

Thoracic member (pectoral girdle and forelimb) bones of *Mylodon darwinii* Owen (Xenarthra, Mylodontidae) from the Late Pleistocene of Central Argentina and their phylogenetic implications

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Abstract A nearly complete skeleton, including most of the thoracic member bones of the sloth *Mylodon darwinii*, have been found in Upper Pleistocene strata from Anisacate River, Argentina. The thoracic member bones resemble their homologues in *Glossotherium robustum*, *Paramylodon harlani*, and *Mylodonopsis ibseni* in the following traits: (1) the olecranon is mediolaterally compressed; (2) the radius has an acute styloid process; (3) the radial diaphysis medial border is straight for two thirds of its length; (4) the radial shaft medial border forms an angle with the medial border of the styloid process. The radius presents a distinctive, mostly proximally facing articular circumference. The unfused epiphyses and feeble muscle attachment ridges indicate a sub-adult ontogenetic stage. Deviation of the olecranon and weak *M. teres major* origin and insertion, suggest a low fossorial specialization. The

structure of the thoracic limb bones does not support climbing habits, because pronation-related features are reduced and the humeral head is not prominent. The structure of the radius suggests graviportal adaptations: the proximal head is mediolaterally expanded and the diaphysis straight. A phylogenetic analysis adding thoracic member characters recovers *M. darwinii* as part of a clade that includes *Glossotherium robustum* and *Paramylodon harlani*, but excludes *Lestodon armatus*. This contrasts with the results of previous analyses focusing on the head skeleton, highlighting the relevance of sampling postcranial characters in phylogenetic analyses of mylodontine sloths.

Keywords *Mylodon darwinii* · Mylodontinae · Osteology · Phylogeny · Late Pleistocene

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Kurzfassung Ein nahezu komplettes Skelett des Faultiers *Mylodon darwinii*, inklusive der meisten Brust-Extremitätenknochen, wurde in oberpleistozänen Schichten des Anisacate-Flusses in Argentinien gefunden. Es erlaubt erstmals eine detaillierte Beschreibung der Schultergliedmaßen und Unterarmknochen. Diese spiegeln die Homologien in *Glossotherium robustum*, *Paramylodon harlani* und *Mylodonopsis ibseni* mit den folgenden Eigenschaften wider: (1) der Ellenbogen ist mediolateral zusammengedrückt; (2) der Radius hat einen spitzen Styloid-Fortsatz; (3) der radiale Diaphysen-Medialrand ist auf 2/3 der Länge gerade; (4) der radiale Schaft-Medialrand bildet einen Winkel mit dem Medialrand des Styloid-Fortsatzes. Der Radius zeigt einen deutlichen hauptsächlich proximal gerichteten Gelenkumfang. Die unverschmolzenen Epiphysen und schwachen Muskelansatzrücken deuten auf ein sub-adultes ontogenetisches Stadium hin. Grazile Unterarmknochen und die Ausbildung eines schwachen

großen Rundmuskels weisen auf eine weniger grabende Spezialisierung hin. Die Struktur der Brust-Extremitätenknochen unterstützt keine Kletterhabitats, da pronationsähnliche Merkmale reduziert sind und der Humeruskopf nicht markant ist. Die Struktur des Radius deutet auf graviportale Anpassungen hin: der proximale Kopf ist mediolateral ausgeweitet und die Diaphyse ist gerade. Eine phylogenetische Analyse mit Merkmalen der Brust-Extremitätenknochen zeigt, dass *M. darwinii* näher mit *Glossotherium robustum* und *Paramylodon harlani* verwandt ist, als die Lestodontini. Dies steht im Gegensatz zu Resultaten früherer Analysen, welche auf den Schädel fokussiert waren und verdeutlicht damit die Relevanz postcranialer Merkmale in phylogenetischen Analysen von mylodontinen Faultieren.

Schlüsselwörter *Mylodon darwinii* · Mylodontinae · Osteologie · Phylogenie · spätes Pleistozän

Introduction

Mylodon darwinii Owen, 1839 is a South American Pleistocene sloth best known by a number of well-studied skulls and mandibles (Owen 1839; Reinhardt 1879; Esteban 1996; Brandoni et al. 2010). Large parts of the postcranial skeleton have also been recovered and described (Roth 1899, 1902; Nordenskiöld 1900; Woodward 1900; Studer 1905; Kraglievich 1928, 1934; Bargo and Deschamps 1996; Martín 2008; Haro et al. 2016; McAfee 2016). Exceptionally preserved remains, including hide, hair, horny claw sheaths, muscles, tendons, and dung (Jacob 1899; Moreno and Woodward 1899; Roth 1899; Philippi 1900, 1901; Woodward 1900; Ridewood 1901; Studer 1905), were recovered at Cueva del Milodón, on the Última Esperanza inlet, southern Chile. In 1999 a specimen of *M. darwinii*, including the skull, mandibles, cervical, dorsal and caudal vertebrae, a scapula, and most of the limb bones, was discovered on the banks of the Anisacate River in central Argentina (Tauber and Di Ronco 2003). This specimen allowed detailed study of the anatomy of bones of the manus (Haro et al. 2016). The variability of one thoracic member skeletal character is widely recognized for its importance in mylodontid phylogeny, the presence or absence of the supracondylar (=entepicondylar) foramen of the humerus (Owen 1842). However, zeugopodial characters have not been previously included in phylogenies of mylodontine sloths (e.g., Gaudin 2004; Rincón et al. 2015; Haro et al. 2016). The present contribution describes the scapula, humerus, radius, and ulna of the Anisacate River specimen of *M. darwinii* comparing them with previously described mylodontine homologous elements, complementing the study of the manus of the same

specimen. Here, we attempt to assess the usefulness of thoracic member character variability in mylodontine phylogeny, and consider several implications for the ontogeny and habits of *M. darwinii*.

Abbreviations

Anatomical abbreviations

Cf1, superior dental arcade caniniform; **cf1**, inferior dental arcade caniniform; **Mf1-4**, superior dental arcade molari-forms 1 to 4; **mf1-3**, inferior dental arcade molariforms 1 to 3.

Institutional abbreviations

BM(NH), Natural History Museum, London, UK; **CORD PZ**, Colección de Paleozoología, Museo de Paleontología, Universidad Nacional de Córdoba, Córdoba, Argentina; **FMNH**, Field Museum of Natural History, Chicago, IL, USA; **LGP-Q**, Laboratório de Geologia e Paleontologia, Fundação Universidade de Rio Grande, Rio Grande, Brazil; **MACNC Pv**, Colección Paleontología de Vertebrados, Museo de Antropología y Ciencias Naturales de Concordia, Concordia, Argentina; **MACN Pv**, Colección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales, “Bernardino Rivadavia,” Buenos Aires, Argentina; **MCN-PV**, Coleção de Paleovertebrados, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MLP**, Museo de La Plata, La Plata, Argentina; **MMCIPAS**, 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; **UCMP**, Museum of Paleontology, University of California, Berkeley, CA, USA; **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), according to the rationale of Harris (2004). Sloth teeth are not readily comparable to those of domestic mammals covered by that book, so we follow the nomenclature in Carlini and Scillato-Yané (2004), as proposed by Miño-Boilini et al. (2014). Mylodontine clade names follow

informal usage in Haro et al. (2016). Skeletal comparisons were based on features mentioned in the literature describing the scapula, humerus, radius, and ulna of mylodontid taxa included in “Appendix 1”.

The phylogenetic analysis was performed with the program TNT (Goloboff et al. 2003, 2008). The analysis was based on equal weights parsimony. It was performed applying the TBR algorithm on 1,000,000 random addition sequence Wagner trees (replications), keeping only one (1) shortest tree per replication. 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 a reduced strict consensus tree. A strict consensus tree and a reduced strict consensus tree were obtained. The latter was obtained after a posteriori pruning of the wildcard OTUs. 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 the OTUs not scored for the characters from the thoracic member here studied or with unstable positions. Variability in a binary character state in *Mylodon darwini* does not help to distinguish or directly establish the phylogenetic position of this taxon, so these characters are not included in the final analysis. Characters with a variation correlated to ontogenetic development are likewise excluded from analysis. Thus, characters related to the presence or prominence of ridges or fossae representing muscular attachment areas are not included because Stock (1925) related prominence of muscle scars to age in sloths.

A small data matrix of phylogenetically informative characters was generated. The matrix adds ten thoracic member characters to a slightly modified version of the character list in Haro et al. (2016) (“Appendix 2”). The data matrix includes 11 mylodontine taxa and six non-mylodontine outgroups. The recognition of the latter as outgroups was based on a previous large phylogenetic study (Gaudin 2004). The 11 mylodontine taxa are: *M. darwini*; *Paramylodon harlani* (Owen, 1839); *Ocnotherium giganteum* (Lund, 1839); *Lestodon armatus* Gervais, 1855; *Thinobadistes segnis* Hay, 1919; *Pseudopreotherium confusum* Hirschfeld, 1985; *Mylodonopsis ibseni* Cartelle, 1991; *Bolivatherium urumaquensis* (Linares, 2004); *Simomylodon uccasamamensis* Saint-André, Pujos, Cartelle, De Iuliis, Gaudin, McDonald, and Mamani Quispe, 2010; *Glossotherium garbanii* Montellano-Ballesteros and Carranza-Castañeda, 1986; and *Glossotherium* Owen, 1839. The latter OTU consists of the closely related species *Glossotherium robustum* (Owen, 1842) and *Glossotherium wegneri* (Spillmann, 1931). We follow Gaudin (2004) in merging these two species into a single OTU because they have been recovered as sister taxa

in the phylogenetic analysis by Esteban (1996). We exclude *G. garbanii* from this OTU following results in Haro et al. (2016). The holotype of *Pseudolestodon hexaspondylus* Rautenberg, 1906 was included as a distinct OTU in order to test its purported referral to *G. robustum* by Cabrera (1936), following its doubtful position in Haro et al. (2016). The six non-mylodontine sloth taxa are: *Scelidotherium* Owen, 1839; *Catonyx* Ameghino, 1891; *Hapalops* Ameghino, 1887; *Mionothropus cartellei* De Iuliis, Gaudin and Vicars, 2011; *Megatherium americanum* Cuvier, 1796; and *Megalonyx jeffersoni* Desmarest, 1822. Outgroup topology was not enforced a priori.

