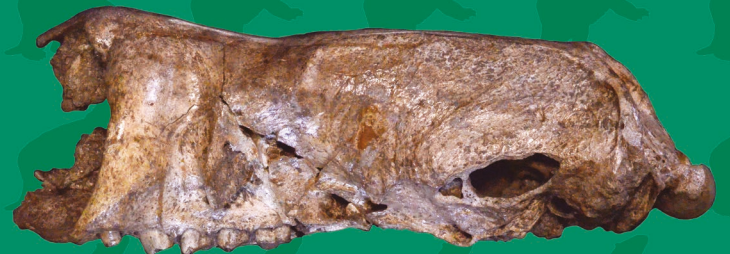# On the status of the giant mylodontine sloth *Glossotherium wegneri* (Spillmann, 1931) (Xenarthra, Folivora) from the late Pleistocene of Ecuador

Gerardo DE IULIIS, Alberto BOSCAINI, François PUJOS, Robert K. MCAFEE,
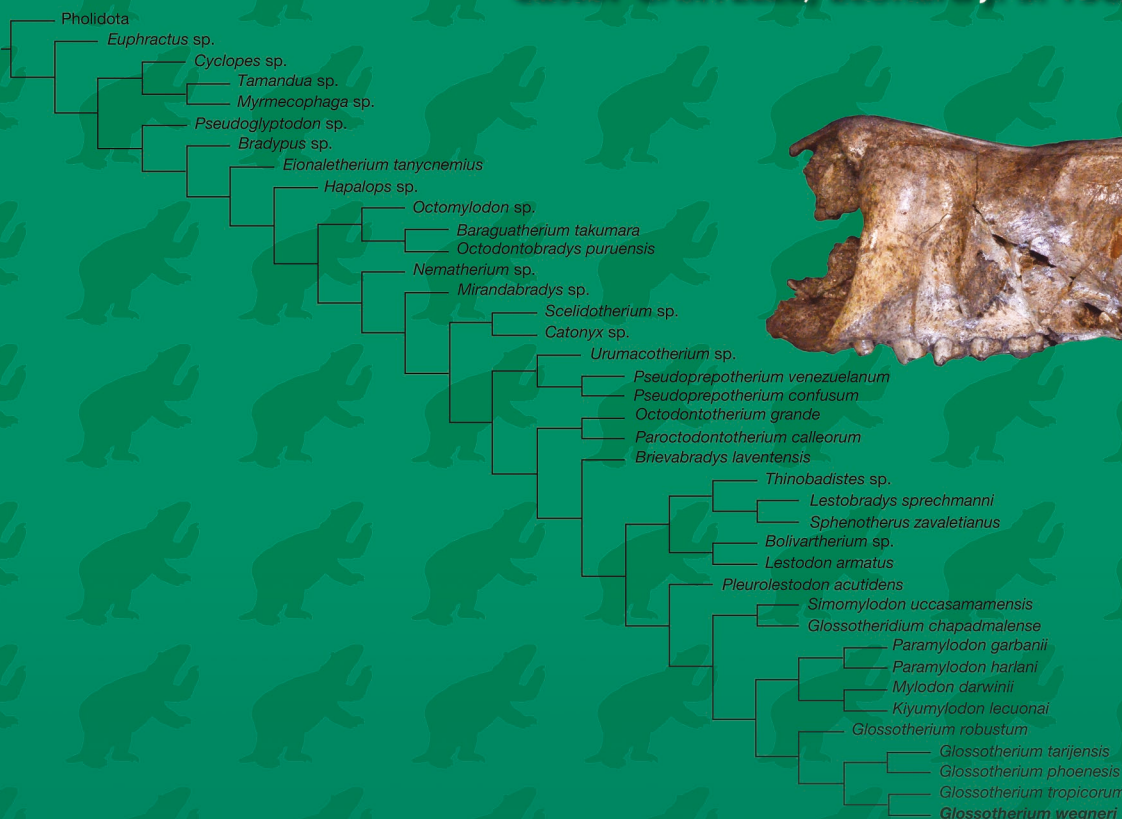Cástor CARTELLE, Leonard J. S. TSUJI & Lorenzo ROOK

On the status of the giant mylodontine sloth *Glossotherium wegneri* (Spillmann, 1931) (Xenarthra, Folivora) from the late Pleistocene of Ecuador

Gerardo DE IULIIS

Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5 (Canada) and Section of Palaeobiology, Department of Natural History, Royal Ontario Museum, 100 Queen's Park Crescent, Toronto, ON M5S 2C6 (Canada) gerry.deiuliis@utoronto.ca (corresponding author)

Alberto BOSCAINI

Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT-CONICET-Mendoza, Avda. Ruiz Leal s/n, Parque Gral. San Martín, 5500 Mendoza (Argentina) *and* Instituto de Ecología, Genética y Evolución de Buenos Aires (IEGEBA – CONICET) DEGE, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Int. Guiraldes 2160, Buenos Aires (Argentina)

François PUJOS

Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CCT-CONICET-Mendoza, Avda. Ruiz Leal s/n, Parque Gral. San Martín, 5500 Mendoza (Argentina)

Robert K. MCAFEE

Department of Biomedical Sciences, PCOM Georgia, Suwanee, GA (United States)

Cástor CARTELLE

Pontifícia Universidade Católica de Minas Gerais (PUC Minas), Avenida Dom José Gaspar, 290 Coração Eucarístico, Belo Horizonte, Minas Gerais (Brazil)

Leonard J. S. TSUJI

Department of Physical and Environmental Sciences, University of Toronto Scarborough, 1265 Military Trail, Scarborough, ON M1C1A4 (Canada)

Lorenzo ROOK

Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Firenze (Italy)

ABSTRACT

The late Pleistocene mylodontine sloth *Glossotherium wegneri* (Spillmann, 1931) (Interandean region, Ecuador) has been assigned to *Glossotherium* Owen, 1839 and *Oreomylodon* Hoffstetter, 1949 (the latter ranked as a subgenus or genus), and synonymized with *G. robustum* (Owen, 1842). However, the phylogenetic and comparative analyses conducted here, which include previously undescribed remains, strongly suggest specific distinction for *G. wegneri* and that there is little, if any, support for generic or subgeneric distinction for *Oreomylodon*. Among the notable features of this species are the

presence of an internasal element, marked expansion of the rostrum anteriorly, and dorsoventrally and the palatal region transversely, increased separation of the caniniform tooth from the anterior edge of maxilla, increased relative braincase width, relatively enlarged hypoglossal foramen, and greatly elongated zygomatic process of the squamosal. The resulting single MPT recovered a monophyletic *Glossotherium*, with the following phylogenetic arrangement of the species of this genus (*G. robustum* + ((*G. wegneri* + *G. tropicorum* Hoffstetter, 1952) + (*G. phoenesis* Cartelle, De Iuliis, Boscaini & Pujos, 2019 + *G. tarijense* Ameghino, 1902))).

