THE MANUS OF *MYLODON DARWINII* OWEN (TARDIGRADA, MYLODONTIDAE) AND ITS PHYLOGENETIC IMPLICATIONS

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ABSTRACT—The first nearly complete and articulated manus of the ground sloth *Mylodon darwini*, from the upper Pleistocene of Argentina, is described. It shares similarities with *Mylodonopsis ibseni* from Brazil, including a cuneiform with a distinct pisiform facet, an obliquely concave ulnar facet, and a prominent distolateral process, as well as a gracile metacarpal III. It shares a flattened pisiform with *Glossotherium robustum*. The trapezoid is unique in the obliquely elongate proportions of its dorsal surface. Shapes of the articular facets indicate different functions in digits II and III, with the former having a greater range of motion and the latter greater stability at the joints. Clear arboreal or fossorial adaptations are absent. A phylogenetic analysis recovered *M. darwini* as closely related to *M. ibseni* and agrees with larger phylogenetic analyses of sloths based on craniomandibular evidence. Our data support more than two mylodontine dispersal events to North America.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

*Mylodon darwini* is one of the earliest fossil ground sloths described, based on a mandible collected by Charles Darwin, and formally described by Richard Owen (1839). This taxon subsequently attracted great interest with the discovery of exceptionally preserved remains assigned to this species recovered at Cueva del Milodón, on the Ultima Esperanza Inlet in southern Chile (Moreno and Woodward, 1899; Roth, 1899; Philippi, 1901; Woodward, 1900; Studer, 1905). The remains include soft tissues, such as hides, hairs, and horny claw sheaths (Jacob, 1899; Ridewood, 1901). These remains suggested the existence of an extant giant ground sloth (*Ameghino*, 1898), which generated much public interest and debate (Roth, 1899). Further remarkable evidence was the presence of feces attributable to this species that indicated a diet composed of a variety of non-arboreal plants (Borrero and Martin, 2012), and that also provided data on its parasites (Ringuelet, 1957). Based on the distribution of the feces in the cave, this species was considered to be domesticated by coeval humans (Hauthal, 1899), a hypothesis that was later discarded (Martinic, 1996). Regarding its skeleton, *M. darwini* is best known from a number of skulls and dentaries (Owen, 1839; Reinhardt, 1879; Esteban, 1996; Brandoni et al., 2010). This material allowed recognition of its distinctive nature, which includes an ossified prenasal bridge connecting the premaxilla to the nasal to separate the external nares in adults (Reinhardt, 1879; Cattoi, 1966; Esteban, 1996). The anatomy of the skull has received much attention (Reinhardt, 1879; Esteban, 1996), including detailed analyses of its basicranial structure (Van der Klaauw, 1931; Patterson et al., 1992). The available sample of skull material has also allowed statistical morphometric studies (Brandoni et al., 2010). Although descriptions of the postcranial skeleton are available, including parts of the manus (e.g., Roth, 1899; Kraglievich, 1934; Bargo and Deschamps, 1996), regarding the manus these descriptions are limited and mostly restricted to the distal phalanges (Roth, 1899, 1902; Nordenskiöld, 1900; Woodward, 1900; Studer, 1905; Martin, 2008).

The genus *Mylodon* has a convoluted taxonomic history. Its type species was given the generic name *Grypotherium* by Reinhardt (1879), a name now considered a junior synonym. The species was later included in the similarly convoluted genus *Glossotherium* by Ameghino (1889) (Kraglievich, 1928; McAfee, 2009). Currently, *M. darwini* is accepted as the type species of the genus *Mylodon* because of the rationale provided by Kraglievich (1928). Four other species have been referred to the genus, namely: *Mylodon zeballozi*, erected by Gervais and Ameghino (1880), *Quatriodon bonariensis*, erected by Ameghino (1881), *Neomyodon listai*, also erected by Ameghino (1898), and *Mylodon insigne*, erected by Kraglievich (1928). Later analyses support the view that *M. darwini* is the only valid species within the genus and consider the other species to be junior synonyms of the type species (Kraglievich, 1928, 1934; Esteban, 1996). In 1999, a new specimen was discovered along the bank of Anisacate River, in central Argentina (Tauber and Di Ronco, 2003). This material consists of a skull, cervical, dorsal, and caudal vertebrae, the scapulae, almost the entire thoracic limb (=forelimb) skeleton (except for some phalanges and finger sesamoids), and most of the pelvic limb (=hind limb) skeleton. The present work deals only with the bones of the hand, comparing
them with those of previously described mylodontines. Among these, the incompletely known species *Mylodonopsis ibseni* has been hypothesized to be closely related to *M. darwini* by Cartelle (1991). *Mylodonopsis ibseni* has a well-described manus (Cartelle, 1980), so comparison with this taxon allows testing of this relationship. Moreover, characters of the hand have not been included in current phylogenies of mylodontine sloths (Esteban, 1996; Gaudin, 2004; Rincón et al., 2015), so the comparisons will allow examination of the usefulness of these characters for studies of mylodontine phylogeny.

**Institutional Abbreviations—CORD PZ, Colección de Paleozoología, Museo de Paleontología, Universidad Nacional de Córdoba, Córdoba, Argentina; FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; MACN Pv, Colección Paleontológica de Vertebrados, Museo Argentino de Ciencias Naturales, ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MACNC Pv, Colección Paleontológica de Vertebrados, Museo de Antropología y Ciencias Naturales de Concordia, Concordia, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMCI PAS, Museo Municipal Centro de Investigaciones Paleontológicas y Arqueológicas de Salto José Fernando Bonaparte, Salto, Argentina; MMP M, Colección Paleontología Vertebrados, Museo Municipal de Mar del Plata ‘Lorenzo Scaglia,’ Mar del Plata, Argentina; MNHN-BOL, Museo Nacional de Historia Natural, La Paz, Bolivia; NHMUK (formerly BM(NH)), Natural History Museum, London, U.K.; UCMP, Museum of Paleontology, University of California, Berkeley, California, U.S.A.; UF, Florida State Museum, University of Florida, Gainesville, Florida, U.S.A.; ZMUC CN, Zoological Museum, University of Copenhagen, Copenhagen, Denmark.

**METHODS**

Anatomical terminology follows the conventions of the Nomina Anatomica Veterinaria (International Committee on Veterinary Gross Anatomical Nomenclature, 2005), in agreement with Harris (2004). Therefore, for nomenclatural purposes, the axis of the hand is considered to be located between the third and fourth digits, although this does not easily apply to the much different proportions of the metacarpals in mylodontids. This is done in order to use the terms axial and abaxial in the same way as they are used for domestic artiodactyls and carnivorans. For comparison, bones were described by accepting the positions used in the first detailed published study of the hand of a mylodontine (Owen, 1842), even if these were not the positions occupied in life. Sloth teeth are not readily comparable to those of domestic mammals covered by the Nomina Anatomica Veterinaria, so we follow the nomenclature proposed by Carlini and Scillato-Yané (2004). We provide the following phylogenetic definitions for Mylodontinae and Scelidotheriinae: the former being all mylodontids closer to *Mylodon darwini* than to *Scelidotherium leptoecephalum*, the latter being all mylodontids closer to *Scelidotherium leptoecephalum* than to *Mylodon darwini*. In order to avoid creation of taxon names within the Mylodontinae, and for the sake of short reference, informal clade names were used in the section on phylogenetic relationships. Comparisons were based on features in descriptions of the manus in the following mylodontine taxa: *Glossotherium robustum*, described by Owen (1842) and others (Rattenberg, 1906; Cartelle, 1980; Saint-André et al., 2010), *Paramylodon harlani*, described by Brown (1903) and others (Lull, 1915; Stock, 1925; Hirschfeld, 1985; McDonald, 1987), *Mylodonopsis ibseni*, described by Cartelle (1980), *Glossotherium garbanii*, described in Montellano and Carranza-Castañeda (1981) and Montellano-Ballesteros and Carranza-Castañeda (1986) and referred to the genus *Paramylodon* by Montellano and Carranza-Castañeda (1981) and Morgan (2008), *Pseudopreotherium confusum*, described by Hirschfeld (1985) and Saint-André et al. (2010), *Thinobadistes segnis*, described by Webb (1989), *Ocnotherium giganteum*, described by Cartelle (1992), and *Simomylodon uccasamanensis*, described by Saint-André et al. (2010). Also included in the comparisons is *UF 10922*, a specimen described and originally referred to *Glossotheridium chapadmalense* by Robertson (1976). This referral has been questioned by Esteban (1996), and the specimen was subsequently referred to *G. garbannii* by Morgan (2008).