The data matrix is presented in “Appendix 3”. Mechanisms of safe taxonomic reduction (Wilkinson 1995) suggested exclusion of some comparative material, such as *Brievabradys laventensis* Villarroel, 2000; the intertropical “*Glossotherium* aff. *G. lettsomi*” of Cartelle (1992); and the specimens referred to the genus *Glossotherium* by Pitana (2011). The character state scores for *Brievabradys laventensis* are a subset of those from *P. confusum*. Scores of the intertropical “*Glossotherium* aff. *G. lettsomi*” are a subset of those from *M. ibseni*. This data matrix was then combined with those of Gaudin (2004) and Rincón et al. (2015). Taxa not included in at least one of these matrices, but included in at least one other, are scored as missing data in the characters of the matrices in which they were not included. The data matrix, ready for use in TNT, is provided as Online Resource 1.

Systematic paleontology

Order **Pilosa** Flower, 1883

Suborder **Tardigrada** Latham and Davies in Forster, 1795

Family **Mylodontidae** Gill, 1872

Subfamily **Mylodontinae** Gill, 1872

Genus ***Mylodon*** Owen, 1839

Type species. *Mylodon darwini* Owen, 1839.

Diagnosis (emended). We follow the diagnosis of Esteban (1996), adding a few distinctive characters based on the thoracic limb material. *Mylodon darwini* is diagnosed by an incisive bone (=premaxilla) dorsally elongated and connected to the nasals by a bony midline bridge; medial ramus of incisive bone longer than the lateral ramus; nasals strongly convex at midlength; dental formula 4/4; lack of a diastema between Mf1 and Mf2; zygomatic (=postorbital) processes of frontal well developed; wide space between temporal lines; rostral border of facial surface of maxilla completely concave; external caudal opening of the mandibular canal caudal to mf3 and entirely rostral to mandibular coronoid process; mandibular coronoid process with short base; cf1 small, non-caniniform, and oval in

section; mfl oval with distal surface less convex than in *Myloodonopsis ibseni*; cuneiform with prominent distolateral process and articular facet for ulna concave in dorso-lateral direction; pisiform flattened; trapezoid dorsal surface elongated perpendicular to main part of scaphoid facet; distal carina on metacarpal III oblique; astragalus with single calcaneal facet and odontoid process set at a wide obtuse angle to lateral part of the astragalar trochlea; and presence of dermal ossicles.

Myloodon darwinii Owen, 1839

Figures 1, 2 and 3.

Holotype. BM(NH) M-16617; mandible with teeth.

Diagnosis. As for the genus by monotypy.

Stratigraphic and geographic distribution. Ensenadan–Lujanian (Pleistocene); South America from southern Bolivia to the southern extremity of Patagonia (Brandoni et al. 2010).

Studied material. The specimen, CORD PZ 4570, is curated at the Museo de Paleontología, Universidad Nacional de Córdoba. Most of the skeleton has been recovered. It includes a left scapula and both sets of humeri, radii, and ulnae. The right ulna and both radii are nearly completely preserved. The humeri are incompletely preserved. The scapula and left ulna are incomplete. The bones were generally well preserved, but locally affected by surface erosion. Web-like rhizoconcretions are attached to the surfaces of the bones, indicating the presence of paleosols.

Description. The following descriptions focus on characters showing variation among myloodontines. Relevant bone measurements are listed in Table 1.

Determination

CORD PZ 4570 is assigned to the taxon *Myloodon darwinii* on the basis of 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 maxilla concave (Esteban 1996); snout dorsoventrally taller than mediolaterally wide (Esteban 1996); Mf2–4 subtriangular (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 astragalar trochlea (Kraglievich 1928). The skull and dentaries of CORD PZ 4570 are not completely prepared, so not all diagnostic features listed in previous diagnoses (e.g., Cattoi 1966; Esteban 1996) were recognized.

Scapula

Myloodon darwinii scapulae have been previously reported from the Última Esperanza Inlet (e.g., Roth 1899;

Nordenskiöld 1900) and partially described by Studer (1905). The fragments of CORD PZ 4570 completely agree with previous accounts of scapular osteology in *M. darwinii* and many other myloodontines (e.g., Owen 1842; Reinhardt 1875; Studer 1905; Stock 1925; Webb 1989; Cartelle 1992). However, some comparative remarks can be made. The preserved portion of the glenoid suggests it was not kidney-shaped, differing from the condition present in the holotype of *Pseudolestodon hexaspondylus* Rautenberg, 1906. The caudal angle of the scapula is angular instead of rounded (Fig. 1a), thus resembling the condition present in *Glossotherium robustum* (Owen, 1842) and differing from the condition in some specimens of *Scelidotherium* (Cuenca Anaya, 1995). The surfaces of the supra- and infraspinal fossae present ridges (Fig. 1a) (Studer 1905). Ridges are also found at the fossae in *G. robustum* (Owen, 1842), in contrast to their lack in the holotype of *P. hexaspondylus* Rautenberg, 1906. The caudal fossa for attachment of the *M. teres major* is small and not expanded.

Humerus

The humerus has been previously reported for *Myloodon darwinii* by Roth (1899), Nordenskiöld (1900), Lehmann-Nitsche (1902), Kraglievich (1934), and Bargo and Deschamps (1996). It has been described in Kraglievich (1934), Bargo and Deschamps (1996), Pitana (2011), and Saint-André et al. (2010). Certain differences with these materials are noted here. The head of the humerus is craniocaudally deeper than mediolaterally wide, as in the *M. darwinii* material from Olavarría and most other myloodontids (Owen 1842; Kraglievich 1934). This articular surface is evenly convex, but corresponds to a reduced share of the surface of a sphere. The greater tubercle is almost as proximally projected as the head. No fossa is developed immediately distal to the head of the humerus and medial to the lesser tubercle on the caudal surface, as in *Paramyloodon harlani* (Webb 1989). This is in contrast to the situation in *Thinobadistes segnis* (Webb 1989). The tuberosity for insertion of the *M. teres major* is absent, contrasting with its presence in *Scelidotherium* (McDonald 1987; Cuenca Anaya 1995). The area limited by the deltoid and pectoral ridges is smooth in CORD PZ 4570 (Fig. 1b), in contrast to the rugged condition in *M. darwinii* from Olavarría (Kraglievich 1934) and *Glossotherium robustum* (Owen, 1842). The prominence of the lateral branch of the deltoidal V-shaped scar is low in CORD PZ 4570 (Fig. 1b), as in *Ocnotherium giganteum* (Cartelle 1992). This contrasts with the well-developed scar present in specimens of *M. darwinii* from Olavarría (Kraglievich 1934), as well as *T. segnis* (Webb 1989). The medial branch of the deltoidal scar is not marked, but is prominently raised. Its