RÉSUMÉ
Sur le statut du paresseux géant mylodontiné Glossotherium wegneri *(Spillmann, 1931) (Xenarthra, Folivora) du Pléistocène supérieur de l'Équateur.*
Le paresseux mylodontiné du Pléistocène supérieur *Glossotherium wegneri* (Spillmann, 1931) (région inter-andine, Équateur) a été attribué à *Glossotherium* Owen, 1839 et *Oreomylodon* Hoffstetter, 1949 (comme un sous-genre ou un genre) et mis en synonymie avec *G. robustum* (Owen, 1842). Cependant, des analyses phylogénétiques et comparatives menées ici et qui incluent de nouveaux restes inédits, suggèrent fortement une distinction spécifique pour *G. wegneri* et non pas une distinction générique ou sous-générique. Parmi les caractères notables de cette espèce on peut mentionner la présence d'un élément internasal, une forte expansion antérieure et dorsoventrale du rostre et transversale de la région palatine, une séparation accrue entre le bord antérieur du maxillaire et la dent caniniforme, une augmentation relative de la largeur de la boite crânienne, un foramen hypoglosse relativement agrandi ainsi qu'un important allongement du processus zygomatique du squamosal. L'unique arbre le plus parcimonieux obtenu montre la monophylie de *Glossotherium* avec les relations phylogénétiques suivantes entre les espèces de ce genre (*G. robustum* + ((*G. wegneri* + *G. tropicorum* Hoffstetter, 1952) + (*G. phoenesis* Cartelle, De Iuliis, Boscaini & Pujos, 2019 + *G. tarijense* Ameghino, 1902))).

INTRODUCTION

Sloths (Folivora synonym of Tardigrada synonym of Phyllophaga; Delsuc *et al.* 2001; Fariña & Vizcaíno 2003) and anteaters (Myrmecophaga) constitute Pilosa, one of the main clades of Xenarthra, the other being the cingulates (Cingulata), which include armadillos, pampatheres, and glyptodonts. Sloths are currently represented only by the two small-sized genera *Bradypus* Illiger, 1811 and *Choloepus* Linnaeus, 1758, which are nearly exclusively arboreal, with peculiar upside-down locomotion, and restricted to the tropical rain forests of South and Central America. However, their fossil representatives document a much more taxonomically and ecologically diverse clade, with at least 90 named genera that ranged throughout much of the New World, particularly South America, from the Oligocene to the Holocene (e.g. McDonald & De Iuliis 2008; Gaudin & Croft 2015). Giant fossil sloths were much larger, with some weighing several tons, and exhibited varied diets (e.g. browser, grazer, mixed feeding; Bargo & Vizcaíno 2008) and locomotory modes (e.g. terrestrial quadrupedal and/or bipedal, semi-arboreal, aquatic; Pujos *et al.* 2017). The main sloth clades, traditionally recognized as families and based on osteological characters, are Bradypodidae, Megalonychidae, Mylodontidae, Nothrotheriidae, and Megatheriidae (e.g. Gaudin 2004; McDonald & De Iuliis 2008; Varela *et al.* 2019). The first clade is monogeneric and includes only the extant three-toed sloth *Bradypus*. This arrangement reflects the longstanding consensus that this genus is the sister clade to the remaining sloths while the other living genus, the two-toed sloth *Choloepus*, is included among megalonychids. These osteologically-based hypotheses have been recently questioned by molecular data (i.e., Delsuc *et al.* 2019; Presslee *et al.* 2019), according to which *Bradypus* is closely related to Nothrotheriidae and Megatheriidae (i.e., Megatherioidea) and *Choloepus* to mylodontids.

The present study focuses on a species of Mylodontidae, a clade known from the late Oligocene to the late Pleistocene of North and South America. Three clades, traditionally regarded as subfamilies, are generally accepted: Mylodontinae, Lestodontinae, and Scelidotheriinae (Pitana *et al.* 2013), although some authors also recognize Urumacotheriinae, Nematheriinae, and Octomylodontinae (see Rinderknecht *et al.* 2010 and Saint-André *et al.* 2010). The species under consideration is itself well characterized following the work of Hoffstetter (1948, 1949, 1952), but has recently been variably referred to as *Glossotherium wegneri* (Spillmann, 1931) and *Oreomylodon wegneri* (Spillmann, 1931), and as a synonym of *Glossotherium robustum* (Owen, 1842) (Boscaini *et al.* 2019c). It has been considered relatively close to the mylodontine *Glossotherium* Owen, 1839, as it has been related with *G. robustum*, *G. tropicorum* Hoffstetter, 1952, and *G. phoenesis* Cartelle, De Iuliis, Boscaini & Pujos, 2019 (De Iuliis *et al.* 2017; Cartelle *et al.* 2019; Boscaini *et al.* 2020). Román-Carrión & Brambilla (2019) performed a phylogenetic analysis, based exclusively on craniodental characters and essentially at the generic level, that resolved *Oreomylodon* Hoffstetter, 1949 as relatively far removed from *Glossotherium*. These authors used their analysis as evidence to support generic distinction for *Oreomylodon*.

The aim of the current paper is to futher consider the taxonomy of this species and consider its phylogenetic affinities and its generic status based on more comprehensive phylogenetic analysis, thus testing the hypothesis of Román-Carrión & Brambilla (2019).

MATERIAL AND METHODS

The remains on which *Glossotherium wegneri* are based were recovered by Spillmann in 1927 in the Quebrada de Chalán (Fig. 1; Spillmann 1931; Hoffstetter 1952). This species was more completely characterized by remains discovered by Hoffstetter in 1946 south of La Cocha, close to Alangasí (Fig. 1; Hoffstetter 1948). The depositional context of these localities were well described by Hoffstetter (1948, 1949, 1952) and are considered Pleistocene (Marshall *et al.* 1984). These localities and those from which additional remains, reported here, were recovered are restricted to the Interandean Depression (see below). These additional remains include those housed in the AMNH and MECN. The former were collected in 1921 and 1931 according to AMNH catalog records, whereas those from MECN are the result of field work carried out between 1987 and 1997 in northern Ecuador by the Dipartimento di Scienze della Terra and Museo di Storia Naturale of the University of Firenze, in collaboration with the MECN. The field work resulted in the discovery of new fossil vertebrate localities (Quebrada Pistud and Quebrada Cuesaca; Fig. 1) near Bolivar, Carchi Province (Ficcarelli *et al.* 1992, 1993). Systematic excavations yielded an abundant collection of large mammal fossils (mostly representing mylodontines and gomphotheres; Ficcarelli *et al.* 1992, 1993; Ferretti 2010) that are housed, and in part exhibited, at the MECN (currently the Instituto Nacional de Biodiversidad, INABIO). The notable collection of mylodontines from Quebrada Pistud and Quebrada Cuesaca, as well as those from the AMNH (not previously described), provide the opportunity for considering the status of *Glossotherium wegneri* and the question of the generic status of *Oreomylodon* based on phylogenetic analysis.

The remains of the MECN (most not previously described) and AMNH collections are analyzed and compared, according to standard protocol for systematic reports in vertebrate paleontology, to those on which Spillmann (1931) erected the species and those that Hoffstetter (1948, 1949, 1952) relied on to further the understanding of its diagnostic features. The phylogenetic analysis was conducted following the protocol established in Boscaini *et al.* (2019c). Craniodental and postcranial features of *G. wegneri* were coded in the matrix of Boscaini *et al.* (2019c) using Mesquite ver. 3.04 (Maddison & Maddison 2011). The dataset was subsequently analyzed using TNT v. 1.5 (Goloboff & Catalano 2016). For the resulting single Most Parsimonious Tree [MPT] (see Results), Bremer, bootstrap, and jackknife support values were calculated. Further information (i.e., list of features, characters ordination, taxon sampling, and parameters used in the search and bootstrap analyses) is available in Boscaini *et al.* (2019c).

