, and ankle joints, a relatively short olecranon, a widely open trochlear notch, and a convex posterior border of the ulna, a radial notch orientated anteriorly and nearly in the same plane as the coronoid process (a condition that increases pronation–supination capabilities), well-developed pronator and flexor muscles, and a wide range of digital flexion, propose climbing capabilities. White (1989, 1993, 1997) suggested climbing abilities based on similar adaptations for some Megalonychidae from the West Indies. Preliminary comparisons with the Santacrucian sloth *Hapalops* and the North American megalonychid *Pliometanastes* suggest an increased gradient of arboreality from *Hapalops* to *D. nordenskioldi*. Furthermore, the poorly stabilized articulations of *Diabolotherium* suggest that it was probably a slow-moving form. The discovery of the well-preserved and nearly complete individual MNHN CPN 9–1 permits extension of the range of adaptations for Tardigrada: apart from the previously known diggers (i.e. Mylodontidae), graviportal bipeds and/or quadrupeds (e.g. Megatheriinae), and swimmers (i.e. nothrotheriid *Thalassocnus*), *D. nordenskioldi* is the first fossil Tardigrada that clearly exhibits climbing adaptations and probably had arboreal habits.

3. The preliminary phylogenetic analysis confirmed that *Diabolotherium* is a Megalonychidae, clearly distinct from all members of this clade. The clades Tardigrada, Megatherioidea, Nothrotheriidae, Megatheriidae, and Megalonychidae are well supported. Nothrotheriidae and Megatheriidae are grouped in the clade Megatheria, which is not supported by unequivocal synapomorphies. Except for the megalonychid *Eucholoeops ingens*, the relationships between Santacrucian sloths (i.e. *Planops martini* and *Hapalops longipes*), the modern three-toed tree sloth *Bradypus variegatus*, and other Tardigrada are not resolved. In contrast with previous phylogenetic analyses (e.g. Gaudin, 2004), *Planops* does not seem to be closely related to Megatheriidae. The Mylodontidae, poorly supported in one of the two MPTs, do not exist in the strict consensus tree. This last result is not surprising with regard to Gaudin's (1995, 2004) works, in which this clade is the least strongly supported.

4. *Diabolotherium nordenskioldi* is the first Pleistocene Megalonychidae of the South American Pacific coast and thus increases the palaeogeographical dis-

tribution of this clade in South America and suggests that a re-evaluation of the evolutionary history of the sloths is required.

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## APPENDIX 1

Measurements of *Diabolotherium nordenskioldi* (MNHN CPN 9–1) in millimetres

## Skull

Diameter of the alveolus of M1 (AP × T)	9.6 × 7.7
Diameter of the alveolus of M2 (AP × T)	9.6 × 10.6
Diameter of the alveolus of M3 (AP × T)	9.1 × 12.8(e)
Diameter of the alveolus of M4 (AP × T)	8.3 × 12.8(e)
Diameter of the alveolus of M5 (AP × T)	5.6 × 10(e)
Length of the tooth row (anterior margin of M1/posterior margin of M5)	53

## Mandible

Diameter of the alveolus of M1 (AP × T)	10.8(e) × –
Diameter of the alveolus of M2 (AP × T)	10.4(e) × –
Diameter of the alveolus of M3 (AP × T)	10.3(e) × –
Diameter of the alveolus of M4 (AP × T)	10.1(e) × –
Length of the tooth row (anterior margin of m1/posterior margin of M4)	43.2

## Axial skeleton

Atlas (C1) diameter (AP × T × DV)	– × 85(e) × 36
Sacrum (T × Ls)	230(e) × 173(e)