The phylogenetic analysis was performed with the program TNT (Goloboff et al., 2003, 2008). The analysis was based on equal-weights parsimony and was performed applying the tree bisection reconnection (TBR) algorithm on 1,000,000 random addition sequence Wagner trees (replications), keeping only one shortest tree per sequence. Such a large number of replicates were required because our first analyses indicated that the number of most parsimonious trees (MPTs) exceeded capacity. The ‘Pruned trees’ command in TNT was used to identify wildcard operational taxonomic units (OTUs). Jackknife (p: 0.36, 10,000 replicates) and Bremer support values were calculated based on the reduced strict consensus tree. The strict consensus tree, majority-rule consensus tree, and reduced strict consensus tree, after a posteriori pruning the wildcard OTUs, were obtained. Only unambiguous optimization was used for reconstruction of character state evolution—TNT does not provide ACCTRAN or DELTRAN reconstructions. Synapomorphies were recognized by a posteriori pruning of OTUs not coded for the characters from the manus or unstable in position. Six sloth taxa were selected as outgroups based on a previous large phylogenetic study (Gaudin, 2004), and outgroup topology was not enforced a priori. One of these outgroup taxa is *Scelidotherium*. The hand in this taxon has been described in detail (Burmeister, 1881; McDonald, 1987; Aranyo, 1988; Esteban et al., 1992; Cuena Anaya, 1995) and is represented by three specimens in the collection of the Museo de Paleontología, Universidad Nacional de Córdoba (CORD PZ 4464, 4586, 11293). Also included in the analysis were *Catonyx caviari* (described in Winge, 1915; McDonald, 1987; Cartelle et al., 2009), Hapalops (described in Scott, 1904; Stock, 1925), Megatherium americanum (described in Owen, 1858; Cabrera, 1929; De Iuliis and Cartelle, 1993), Mionothropus cartellei (described in De Iuliis et al., 2011), and Megalonyx jeffersonii (described in Leidy, 1855; Stock, 1925; McDonald, 1977).

**SYSTEMATIC PALEONTOLOGY**

TARDIGRADA Latham and Davies, in Forster, 1795  
MYLODONTIDAE Gill, 1872  
**MYLODONTINAE** Gill, 1872  
**MYLODON** Owen, 1839

**Type Species—**Mylodon darwini** Owen, 1839.**  
**Diagnosis—**As for type and only species.

**MYLODON DARWINII** Owen, 1839  
(Figs. 2–6)

*Mylodon darwini* Owen, 1839:63, pls. XVIII, XIX, figs. 1–4 (original description).  
**Gryrotherium darwini** (Owen, 1839): Reinhardt, 1879:368, figs. 1–3 (new combination).  
**Myloodon zeballozi** Gervais and Ameghino, 1880:156 (original description).  
**Quatrodon bonariensis** Ameghino, 1881:307 (original description).  
**Tetrodon bonariensis** (Ameghino, 1881): Ameghino, 1882:4 (new combination).  
**Mesodon zeballozi** (Gervais and Ameghino, 1880): Ameghino, 1882:41 (new combination).
**Glossotherium darwinii** (Owen, 1839): Ameghino, 1889:737, pl. XLIV, figs. 4, 5, pl. XLV, fig. 1 (new combination).

**Glossotherium zeballosi** (Gervais and Ameghino, 1880): Ameghino, 1889:738, pl. LXXXVIII, fig. 1 (new combination).

**Glossotherium bonaerense** (Ameghino, 1881): Ameghino, 1889:738, pl. XLIV, fig. 8 (new combination).

**Grypotherium bonaerense** (Ameghino, 1881): Roth, 1899:434 (new combination).

**Neomyodon listai** Ameghino, 1898: Woodward, 1900:74, pl. V, figs. 1–3, pl. VI, figs. 1–4, pl. VII, fig. 1, pl. VIII, figs. 1, 2, pl. IX, fig. 1 (new combination).

**Myloodon listai** Ameghino, 1898: Kraglievich, 1928:182 (new combination).

**Myloodon insignis** Kraglievich, 1928:182 (original description).

### Holotype—NHMUK M-16617, a mandible with teeth.

**Revised Diagnosis**—We follow the diagnosis of Esteban (1996) and add some distinctive characters. Apomorphies of taxon: premaxillae dorsally elongated and contacting the nasals in the midline; medial ramus of the premaxilla longer than the lateral; nasals strongly convex at mid-length; dental formula 4/4; postorbital processes of frontal well developed; wide, dorsally flattened space between temporal fossae; caudal external opening of the dentary canal caudal to distal-most tooth and entirely rostral to coronoid process; coronoid process with short base; pisoliform flattened; and trapezoid dorsal surface elongated perpendicular to main scaphoid facet. Differing from *Glossotherium robustum*, *Paramyloodon harlani*, and *Leiostodon armatus* in: rostral border of maxilla completely concave. Differing from *G. robustum* and *P. harlani* in: cuneiform with prominent laterodistal process and articular facet for ulna concave in dorsolateral direction; and astragalus with odontoid process set at a wide obtuse angle to lateral part of the articular surface for the tibia. Differing from *Myloodonopsis ibseni* in: second mandibular tooth oval and with distal surface less convex. Differing from *Onootherium* giganteum in: lacking diastema between second and third maxillary teeth. Differing from *Simomylodon uccasamensis* in: mesial-most mandibular tooth small, non-cainiform, and oval in section; and single astragalocalcaneal facet. Differing from *Glossotherium garbani* in: second mandibular tooth oval and distal carina on metacarpal III oblique. Further differences in the bones of the manus are noted in Supplementary Data 1.

**Referred Specimens**—FMNH P14288 (skull); MACN Pv 991 (mandible with teeth); MACN Pv 2219 (astragalus); MACN Pv 5980 (premaxillae and mandible); MACN Pv 11346 (mandible); MACN Pv 11502 (mandible); MACN Pv 11617 (caudal part of skull); MACN Pv 13882 (skull); MACN Pv 13911 (mandible); MACN Pv 15348 (skull); MACNC Pv 2334 (skull and mandible); MLP 3–122 (skull); MLP 3–762 (partial skeleton); MLP 3–763 (partial skeleton); MLP 3–764 (skull); MLP 36–VIII–12–1 (skull); MLP 54–III–8–1 (caudal part of skull); MLP 94–VIII–10–1 (caudal part of skull); MLP 94–VIII–10–6 (maxilla with all teeth); MLP 94–VIII–10–2 (skull); MLP 94–VIII–10–3 (maxilla); MLP 94–VIII–10–4 (maxilla); MLP 94–VIII–10–5 (mandible); MMCPAS B-50–2458 (skull); MMP M 4701 (mandible); MNHN-BO-LV 006470 (skull); ZMUC CN 43 (skull and mandible with teeth); CORD PX 4570 (partial skeleton, including nearly complete skull, dentaries, several vertebrae, ribs, and many limb bones in articulation).