GEOGRAPHIC AND STRATIGRAPHIC CONTEXT

The physiographic and stratigraphic setting of the fossiliferous localities Quebrada Pistud and Quebrada Cuesaca, as well as their chronological (radiometric) placement, were reported and described by Ficcarelli *et al.* (1992, 1993) and Coltorti *et al.* (1998). The Ecuadorian Andes are part of the Cordillera range which borders the western side of South America (Fig. 1). In this area of South America, the Andes are subdivided into "western" and "eastern" Cordilleras separated by a deep tectonic depression, also called the Interandean Depression. The latter, located at elevations between 2000-3000 m, is filled with alluvial fan, fluviatile, lacustrine, and volcanic deposits which, at places, are more than 1000 m thick. During the last and the penultimate glaciations features higher than approximately 3000-3500 m in the Ecuadorian Andes were glaciated. The Interandean Depression, located between two glaciated Cordilleras, was the site of considerable aeolian activity that formed aeolian deposits up to more than 100 m thick. These aeolian sediments characterise the Cangahua Fm. (Clapperton & Vera 1986).

In Quebrada Cuesaca and Quebrada Pistud (Carchi Province), two sequences well representative of the Cangahua Fm. are observable. In both localities there are fossiliferous levels that yielded abundant large mammal bones. In Quebrada Cuesaca the sequence is more than 15 m thick. The two lower fossiliferous layers, which contain the larger remains of the fauna, are in contact and locally are up to 1 m thick. Radiometric dating of bones from this layer yielded an age of 16 670 ± 80 years BP (Coltorti *et al.* 1998). The sequence at Quebrada Pistud is more condensed (up to 9 m thick). The majority of the *Glossotherium* sample was recovered from the upper levels of this site. Radiometric dating of bones from these layers yielded ages between 14 450 ± 70 and 12 350 ± 70 years BP (Coltorti *et al.* 1998).

TAXONOMIC HISTORY

The early taxonomic history of the species has been well documented by Hoffstetter (1952) and only a cursory account is provided here. It was erected as *Mylodon wegneri* by Spillmann (1931: 15-17) on a partial left maxilla with Mf1-Mf4 and a nearly complete left dentary (without coronoid process) with cf1 and mf1-mf3 from Quebrada de Chalán (Spillmann 1931: 16; Fig. 1). These remains, which were only briefly described, have long been lost and were unavailable to Hoffstetter (1948, 1949, 1952). However, Spillmann's (1931) figure sufficiently illustrated features that allowed Hoffstetter (1948, 1949, 1952) to recognize the remains as conspecific with subsequently recovered and more complete remains. Hoffstetter (1948) considered that all these remains, from the Interandean region of northern Ecuador, represented a species more closely related to those of *Glossotherium* rather than *Mylodon* Owen, 1839, and formally transferred the species to *Glossotherium*, designating a neotype (EPN V 120; see Montellano-Ballesteros & Román-Carrión 2011), a reasonably complete skull associated with postcranial elements from La Cocha, close to Alangasí (Fig. 1). Hoffstetter (1949) dealt again with this species and considered it sufficiently distinct from other *Glossotherium* species to recognize it as a distinct subgenus, *Oreomylodon*. This arrangement was reaffirmed (Hoffstetter 1952, 1958) and maintained (Hoffstetter 1970, 1986) by this researcher.

Dechaseaux (1971), in a non-taxonomic paper on the cranial and endocranial analyses of the species, raised without explanation *Oreomylodon* to generic status, whereas Simpson & Paula Couto (1981) maintained the subgeneric status of *Oreomylodon*. Esteban (1996), in an unpublished doctoral dissertation, conferred generic status on *Oreomylodon* and provided a diagnosis, but did not otherwise address or describe the genus and species. Coltorti *et al.* (1998) and Tomiati & Abbazzi (2002) recognized the species as *Glossotherium wegneri*. McAfee (2007) treated *Oreomylodon* as a distinct genus and later erroneously synonymized *G. wegneri* under *G. robustum* (McAfee 2009); Varela & Fariña (2016) followed this synonymy. Román-Carrión (2007, 2012) maintained the species in *Glossotherium*, as *G. wegneri* and *G. (Oreomylodon) wegneri*, respectively. Saint-André *et al.* (2010) and Pitana *et al.* (2013) recognized *G. wegneri*, as did De Iuliis *et al.* (2017; see also Cartelle *et al.* 2019), but the latter authors remarked that there were questions regarding its generic assignment, whereas Püschel *et al.* (2017), following McAfee (2009), considered this species as conspecific with *G. robustum*. However, Püschel *et al.* (2017) made use of McAfee's (2007) data set, which did not include any *G. wegneri* specimens. Finally, Román-Carrión & Brambilla (2019) recently reconsidered *Oreomylodon wegneri* as valid based on an effectively generic level analysis that included only craniodental evidence.

It is clear from this history that there has been considerable inconsistency in the recent literature in the generic status of *Oreomylodon*, as well as in the validity of Spillmann's (1931) species, "*Mylodon*" *wegneri*.

SYSTEMATIC PALEONTOLOGY

Superorder XENARTHRA Cope, 1889
Order PILOSA Flower, 1883
Suborder FOLIVORA
Delsuc, Catzeflis, Stanhope & Douzery, 2001
Family MYLODONTIDAE Gill, 1872

Genus *Glossotherium* Owen, 1839

Oreomylodon Hoffstetter, 1949: 67.

TYPE SPECIES. — *Glossotherium robustum* (Owen, 1842).

DISTRIBUTION. — Late Pleistocene of many localities throughout southern cone, between latitudes of 20°S and 40°S (Pitana *et al.* 2013).

Glossotherium wegneri (Spillmann, 1931)

NEOTYPE. — EPN V. 120. Skull without mandible, atlas, right scapula, elements of the third digit of the left manus (third metacarpal, proximal and distal phalanges, lateral sesamoid), fragment of pelvis, left navicular, and dermal ossicles. La Cocha, close to Alangasí, late Pleistocene (Montellano-Ballesteros & Román-Carrión 2011: fig. 2) (Fig. 1).

REFERRED MATERIAL. — See Figures 2-4 and Appendices 1-4.

REVISED DIAGNOSIS. — Cf1 is intermediate in size (neither the largest nor the smallest tooth of the upper tooth row); there is pronounced separation of Cf1 from the anterior edge of maxilla; the mandibular symphysis is short and ends anteriorly to cf1; the upper tooth rows are markedly divergent, particularly due to the lateral position of the Cf1s; an internasal element, anterior to the nasals and resting on the vomer, is present and the nasals diverge anteriorly at the midline; in ventral view, the maxilla extends both laterally and anteriorly well beyond the position of the teeth; the braincase width is relatively large; the rostrum is anteroposteriorly elongated; the anterior part of the rostrum is markedly expanded transversely and dorsoventrally; the premaxilla is tightly sutured to the skull; the palate is not conspicuously extended posteriorly; the zygomatic process of the squamosal is greatly elongated; the hypoglossal foramen is relatively enlarged; the ventral margin of the dentary is markedly concave; the mandibular spout is strongly expanded transversely; the proximal epiphysis of the radius is subcircular in shape; in the ulna, the angle between the olecranon and the posterior border is approximately orthogonal.