## Forelimb

Scapula (DV × AP)	122 × 202(e)
Humerus length	240
Humeral head diameter (T × AP)	37 × 39(e)
Proximal epiphysis, T diameter	58
Midshaft diameter (T × AP)	30 × 30
Distal epiphysis, T diameter	87(e)
Ulna length	230
Olecranon diameter (T)	32
Proximal articular facets (T × AP)	39 × 45
Midshaft diameter (T × AP)	13 × 23
Distal epiphysis diameter (T × AP)	29 × 26(e)
Radius length	184
Head diameter (T × AP)	29(e) × 28(e)
Midshaft diameter (T × AP)	27 × 14
Distal epiphysis diameter (T × AP)	48 × 36(e)
Scaphoid diameter (T × AP × DPa)	37 × 27 × 33
Lunar diameter (T × AP × DPa)	20 × 17 × 24(e)
Cuneiform (T)	29(e)
Unciform (T × AP)	26 × 17(e)
Mc II diameter (L × DPa proximal × DPa distal × T proximal × T distal)	39(e) × 25(e) × 24 × – × –
Mc III diameter (L × DPa proximal × DPa distal × T proximal × T distal)	41 × – × 21 × 26 × 17(e)
Mc IV diameter (L × DPa proximal × DPa distal × T proximal × T distal)	39(e) × 28(e) × 25 × – × 14
P3-III (L.)	60(e)

## Hind limb

Astragalus diameter (T × AP × DPl)	43 × 40 × 28(e)
Calcaneum diameter (T × AP × DPl)	56 × 77 × 34
Cuboid (AP × DPl)	18(e) × 24
Mt III diameter (DL/MP1 proximal × T × DM/LPl distal × L)	35(e) × 28 × 17(e)
Mt V diameter (T proximal × T distal × DM/MP1 proximal × DM/LPl distal × L)	17 × – × 15(e) × – × 34
P1-III diameter (DL/MP1 × DM/LPl × L)	19 × 27 × 29
P3-III diameter (DL/MP1 × DM/LPl × L)	15(e) × – × 45(e)

AP, anteroposterior; BL, body length; DL/MP1, dorsolateral/mediopltar; DM/LPl, dorsomedial/lateropltar; DPa, dorsopalmar; DPl, dorsoplantar; DV, dorsoventral; e, estimated; L, length; Ls, length of the sacrum; max., maximal; MC, metacarpal; MH, maximal height; min, minimal; P, phalanx; PD, proximodistal; T, transverse; Ta, minimum transverse diameter between acetabulum fossae; –, nonmeasurable.

## APPENDIX 2

## Characters related to locomotor behaviour in fossil and modern Phyllophaga

Characters		Other		Hapalops		Megatheriidae	Nothrotheriidae	Mylodontidae	Modern tree sloths
Scapula	Triangular and postscapular fossa	Megalonychidae	Quadrangular	Triangular but no postscapular fossa	Triangular	Long and slender in <i>Planops</i> , short and robust in others	Quadrangular	Quadrangular	Triangular but no postscapular fossa
	General morphology: long and slender		Variable but generally more robust than in <i>Diabolotherium</i>	Long and slender			Short and robust	Short and robust	Extremely thin and elongated
Humerus	Deltopectoral crest long but not prominent		More developed (especially in North American forms) than in <i>Diabolotherium</i>	More developed than in <i>Diabolotherium</i> and less than in Mylodontidae and <i>Megalonyx</i>	Reduced especially in Quaternary forms	Same relative development as in <i>Hapalops</i>	Prominent		Almost non-existent
	Entepicondylar foramen absent		Present except in <i>Parocnus</i>	Present	Absent	Present	Present or absent		Absent
Ulna	Horizontal trochleocapitular axis		Horizontal except in <i>Eucholoeops</i>	Oblique*	Horizontal	Horizontal	Horizontal	Horizontal	Horizontal
	Olecranon slightly shorter than the trochlear notch		Shorter than the trochlear notch	Slightly shorter than the trochlear notch	Shorter than the trochlear notch except in <i>Planops</i>		Shorter than the trochlear notch	Longer than the trochlear notch	Extremely short
	Trochlear notch wide open		More open than in <i>Diabolotherium</i> especially in North American forms	Wide open	Wide open but coronoid process extremely prominent as in <i>Megalonyx</i>	Wide open but coronoid process extremely prominent as in Megatheriids	Wide open but coronoid process extremely prominent as in Nothrotheriids	Wide open but coronoid process extremely reduced	
	Radial notch almost in the same plane as the coronoid process in anterodistal view		Radial notch facing more laterally than in <i>Diabolotherium</i>	Radial notch facing more laterally than in <i>Diabolotherium</i>	Radial notch facing more laterally than in <i>Diabolotherium</i>	Radial notch facing more laterally than in <i>Diabolotherium</i>	Radial notch facing more laterally than in <i>Diabolotherium</i>	Radial notch facing more laterally than in <i>Diabolotherium</i>	
	Sigmoid shaft		Straight to convex	Sigmoid	Sigmoid in <i>Planops</i> and straight in others	Straight	Straight, short, and massive		Thin and elongated
	Styloid process spatulate		Styloid process not spatulate	Styloid process not spatulate	Styloid process not spatulate	Styloid process not spatulate	Styloid process not spatulate	Styloid process not spatulate	Styloid process spatulate