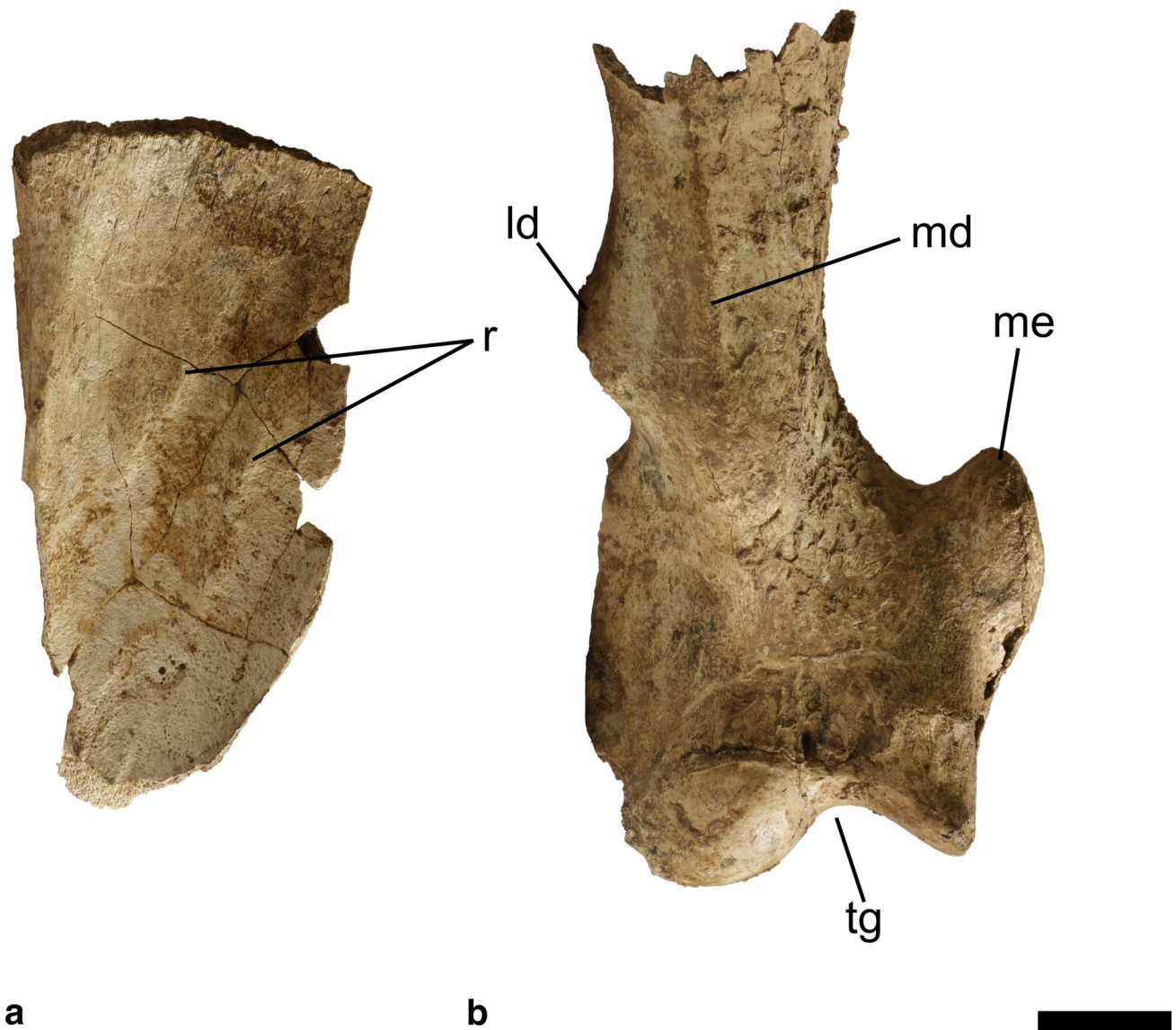


Fig. 1 Proximal thoracic member bones from the *Mylodon darwini* specimen CORD PZ 4570. **a** Lateral view of scapular caudoventral fragment, dorsal to the top; **b** cranial view of right humerus, proximal

to the top. *ld* lateral branch of deltoid ridge, *md* medial branch of deltoid ridge, *me* medial epicondyle, *r* ridges, *tg* groove of the humeral trochlea. Scale bar equals 50 mm

prominence resembles the condition of *Lestodon armatus* (Kraglievich 1934), but contrasts with the less prominent state in both *M. darwini* from Olavarría (Kraglievich 1934) and *P. harlani* (Hirschfeld 1985). The pectoral ridge is relatively poorly developed in CORD PZ 4570, as in most specimens of *P. harlani* (Stock 1925; Webb 1989). By contrast it is well marked in other specimens of *M. darwini* (Kraglievich 1934) and *Glossotherium wegneri* (Hoffstetter 1952).

On the distal humerus of CORD PZ 4570, the supracondylar (=entepicondylar) foramen is absent (Fig. 1b), as in other material assigned to *M. darwini* (Kraglievich 1934). This feature is shared by most other mylodontines, including *G. robustum* (Owen, 1842) and *L. armatus*

(Gervais 1873). This contrasts with the presence of the foramen in the Miocene mylodontines *Pseudopotherium confusum* (Hirschfeld 1985; Saint-André et al. 2010) and *Brievabradys laventensis* (McDonald 1997). The medial epicondyle presents a proximal projection (Fig. 1b), as in other material assigned to the same taxon (Kraglievich 1934), as well as in *P. harlani* (Lull 1915; Saint-André et al. 2010), but contrasting with the lack of the projection in *P. confusum* (Hirschfeld 1985; Saint-André et al. 2010). The fossa for the olecranon in the caudal surface of the distal humerus is not marked, as it is in *G. wegneri* (Hoffstetter 1952). This is in contrast to the presence of a well-developed fossa in *Simomylodon uccasamamensis* (Saint-André et al. 2010). The angle between the surfaces

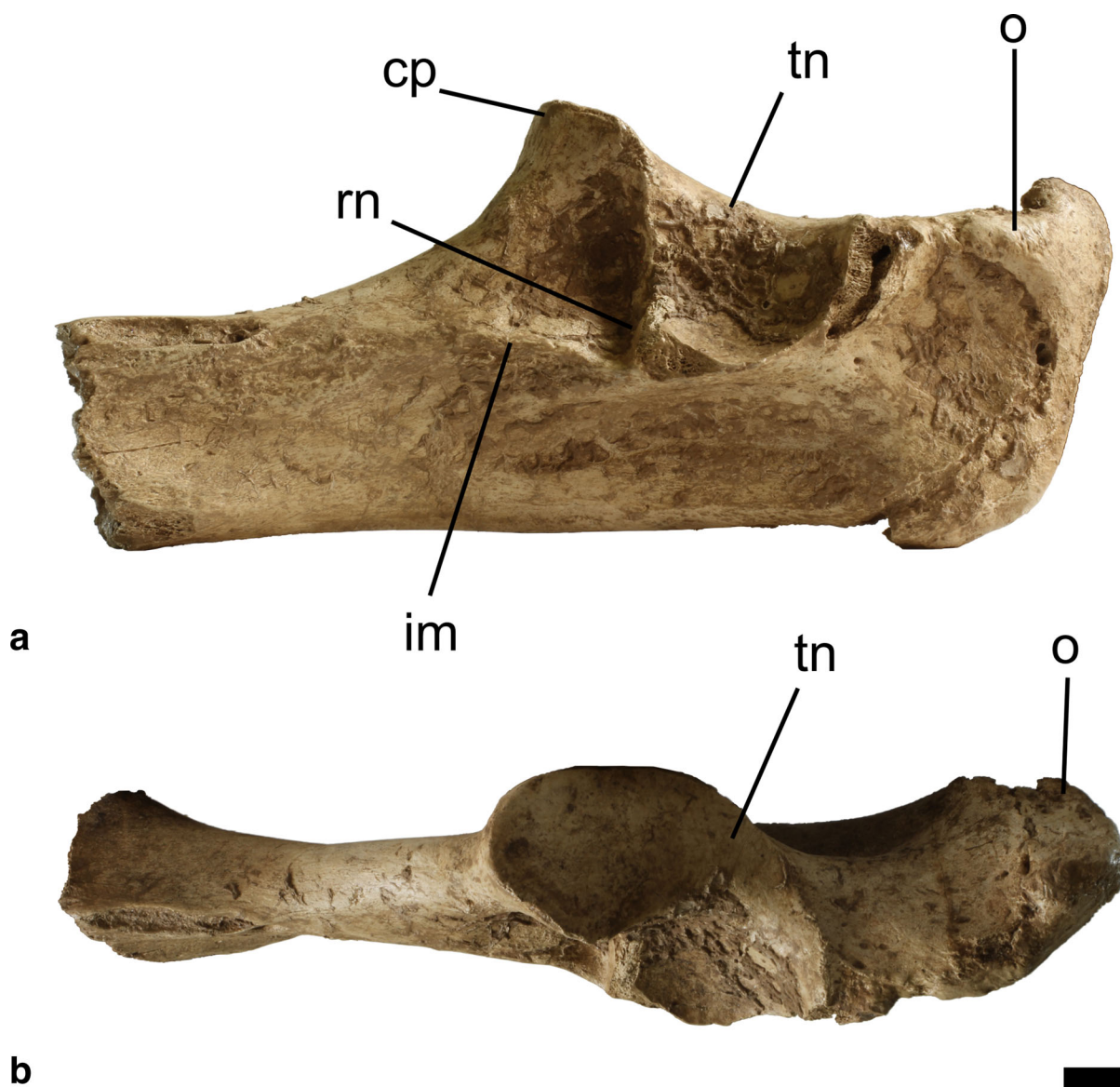


Fig. 2 Left ulna, excluding the distal epiphysis, of the *Mylodon darwinii* specimen CORD PZ 4570. **a** Lateral view, proximal to the top; **b** cranial view, proximal to the top. *cp* coronoid process, *im*

interosseal margin, *o* olecranon, *rn* radial notch, *tn* trochlear notch. Scale bar equals 50 mm

surrounding the trochlear groove in the humeral condyle is close to 90° in cranial and caudal views (Fig. 1b), as in *L. armatus* (Reinhardt 1875). This contrasts with the obtuse angle in *G. robustum* (Reinhardt 1875). The medial part of the distal articular surface is largely concave mediolaterally.