**Occurrence**—Ensenadan–Lujanian (Pleistocene); southern South America from southern Bolivia to southernmost Patagonia (Brandoni et al., 2010).

**Hypodigm**—The specimen studied here is deposited in the Museo de Paleontología, Universidad Nacional de Córdoba, under the label CORD PX 4570. Remains of both articulated hands are present. The left hand is in general well preserved, whereas the bones of the right manus are more incompletely preserved. The bones of the manus preserved include both scaphoids, lunars, cuneiforms, trapezia, trapezoids, magna, metacarpals II and III, full sets of phalanges of digit II, and axial sesamoids of digit IV, pisiform, uniciform, metacarpals I, IV, and V, abaxial sesamoid of digit III, palmar sesamoid from the left manus, and proximal phalanges of digits III–V from the right manus. The specimen is assigned to *Myloodon darwinii* based on the following features: nasals strongly convex in rostrocaudal direction at mid-length (Esteban, 1996), nasals surpassing the rostral border of the maxilla (Kraglievich, 1928), rostral border of the facial surface of the maxilla concave (Esteban, 1996), snout dorsoventrally taller than mediolaterally wide (Esteban, 1996), M2–M4 subtriangular in shape (Cattoi, 1966); mandible elongate (Kraglievich, 1928), and articular surface for tibia on odontoid process of the astragalus set at an obtuse angle to lateral part of the articular surface for the tibia (Kraglievich, 1928). The skull and dentaries of the specimen are not completely prepared, so not all diagnostic features listed in previous diagnoses (Cattoi, 1966; Esteban, 1996) were recognized. Of these, the rostrocaudal convexity of the nasals has been deemed unique for this taxon (Esteban, 1996).

**Locality and Horizon**—The fossil was collected near the town of La Bolsa, Córdoba Province, in central Argentina (Tauber and Di Ronco, 2003) (Fig. 1A, B). It was collected from the northern gully of the Anisacate River, on its left bank (31° 41′ 12.85″ S, 64° 21′ 24.40″ W; 455 m above sea level [a.s.l.])(Fig. 1C), from an aeolian silt stratum. The silt layer was radio-carbon-dated at 13,570 ± 0.16 ka before present (Tauber, 1999) and dated by thermoluminescence at 10.010 ± 0.66 ka before present (Sanabria, 2000; Sanabria and Argüello, 2003). The associated mammalian assemblage (Tauber et al., 2008a, 2008b) includes Glyptodon perotorus, which indicates a Lujanian Age (Tauber et al., 2008a). The layer has been correlated with the La Invernada Formation (Kröhling and Carignano, 2014).

**Taphonomy**—The bones were generally well preserved, except for some damage attributable to surface erosion. The bones of the manus were found articulated; the right manus was recovered with digit II adjacent to the left nostril. Web-like rhyzoconcretions were found attached to the surfaces of the bones, which indicate the presence of paleosols.

**DESCRIPTION**

The following description focuses on characters showing variation among mylodontines. Measurements of the bones described below are listed in Supplementary Data 1. Supporting photographic material is presented in Supplementary Data 2. Further comparisons with other mylodontine sloth species are presented in Supplementary Data 3.

**Carpus**

In this section we will describe all the carpals and metacarpal I, because the latter element is coossified with a carpal bone, the trapezium.

**Scaphoid**—The scaphoid is proximodistally depressed and approximately triangular in proximal and distal views, with a mediolaterally concave palmar surface (Fig. 2A). The trapezium-metacarpal I facet is separated from the articular facet for the trapezoid (Fig. 2A), as in *Glossotherium robustum* (Owen, 1842) and *Paramyloodon harlani* (Hirschfeld, 1985), but in contrast to the confluent condition of the facets of *Pseudopreprototherium confusum* (Hirschfeld, 1985) and selciolitheres (McDonald, 1987). The articular surface for the radius is convex laterally (Fig. 2B) and concave medially, especially in the dorso-palmar direction, to receive the styloid process of the radius, as in *G. robustum* (Owen, 1842), but unlike the uniformly convex
Haro et al.—Manus of *Mylodon darwinii* (e1188824-4)

**FIGURE 1.** Maps indicating provenance of CORD PZ 4570, a partial manus of *Mylodon darwinii*. A, map of South America indicating placement of Córdoba Province (light gray) within Argentina (white). B, close-up of square in A. C, close-up of square in B. Black dots in B and C represent urban centers, dashed lines indicate the course of the Anisacate River, and pentagons with numbers within represent highway routes. Gray field in C indicates the lower terrace of the Anisacate River, and crossed-bone symbol indicates the location of the material.

**FIGURE 2.** *Mylodon darwinii*, left carpals from the proximal row of CORD PZ 4570. A, distal view of scaphoid; dorsal to the top. B, lateral view of scaphoid; proximal to the top. C, proximal view of lunar; dorsal to the top. D, dorsal view of lunar; proximal to the top. E, lateral view of cuneiform; proximal to the top. F, dorsomedial view of cuneiform; proximal to the top. G, dorsal view of cuneiform; proximal to the top. H, dorsal view of pisiform; proximal to the top and right. I, proximomedial view of pisiform; dorsal to the top. *Abbreviations*: *af*, continuous articular surface for cuneiform and ulna; *cf*, articular facet for cuneiform; *dmp*, dorsomedial process; *dp*, distal process of scaphoid; *g*, groove on dorsal surface of cuneiform, immediately distal to lower part of rough ridge; *hp*, hooked process; *ldp*, laterodistal process; *lf*, articular facet for lunar; *mf*, articular facet for magnum; *mVf*, articular facet for metacarpal V; *nf*, pair of nutrient foramina; *pf*, articular facet for pisiform; *rf*, articular facet for radius; *rr*, rough ridge; *tf*, articular facet for trapezoid; *tmf*, articular facet for trapezium-metacarpal I; *tp*, process contacting trapezium-metacarpal I; *uf*, articular facet for ulna; *unf*, articular facet for unciform. Scale bar equals 10 mm.
surface of the holotype of *Pseudolestodon hexaplyodon* (Rautenberg, 1906). The lunar facet is single, as in *P. harlani* (Stock, 1925; McDonald, 1987), but unlike the two facets present in *Thinobadistes segnis* (Webb, 1989), *P. confusum* (Hirschfeld, 1985), and most scelidotherines (McDonald, 1987). A single magnus facet is present (Fig. 2A, B), as in *P. harlani* (Stock, 1925), but unlike the two facets of the holotype of *P. hexaplyodon* (Rautenberg, 1906). This facet is not located on a dorsal process, unlike in *P. confusum* (Hirschfeld, 1985). The facets for trapezoid and magnus are contiguous (Fig. 2A), as in *G. robustum* (Cartelle, 1980; Saint-André et al., 2010) and *T. segnis* (Webb, 1989), but in contrast to the separated condition of *Mylopondopsis ibseni* (Cartelle, 1980) and *Simomyloydon uccasamensis* (Saint-André et al., 2010). The trapezoid facet is slightly deeper dorsopalmarly than it is mediolaterally wide (Fig. 2A), unlike the mediolaterally wider condition of *S. uccasamensis* (Saint-André et al., 2010).