Radius	Pronator crest well developed and shaft regularly anteriorly convex	Pronator crest more developed in gigantic forms	Pronator crest reduced and shaft slender	Pronator crest well developed and angulated	Development of pronator crest variable but shaft of radius usually angulated	Shaft short and robust	Extremely thin
Manus	Probably all (five) clawed digits	Four clawed digits (I–IV)	Five clawed digits	Two (III–IV, <i>Eremotherium laurillardii</i> ), three (II–IV, <i>Megatherium</i> sp.), or four (I–IV, <i>E. eomigrans</i> ) clawed digits	Three (II–IV, <i>Nothrotheriops</i> sp.) or four (I–IV, <i>Thalassocnus</i> sp.) clawed digits	Three (I–III) clawed digits	Two ( <i>Choloepus</i> sp.) or three ( <i>Bradypus</i> sp.) clawed digits
Innominate	McII = McIII = McIV	Variable (e.g. <i>Megalocnus</i> : McII = McIV < McII I: <i>Eucholoepus</i> McIV > McIII)	McII < McIII < McIV	McII < McIII < McIV	McII < McIII < McIV	McII < McIII < McIV	Metacarpals subequal in length in clawed digits
Tuber calcanei	Ilia not prominent laterally and subparallel to sacral vertebrae	Variable in the family	Ilia not prominent laterally and subparallel to sacral vertebrae	Ilia prominent dorsally and laterally except in <i>Planops</i>	Ilia prominent dorsally and laterally	Ilia prominent dorsally and laterally	Ilia not prominent laterally and subparallel to sacral vertebrae
Astragalus	Wing shape	Wing shape except <i>Megalonyx</i>	Wing shape	Tuberous	Tuberous	Tuberous	Wing shape
	Obtuse angle between discoid and odontoid facets	Obtuse angle in <i>Pliometanastes</i> and acute angle in <i>Megalonyx</i>	Obtuse angle	Acute angle	Acute angle	Acute angle (but less than in Megatheriidae)	Highly specialized morphology of the astragalus for all characters
	Medial astragalus head	Astragalus head medial in <i>Pliometanastes</i> , located in the middle of the anterior face in <i>Megalonyx</i>	Medial astragalus head	Central astragalus head	Central astragalus head	Central astragalus head	
	Ectal facet L-shaped	Ectal facet L-shaped in <i>Pliometanastes</i> , rectangular in <i>Megalocnus</i>	Curved ectal facet	Rectangular	Rectangular	Reduced in <i>Scelidotherrium</i> and fused to the sustentacular facet in <i>Glossotherium</i>	

\*Trochlea located more proximally than the capitulum.

## APPENDIX 3

Data matrix of the 42 characters. The symbol “?” represents missing data, ‘N’ a non-applicable character, and “†” extinct taxa. The following symbols are used to represent character states in polymorphic taxa: a = (0, 1); b = (1, 2); c = (0, 2)]