Ulna

The ulna of the *Mylodon darwinii* specimen, CORD PZ 4570, is relatively gracile, with a maximum length/maximum craniocaudal depth (at the level of the coronoid process tip) ratio of 2.71. This is similar to the 2.65 ratio in

Glossotherium wegneri (Hoffstetter 1952) and the 2.64 ratio in the FMNH P 14288 specimen of *M. darwinii* (McAfee 2016), but larger than the mean of 2.42 in *Glossotherium robustum* (McAfee 2016) and smaller than the 3.01 ratio in *Thinobadistes segnis* (Webb 1989). The olecranon of CORD PZ 4570 is proportionally short, representing 0.22 of the total length. This is less than in *G. robustum*, in which the ratio exceeds 0.25 (Owen 1842). Thus, the Index of Fossorial Ability (IFA; Vizcaíno et al. 1999) is very low, approximately 0.44 (Tauber et al. 2011). By comparison, the IFA of *Lestodon armatus* is 0.53, that one in *Scelidotherium leptocephalum* Owen, 1839 is 0.54, and that one in a specimen of *G. robustum* is 0.56 (Bargo

et al. 2000). The IFA more closely resembles the value in a gracile specimen of *G. robustum* (0.47; Christiansen and Fariña 2000). The olecranon is mediolaterally compressed (Fig. 2a, b), as in *Paramyiodon harlani*, but contrasting with the mediolaterally expanded condition in *T. segnis* (Webb 1989). The olecranon is medially, but not caudally, bent. The proximocranial projection of the CORD PZ 4570 olecranon is prominent (Fig. 2a), as in *G. robustum* (Cartelle 1992). This is in contrast to the lesser development in the intertropical “*Glossotherium* aff. *G. lettsomi*” (Cartelle 1992). The proximocaudal corner of the CORD PZ 4570 olecranon is angular, as exposed in medial and lateral views (Fig. 2a), similar to this trait in *G. wegneri* (Hoffstetter 1952). This contrasts with the rounded condition present in *G. robustum* (Hoffstetter 1952). The craniocaudal expansion of the CORD PZ 4570 olecranon (ratio between craniocaudal depth of olecranon and total length of bone: 0.33) is somewhat deeper than in *Scelidothierium* (ratio: 0.25–0.28; Aramayo 1988; pers. obs., CORD PZ 4464, 11293). The dorsomedial surface of the olecranon is proximodistally concave and transversely convex. The trochlear notch (=articular surface for the humerus) is longer than wide, as in FMNH P 14288 (McAfee, pers. comm.), but contrasting with the wider than long articular surface in *G. robustum* (Owen, 1842). In CORD PZ 4570 a rounded notch invades this articular surface at its distal contour, as in *P. harlani* (Allen 1913). The trochlear notch presents a ridge fitting into the trochlear groove of the humerus, which projects from the rest of the surface craniolaterally. The region of the trochlear notch medial to that ridge is proximodistally longer relative to its mediolateral width than in *G. robustum*, as in some specimens of *P. harlani* (Harlan 1843). The region lateral to the previously mentioned ridge is strongly concave, as in *G. robustum* (Owen, 1842). This trait contrasts with the convex condition present in *Pseudopreoptherium confusum* Hirschfeld, 1985. The latter region is mediolaterally narrow relative to its proximodistal length, as in *P. harlani*, and contrasting with the condition present in *G. robustum* (Allen 1913). The anconeal process is located proximomedial to the part of the trochlear notch lateral to the ridge, as in *P. harlani* (Harlan 1843), instead of proximolateral to it as in *P. confusum* Hirschfeld, 1985. The part of the trochlear notch lateral to the ridge presents a slightly concave distal border, contrasting with the convex border of *Scelidothierium* (pers. obs., CORD PZ 11293). The radial notch (=articular surface for radius) contacts the part of the trochlear notch lateral to the ridge, as in *G. robustum* (Owen, 1842). This contrasts with the lack of contact in some specimens of *P. confusum* Hirschfeld, 1985. The radial notch does not contact the part of the trochlear notch medial to the ridge (Fig. 2a, b), unlike the condition in *P. confusum* Hirschfeld, 1985. The radial notch is not

rugged, contrasting with the condition in *T. segnis* (Webb 1989). The radial notch is set in a plane orthogonal to that of the coronoid process. The radial notch contacts the trochlear notch at a straight border, and is approximately semicircular in shape. It is instead described as oval in FMNH P 14288 (McAfee 2016).

In cross-section, the ulna is elongate, sinuous, and not trihedral, unlike *P. harlani* (Lull 1915). A fossa is present on the internal surface of the ulna (for origin of *M. flexor digitorum profundus*), as in *G. robustum* (Owen, 1842), but in contrast to *P. confusum* Hirschfeld, 1985. A strong, but dull ridge proximocaudally limits the fossa on the internal surface of the ulna. Its prominence is similar to that of *P. harlani*, but unlike its lesser development in *P. confusum* Hirschfeld, 1985. In the ulna of CORD PZ 4570 the oblique ridge on the medial surface near the distal end of the bone, which likely limited the attachment area of the *M. pronator quadratus*, is very reduced, contrasting with the condition in FMNH P 14288 (McAfee 2016). On the proximal half of the lateral surface, the interosseal margin is located caudal to the cranial border of the ulna (Fig. 2a), as in *P. harlani* (Lull 1915). By contrast, in *P. confusum* the interosseal margin reaches the cranial border within the proximal half (Hirschfeld 1985). This ridge, extending distally from the distolateral angle of the trochlear notch, presents the distal part reduced (Fig. 2a, b), and thus less prominent than in FMNH P 14288 (McAfee 2016) and *G. robustum* (Owen, 1842). The oblique ridge caudal to the interosseal margin on the lateral surface (Fig. 2a), which likely separated the fossae for attachment of the origins of *Mm. abductor digiti I longus* and *extensor digiti II*, is less marked than in FMNH P 14288 (McAfee 2016) and *Scelidothierium* (pers. obs., CORD PZ 4464, 11293). The distal part of the lateral surface of the shaft is for the most part transversely concave, as in *Scelidothierium* (pers. obs., CORD PZ 11293). This is in contrast to the convex transverse relief of *G. robustum* (Owen, 1842). Reticular ridges are not developed upon the lateral surface of the ulna (Fig. 2a), in contrast to their presence in *G. robustum* (Owen, 1842). The caudal margin of the ulna is nearly straight in lateral view (Fig. 2a). The caudal margin of the ulna is transversely convex, in contrast to the flat caudal margin of *G. robustum* (Owen, 1842). The styloid process, which bears the carpal articular surface (for articulation with the cuneiform and pisiform), is distally directed (Fig. 2b), as in *P. harlani* (Hirschfeld 1985), distinct from the oblique direction present in *P. confusum* (Hirschfeld 1985). The part of the carpal articular surface in contact with the cuneiform is slightly convex (Fig. 2a, b). In *Scelidothierium* it is at least partly concave (Cuenca Anaya 1995). The cuneiform facet is oriented distally, distinct from the more oblique craniodistal facet in *Scelidothierium* (pers. obs., CORD PZ 11293).

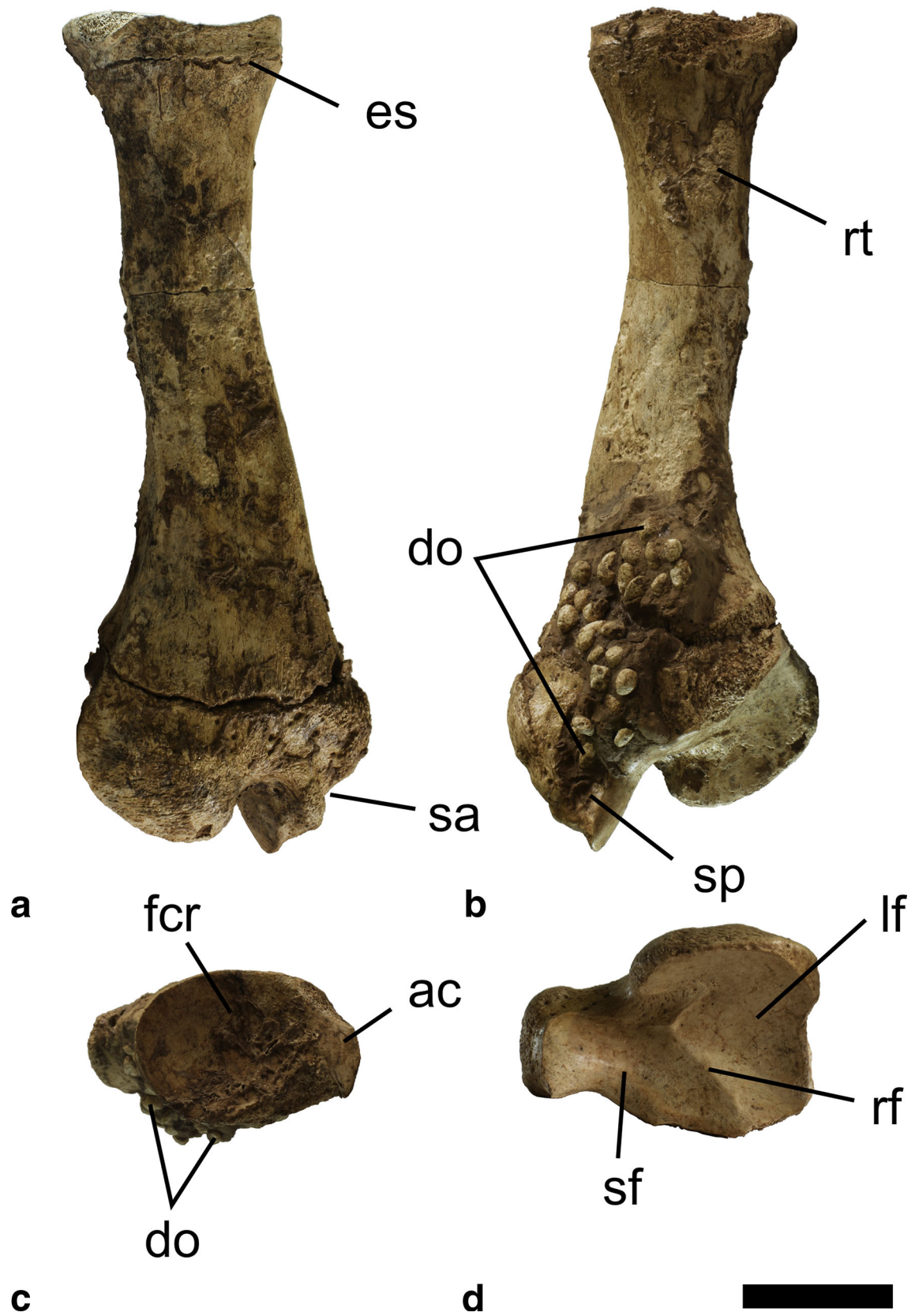


Fig. 3 Radii of the *Myiodon darwinii* specimen CORD PZ 4570. **a** Cranial view of right bone, proximal to the top; **b** caudal view of right bone, proximal to the top; **c** proximal view of right bone, cranial to the top; **d** distal view of left bone, cranial to the top. *ac* articular circumference, *do* dermal ossicles, *es* proximal epiphyseal suture, *fer* radial head fovea, *lf* lunar articular facet, *rf* ridge in carpal articular surface between facets for scaphoid and lunar, *rt* radial tubercle, *sa* sulcus for *M. adductor digiti I longus*, *sf* scaphoid articular facet, *sp* styloid process. Scale bar equals 50 mm