COMPARATIVE DESCRIPTION
The skull of *G. wegneri* (Fig. 2) is particularly distinct from that of other *Glossotherium* species in possessing an internasal element, which is not present in *G. robustum*, *G. tropicorum*, and *G. phoenesis* (e.g. Owen 1842; Pitana *et al.* 2013; De Iuliis *et al.* 2017; Cartelle *et al.* 2019), and in the dorsoventral expansion of the rostrum anteriorly, which is reflected in the rising dorsal profile of the rostrum in lateral view (Fig. 2B). An anterior ossification is present in *Mylodon darwinii* Owen, 1839 (Hoffstetter 1952) but is not homologous to the internasal described for *G. wegneri*; in the former the ossification results from dorsal extension of the premaxillae to contact the nasals and forms a characteristic bony arch that is absent in the latter. The dorsal profile is either nearly horizontal for most of its length and declines only at its anteriormost extremity
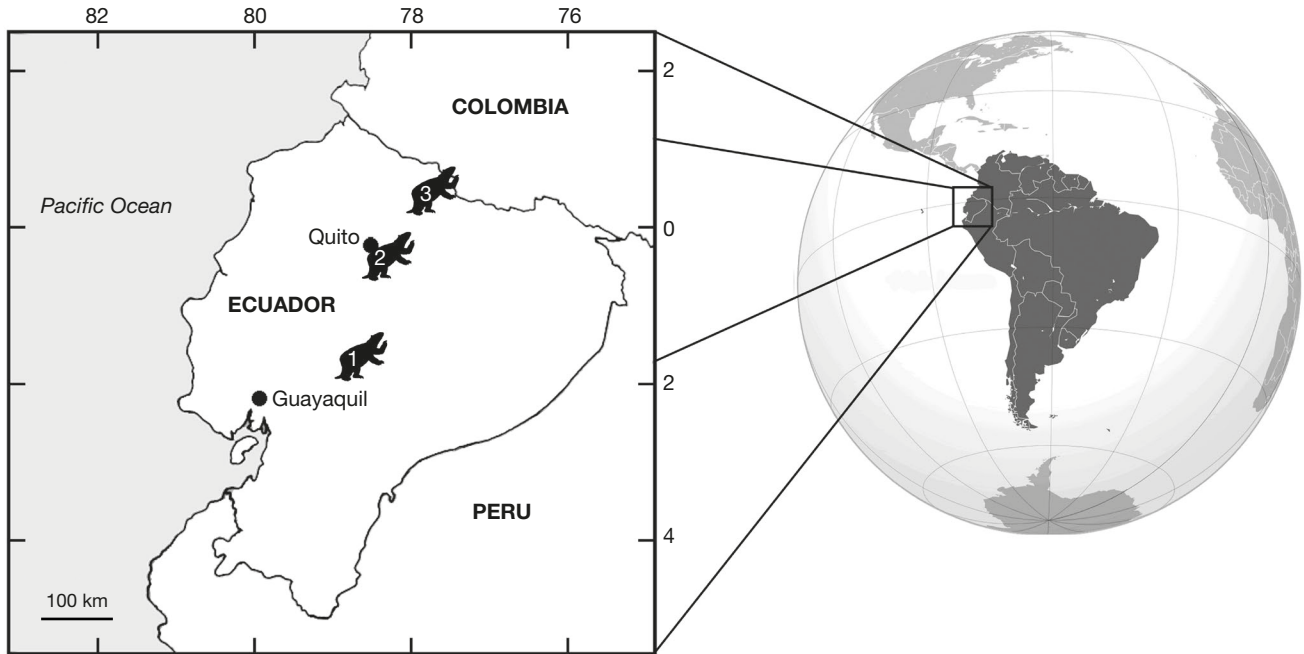
Fɪɢ. 1. — Map showing the main localities from which remains of the mylodontid sloth *Glossotherium wegneri* (Spillmann, 1931) from the Pleistocene of Ecuador have been recovered: **1**, Quebrada de Chalán; **2**, La Cocha (close to Alangasí); and **3**, Quebradas Pistud and Cuesaca (close to Bolivar).

in *G. robustum* (e.g. Owen 1842) or descends gradually anteriorly in *G. tropicorum* and *G. phoenesis* (De Iuliis *et al.* 2017; Cartelle *et al.* 2019). *Paramylodon harlani* Owen, 1839 resembles more the condition in *G. robustum* (Stock 1925). The dorsal profile of *M. darwinii* bears a convexity approximately at about the midpoint of the rostrum, but it descends farther anteriorly (Hoffstetter 1952). Thus, a portion of the rostrum does rise, but this condition is distinct from that in *G. wegneri*, in which the rostrum does not decline anteriorly in lateral view (Fig. 2B; Appendices 2-4). The condition in MNHN.F.PUN220 (Appendix 4), with the anteriormost part of the rostrum declining, represents an exception, and is probably due to an extended ossification of the cartilage at the tip of the nasals, variably observed in other mylodontids (e.g. *Simomylodon uccasamamensis* Saint-André, Pujos, Cartelle, De Iuliis, Gaudin, McDonald, and Mamani Quispe, 2010; Boscaini *et al.* 2019a). In ventral view, the upper tooth rows diverge in all *Glossotherium* species and *P. harlani* (Owen 1842; Stock 1925; McAfee 2009; Pitana *et al.* 2013; De Iuliis *et al.* 2017; Cartelle *et al.* 2019), but is most marked in *G. wegneri* (Fig. 2C, E) and least marked in *P. harlani*, with the differences reflected in the curvature of the tooth rows.

Glossotherium wegneri differs notably from the other species so far noted in the degree of transverse expansion of the maxillae, particularly anteriorly near the level of the caniniform teeth (Gaudin 2004). In *G. wegneri* (Fig. 2C, E), the maxilla extends laterally and anteriorly to a greater extent than in the other *Glossotherium* species (Owen 1842; Pitana *et al.* 2013; De Iuliis *et al.* 2017; Cartelle *et al.* 2019). The degree of this expansion imparts a strongly and abruptly widened palatal region, especially as compared to the postorbital constriction of the skull, whereas in the other species, particularly *P. harlani*,

the palatal region is less expanded and the skull overall appears more elongated and narrow (Stock 1925; McAfee 2009). This is particularly true in *M. darwinii*, in which the rostrum is long and narrow, and the tooth rows are essentially parallel (Hoffstetter 1952). This latter species also differs from the *Glossotherium* species in the absence of a caniniform tooth, so that only four upper teeth are present on each side (although four lower teeth are present in each dentary, as in *Glossotherium* species and *P. harlani*). Stock (1925) noted the occasionally absence of the first upper tooth in *P. harlani*, although this loss is restricted to late Pleistocene (Rancholabrean NALMA) specimens and occurs at a frequency of nearly 50% (McAfee 2015; McDonald 1995).

The occiput of *Glossotherium robustum* in posterior view was characterized as low and wide among mylodontids by Brambilla & Ibarra (2018), but this morphology is not clearly diagnostic generically for *Glossotherium*. Indeed, the occiput of *G. wegneri* (Hoffstetter 1952) is relatively higher, and it is progressively higher in *G. tropicorum* (De Iuliis *et al.* 2017) and *G. phoenesis* (Cartelle *et al.* 2019), so that in the latter it is nearly semicircular, and thus more closely resembles the occiput of *Mylodon darwinii*, as illustrated in Brambilla & Ibarra (2018).