**Lunar**—The lunar resembles a wedge or cone in proximal view. The proximal articular surface, which contacts the radius, has a dorsal border that is much wider than its palmar edge (Fig. 2C), as in *Thinobadistes segnis* (Webb, 1989) and the *Pseudolestodon harlani* material from Rancho La Brea (Stock, 1925), but unlike the palmarly expanded condition observed in material originally referred to *Paramyloydon nebrascensis* (Brown, 1903) and in *Psuedopreotherium confusum* (Hirschfeld, 1985). The dorsal surface of the bone is approximately hexagonal (Fig. 2D).

On the dorsal surface, the medial border, located between the articular facets for radius and magnus, is shorter than the part of the distal border formed by the facet for the unciform, as in *Glossotherium robustum* (Owen, 1842), *P. harlani* (Montellano-Ballesteros and Carranza-Castañeda, 1986), and *Mylopondopsis ibseni* (Cartelle, 1980), but unlike that found in *Glossotherium garbanii*, in which the medial border is longer (Montellano-Ballesteros and Carranza-Castañeda, 1986), or longer as in *G. robustum* (Cartelle, 1980). The scaphoid and magnus facets are almost parallel, meeting at a widely obtuse angle, more closely resembling the nearly parallel condition of *P. harlani* than the approximately 90° angle of *P. confusum* (Hirschfeld, 1985).

**Cuneiform**—The cuneiform is wedge-shaped, and its dorsopalmar depth decreases distally (Fig. 2E). Its maximal dorsopalmar depth is less than its proximodistal length, as in the *Mylopondopsis ibseni* (Cartelle, 1980) and *Ocnotherium giganteum* (Cartelle, 1992), but unlike the relatively thicker elements of *Glossotherium robustum* (Owen, 1842), *P. harlani* (Montellano-Ballesteros and Carranza-Castañeda, 1986), and *Simomyloydon uccasamamensis* (Saint-André et al., 2010). The dorsopalmar depth of the ulnar facet is less than the cuneiform proximodistal length, as in UF 10922 (Robertson, 1976), but unlike the relatively deeper facet of *Paramyloydon harlani* (Robertson, 1976). The proximodistal length in turn is less than the maximum mediolateral width, as in *P. harlani*, UF 10922 (Robertson, 1976), and *G. garbanii* (Montellano-Ballesteros and Carranza-Castañeda, 1986), but unlike in *M. ibseni* (Cartelle, 1980), *O. giganteum* (Cartelle, 1992), and *S. uccasamamensis* (Saint-André et al., 2010). The articular surface for the ulna is approximately elliptical, with an almost dorsopalmarly directed long axis. This resembles more closely the state of *M. ibseni* (Cartelle, 1980) and *S. uccasamamensis* (Saint-André et al., 2010) than the conditions of *P. harlani* (Cartelle, 1980) and *G. robustum* (Montellano-Ballesteros and Carranza-Castañeda, 1986). The medial border of the ulnar facet is concave. The surface of the facet is concave in the dorsolateral direction (Fig. 2F). The facet is less concave than in *M. ibseni* (Cartelle, 1980). This facet is flat in *G. robustum* (Owen, 1842; Cartelle, 1980), *P. harlani* (Stock, 1925; Cartelle, 1980), and *Thinobadistes segnis* (Webb, 1989). The dorsal surface does not present a prominent transverse ridge dorsal to the articular surface for the ulna, similar to the condition present in *M. ibseni*, but unlike in *G. robustum* (Cartelle, 1980). The articular facet for the pisiform is separated from the articular surface for the ulna (Fig. 2E), similar to the condition in *M. ibseni* (Cartelle, 1980) and *O. giganteum* (Cartelle, 1992), but in contrast to the contiguous condition of the facets in *G. robustum* (Owen, 1842), the holotype of *Pseudolestodon hexaplyodon* (Rautenberg, 1906), *P. harlani* (Stock, 1925), *T. segnis* (Webb, 1989), and *G. garbanii* (Montellano-Ballesteros and Carranza-Castañeda, 1986). The dorsolaterally facing articular surface for metacarpal V is located on a pronounced distal process situated on the lateral part of the bone (Fig. 2G) that also bears the lateral part of the unciform facet. The great development of this feature resembles that of *M. ibseni* (Cartelle, 1980), unlike the less developed process of *G. garbanii* (Montellano-Ballesteros and Carranza-Castañeda, 1986). The process is absent in *P. harlani* and *G. robustum* (Cartelle, 1980).

**Pisiform**—This bone is dorsopalmarly flattened and approximately oval in dorsal view (Fig. 2H, I). Its flattening (ratio between maximum thickness and maximum width: 0.67) is greater than in *Ocnotherium giganteum* (Cartelle, 1992) and UF 10922 (ratio: 0.9; Robertson, 1976) and is unlike the nodular shape present in *Paramyloydon harlani* (mean ratio: 1.05; Stock, 1925), the half-walnut-shaped condition of the holotype of *Pseudolestodon hexaplyodon* (Rautenberg, 1906), and the pyramidal aspect of *Thinobadistes segnis* (ratio: 0.81; Webb, 1989). Among mylodontines, a flattened pisiform was also noted in *Glossotherium robustum* (Owen, 1842).

**Trapezoid**—The dorsal surface of the bone resembles an irregular pentagon (Fig. 3A), with elongate proximolateral and distomedial borders, unlike the subtriangular trapezoid in *Glossotherium robustum* (Owen, 1842) and *Paramyloydon harlani* (Stock, 1925), and also the more proximodistally flattened shape in scelidotherines (McDonald, 1987). The dorsal surface long axis is perpendicular to the dorsal border of the medial region of the scaphoid facet. The ratio between this dimension and the width of the surface, as measured perpendicular to its long axis, is 1.5, higher than the mean ratio of 0.85 present in *P. harlani* (Stock, 1925). The dorsal third of the facet for metacarpal II is convex in the dorsopalmar direction, whereas the palmar two-thirds bear a very pronounced concavity (Fig. 3B, C).

**Magnum**—The magnum is irregular in dorsal view and mediolaterally compressed (Fig. 3D). It is proximodistally longer palmarwards. If the autopod is reconstructed in articulation, the contact between magnum and metacarpal II is not exposed in dorsal view, as in *Glossotherium robustum*, but unlike the condition present in *Mylopondopsis ibseni* (Cartelle, 1980). Distally, the bone presents two articular facets for metacarpal III (Fig. 3D), as in *G. robustum* (Owen, 1842; Cartelle, 1980), but unlike the condition of *Psuedopreotherium confusum* and scelidotherines, in which only one is present (Hirschfeld, 1985; McDonald, 1987).

**Unciform**—The nearly flat dorsal surface of this bone is ‘L’-shaped (Fig. 3E). The proximolateral border of the surface corresponds to the dorsal border of the articular facet for the cuneiform. It is quite sigmoid, unlike the straighter border of *Glossotherium robustum* (Owen, 1842). Proximally, a wedge-shaped process penetrates between the lunar and the cuneiform (Fig. 3E). As in *Paramyloydon harlani*, this process is taller and more distinctive than in *Psuedopreotherium confusum* (Hirschfeld, 1985). It is less medi ally set than in scelidotherines (McDonald, 1987). The articular surface for the cuneiform expands dorsopalmarly at the lateral border (Fig. 3F), as in *P. harlani*, but in contrast to the unexpanded condition present in *P. confusum* (Hirschfeld, 1985). On the medial surface, two
articulat facets for metacarpal III are present, unlike the single facet for metacarpal III present in scelidotherines (McDonald, 1987). As in *Paramylodon harlani*, the dorsal facet for metacarpal III does not form a deep indentation on the dorsal surface of the unciform (Fig. 3E), unlike in *Pseudoprepotherium confusum* (Hirschfeld 1985).