Radius

The radius of CORD PZ 4570 is relatively gracile (Fig. 3a, b), as in *Lestodon armatus* (Reinhardt 1875). By comparison the radius of *Ocnotherium giganteum* is robust (Cartelle 1992). The ratio between the maximum length and maximum width (measured at the distal end) of CORD PZ 4570 is 2.73 in the right radius and 2.88 in the left radius. It more closely approaches the ratio in *Simomyiodon uccasamamensis* (2.91; Saint-André et al. 2010), than that of *Thinobadistes segnis* (3.02–3.28; Webb 1989) or the FMNH P 14288 specimen of *Myiodon darwinii* (3.2;

McAfee 2016). The ratio is much higher than in *Pseudopreotherium confusum* (2.47–2.58; Hirschfeld 1985). The general shape of the radius is rather straight, as in *Paramyiodon harlani*, but unlike the sinuous shape observed in scelidotheriines (McDonald 1987). McAfee (2016) also reported a straight radius for other *M. darwinii* material. The radial head is distinctly expanded mediolaterally, so the medial border of the radial head is quite prominent relative to the neck, as is the medial part of the proximal epiphyseal suture (Fig. 3a, b). These contrast with the less prominent condition of both structures present in *Scelidotherium* (pers. obs.; specimen CORD PZ 4464). The long axis of the radial head fovea (=proximal articular surface for the humerus) is approximately coplanar with the long axis of the carpal articular surface, as in *P. harlani*, but in contrast to the 45° twist of *P. confusum* Hirschfeld, 1985. The articular circumference (=articular surface for the ulna) is angularly deflected; this deflection divides the circumference into a larger part directed mostly proximally and a smaller part facing laterally. The relatively greater proximal exposition of the facet is more similar to *Glossotherium robustum* and differs from the

Table 1 Selected measurements of described bones of *Myiodon darwinii* specimen CORD PZ 4570. Measurements are of actual bone or bone fragment, not estimated

Humerus	
Craniocaudal length of caput	109.1 mm (L)
Mediolateral length of caput	95.6 mm (L)
Radius	
Greatest length	295.8 mm. (R); 304 mm (L)
Greatest diameter of proximal end	75.15 mm (R); 70.1 mm (LI)
Short diameter of proximal end	52 mm (RI); 47.2 mm (LI)
Greatest diameter of distal end	108.2 mm (R); 105.7 mm (L)
Short diameter of distal end	68.8 mm (RI); 70.4 mm (LI)
Long diameter of neck constriction	44.9 mm (R); 47.2 mm (L)
Short diameter of neck constriction	32.7 mm (R); 32.5 mm (L)
Distance from proximal surface to distal end of biceps tubercle	79.7 mm (R); 84.4 mm (L)
Mediolateral diameter of distal end of diaphysis	85.1 mm (R); 90.3 mm (L)
Ulna	
Maximal length	375 mm (L)
Length of olecranon (from level of anconeal process to level of proximal tip)	81.1 mm (L)
Craniocaudal depth of shaft at mid-length	73.35 mm (L); 72.15 mm (RI)
Length from caudal border to tip of coronoid process	138.15 mm (L)
Length from proximal end of olecranon to tip of coronoid process	185.15 mm (L)
Maximal craniocaudal depth of olecranon	123.2 mm (L)
Maximal extension of distal articular surface	53.4 mm (L)
Mediolateral width of shaft at mid-length	30.4 mm (L); 28.9 mm (R)
Craniocaudal depth of diaphysis at distal end	73.8 mm (L); 72.15 mm (RI)
Lesser craniocaudal depth of distal epiphysis at distal end	43.45 mm (L); 38 mm (RI)

I incomplete, *L* left bone, *R* right bone

more lateral facet of *S. uccasamamensis* (Saint-André et al. 2010). The lateral border of the expanded head is proximodistally narrow (Fig. 3a, b), which makes the articular circumference proximodistally short. This contrasts with the more extensive facet of *L. armatus* (Reinhardt 1875). In CORD PZ 4570 the radial neck is narrower between the medial and lateral borders than in *G. robustum*, as in *Glossotherium wegneri* (Hoffstetter 1952). In CORD PZ 4570 the medial margin of the neck is strongly excavated relative to the radial head at the proximal epiphyseal suture, distinct from the shallow excavation in *Scelidotherium leptocephalum* (pers. obs., CORD PZ 4464). In CORD PZ 4570 the radial tubercle is located well proximal to the proximal third of the radius. By contrast, in *O. giganteum* the tubercle is located distal to that point (Cartelle 1992).

The cranial surface of the radius lacks a marked ridge close and parallel to the medial margin (Fig. 3a), as in *Myloodonopsis ibseni* (Cartelle 1980). The ridge is present (and likely separated the insertion areas of *M. supinator* from *M. pronator teres*) in *G. robustum* (Owen, 1842). The ridge that separates the insertion areas of the *Mm. supinator* and *abductor digiti I longus* is scarcely marked on the cranial surface (Fig. 3a), as seen in the holotype of *Pseudolestodon hexaspondylus* Rautenberg, 1906, distinct from the well-marked condition present in *G. robustum* (Owen, 1842). Only one muscle insertion fossa, likely representing the insertion area of *M. supinator*, is present on the cranial surface of the CORD PZ 4570 radius, as in *M. ibseni* (Cartelle 1980). In *G. robustum* there are two fossae (Owen 1842). The medial border of the supinator fossa in the CORD PZ 4570 radius is convex and confluent with the medial border of the bone, but distinctly separate in *G. robustum* (Owen, 1842). A short, longitudinal ridge is barely distinguishable on the distal part of the fossa, but is prominent in *L. armatus* (Reinhardt 1875). The medial margin of the diaphysis is smooth, as in FMNH P 14288 (McAfee 2016), not rugous as in *G. robustum* (Owen, 1842). The margin lacks a clearly marked angle, a trait shared with *G. robustum*, in contrast to the clearly marked angle of *L. armatus* (Reinhardt 1875). The margin is approximately straight at the distal third of the diaphysis (Fig. 3a, b), as in *G. robustum* (Owen 1842; Reinhardt 1875; Saint-André et al. 2010), but not convex as in *L. armatus* (Reinhardt 1875). The lateral margin is mostly concave in cranial view (Fig. 3a), as in *L. armatus* (Reinhardt 1875). By contrast, in the holotype of *P. hexaspondylus* the lateral margin is straight (Rautenberg 1906). The lateral surface is not separated from the cranial and caudal surfaces by sharp edges in the new material, distinct from *P. harlani* (Lull 1915). We were unable to find a nutrient foramen, probably due to sub-optimal preservation.

The distal end of the diaphysis in CORD PZ 4570 is wider than the radial head. This is distinct from a similar width in *S. uccasamamensis* and a lesser width in *G. robustum* (Saint-André et al. 2010). The medial margin of the radius presents a well-marked angle between the medial borders of the diaphysis and the styloid process at the distal epiphysis (Fig. 3b), as in *G. robustum*, and distinct from the poorly marked angle present in the holotype of *P. hexaspondylus* Rautenberg, 1906. The styloid process of the CORD PZ 4570 radius forms a distally acute angle (Fig. 3b), as in *G. robustum*, in contrast to the rounded condition of the holotype of *P. hexaspondylus* Rautenberg, 1906. An oblique ridge is present on the cranial surface of the styloid process. It is located principally on the cranial surface of the styloid process (Fig. 3a). This ridge marks the distal limit of the sulcus for the tendon of *M. adductor digiti I longus*. The mediolateral prominence of the ridge is relatively low, as in *O. giganteum*, distinct from the greater mediolateral prominence of *L. armatus* (Cartelle 1992). The carpal articular surface is not medially displaced relative to the radial head fovea (Fig. 3a, b), as in *P. harlani*, but contrasting with the condition found in *Scelidotherium* (McDonald 1987). The carpal articular surface is medio-laterally wider than craniocaudally deep (Fig. 3d), as in *L. armatus*, and unlike the subequal width and depth in *O. giganteum* (Cartelle 1992). The cranial border of the carpal articular surface does not present an angle in distal view (Fig. 3d). This condition is shared with *G. robustum*, and distinct from the significant angle present in *L. armatus* (Reinhardt 1875). The carpal articular surface is subdivided into scaphoid and lunar articular facets by an oblique ridge (Fig. 3d, e), as in *G. robustum* (Rautenberg 1906). It contrasts with the sulcus found in *M. ibseni* (Cartelle 1980); and the lack of subdivision present in the “*Glossotherium* aff. *G. robustum*” specimen MCN-PV 9718 (Pitana 2011). The scaphoid facet is trapezoidal in shape (Fig. 3d), in contrast to the triangular shape of *P. harlani* (Lull 1915). The scaphoid facet is mediolaterally concave (Fig. 3e), as in *P. harlani* (Lull 1915). This is in contrast to the flat facet in *O. giganteum* (Cartelle 1992) and the convex facet in the holotype of *P. hexaspondylus* Rautenberg, 1906. The lunar facet approximates a triangle or a semicircle in shape (Fig. 3d), as in the holotype of *P. hexaspondylus* Rautenberg, 1906. It thus presents a contrast to the suboval shape of *P. harlani* (Lull 1915) and the quadrangular shape of MCN-PV 9718 (Pitana 2011).