In lateral view, the ventral margin of the dentary beneath the tooth row is concave in *G. wegneri* (Fig. 3), in contrast to the nearly rectilinear or slightly convex margin in the other mylodontines (Gaudin 2004). The depth of the horizontal ramus tends to be nearly constant below the tooth row in *G. robustum*, *G. tropicorum*, *G. phoenesis*, and *P. harlani* (Owen 1842; Pitana *et al.* 2013; De Iuliis *et al.* 2017; Cartelle *et al.* 2019). Although this is not the case in *G. wegneri*, owing to the concave ventral margin, the anterior and posterior

A

B

C

D

E
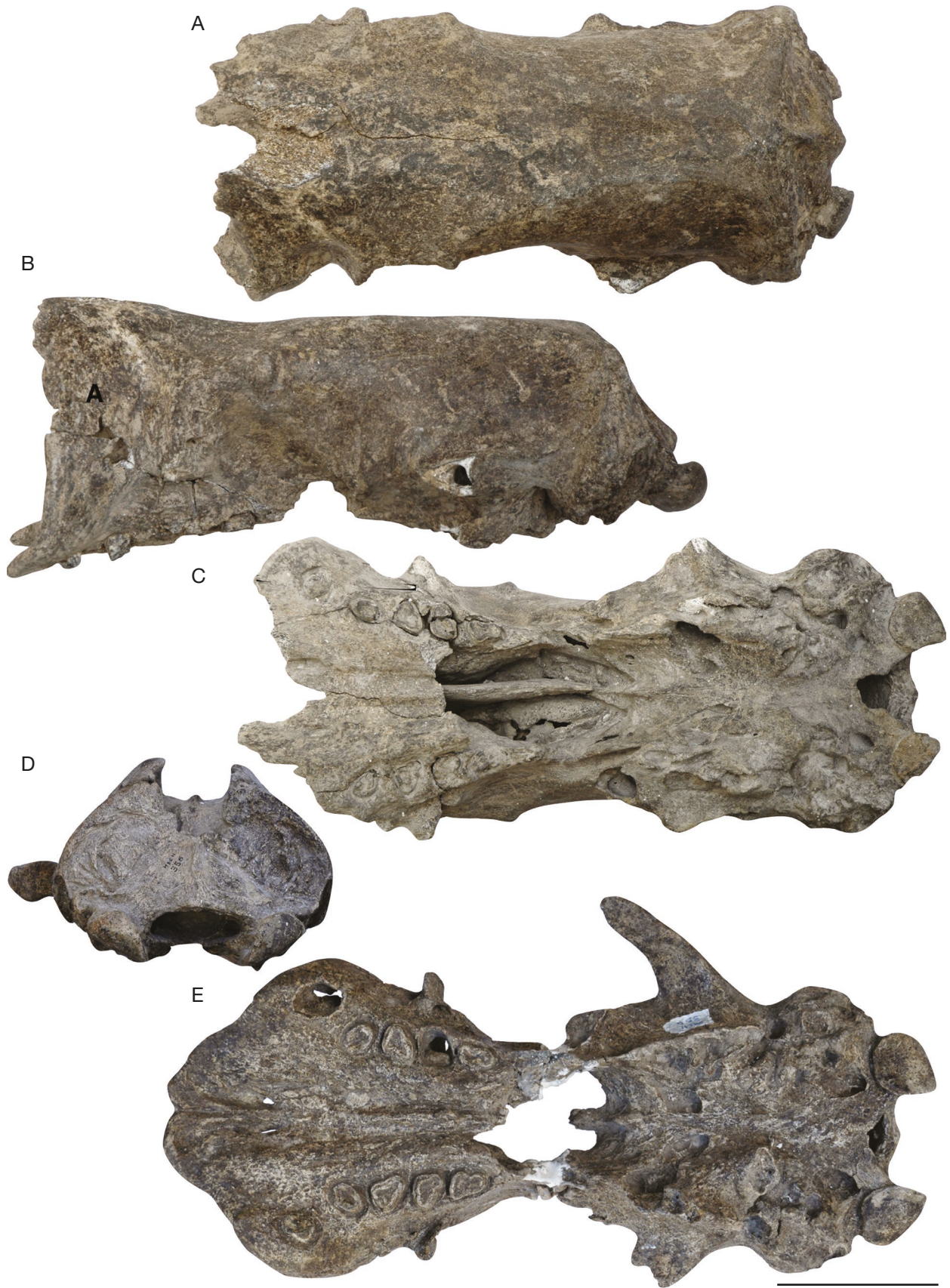
Fig. 2. — Skulls of the mylodontid sloth *Glossotherium wegneri* (Spillmann, 1931) from the Pleistocene of Ecuador: **A-C**, MECN 505 in dorsal, lateral, and ventral views respectively; **D**, **E**, MECN 356 in posterior and ventral views respectively. Scale bar: 10 cm.

Fig. 3. — Mandibular remains of the mylodontid sloth *Glossotherium wegneri* (Spillmann, 1931) from the Pleistocene of Ecuador: **A-C**, partial left dentary with cf1–mf2 (MECN 358) in lateral, occlusal, and medial views respectively; **D**, **E**, mandibular symphysis (AMNH 9971) with fragmented right cf1–mf2 in occlusal and lateral views respectively; **F-H**, left partial dentary with cf1 and part of mf1 (AMNH 96220) in lateral, occlusal, and medial views respectively; **I-K**, nearly complete left dentary without dentition (MECN 357) in lateral, occlusal, and medial views respectively. Scale bar: 10 cm.

portions of the dentary are approximately of the same height (Fig. 3I-K). In *M. darwinii*, however, the height decreases anteriorly, so that the ramus tapers (Hoffstetter 1958). The mandibular spout of *G. wegneri* is anteriorly flat in occlusal view (Fig. 3D), whereas it is anteriorly rounded in *G. tropicorum* and *G. phoenesis* (De Iuliis *et al.* 2017; Cartelle *et al.* 2019). As in *G. tropicorum* (De Iuliis *et al.* 2017), the coronoid process of the mandible is not hooked posteriorly, and the condyloid process is relatively shorter, in comparison to all the other *Glossotherium* species (e.g. Pitana *et al.* 2013; Cartelle *et al.* 2019).

In the postcranial elements, we observed a general resemblance between *G. wegneri* and the remains attributed to the other Mylodontinae species (Boscaini *et al.* 2019c).