Cranial characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
<i>Propalaeohoplophorus australis</i> †	0	0	0	0	0	0	0	0	2	N	0	0	0	1	2	2	2	0	2	0	1	0	N	0	0	
<i>Dasyus novemcinctus</i>	0	0	0	0	0	0	0	N	0	N	0	0	0	0	1	0	0	0	0	0	1	0	N	0	1	
<i>Bradypus variegatus</i>	1	0	0	0	1	0	1	0	2	1	0	0	0	0	0	1	0	2	0	1	0	2	a	0	1	
<i>Planops martini</i> †	1	1	0	0	0	1	1	?	1	?	0	1	1	0	1	1	0	2	1	1	0	2	0	2	1	
<i>Hapalops longipes</i> †	1	1	0	0	a	1	1	1	0	1	0	1	1	0	1	1	0	2	b	1	0	2	0	a	1	
<i>Megatherium americanum</i> †	1	0	2	2	0	0	3	2	0	0	0	1	1	0	0	1	1	1	0	1	1	1	1	0	1	
<i>Eremotherium laurillardi</i> †	1	0	2	2	0	0	3	1	0	0	1	1	1	0	0	2	1	1	0	1	a	1	1	0	1	
<i>Nothrotherium maquinensis</i> †	2	0	N	N	0	N	2	1	0	1	2	?	1	0	0	2	0	0	0	1	0	2	0	2	1	
<i>Nothrotheriops shastensis</i> †	2	0	N	N	0	N	2	1	0	0	2	2	1	0	0	2	0	0	0	1	0	2	0	0	1	
<i>Choloepus hoffmanni</i>	1	1	1	1	1	1	1	0	1	1	2	a	1	1	2	0	2	1	1	1	1	0	0	0	1	
<i>Acratocnus odontrigonus</i> †	1	1	1	1	1	1	1	0	1	1	0	2	0	1	2	1	2	c	2	1	1	1	0	2	1	
<i>Megalocnus rodens</i> †	1	1	1	1	1	1	1	0	2	1	2	1	?	1	2	1	2	?	?	2	1	1	0	0	2	1
<i>Diabolotherium nordenskioldi</i> †	1	0	1	2	0	0	2	?	2	?	0	2	1	1	2	?	?	0	2	1	?	2	0	?	1	
<i>Megalonyx jeffersonii</i> †	1	1	1	1	1	1	1	0	2	1	0	1	1	1	2	2	2	0	2	1	1	0	0	0	1	
<i>Pliometanastes prostitus</i> †	1	1	1	1	1	1	1	?	2	?	0	1	?	1	2	?	2	0	?	1	1	1	0	2	1	
<i>Euchloeops ingens</i> †	1	1	1	1	1	1	1	0	1	?	0	1	1	0	1	1	0	0	2	1	0	2	0	0	1	
<i>Scelidodon chiliensis</i> †	1	0	2	2	0	0	0	1	1	0	1	2	0	0	1	0	0	1	0	1	0	0	0	2	0	
<i>Mylodon darwini</i> †	1	1	0	0	1	0	0	0	1	0	1	1	0	0	1	1	0	1	2	1	0	0	0	2	0	
Postcranial characters	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42									
<i>Propalaeohoplophorus australis</i> †	0	0	0	0	0	0	0	0	0	N	1	0	0	0	0	1	0									
<i>Dasyus novemcinctus</i>	0	0	0	0	0	0	0	0	0	N	1	0	0	2	0	1	0									
<i>Bradypus variegatus</i>	1	1	1	0	N	N	0	N	2	N	N	N	N	1	N	0	N									
<i>Planops martini</i> †	0	0	?	?	?	0	0	0	2	0	0	1	0	0	?	?	?									
<i>Hapalops longipes</i> †	0	0	0	0	2	0	0	1	1	1	1	0	0	1	0	0	1									
<i>Megatherium americanum</i> †	1	1	0	1	2	1	1	2	a	0	0	1	0	0	a	1	0									
<i>Eremotherium laurillardi</i> †	1	1	0	1	2	1	1	2	1	0	0	1	0	0	1	1	0									
<i>Nothrotherium maquinensis</i> †	1	0	0	0	1	1	2	1	2	0	0	1	0	1	1	1	1									
<i>Nothrotheriops shastensis</i> †	1	0	0	0	1	1	2	1	2	0	0	1	0	1	1	1	1									
<i>Choloepus hoffmanni</i>	1	0	1	0	N	N	0	N	2	N	N	N	N	1	?	0	N									
<i>Acratocnus odontrigonus</i> †	0	1	0	0	2	0	0	0	2	?	?	?	?	1	1	?	?									
<i>Megalocnus rodens</i> †	0	0	0	0	2	2	0	0	2	1	1	?	2	1	1	0	1									
<i>Diabolotherium nordenskioldi</i> †	1	1	1	?	2	?	?	?	?	2	2	0	1	1	?	?	1									
<i>Megalonyx jeffersonii</i> †	0	0	0	0	2	0	2	1	2	0	1	0	2	1	1	1	1									
<i>Pliometanastes prostitus</i> †	0	0	?	?	?	?	?	?	2	2	1	?	1	1	?	?	?									
<i>Euchloeops ingens</i> †	0	1	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?									
<i>Scelidodon chiliensis</i> †	0	0	0	0	0	1	0	1	2	0	N	1	2	2	1	1	1									
<i>Mylodon darwini</i> †	0	1	0	0	2	1	0	1	2	0	0	1	2	2	2	0	1									