Dermal ossicles

Small pea-sized ovoid to subspherical dermal ossicles were found in contact with the scapula, humerus and radius. Many densely packed dermal ossicles were found adjacent to the right scapula and ribs. Notably, the scapula is not

located between the dermal ossicles and the ribs. This is likely due to diagenetic compression of the ribcage, forcing contact with elements from the opposite side of the body. A single osteoderm was found in situ at the medial border of the proximal half of the right humerus. While dermal ossicles are densely packed upon the distal part of the caudal surface of the right radius (Fig. 3b), they are absent on the left radius. Thus, the association of dermal ossicles found upon the right radius may not be natural.

Phylogenetic analysis

The phylogenetic analysis yielded 207,464 most parsimonious trees (MPTs) ($L = 1856$; $CI = 0.310$; $RI = 0.648$). The strict consensus tree allowed recognizing the monophyly of sloths, and the sister-group relationships between *Bradypus* Linnaeus, 1758 and all the other sloths (Fig. 4). Three other groups were recovered in that tree. The first is formed by *Scelidotherium* and *Catonyx*, representing the Scelidotheriinae. The second is a monophyletic trichotomy formed by *Paramylodon harlani*; *Mirandabradys socorrensis* Carlini, Scillato-Yané and Sánchez, 2006a and *Mirandabradys urumaquensis* Carlini, Scillato-Yané and Sánchez, 2006b (clade 1) (Fig. 4). The third is a group formed by *Pseudopreotherium confusum* and *Bolivartherium urumaquensis* (clade 3). No further sloth clades were recovered in the strict

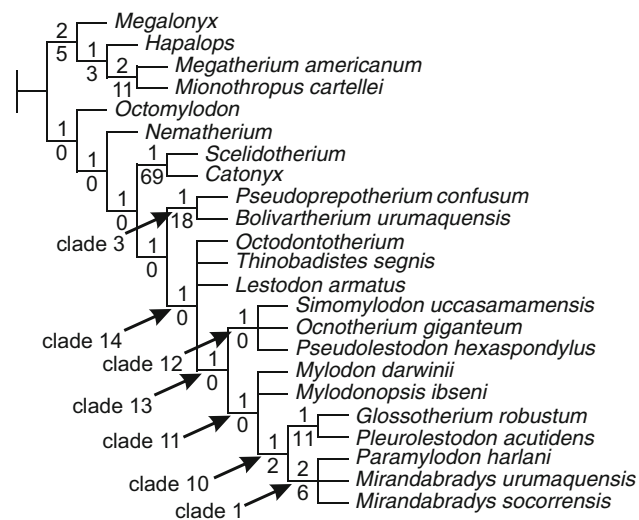


Fig. 4 Results of the phylogenetic analysis. Strict consensus of 207,464 most parsimonious trees (MPTs) ($L = 1856$; $CI = 0.310$; $RI = 0.648$) obtained after pruning *Glossotherium garbanii* and eight mylodontid taxa that included only pelvic limb bone character scores in the phylogenetic analysis by Rincón et al. (2015). Only the phylogenetic position of non-mylodontid taxa scored for thoracic limb characters is depicted. Numbers above branch leading to a group of leaves represent the Bremer supports of the group. Numbers below the branch represent the Jackknife frequency values of the group. These values were obtained upon the reduced strict consensus. Arrows indicate informal clades. See text for details

consensus. A reduced strict consensus (Fig. 4) including the largest possible number of resolved nodes was obtained after a posteriori pruning the following nine OTUs: *Glossotherium garbanii*; *Urumacotherium garciai* Bocquentin-Villanueva, 1984; *Chubutherium ferrelloi* Cattoi, 1962; *Pseudopreotherium venezuelanum* (Collins, 1934); *Eionaletherium tancynemius* Rincón, McDonald, Solórzano, Núñez Flores and Ruiz-Ramoni, 2015; *Mirandabradys zabasi* Carlini, Scillato-Yané and Sánchez, 2006b; *Urumaquia robusta* Carlini, Brandoni and Sánchez, 2006a; *Pyramiodontherium scillatoyanei* De Iuliis, Ré and Vizcaíno, 2004; and *Pyramiodontherium brevirostrum* Carlini, Brandoni, Scillato-Yané and Pujos, 2002. The results of the a posteriori pruning allowed recognizing additional groups. The OTU formed by *Glossotherium robustum* and *Glossotherium wegneri* is recovered as the sister taxon of *Pleurolestodon acutidens* Rovereto, 1914. These later two OTUs, together with clade 1, conform a clade, here informally called “clade 10” (Fig. 4). Clade 10, *M. darwini* and *M. ibseni* are closely related, together forming a monophyletic trichotomy here informally called “clade 11” (Fig. 4). *Simomylodon uccasamamensis*, *Ocnotherium giganteum* and the holotype of *Pseudolestodon hexaspondylus* form a monophyletic trichotomy, here called “clade 12” (Fig. 4). Together, clades 11 and 12 constitute a clade here informally called “clade 13” (Fig. 4). Clade 13; *Lestodon armatus*; *Thinobadistes segnis*; and *Octodontotherium* Ameghino, 1894 form another monophyletic polytomy, here informally called “clade 14” (Fig. 4), which excludes clade 3. Apomorphic character states of some of these recovered clades are noted in “Appendix 4”.

The relationships of each of the pruned OTUs were then investigated individually by sequentially pruning eight of them from the strict consensus of 207,464 MPTs and then constructing a strict reduced consensus tree for each. *Glossotherium garbanii* is recovered as a sloth more derived than *Bradypus* and never recovered within the Nothrotheriinae, the Scelidotheriinae, clades 3, 10, or 12. *Chubutherium ferrelloi* is recovered as a mylodontine excluded from clades 3 and 11. *Urumacotherium garciai* is recovered as a mylodontine more derived than clade 3, but excluded from clade 1. *Mirandabradys zabasi* and *P. venezuelanum* are recovered as mylodontines excluded from clades 1, 3, and 12. *Eionaletherium tancynemius* is recovered as a mylodontine more derived than clade 3, and excluded from clades 1 and 12. *Urumaquia robusta*, *P. scillatoyanei*, and *P. brevirostrum* were always recovered as megatherians.

Discussion

The *Mylodon darwini* specimen, CORD PZ 4570, seemingly represents a subadult ontogenetic age, due to two traits: (1) a lack of fusion of the epiphyses at the proximal

and distal ends of radius and ulna (Figs. 2a, 3a); and (2) the relatively feeble muscle attachment scars, compared to material assigned to adult specimens of *Glossotherium robustum* (Owen, 1842) and *Paramylodon harlani* (Stock 1925). In CORD PZ 4570 the feeble scars include ridges for the insertion of *Mm. deltoideus* and *pectoralis* on the humerus, for the *Mm. adductor digiti I longus* and *supinator* on the radius, and for the *Mm. pronator quadratus*, *abductor digiti I longus* and *extensor digiti II* on the ulna. The first two ridges are well-marked on the humeri of the *M. darwinii* specimens studied by Kraglievich (1934). The ulna of CORD PZ 4570 differs from its homologue in FMNH P 14288 in the feebleness of the ridges that limit the attachment areas of the *Mm. pronator quadratus*, *abductor digiti I longus* and *extensor digiti II* (McAfee 2016). As size is similar between specimens CORD PZ 4570 and FMNH P 14288 (Table I; McAfee 2016), it is not clear whether or not these differences in muscle scar prominence are related to age. The differences between both specimens may alternatively be related to intraspecific variability, perhaps related to sexual dimorphism or geographical separation. This indicates that for these thoracic member bones, variation in muscle scar prominence and definition occurs in *M. darwinii*, as previously reported by Stock (1925) for the humeri of North American sloths. Thus, the differences in ridge development noted by Cartelle (1980) between the radii of *Mylodonopsis ibseni* and *G. robustum* likely represent distinct ontogenetic stages, or intraspecific variability, rather than taxonomic differences.

The fossorial abilities of *M. darwinii* were previously considered low, based on the relatively low IFA value (Tauber et al. 2011). However, the great range of intraspecific variability in the closely related *G. robustum*, nearly encompasses the differences between *M. darwinii* and the less closely related *Lestodon armatus* or *Scelidotherium leptocephalum* (Bargo et al. 2000; Christiansen and Fariña 2003; Tauber et al. 2011). Furthermore, McAfee (2016) described the prominence of the olecranon in FMNH P 14288 as comparable to that of the *G. robustum*, *L. armatus*, and *S. leptocephalum* specimens studied by Bargo et al. (2000). This suggests the IFA was larger in FMNH P 14288 than in CORD PZ 4570. Thus, this feature suggests no meaningful difference between *M. darwinii* and *G. robustum*. Reduced fossorial ability in *M. darwinii* is suggested by the structure of the manus (Haro et al. 2016; McAfee, pers. comm.). The feeble development of the origin and insertion of the *M. teres major* in CORD PZ 4570, typically well developed in fossorial mammals, may seem to support this hypothesis (Hildebrand 1974). However, this may be due to the immaturity of the specimen (McAfee, pers. comm.). CORD PZ 4570 resembles digging mammals in the lack of caudal deviation in the olecranon

(White 1993). However, this may have to do with the shape of the trochlear notch in mylodontids, in which the ridge fitting the trochlear groove is craniolaterally projected. This suggests the humerus articulated leaning towards the lateral side of the ulna. Thus, the medial bending of the olecranon in *M. darwinii* likely provides an analog to the caudal bending of most other terrestrial mammals that do not dig. Thus, available evidence suggests relatively low fossorial ability in *M. darwinii*.