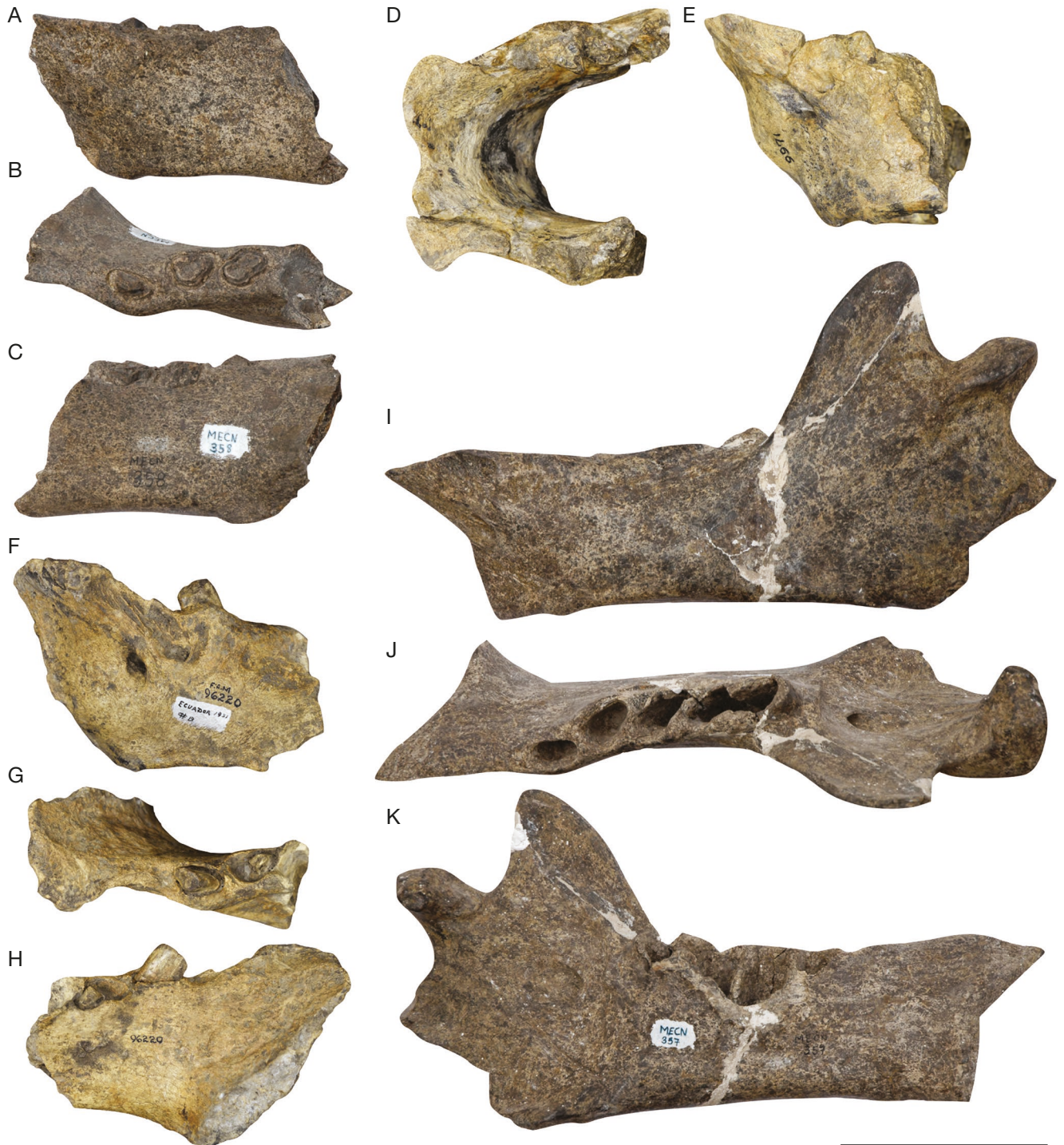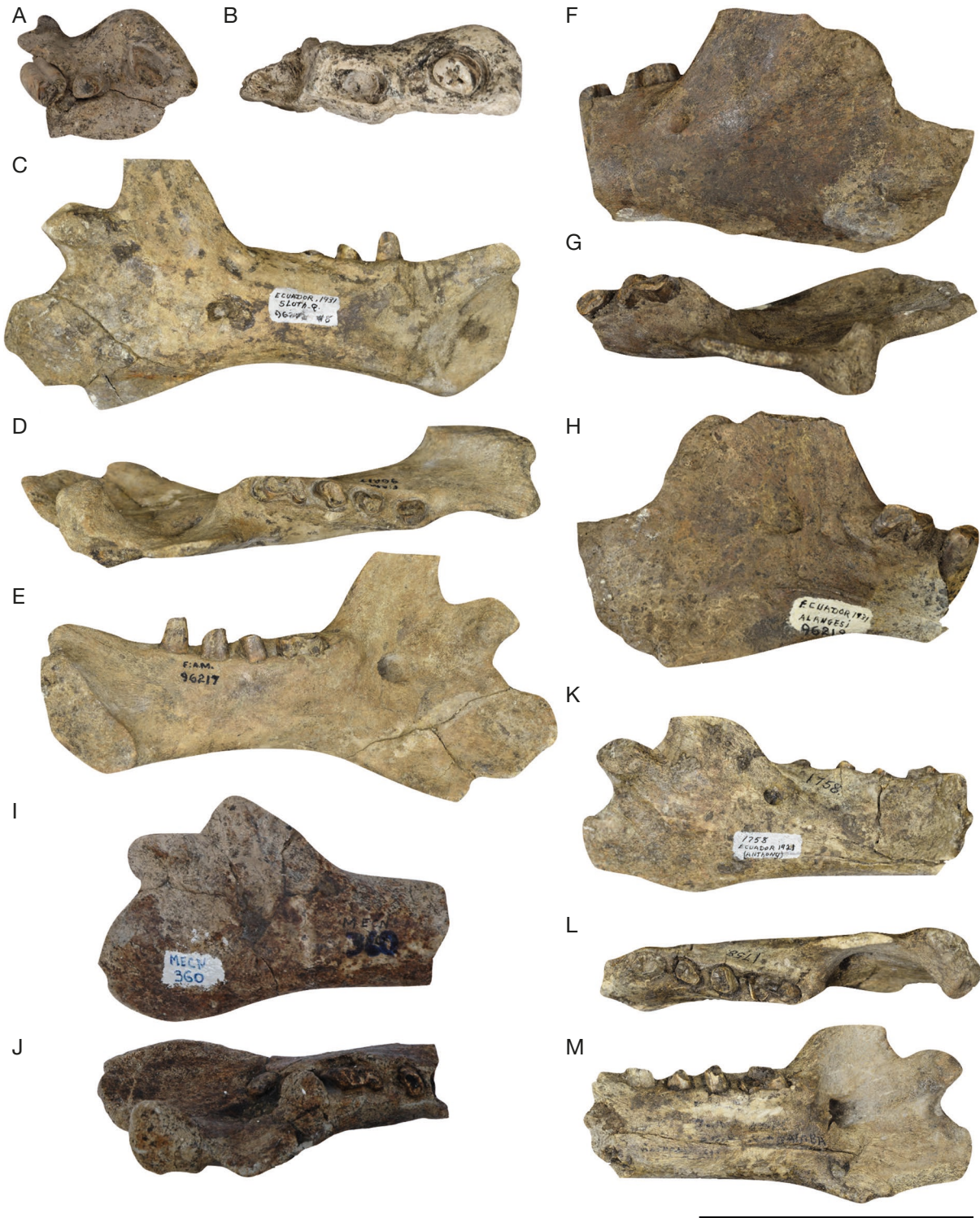Fig. 4. — Maxillary and mandibular remains referred to juvenile specimens of the mylodontid sloth *Glossotherium wegneri* (Spillmann, 1931) from the Pleistocene of Ecuador: **A**, right maxillary fragment with Cf1-Mf2 (MECN 125) in occlusal view; **B**, right maxillary fragment with Cf1 and alveoli of Mf1-Mf2 (MECN 55) in occlusal view; **C-E**, nearly complete right dentary with dentition (AMNH 96217) in lateral, occlusal, and medial views respectively; **F-H**, partial left dentary with mf3-mf4 (AMNH 96219) in lateral, occlusal, and medial views respectively; **I, J**, partial right dentary with mf3-mf4 (MECN 360) in lateral and occlusal views respectively; **K-M**, partial right dentary with dentition (AMNH 1758) in lateral, occlusal, and medial views respectively. Scale bar: 10 cm.

Only two postcranial features are worth mentioning, as they appeared to be autapomorphies of *G. wegneri*: the subcircular shape of the proximal articulation of the radius, and the roughly orthogonal angle between the ulnar olecranon and posterior border in lateral view. Both features are unusual among Mylodontini and resemble more the conditions observed in scelidotheres and some lestodontine sloths (Boscaini *et al.* 2019c).