**Trapezium-Metacarpal I**—The suture between trapezium and metacarpal I is fused, except at its distal and axial parts (Fig. 4A). The resulting element is ‘L’-shaped (Fig. 4A), with arms meeting at an acute angle. The proximomaxial arm is shorter relative to the distoabaxial arm than in *Paramylodon harlani* (Stock, 1925). However, as in *P. harlani* and *Glossotherium robustum*, it is relatively longer than in *Thinobadistes segnis*.
(Webb, 1989). The articular surface for the scaphoid is axioabaxially concave (Fig. 4A) and slightly convex dorsopalmarly. Its convexity resembles the condition of scelidotherines and is unlike the flat surface in Glossotherium and Paramylodon (McDonald, 1987). The very small trapezoid articular facet faces axially. The presence of this facet is a trait shared with scelidotherines (Stock, 1925; McDonald, 1987); but this facet is lacking in Paramylodon harlani and Glossotherium robustum (Stock, 1925; McDonald, 1987).

Metacarpus

Only metacarpals II–V are described in this section. Metacarpal I was described above with the carpal bones because it is ossified to the trapezium.

Metacarpal II—The bone is proportionally less robust than in Paramylodon harlani (Stock, 1925), thus resembling metacarpal II in Mylododonopsis ibseni (Cartelle, 1980). Its gracility was previously noted in material from Olavarria (Krögliichev, 1934). The dorsopalmar depth of the diaphysis is lower, relative to its length (ratio: 0.38), than in P. harlani (mean ratio: 0.49; Stock, 1925), Pseudopreotherium confusum (ratio: 0.46–0.73; Hirschfeld, 1985), and Scelidotherium (0.46–0.47; pers. observ., JAH). More closely resembles the ratio present in Simomylodon uccasamensis (ratio: 0.35; Saint-André et al., 2010). The small articular facet for the trapezium-metacarpal I is proximodistally concave (Fig. 4B), as in Glossotherium garbani (Montellano and Carranza-Castañeda, 1981; P. harlani, and P. confusum (Hirschfeld, 1985), but unlike the flat facet of the holotype of Pseudolestodon hexapondylus (Rautenberg, 1906) and the slightly convex facet of Simomylodon uccasamensis (Saint-André et al., 2010). The facet for metacarpal III is axially located. This facet is concave, as in G. robustum (Owen, 1842), the holotype of P. hexapondylus (Rautenberg, 1906), and P. harlani (Stock, 1925), but unlike the nearly flat condition of the homologous surface of P. confusum (Hirschfeld, 1985) and Scelidotherium (McDonald, 1987). The facet is separate from the magnus facet (Fig. 4C), as in G. robustum and S. uccasamensis, but unlike P. confusum (Saint-André et al., 2010) and Scelidotherium (Cuenca Anaya, 1995). At the distal end, the epiphysial suture is well marked (Fig. 4B, C). The distal articular surface presents a strong, dorsopalmarly convex carina (Fig. 4B, C), unlike the straighter carina of scelidotherines (McDonald, 1987).

Metacarpal III—Metacarpal III is longer than metacarpal II. In dorsal view, the shape of metacarpal III resembles a combination of the letters ‘T’ and ‘Y’ (as indicated in G. robustum and Thinobadistes segnis, respectively; Owen, 1842; Webb, 1989) (Fig. 4D), differing from the more robust, blocky shape of the holotype of Pseudolestodon hexapondylus (Rautenberg, 1906), or Scelidotherium (McDonald, 1987). The proximal end is expanded (Fig. 4D, E). The palmar process of metacarpal III is pronounced (Fig. 4E). The shaft is relatively gracile, unlike in Paramylodon harlani (Stock, 1925) and Glossotherium robustum (Owen, 1842). The ratio between the axioabaxial width at the shaft and the proximodistal length of the bone is 0.29, more closely approaching that in Mylododonopsis ibseni (ratio: 0.31; Cartelle, 1980), and to a lesser degree those in Pseudopreotherium confusum and Simomylodon uccasamensis (ratio: 0.34; Hirschfeld, 1985; Saint-André et al., 2010), than those of G. robustum (ratio: 0.46–0.47; Cartelle, 1980) and P. harlani (ratio: 0.41–0.42; Stock, 1925; Cartelle, 1980). There are two distinct articular facets for the magnus on the proximal surface of metacarpal III, as in P. harlani (Stock, 1925), but unlike the condition in P. confusum and scelidotherines, in which only one facet is present (Hirschfeld, 1985; McDonald, 1987). A rounded process bears the abaxial facet for the magnus proximally (Fig. 4D). A strongly convex articular facet for metacarpal II is present on the abaxial region of the proximal end (Fig. 4D), as in P. harlani (Stock, 1925) and G. robustum (Saint-André et al., 2010), but unlike the weakly convex metacarpal II facet of S. uccasamensis (Saint-André et al., 2010) or the flattened facet of scelidotherines (McDonald, 1987; Cuenca Anaya, 1995). The position of the facet for metacarpal II in this process forces a distal divergence between the long axes of metacarpals II and III. The metacarpal IV facet is single (Fig. 4E), as in scelidotheres, but unlike the subdivided condition in Glossotherium and Paramylodon (McDonald, 1987). The epiphysis is partially fused to the shaft, with the suture remaining largely visible (Fig. 4D, E). The carina of the distal articular surface is obliquely set, extending from the dorsal and axial regions of the distal end to the mid-width of the palmar region (Fig. 4F), as in G. robustum (Owen, 1842) and P. harlani (Stock, 1925), but unlike the more directly dorsopalmar orientation of the carina present in Glossotherium garbani (Montellano and Carranza-Castañeda, 1981; Montellano-Ballesteros and Carranza-Castañeda, 1986) and P. confusum (Hirschfeld, 1985). In the distal articular surface, the portion axial to the carina is reduced, only extending near the sesamoid articular facet (Fig. 4F), as in P. harlani (Stock, 1925) and the holotype of P. hexapondylus (Rautenberg, 1906), but unlike its absence in G. robustum (Owen, 1842). The dorsal end of the carina is unsupervised (Fig. 4D). Although the presence of an expansion of the carina on the dorsal surface is uncertain, it was in any case clearly much smaller than that in Paramylodon harlani (Stock, 1925) (Fig. 4D). In this, it resembles the conditions in G. garbani (Montellano and Carranza-Castañeda, 1981; Montellano-Ballesteros and Carranza-Castañeda, 1986), P. confusum (Hirschfeld, 1985), and scelidotherines (McDonald, 1987). The carina is much stricter in axial or abaxial view (Fig. 4E) than in P. harlani (Stock, 1925), resembling the condition in the scelidotherines (Cuenca Anaya, 1995).

Metacarpal IV—This is the longest metacarpal and is almost completely preserved, except at the proximal and distal ends (Fig. 5A–C). The dorsal surface of the distal end is much damaged (Fig. 5C). At the proximal end, a single articular surface for metacarpal III is present (Fig. 5A). The latter is mainly concave dorsopalmarly and axioabaxially, especially at its palmar region, as in Glossotherium robustum and Simomylodon uccasamensis (Saint-André et al., 2010), but unlike the slightly convex to flat condition of the palmar part of the facets in Pseudopreotherium confusum (Hirschfeld, 1985) and Paramylodon harlani (Lull, 1915). The palmar expansion of the articular surface for metacarpal V exceeds that of the palmar surface at the shaft constriction, as in G. robustum, but unlike the state in S. uccasamensis (Saint-André et al., 2010). The facet is narrow proximodistally, as in P. harlani, but in contrast to P. confusum (Hirschfeld, 1985) and Scelidotherium (Cuenca Anaya, 1995).