Many features suggest a low ability to climb in *M. darwinii*. Chief among these is a relatively large size, in excess of one metric ton (Christiansen and Fariña 2003). The proximally placed greater tubercle in the humerus relates to a reduction in the spherical aspect of the articular surface of the humeral head. This suggests a reduction in the range of motion at the shoulder joint, distinct from the condition in most mammalian climbers (Hildebrand 1974). In the radius, the reduction in the medial prominence of the insertion area of *M. pronator teres* (implied by the lesser prominence of the contiguous medial border of the radius) and the mediolaterally widened head further suggest a reduced ability to pronate and supinate (as noted by McAfee 2016), which is not consistent with climbing habits (Hildebrand 1974). Regarding the ulna, the straight caudal border and the radial notch orthogonal to the coronoid process do not support climbing habits (Pujos et al. 2007).

The position of the articular circumference in the radius of CORD PZ 4570, facing mostly proximally instead of laterally, suggests emphasis on transmission of proximal rather than lateral forces from the ulna, relative to the purportedly fossorial mylodontid *Scelidotherium*. The mediolateral expansion of the radial head in CORD PZ 4570 and FMNH P 14288 (McAfee 2016) suggests enhanced stabilization of the humeroradial articulation compared to *Scelidotherium*. Compared to the relatively sinuous radius in scelidotheriines (McDonald 1987), the straight radius in CORD PZ 4570 and FMNH P 14288 (McAfee 2016) suggests greater capacity to transmit high proximodistally aligned forces. These features suggest an increase in graviportal adaptation in *M. darwinii* compared to *Scelidotherium*. This is consistent with the relatively large size of *M. darwinii* compared to most mylodontids, other than *L. armatus* (Kraglievich 1928). More detailed functional aspects of these thoracic member bones will be presented elsewhere.

In our data matrix, a greater number of characters in the radius than in the ulna may be expected because for many included OTUs (e.g., *Lestodon armatus*, the holotype of *Pseudolestodon hexaspondylus*, *M. ibseni*, *Simomyodon uccasamamensis*) the ulna is not described (Reinhardt 1875; Rautenberg 1906; Cartelle 1980; Saint-André et al. 2010). The many differences in humeral

morphology between included *M. darwinii* specimens likewise produced a greater number of radius than humerus characters. The most remarkable result recovered by our phylogenetic analysis is the new nesting of *M. darwinii* in a clade that includes *G. robustum* and *P. harlani*, but excludes *L. armatus*. This contradicts the results of prior analyses by Esteban (1996), Gaudin (2004), and Haro et al. (2016). The recovery of a more basal position for *L. armatus* clearly indicates the importance of sampling skeletal regions other than the character-rich head skeleton, even if they imply a smaller set of characters. Our results are consistent with McAfee's (2009) assertion of closer relationships between *P. harlani* and *G. robustum* than with *L. armatus* or *M. darwinii*. The lack of unambiguous support in the reduced strict consensus tree for a clade including *L. armatus* and *T. segnis*, but excluding *G. robustum*, *P. harlani*, and *M. darwinii*, contrasts with the results in Esteban (1996), Gaudin (2004), and Haro et al. (2016). Neither is there unambiguous support in the reduced strict consensus tree for a clade including *M. darwinii* and *M. ibseni*, but excluding *G. robustum* and *P. harlani*, contrasting with the results in Haro et al. (2016). Characters from the zeugopod recover the clade including *M. darwinii*, *G. robustum*, and *P. harlani*, but excluding *L. armatus*. This is true whenever the number of articular facets for the calcaneum in the astragalus and the presence/absence of dermal ossicles are included in the character set. Characters from both the thoracic limb zeugopodial and autopodial skeleton support the hypothesis that the holotype of *P. hexaspondylus* cannot be referred to the species *G. robustum* and *G. wegneri*. They never cluster together to the exclusion of other OTUs (Haro et al. 2016). This contrasts with the results of the pre-cladistic analysis of skull characters by Cabrera (1936). Our hypothesis does not review the complete osteology of the holotype of *P. hexaspondylus*, and is thus provisional. But it suggests to us that the cranial features suggesting referral of *P. hexaspondylus* to *G. robustum* by Cabrera (1936) should be re-analyzed in an explicit cladistic analysis.

Conclusions

The principal ideas resulting from this work are: (1) In mylodontines the thoracic limb presents a considerable amount of variability between taxa useful for phylogenetic study. (2) Preliminary comparisons support the hypothesis that *Myiodon darwinii* had reduced fossorial abilities. (3) Phylogenetic relationships proposed by inclusion of characters from the thoracic limb skeleton to large data matrices of previous studies indicate *M. darwinii* forms

part of a clade that includes *Glossotherium robustum* and *Paramyiodon harlani*, but excludes *Lestodon armatus*. The latter point conflicts with the results of previous phylogenetic analyses based largely on material from the skeleton of the head (Esteban 1996; Gaudin 2004).

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Appendix 1: Sources of comparative data in the literature

<i>Myiodon darwinii</i> Owen, 1839	Lehmann-Nitsche (1902), Roth (1899), Nordenskjöld (1900), Studer (1905), Kraglievich (1934), Bargo and Deschamps (1996), Pitana (2011), Saint-André et al. (2010), McAfee (2016)
<i>Glossotherium robustum</i> (Owen, 1842)	Owen (1842), Rautenberg (1906), Reinhardt (1875), Allen (1913), Lull (1915), Stock (1925), Kraglievich (1934), Hoffstetter (1952), Cartelle (1980), McDonald (1987), Saint-André et al. (2010), Pitana (2011), McAfee (2016)
<i>Glossotherium wegneri</i> (Spillmann, 1931)	Hoffstetter (1952), Cartelle (1992)
<i>Paramyiodon harlani</i> (Owen, 1839)	Harlan (1843), Leidy (1855), Allen (1913), Lull (1915), Stock (1925), Kraglievich (1934), Hoffstetter (1952), Hirschfeld (1985), McDonald (1987), Cartelle (1992), Saint-André et al. (2010)
<i>Myiodonopsis ibseni</i> Cartelle, 1991	Cartelle (1980), Cartelle and Fonseca (1981)
<i>Pseudopreotherium confusum</i> Hirschfeld, 1985	Hirschfeld (1985), Saint-André et al. (2010)
<i>Thinobadistes segnis</i> Hay, 1919	Webb (1989), Saint-André et al. (2010)
<i>Ocnotherium giganteum</i> (Lund, 1839)	Cartelle (1992)
<i>Simomyiodon uccasamamensis</i> Saint-André, Pujos, Cartelle, De Iuliis, Gaudin, McDonald, and Mamani Quispe, 2010	Saint-André et al. (2010)

<i>Lestodon armatus</i> Gervais, 1855	Gervais (1873), Reinhardt (1875), Kraglievich (1934), McDonald (1987), Cartelle (1992), Bargo et al. (2000), Saint-André et al. (2010), Pitana (2011)	317	Articular facet for lunar on scaphoid: subdivided in two parts (0); unique (1) (modified from Hirschfeld 1985).
<i>Brievabradys laventensis</i> Villarroel, 2000	Hirschfeld (1985), McDonald (1997)	318	Relationship between mediolateral widths of dorsal and palmar borders of radial articular surface in lunar: dorsal border narrower or not much wider (0); dorsal border more than twice palmar border (1) (Hirschfeld 1985).
<i>Bolivartherium urumaquensis</i> (Linares, 2004)	Carlini et al. (2006b)	319	Extent of dorsal border of the facet for the unciform relative to extent of border of dorsal surface between facets for radius and magnum in lunar: shorter (0); longer (1) (Cartelle 1980).
Unnamed Intertropical “ <i>Glossotherium</i> aff. <i>G. lettsomi</i> ” sensu Cartelle (1992)	Cartelle (1992), Pitana (2011)	320	Angle between articular facets for scaphoid and magnum in lunar: lesser to 145° (0); greater to 145° (1) (Hirschfeld 1985).
“ <i>Glossotherium</i> aff. <i>G. robustum</i> ” specimen LAP-Q 0004 sensu Pitana (2011)	Pitana (2011)	321	Relief of articular surface for ulna in cuneiform in the axis extending from dorsomedial to palmolateral: approximately straight (0); clearly concave (1) (Cartelle 1980).
“ <i>Glossotherium</i> aff. <i>G. robustum</i> ” specimen MCN-PV 9718 sensu Pitana (2011)	Pitana (2011)	322	Contact between the articular facets for ulna and pisiform in the cuneiform: present (0); absent (1) (Cartelle 1980).
<i>Catonyx</i> Ameghino, 1891	Winge (1915), McDonald (1987) Cartelle et al. (2009)	323	Distolateral process of cuneiform: poorly developed (0); well developed (1) (Cartelle 1980).
<i>Scelidotherium</i> Owen, 1839	Owen (1839), Burmeister (1881), McDonald (1987), Aramayo (1988), Esteban et al. (1992), Cuenca Anaya (1995), Miño-Boilini (2012), Miño-Boilini et al. (2014), Owen (1842), Cartelle et al. (2009)	324	Relationship of proximodistal length to dorsopalmar depth in cuneiform: lesser (0); greater (1) (modified from Robertson 1976).
<i>Megatherium americanum</i> Cuvier, 1796	Owen (1858)	325	Relationship between proximodistal length and mediolateral width in the cuneiform: lesser than 0.93 (0); larger than 0.93 (1) (modified from Robertson 1976).
<i>Megalonyx jeffersoni</i> Desmarest, 1822	Leidy (1855), Stock (1925), McDonald (1977)	326	Prominent ridge on proximal region of the dorsal surface of the cuneiform: present (0); absent (1) (Cartelle 1980).
<i>Mionothropus cartellei</i> De Iuliis, Gaudin, and Vicars, 2011	De Iuliis et al. (2011)	327	Proximal facet of trapezium: concave (0); flat (1) (McDonald 1987).
<i>Hapalops</i> Ameghino, 1887	Scott (1904), Stock (1925)	328	Contact between trapezium and trapezoid: present (0); absent (1) (McDonald 1987).
		329	Exposition in dorsal view of articulated manus of contact between metacarpal II and magnum: present (0); absent (1) (Cartelle 1980).
		330	Proportions of lateral extremity of articular facet for cuneiform in unciform: dorsopalmarly reduced (0); dorsopalmarly expanded (1) (modified from Hirschfeld 1985).
		331	Mediolateral development of the axial process of trapezium-metacarpal I: low (0); high (1) (Stock 1925).
		332	Ratio between length of metacarpal II and dorsopalmar depth of narrowest point in the shaft: more than 0.42 (0); less than 0.42 (1) (modified from Cartelle 1980).