## APPENDIX 4

Character distributions at major nodes and terminal taxa in the cladogram. The homoplastic characters are in roman font, the homoplastic characters present in the ingroup and one or both of the outgroups are in italic, and the unequivocal synapomorphies are in bold

Node	Characters
A (Phyllophaga)	<b>1<sup>1</sup>, 7<sup>1</sup>, 12<sup>1</sup>, 18<sup>2</sup>, 20<sup>1</sup>, 21<sup>0</sup>, 22<sup>2</sup>, 30<sup>2</sup>, 34<sup>2</sup>, 41<sup>0</sup>, 42<sup>1</sup></b>
B (Megatherioidea)	7 <sup>0</sup> , <b>10<sup>0</sup>, 11<sup>1</sup></b> , 18 <sup>1</sup> , <b>31<sup>1</sup></b> , 33 <sup>1</sup> , 36 <sup>0</sup> , 37 <sup>1</sup>
C (Megatheria)	9 <sup>0</sup> , 15 <sup>0</sup> , 26 <sup>1</sup>
D (Nothrotheriidae)	<b>1<sup>2</sup>, 11<sup>2</sup>, 18<sup>0</sup>, 30<sup>1</sup></b>
E (Megatheriidae)	<b>73, 171, 231</b> , 271, <b>291, 321, 332</b> , 341, 42 <sup>0</sup>
F (Megalonychidae)	<b>3<sup>1</sup>, 4<sup>1</sup></b> , 5 <sup>1</sup> , 18 <sup>0</sup>
G	141, 152, 17 <sup>2</sup> , 211, 220
H	9 <sup>2</sup>
I	24 <sup>2</sup>
J	22 <sup>1</sup> , <b>38<sup>1</sup></b>
K	12 <sup>2</sup> , 27 <sup>1</sup>
<i>Bradypus variegatus</i>	51, 92, 12 <sup>0</sup> , 150, 261, 271, 281
<i>Planops martini</i>	19 <sup>1</sup> , 24 <sup>2</sup> , 36 <sup>0</sup> , 37 <sup>1</sup> , 39 <sup>0</sup>
<i>Hapalops longipes</i>	8 <sup>1</sup> , 9 <sup>0</sup> , 33 <sup>1</sup> , 34 <sup>1</sup> , 35 <sup>1</sup>
<i>Scelidodon chiliensis</i>	122, 160, 30 <sup>0</sup>
<i>Mylodon darwini</i>	5 <sup>1</sup> , 27 <sup>1</sup> , <b>40<sup>2</sup></b>
<i>Nothrotherium maquinensis</i>	10 <sup>1</sup>
<i>Megatherium americanum</i>	<b>8<sup>2</sup></b> , 11 <sup>0</sup>
<i>Eucholoeops ingens</i>	27 <sup>1</sup>
<i>Choloepus hoffmanni</i>	11 <sup>2</sup> , 16 <sup>0</sup> , 18 <sup>1</sup> , 19 <sup>1</sup> , 26 <sup>1</sup> , 28 <sup>1</sup>
<i>Megalonyx jeffersonii</i>	16 <sup>2</sup> , 32 <sup>2</sup> , 33 <sup>1</sup> , 41 <sup>1</sup>
<i>Megalocnus rodens</i>	11 <sup>2</sup> , <b>31<sup>2</sup></b>
<i>Acratocnus odontrigonus</i>	9 <sup>1</sup> , 13 <sup>0</sup>
<i>Diabolotherium nordenskioldi</i>	2 <sup>0</sup> , 4 <sup>2</sup> , 5 <sup>0</sup> , 6 <sup>0</sup> , 7 <sup>2</sup> , 22 <sup>2</sup> , 26 <sup>1</sup> , 28 <sup>1</sup>