The shaft at mid-length is axioabaxially wider than in metacarpal III, unlike the mean condition in P. harlani (Stock, 1925) and the conditions of Ocnotherium giganteum (Cartelle, 1992) and Scelidotherium leptoecephalum (Burmeister, 1881). On the distal end, the epiphysis is partially fused to the shaft of the bone (Fig. 5A, B). The distal articular surface for the proximal phalanx is mostly convex along the directions of both its longest and shortest axes, as in P. harlani (Stock, 1925), but unlike the flat surface of the holotype of Pseudolestodon hexapondylus (Rautenberg, 1906) and the partially concave surface of Scelidotherium (Cuenca Anaya, 1995). Axial to this carina-like convexity, the distal articular surface is much reduced (Fig. 5C), as in P. harlani (Stock, 1925) and G. robustum (Owen, 1842), but unlike Pseudopreotherium confusum (Hirschfeld, 1985) and scelidotherines (McDonald, 1987).

Metacarpal V—The proximal and distal ends are transversely expanded to a similar degree. The insertion area of the M. extensor carpi ulnaris is abaxially prominent on the dorsobulbar surface of the proximal end. The cross-section of the shaft is
resembling *Mylodonopsis ibseni* in this respect and differing from *Paramylodon harlani* (Cartelle, 1980) and *Scelidotherium* (Cuenca Anaya, 1995). The distal articular trochea is much more rounded in a parasagittal plane than in the proximal phalanx.

**Distal Phalanx of Digit II**—This claw-bearing phalanx is partially preserved (Fig. 6). It presents a roughly conical ungual process that is covered by the poorly preserved ungual crest proximally. The base of the ungual process is axioabaxially wider than dorsopalmarly deep, unlike the condition in the holotype of *Pseudolestodon hexaspondylus* (Rautenberg, 1906).

**Proximal Phalanx of Digit III**—The phalanx (Fig. 6) is quite short proximodistally. The palmar surface presents large perforations and a small, shallow pit. The abaxial surface does not bear a greater prominence than in the proximal phalanx of digit II, unlike in *Glossotherium robustum* (Owen, 1842). In the distal articular surface, the dorsal part of the intercondylar groove is concave both axioabaxially and dorsopalmarly. The axial condyle is invaded by a pitted surface, as in *Paramylodon harlani* (Stock, 1925), whereas the abaxial condyle presents a conical projection, unlike the flat condyle of *P. harlani* (Stock, 1925).

**Proximal Phalanx of Digit IV**—The phalanx (Fig. 6) is much shorter proximodistally than deep dorsopalmarly or wide axioabaxially. The articular facet for the axial sesamoid converges with the articular fovea at an obtuse angle, unlike the 90° angle of *Paramylodon harlani* (Stock, 1925). The dorsal surface lacks a clearly defined canal leading to the nutrient foramina of the abaxial surface, unlike in *P. harlani* (Stock, 1925). On the distal aspect of the bone, the distal articular facet is dorsopalmarly centered, unlike the more dorsally located facet of *Glossotherium robustum* (Owen, 1842). The facet is approximately as wide axioabaxially as it is deep dorsopalmarly, unlike in *P. harlani* (Stock, 1925). The axial part of the facet is larger than the abaxial one, as in *P. harlani* (Stock, 1925), but in contrast to the more symmetrical condition of the holotype of *Pseudolestodon hexaspondylus* (Rautenberg, 1906).

**Proximal Phalanx of Digit V**—This bone is approximately hemispherical (Fig. 6), unlike the crescent-shaped element in the holotype of *Pseudolestodon hexaspondylus* (Rautenberg, 1906). The phalanx is approximately as wide axioabaxially as deep dorsopalmarly, unlike in *Paramylodon harlani* (Stock, 1925). It is also shorter proximodistally than it is deep dorsopalmarly. The distal articular facet is exposed strictly distally, in contrast to the distodorsally facing condition in *P. harlani* (Stock, 1925).

**Other Bones**

**Abaxial Sesamoid of Digit III**—The sesamoid is approximately prismatic, and not ‘keel-like’ as in the holotype of *Pseudolestodon hexaspondylus* (Rautenberg, 1906). It is twice as long as wide, longer than in *Paramylodon harlani* (ratio = 1.54; Stock, 1925) or the holotype of *P. hexaspondylus* (ratio = 1.5; Rautenberg, 1906). It presents an almost square transverse section, unlike the triangular cross-section of all digital sesamoids recovered in the holotype of *Glossotherium robustum* (Owen, 1842) and the depressed condition of *P. harlani* (Stock, 1925).

**Axial Sesamoid of Digit IV**—This sesamoid is also elongate, but is nearly triangular in transverse section at mid-length. The articular surface for the proximal phalanx is slightly developed, whereas it is absent in *Paramylodon harlani* (Stock, 1925).

**Palmar Sesamoid**—This bone is flattened, oblong, and provided with rounded borders. It lacks articular surfaces. The dorsal and palmar surfaces are heavily striated. The bone was preserved lying on the palmar aspect of the partially articulated magnum, unciform, and metacarpal III. The most concave surface faces palmarwards, as in *Megatherium* (Cabrera, 1929). The wider edge is laterodistally directed.
specialist fossorial taxa are very short proximodistally (Hildebrand and Goslow, 2001). A further argument against a palmar sesamoid, which is also present in the mostly fossorial Recent Cingulata (Flower and Gadow, 1885), would suggest some degree of fossoriality. In addition, metacarpal III is gracile relative to other metacarpals compared with myrmecophagid anteaters (Taylor, 1978; Orr, 2005). This suggests that it was much less suited for forceful tearing. On the other hand, the length difference in metacarpals II–IV suggests less branch-grasping ability than in Recent sloths, in which the aforementioned metacarpals are similar in length (Pujos et al., 2007). Notably, a metacarpal IV significantly longer than metacarpal III (as found in M. darwinii) is, among the Recent Pilosa, only found in its largest and most terrestrial representative, the giant anteater (Orr, 2005). The shapes of the articular facets in digits II and III support different functions. In digit II, the dorso-palmarly convex distal articular surface of the metacarpal and the trochlea-like distal articular facet on the proximal phalanx indicate certain flexor mobility that has been related to grasping ability (Pujos et al., 2007). On digit III, the dorso-palmarly straighter distal articular surface in the metacarpal and the irregular distal articular facet of the proximal phalanx indicate less mobility and more stability.

A differing function for digits II and III is further supported by the angle between their long axes when articulated, related to the size of the abaxial prominence in metacarpal III. The concavo-convex articulation between metacarpals II and III suggests some mobility between them. The palmar expansion at the proximal end of metacarpal III would suggest palmigrady (Pujos et al., 2007), but the relatively stiff joints in the third digit, lacking the ability to hyperextend, do not support this interpretation. The stiffness and relative robustness of digit III suggests that it was better suited for support than digits I–II. Digits IV and V, with their reduced intermediate and distal phalanges, are probably ill suited for digging. Metacarpals IV and V, being relatively longer and thicker than metacarpals I–II, would have had a more important role than the latter for support. More detailed functional analyses will be presented elsewhere.