Appendix 2: Description of characters used in the phylogenetic analysis

These 45 characters were added to our larger matrix formed by combining Gaudin (2004) and Rincón et al. (2015); therefore, their numbering reflects their inclusion in the total character list.

- 312 Supracondylar foramen in humerus: present (0); absent (1) (Owen 1842).
- 313 Calcaneal facets in astragalus: unfused (0); fused (1) (Owen 1842).
- 314 Dermal ossicles: absent (0); present (1) (Ameghino 1881).
- 315 Contact between articular facets for trapezium-metacarpal I and trapezoid in scaphoid: present (0); absent (1) (Hirschfeld 1985).
- 316 Contact between articular facets for trapezoid and magnum in the scaphoid: present (0); absent (1) (Cartelle 1980).

- 333 Relationship between articular facets for metacarpal III and magnum in metacarpal II: contacting (0); separated (1) (Saint-André et al. 2010).
- 334 Articular facet for trapezium in metacarpal II: not concave (0); concave (1) (Saint-André et al. 2010).
- 335 Articular facet for the magnum in metacarpal III: single facet (0); subdivided, with separate dorsoabaxial facet (1) (Hirschfeld 1985).
- 336 Dorsal part of articular facet for metacarpal II in metacarpal III: approximately flat (0); markedly convex (1) (Saint-André et al. 2010).
- 337 Ratio between width of body and bone length in metacarpal III: More than 0.37 (0); 0.37 or less (1) (Haro et al. 2016).
- 338 Expansion of the distal carina upon the dorsal surface of metacarpal III: absent or minimal (0); present, well expanded (1) (Stock 1925).
- 339 Orientation of the distal carina of metacarpal III: dorsopalmar (0) oblique from the middle of the palmar border to the dorsoaxial corner of the distal surface (1) (Stock 1925).
- 340 Proximodistal extension of the articular facet for the metacarpal V in the metacarpal IV: relatively extensive (0); quite narrow (1) (Hirschfeld 1985).
- 341 Relief of palmar region of articular surface for metacarpal III in metacarpal IV: convex (0); concave (1) (Hirschfeld 1985).
- 342 Axial offset in distal articular surface of metacarpal IV: well developed (0); reduced or absent (1) (Hirschfeld 1985).
- 343 Relief of carina on distal articular surface of metacarpal IV in the dorsopalmar direction: flat or concave (0); convex (1) (Rautenberg 1906).
- 344 Palmar extension of articular facet for metacarpal V relative to palmar surface at waist of body in metacarpal IV: does not surpass it (0); surpasses it (1) (Saint-André et al. 2010).
- 345 Ratio between maximal dorsopalmar and axioabaxial extents of proximal phalanx of manual digit II: lesser than 1.27 (0); greater than 1.27 (1) (modified from Stock 1925).
- 346 Dorsopalmar keel in proximal surface of intermediate phalanx in manual digit II: not covered with articular surface (0); mostly covered with articular surface (1) (Cartelle 1980).
- 347 Mediolateral compression in olecranon: absent (0); present (1) (Hirschfeld 1985).
- 348 Distal part of lateral surface of ulna: concave (0); convex (1) (Owen 1842).
- 349 Articular circumference proximal exposition: scarce (0); great (1) (Saint-André et al. 2010).
- 350 Bicipital tubercle location in radius: within proximal third (0); exceeding proximal third (1) (Lull 1915).
- 351 Angle in medial border of radius at pronator crest: well marked (0); not marked (1) (Reinhardt 1875).
- 352 Medial border of radius with convexity expanded along distal half of diaphysis: present (0); absent (1) (Reinhardt 1875).
- 353 Angle in medial border of radius at the distal end: not marked (0); well-marked (1) (Rautenberg 1906).
- 354 Styloid process of radius: not acutely pointed (0); acutely pointed (1) (Rautenberg 1906).
- 355 Separation between articular facets for scaphoid and lunar in the radius: ridge (0); groove (1) (Cartelle 1980).
- 356 Relief of articular surface for scaphoid in radius in mediolateral direction: not concave (0); concave (1) (Rautenberg 1906).

Appendix 3: Data matrix

The following data matrix includes only thoracic member and a few other postcranial skeletal characters. It was analyzed after being fused with those of Gaudin (2004) and Rincón et al. (2015), as explained in the main text. Abbreviations—**P**, polymorphic, both states 0 and 1 present; **X**, not applicable.

	321	331	341	351
<i>Hapalops longiceps</i>	000??1?0X?	??????1??	???0???????	??????0??
<i>Scelidotherium</i>	0000PP0000	P000000000	0000000?0P	00000P0000
<i>Pseudopreopotherium confusum</i>	0000?00?0?	??????0?	0010?10000	0????0??0?
<i>Mylodon darwinii</i>	1111P11111	1110100111	11111101PP	1111110101
<i>Glossotherium robustum</i>	11110??1?0	00000111?1	?1P?10?1?1	1?1????11?1
<i>Paramylodon harlani</i>	1111P11110	0000?11?11	0?11101110	11?0011?1?
<i>Mylodonopsis ibseni</i>	?11?1??1?1	11111??0??	?????1?????	?????1?????
<i>Glossotherium garbanii</i>	??1????0??	0100???????	0?1????00??	????0???????
<i>Pseudolestodon hexaspondylus</i>	11?????????	0???????????	??0?????????	?0?1?????1?
<i>Simomylon uccasamamensis</i>	10011?????	??01????????	110?011???	??0?????0??
<i>Thinobadistes segnis</i>	100?001???	0?PP???????	?????????????	??????0?????
<i>Ocnotherium giganteum</i>	?00?????????	1?11????????	?????????????	?????????1?
<i>Lestodon armatus</i>	100?????????	?????????????	?????????????	?????????????
<i>Pleurolestodon acutidens</i>	?01?????????	?????????????	?????????????	?????????????
<i>Catonyx</i>	P000???????	P??P?0P???	???0??0P??	00?0P0?????
<i>Megatherium americanum</i>	100POP??X	X?????00??	?01?????????	00????1?000
<i>Megalonyx jeffersoni</i>	000??1?0?0	01?1?P1100	?0P0??000?	0??P??0?0?
<i>Glossotherium wegneri</i>	1?1?????????	?????????????	?????????????	??????1?????
<i>Bolivartherium urumaquensis</i>	1???????????	?????????????	?????????????	?????????????

	356
<i>Hapalops longiceps</i>	???X?
<i>Scelidotherium</i>	?00?1
<i>Pseudopreopotherium confusum</i>	0????
<i>Mylodon darwinii</i>	11101
<i>Glossotherium robustum</i>	1110?
<i>Paramylodon harlani</i>	????1
<i>Mylodonopsis ibseni</i>	????1?
<i>Glossotherium garbanii</i>	?????
<i>Pseudolestodon hexaspondylus</i>	?0000
<i>Simomylon uccasamamensis</i>	0????
<i>Thinobadistes segnis</i>	?????
<i>Ocnotherium giganteum</i>	?????0
<i>Lestodon armatus</i>	0??1?
<i>Pleurolestodon acutidens</i>	?????
<i>Catonyx</i>	?????
<i>Megatherium americanum</i>	1?0??
<i>Megalonyx jeffersoni</i>	0?01?
<i>Glossotherium wegneri</i>	??1?1
<i>Bolivartherium urumaquensis</i>	?????

Appendix 4: Apomorphic thoracic limb skeleton character states, other than from the manus, of recovered clades

- Clade 10: Character 348: 0 → 1. Distal part of lateral surface of ulna convex.
- Clade 11: Character 349: 0 → 1. Articular circumference in radius with great proximal exposure.
Character 352: 0 → 1. Medial border of radius nearly straight along distal half of diaphysis (convergence in *Megatheria*).
Character 353: 0 → 1. Angle well marked in medial border of radius at the distal end.
Character 354: 0 → 1. Styloid process of radius acutely pointed.
- Clade 12: Character 356: 1 → 0. Articular surface for scaphoid in radius flat or convex in mediolateral direction.
- Clade 12 or 13 (uncertain): Character 347: 0 → 1. Olecranon mediolaterally compressed (convergence in *Megatherium*).
Character 351: 0 → 1. Angle in medial border of radius at pronator crest not marked.

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