RESULTS AND DISCUSSION

The species studied here has been consistently considered as being very similar morphologically to species that have been assigned to the South American mylodontine *Glossotherium*, including *G. robustum*, *G. tropicorum*, and *G. phoenesis* (see De Iuliis *et al.* 2017; Cartelle *et al.* 2019; Boscaini *et al.* 2020), particularly *G. robustum*, as is evident from the taxonomic history. A wide range of morphological and metric variation, generally linked to sexual dimorphism, has recently been documented among fossil and living sloth species, including *G. robustum* (for a review, see Boscaini *et al.* 2019b). The remains on which such intraspecific variation has been recognized include specimens, from the same or similar localities, that span the range of purported variation; i.e., it is not the case that specimens from one part of the spectrum of variation occur in one or some localities and specimens from the other part occur in others. In the case of Spillmann's species, the specimens were recovered from relatively few localities in the Interandean region of Ecuador (Fig. 1). All the specimens exhibit a combination of morphological features that are not encountered in remains from other localities – for example, in the lower elevation, coastal localities of Ecuador, the remains do not exhibit the features present in those from the Interandean region. This would strongly supports specific distinction for the Interandean remains instead of documenting intraspecific variation. The only possible exception is the unconfirmed assignment by Simpson & Paula Couto (1981), of an ulna and a tibia from the Vale do Rio Juruá, Acre, Brazil, to *G. wegneri*. However, as noted by Pitana *et al.* (2013), this assignment was made largely on the proximity of the Brazilian locality to the type locality of *G. wegneri* at Alangasí, Ecuador, but the scant remains are unreliable for confident identification.

Hoffstetter (1948, 1949, 1952) noted several striking features that unambiguously distinguish the Interandean remains from other *Glossotherium* species and *Mylodon darwinii*. Among them, are the presence of an internasal element (although considerably smaller than that of *M. darwinii*), anterior to the nasals and resting on the vomer, with the nasals diverging anteriorly at the midline to accommodate this element; marked transverse and dorsoventral expansion of the rostrum anteriorly (Fig. 2B); markedly concave ventral margin of the dentary (Fig. 3I-K); a transversely expanded mandibular spout (Fig. 3D); and upper tooth rows that diverge markedly (Fig. 2C, E), particularly due to the lateral position of the Cf1s (others are considered below in the results of the phylogenetic analysis). Several of these features, such as an anteriorly expanded rostrum (but only transversely and not dorsoventrally) and anteriorly divergent upper tooth rows (Fig. 2C, E), also occur in other *Glossotherium* species, but not to the degree exhibited by *G. wegneri*. Hoffstetter (1948, 1949, 1952) discussed, described, and compared these features so thoroughly that further detailed commentary is unnecessary. We may add here, however, yet another distinguishing feature of *G. wegneri* that has apparently not been noted in the literature. Indeed, in ventral view the maxilla extends both laterally and anteriorly well beyond the position of the teeth (Fig. 2C, E), whereas in *Glossotherium* species these surfaces (particularly the lateral) lies much nearer to the dentition.

As noted in taxonomic history, McAfee (2009) erroneously included *G. wegneri* within the synonymy for *G. robustum*. Montellano-Ballesteros & Román-Carrión (2011) additionally, and incorrectly, noted that this conclusion was based on MNHN.F.PUN220 (from Punín, Ecuador) rather than the neotype of the species, EPN V. 120 from south of La Concha, near Alangasí, while the type came from Quebrada de Chalán, Ecuador (Hoffstetter 1952; Fig. 4). However, the basis for this comment is unclear as none of the *G. wegneri* specimens were utilized in the data sets of McAfee (2007, 2009). The statement is also unclear as MNHN.F.PUN220 (formerly EPN V. 107) is one of the two specimens, nearly complete skulls (a third specimen, a partial maxilla EPN V. 803, was also considered), from which Hoffstetter (1949, 1952) was able to discern the features peculiar to *G. wegneri*. Indeed, it is MNHN.F.PUN220 that preserves the internasal element, confirming Hoffstetter's (1948) earlier suspicion of its presence in EPN V. 120 (the neotype). From the descriptions and images available in the literature, as well as the additional material housed in the AMNH and MECN noted here, there is convincing evidence that *G. wegneri* is distinct and easily distinguishable from other *Glossotherium* species, as well as from other mylodontines (for a detailed review, see Boscaini *et al.* 2019c). The restricted localities from which remains of this species have been recovered (i.e., the Interandean region) combined with the fact that its distinctive features are present in all and in only such remains but absent in specimens recovered from other localities yielding *Glossotherium* remains argue strongly against attributing its features to sexual dimorphism; in contrast to the listing in McAfee (2009) and Püschel *et al.* (2017), there is no basis for considering it synonymous with *G. robustum*. Furthermore, the phylogenetic analysis conducted here recovers 13 autapomorphies for *G. wegneri* (see below).

The phylogenetic results and conclusions reported here are in marked contrast to those obtained by Román-Carrión & Brambilla (2019). There are several reasons that may account for the differences. Among them is that the analysis of the latter authors is based on Gaudin's (2004) data set, which included 286 exclusively craniodental characters coded by Román-Carrión & Brambilla (2019) for 21 taxa at, effectively, the generic level. As well, they did not incorporate published information on other *Glossotherium* species available in Cartelle *et al.* (2019). However, inclusion of other *Glossotherium* species is fundamentally important in order to test: a) its monophyly, and therefore the validity of *Glossotherium* as a natural group; and b) whether or not *G. wegneri* should be included in the genus. By contrast, the current report incorporates many more characters (including cranial and postcranial) and taxa (see Phylogenetic analysis, below), with Mylodontinae considered at the species level, resulting in a more robust hypothesis.

The new remains assigned to *G. wegneri* (Figs 2-4; Appendices 1-4) provide insight into the ontogeny of the dentition and dentary. Indeed, several juvenile specimens preserve the dentition (Fig. 4). As has been reported for other sloths
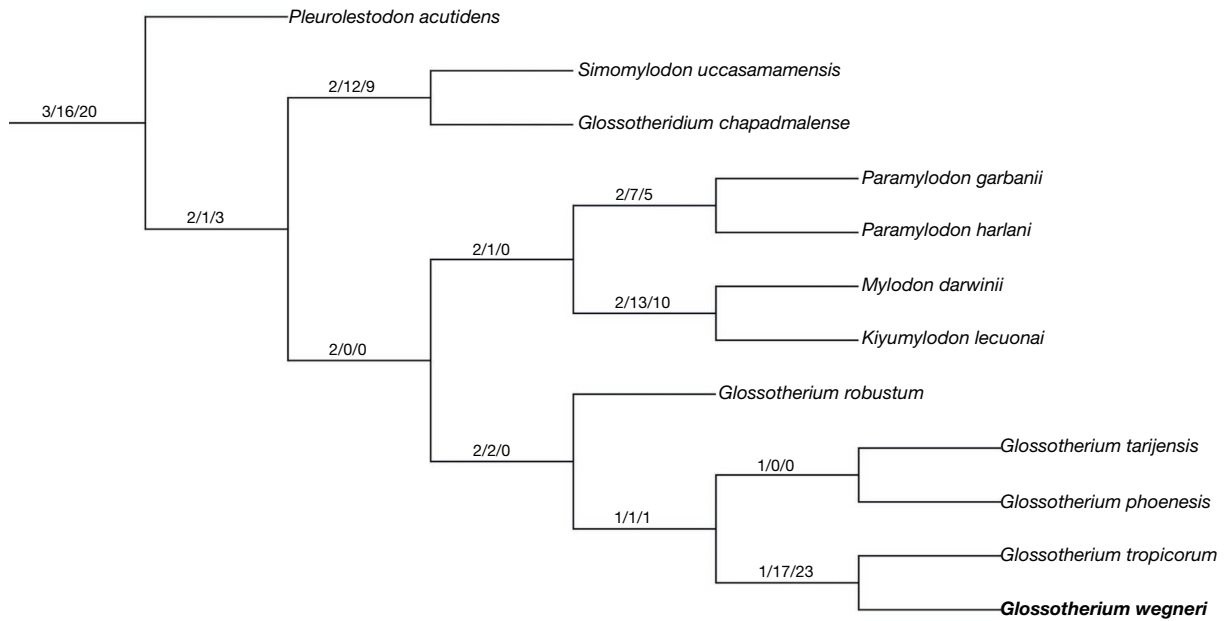
FIG. 5. — Single most parsimonious tree (tree length = 1167 steps; consistency index = 0.545; retention index = 0.887) showing the phylogenetic relationships among Mylodontini and the phylogenetic position of the mylodontid sloth *Glossotherium wegneri* from the Pleistocene of Ecuador within the clade. Numbers at each node represent Bremer, bootstrap, and jackknife support values, respectively. The complete matrix and tree, that resulted from the present phylogenetic analysis, are available in Appendices 5; 6.