**Taxonomy and Phylogeny**—Detailed comparison of the manus of CORD PZ 4570 with other mylodontines reveals differences with all of them. The extent to which CORD PZ 4570 differs from the other mylodontines is related both to actual anatomical differences and the number of corresponding preserved and described bones. Considering the features that vary among the sample of mylodontines compared, the highest ratios of similarities to differences are shared with UF 10922, Ocnotherium giganteum, and Mylodonopsis ibseni. For the last, a larger number of comparisons were performed. Our comparisons revealed distinctive morphologies in the holotype of Paramylodon.
nebrascensis—referred to Paramylodon harlani by Stock (1925)—and the holotype of Pseudolestodon hexaspodylus—referred to Glossotherium robustum by Cabrera (1936). The holotype of P. nebrascensis differs from P. harlani in having a lunar with a proximal articular surface wider mediolaterally at the palmar border than at the dorsal border (Brown, 1903; Stock, 1925). Although this single difference represents a poor basis to support elevation of P. nebrascensis to the status of species, some importance may be attributed to this feature because a relatively broad palmar border is characteristic of basal mylodontine taxa (e.g., Pseudopretherium confusum; Hirschfeld, 1985) and the outgroups of the Mylodontidae (Scelidotherium; pers. observ., JAH), but not derived mylodontines (e.g., Brown, 1903; Hirschfeld, 1985; Webb, 1989). Several differences in the structure of the manus have also been noted in the published descriptions of the holotypes of G. robustum and P. hexaspodylus by Owen (1842) and Rautenberg (1906), respectively. These include (1) the proximal articular surface on the scaphoid is medially concave in the former, but uniformly convex in the latter; (2) the scaphoid bears two articular surfaces for the magnum in the latter, but only one in the holotype of G. robustum; (3) the cuneiform is the largest carpal in the holotype of G. robustum, but the second largest in the holotype of P. hexaspodylus; (4) metacarpal III is ‘T’-shaped in the former, but cube-like in the latter; and (5) the part of the distal articular surface located axially to the carina in metacarpal III is present in the latter, but absent in the former. However, determination of the taxonomic status of P. hexaspodylus would require anatomical comparisons of features from the rest of the skeleton, but that is beyond the scope of this work. We were unable to find morphological differences between UF 10922 and the holotype of G. robustum, which, besides the smaller size of the former (Montellano-Ballesteros and Carraza-Castañeda, 1986). Although Morgan (2008) refers UF 10922 to G. garbanii on the basis of age and its plesiomorphic body size, more exhaustive comparisons are necessary to support this referral.

A small data matrix of phylogenetically informative characters was generated based on comparisons between the new Mylodon material and other mylodontines. The data matrix is composed of nine mylodontine taxa, representing all those used for comparisons. In addition, in order to test the affinities of the holotype of P. hexaspodylus to G. robustum and of UF 10922 to G. garbanii, we incorporated anatomical information from these two specimens as two other separate operational taxonomic units (OTUs). Because there is little evidence regarding the morphology of the manus in the holotype of P. nebrascensis, which could be coded for a single feature only, this taxon was not included in the final analysis. Thirty-seven binary characters were used in the phylogenetic analysis (see Supplementary Data 4). In addition to characters from the bones of the manus here sampled, the matrix includes three postcranial skeletal characters previously considered important in mylodontine systematics: the presence of a supratrochlear foramen in the humerus, the number of articular facets for the calcaneum in the astragalus, and the presence of osteoderms. Regarding the last character, we only scored osteoderms as absent if the taxa are known by most of the skeleton or from many skeletons. Although this is not absolute evidence of absence, it seems unlikely given how many osteoderms are present in complete mylodontids that they were present but completely unobserved when that many other bones are present. If any osteoderms were recovered, they were scored as present regardless of the completeness of the skeleton. Some of the characters of the cuneiform were based on ratios involving a common measurement; this raises the possibility of character correlation if the change in each ratio results from a change in the shared measurement. However, these characters, namely, characters 323–326, were kept for two reasons. Because of the distribution of the missing entries, character 325 supports a group different from those supported by characters 323 and 324. In characters 323, 324, and 326, the distribution of at least one character state among the taxa overlaps that of both alternative character states of the other characters. This implies that modification of at least one of the measurements not shared could be responsible for the variation. To remove them would therefore result in a loss of relevant information. This data matrix (available in Supplementary Data 5) was then combined with those of Gaudin (2004) and Rincón et al. (2015). Taxa not included in at least one of the matrices, but which are included in at least one of the others, are scored with missing data in the characters of the matrices in which they were not included. We merged Glossotherium robustum and Glossotherium wegneri into a single OTU, as in Gaudin (2004). These species have been recovered as sister groups by Esteban (1996).

The phylogenetic analysis (file ready for use in TNT available in Supplementary Data 6) yielded over a million MPTs of 1842 steps (consistency index [CI]: 0.308, retention index [RI]: 0.649). Only a million MPTs were recovered. The strict consensus tree was almost completely unresolved, yielding only a monophyletic trichotomy formed by P. harlani, Mirandabrady soborrensis, and Mirandabrady urumaquensis. We informally call this group ‘clade 1’ (Fig. 7A). This indicates that the species of the genus Mirandabrady do not form a monophyletic group exclusive of other species. A reduced strict consensus (Fig. 7A) including the largest possible number of resolved nodes was obtained after a posteriori pruning the following 12 OTUs: Ocnotherium gigan
terus, Glossotherium garbanii, the holotype of Pseudolestodon hexaspodylus, Simonylonodon uccasammenensis, Uruscomotherium garciai, Chubutherium ferelloi, Pseudopretherum venezuelanum, Eionaletherium tanycennicus, Mirandabrady zabasi, Urumaquia robusta, Pyramiodontherium scillatoyanei, and Pyramiodontherium brevirostrum. The relationships of each of the 12 pruned OTUs were then investigated individually by sequentially pruning 11 of them from the 1,000,000 MPTs and then constructing a strict reduced consensus tree for each.

The results of the a posteriori pruning allowed recovery of the general relationships among non-mylodontids seen in Gaudin (2004). The only difference observed was the lack of resolution in the clade including G. robustum, P. harlani, Pleurolestodon acutidens, and the Lesiodontidae (sensu Webb, 1989), here informally called ‘clade 2’ (Fig. 7A). As in Rincón et al. (2015), a clade was recovered including Bolivartherium urumaquensis and P. confusum, here informally called ‘clade 3’ (Fig. 7A). However, compared to Rincón et al. (2015), the most complete and conditionally complete occurrence of the manus in the holotype of P. harlani, as recovered as a true mylodontid, but Hapalops was not. Our results, therefore, agree in these two statements with the original hypotheses in Saint-André et al. (2010) and Ameghino (1889), respectively. Pseudopretherium confusum is recovered as basal to a group including Paramylo
don harlani and Glossotherium wegneri, as in Gaudin (2004), but in contrast to Rincón et al. (2015), in which P. confusum is more closely related to G. wegneri than P. harlani. A clade was recovered, here informally called ‘clade 4’ (Fig. 7A), formed by Mylodon darwini, Mylo
donopsis ibesi, and UF 10922. A fifth clade, here informally called ‘clade 5’ (Fig. 7A), is formed by clades 2 and 4, with Octodontherium as its sister taxon.

Regardless of the position of the wildcard taxa, O. giganteum is never recovered within clade 2. Glossotherium garbanii is recovered as a soloth more derived than Bradypus, and never recovered within the Megatheria or clade 5 mylodontines. The holotype of P. hexaspodylus is recovered as a mylodontine more derived than Nematherium, but never as a member of the mylodontine clade 2 or 3. Simonylonodon uccasammenensis is recovered as a mylodontine more derived than those in clade 3 but never included within clade 2. Chubatherium ferelloi is recovered as a mylodontine not included within clades 2 and 3. Uruscomotherium garciai is recovered as a mylodontine more derived than
clade 3 but not included within clade 1. *Eionaletherium tanycremnus* is recovered as a mylodontine more closely related to *M. darwinii* than to clade 3, but not included in clade 1 or 4. *Mirandabradyz zabasi* and *P. venezuelanum* are recovered as mylodontines not included within clade 1, 3, or 4. *Uramaquia darwinii*, *P. venezuelanum* and *S. uccasamamensis* are suggested to form another possible clade, here called 'clade 6' (Fig. 7B).

A majority-rule consensus was obtained (cutoff: 50%; Fig. 7B) and suggests a placement for some of these wildcard taxa, as well as the OTU formed by *Glossotherium robustum* and *Glossoth-erium wegeneri*. The latter OTU is suggested as the closest relative to the Lestodontinae, as in Gaudin (2004). We informally call this possible group 'clade 6' (Fig. 7B). *Mirandabradyz zabasi* and *P. venezuelanum* are suggested to form a possible group here informally called 'clade 7' (Fig. 7B). C. clades 3 and 7 are suggested to form another possible clade, here called 'clade 8' (Fig. 7B). *Chubatherium ferrelli* is suggested to represent the sister taxon of *S. uccasamamensis*, forming a possible clade here informally called 'clade 9' (Fig. 7B). This clade is suggested to be outside clade 4. *Octoetherium giganteum* is suggested to represent a clade of the mylodontid group defined by the most recent common ancestor of *Octomylopon* and *Mylodon. Glossoth-erium garbani*, *P. hexapontylos*, *E. tanycremnus*, and *U. gar- ciai* are suggested to represent mylodontines more derived than *Nematherium*, but not included in the Scelidotheriinae, nor in clade 1, 4, 6, 8, or 9. The groups obtained from the majority-rule consensus are only suggestive and cannot be preferred on the basis of parsimony, because they are contradicted by some MPTs that represent equally parsimonious possibilities. A second phylogenetic analysis, in which all taxa not scored for characters of the hand were excluded, provides further suggestive positions (Fig. 7C). Clades 2 and 6 were recovered. A reduced consensus, obtained after pruning the wildcard taxa *O. giganteum* and *G. garbani*, allowed recovery of the holotype of *P. hexapontylos* and *S. uccasamamensis* as successive sister taxa to clade 5, which may be seen as suggestive of their actual position. Clade 4 was also recovered. However, some results depart from those of Gaudin (2004) and our first analysis, such as the position of *P. confusum* as a non-mylodontine mylodontid, or the stronger sister-group relationship between *Megatherium americanum* and *Glossotherium jeffersoni* to the exclusion of *Hapa-lops* sp. and *Mionotherpus cartellei*. The results of this second analysis are produced by excluding relevant data from the excluded taxa and are therefore globally less parsimonious. Constraining the topology produced by the smaller analysis in a search using all the taxa and characters reduces constraints (100 steps).

The results of our phylogenetic analysis lend support to the hypothesis of a closer relationship between *M. darwinii* and *M. ibseni* than with *P. harlani*, *T. segnis*, *G. robustum*, *G. garbani*, and *P. confusum*. This agrees with the hypothesis of close relationship between the two taxa offered by Cartelle (1991) on the basis of cranial, mandibular, and dental evidence. Several features from the cuneiform previously thought to separate *M. ibseni* from *G. robustum* and *P. harlani* by Cartelle (1980) represent synapomorphies shared by *M. darwinii* and *M. ibseni*. These include the ulnar facet concave along an oblique axis, the ulnar and pisiform articular facets separated, and the greater degree of development of the distolateral process. The lack of resolution among *P. harlani*, *G. robustum*, and the Lestodontinae sensu
CONCLUSIONS

The principal ideas derived from this work are (1) the anatomy of the manus of Mylodon darwinii is different from all the other mylodontine hand skeletons described to date, especially regarding the structure of the trapezoid; (2) a considerable amount of variability useful for phylogenetic study is found in the hand elements of mylodontines; (3) M. darwinii presents different adaptations in digits II and III, with the latter being more specialized for stability; (4) phylogenetic relationships proposed by inclusion of characters of the hand mostly agree with results of previous analyses predominantly based on craniodental evidence (Esteban, 1996; Gaudin, 2004); (5) the analysis provides evidence of close relationships between M. darwinii and Mylodonopsis ibseni, principally supported by the morphology of the cuneiform; and (6) the results of our phylogenetic analysis suggest four different dispersal events to North America in mylodontine history.

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Webb (1989) contrasts with the better resolution of these taxa in the analyses of Esteban (1996) and Gaudin (2004). Our results suggest that the holotype of P. hexaspindylus cannot be referred to the species G. robustum, which contrasts with the conclusions of Cabrera (1936) based on skull anatomy. The referral would only be possible from a phylogenetic standpoint if the holotypes of P. hexaspindylus and Glossotherium were recovered as sister groups. Our analysis also suggests that UF 10922 cannot be referred to the species G. garbanii, because the former belongs to clades 4 and 5, whereas the latter is excluded from both. The results suggest that G. garbanii is not closely related to either G. robustum or P. harlani, in spite of being assigned those genera by previous authors (Montellano and Carranza-Castañeda, 1981; Montellano-Ballesteros and Carranza-Castañeda, 1986; Morgan, 2008).

Autapomorphies of the Manus—The phylogenetic analysis reveals a possible autapomorphy of Mylodon darwinii, namely, the flattened pisiform. Its presence in Glossotherium robustum is thus interpreted as convergent in the context of the present analysis. Another possible autapomorphy of M. darwinii not included in the phylogenetic analysis is having the long axis of the dorsal surface of the trapezoid perpendicular to the main part of the scaphoid facet, a feature not found in other mylodontids (Stock, 1925; Webb, 1989; pers. observ., JAH). The direction of the long axis of the trapezoid dorsal surface likely correlates with its irregular pentagonal shape. This shape is unique to M. darwinii—in other mylodontids the outline is roughly subtriangular (Owen, 1842; Stock, 1925; pers. observ., JAH). The relative elongation along the axis perpendicular to the main part of the scaphoid facet is probably related to the remarkable depth of the dorso-palmar concavity on the palmar part of the articular facet for metacarpal II.

Morphological Evolution—Apomorphic character states of the different clades for the characters in our original data matrix are presented in Supplementary Data 7. These do not unambiguously support the recovered clades, either because of missing data in some basal members of the ingroup or in the most immediate outgroups. Mylodontines of clade 5 present many apomorphies, representing a huge morphological gap between Pseudoprepotherium confusum and members of clade 5, and a few others separate them from Glossotherium garbanii. An intriguing aspect of the results of our phylogenetic analysis is that most of the features linking M. darwinii to the group including M. ibseni, but excluding G. robustum and P. harlani, come from a single bone, the cuneiform. This suggests correlation of some sort among the characters of the same bone in both cases, but we cannot invoke a logical correlation on purely morphological grounds. Anyway, the presence in G. garbanii of a cuneiform distolateral process—shared with M. darwinii and M. ibseni, but not G. robustum and P. harlani—and confluent articular facets for ulna and pisiform—found in the latter two, but not in M. darwinii nor M. ibseni—indicates that at least some of these features are not correlated.

Biogeographical Remarks—The resulting consensus tree in the data matrix produced here indicates that the North American taxa are not closely related to each other; consequently, four mylodontine dispersal events between South and North America occurred: one involved Thinobadistes; another involved the basal taxon Glossotherium garbanii; yet another involved a member—UF 10922—of the most exclusive group including Mylodon darwinii; and the last involved Paramylyodon harlani. This contrasts with the hypothesis of close relationships between all North American mylodontines except for Thinobadistes (Morgan, 2008, and references therein). However, the anatomy of North American Blancan mylodontines is still poorly known, so our conclusions are only preliminary.
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