(see e.g. Cartelle & De Iuliis 2006; Cartelle *et al.* 2014; Boscaini *et al.* 2019a) the teeth in very young individuals are conical (e.g. Fig. 4C, E), with the surfaces of the teeth converging apically. The ventral margin of the dentary is concave in both juvenile and adult individuals (Fig. 4), but apparently more so in juveniles than in older individuals, suggesting a change in form during growth; however, the sample size is small, so this assertion requires additional remains for confirmation. Although little information on ontogenetic changes have been reported among sloths, Boscaini *et al.* (2019a) reported that there is no substantial shape transformation in the dentary between juvenile and adult individuals of the mylodontine *Simomylodon uccasamamensis*. Also, De Iuliis (1996) and Cartelle & De Iuliis (2006) noted that maintenance in the form of the ventral margin occurred during ontogeny in the giant tropical megatheriine *Eremotherium laurillardi* (Lund 1842), but not in its close relative *Megatherium americanum* Cuvier, 1796. In megatheriines the ventral margin is convex rather than concave, and in *M. americanum* the depth of this ventral bulge increased dramatically during growth.

PHYLOGENETIC ANALYSIS

The present phylogenetic analysis was based on 39 taxa and 383 cranial and post cranial characters (for the complete character list and data matrix see Boscaini *et al.* 2019c; Appendices 5; 6 for the coding of *G. wegneri*). The analysis resulted in a single MPT, available in Appendices 5; 6 (tree length: 1167 steps; consistency index: 0.545; retention index: 0.887). *Glossotherium wegneri* is recovered among Mylodontini (Fig. 5), and deeply nested among the other *Glossotherium* species, strongly suggesting that this taxon is also a member of the genus. Moreover, the analysis recovers *G. tropicorum*

as the sister species of *G. wegneri*, both of them restricted to the Pleistocene of northwestern South America (De Iuliis *et al.* 2017). Although not particularly elevated, the support values of the clade uniting *G. tropicorum* and *G. wegneri* are the highest within the genus (Fig. 5). The present results fully resolve the phylogenetic relationships among *Glossotherium* species, with *Glossotherium* recovered as a monophyletic clade and sister group of the clade comprising (*Paramylodon*, (*Mylodon*, *Kiyumylodon*)) (Fig. 5).

The three synapomorphies that support and diagnose *Glossotherium* include a relative shallowing and elongation of the mandible (37: 4 → 3), a reduced ossification of the auditory bulla (213: 1 → 2), and a relatively shorter and broader third metacarpal (341: 0 → 1). All *Glossotherium* species, except *G. robustum*, are clustered into a subsequent node (Fig. 5), diagnosed by three synapomorphies: the presence of a diastema between Mf1 and Mf2 (25: → 1), intermediate development of the mandibular coronoid process (47: 2 → 1), and the partial closing of the canal for the opening of the occipital artery on the lateral braincase (270: 3 → 2). A single synapomorphy from the ear region is recovered as corroborating the monophyly of *G. phoenesis* and *G. tarijense* (Ameghino, 1902): the presence of a weak groove connecting the stylomastoid foramen to the ventral opening of the occipital artery (260: 3 → 2). The monophyly of the clade constituted by *G. tropicorum* and *G. wegneri* is corroborated by two synapomorphies: the mandibular coronoid process not hooked posteriorly (45: 1 → 0) and increase of the relative elongation of the mandibular condyloid process (51: 0 → 1).

Thirteen features are recovered by the present analysis as autapomorphies of *Glossotherium wegneri*. These include: intermediate size of Cf1 (13: 0 → 2), increase of the separa-

tion of Cf1 from the anterior edge of maxilla (21: 0 → 1), a short mandibular symphysis (62: 2 → 1) ending anteriorly to cf1 (63: 1 → 0), increase of relative braincase width (82: 2 → 3), snout relatively anteroposteriorly long (85: 3 → 2) and mediolaterally wide (86: 2 → 3), premaxilla tightly sutured to the skull (113: 1 → 0), palate not conspicuously extended posteriorly (124: 1 → 0), zygomatic process of the squamosal greatly elongated (168: 2 → 3), relatively enlarged size of the hypoglossal foramen (187: 1 → 2), subcircular shape of the proximal epiphysis of radius in proximal view (315: 1 → 2), and ulna exhibiting a roughly orthogonal angle between the olecranon and the posterior border (323: 2 → 1). Additionally, the dorsoventral expansion of the rostrum anteriorly is unique to *G. wegneri*, although this particular aspect of rostral height was not reflected in Gaudin's (2004) character list.

Considering the results of the phylogenetic analysis that *G. wegneri* falls well within *Glossotherium* and is the sister species of *G. tropicorum* (Fig. 5), it becomes difficult to support a generic distinction for the former species, in contrast to the recent conclusion of Román-Carrión & Brambilla (2019). Given the state of knowledge of the *Glossotherium* species and the phylogenetic results obtained here, there appear to be no compelling reasons to recognize *Oreomylodon* as a distinct genus.

CONCLUSIONS

The late Pleistocene mylodontine sloth *Glossotherium wegneri* from the Interandean region of Ecuador is a valid species, based on a phylogenetic analysis that identified 13 autapomorphies. Among these notable features are the presence of an internasal element and expansion of the rostrum dorsoventrally and of the palatal region transversely, particularly at the level of the caniniform teeth. This palatal expansion is typical of *Glossotherium* species, but is particularly marked in *G. wegneri*. A phylogenetic analysis that considers several undescribed remains in the collections of the MECN and AMNH, as well as those already known from the literature, results in a single MPT that recovers a monophyletic *Glossotherium* including *G. wegneri*. The latter species is well nested within this clade and is sister species to *G. tropicorum*. These two species are known only from a fairly restricted geographical region, the northwestern part of South America, with the remains of *G. wegneri* deriving from the Interandean region of Ecuador and *G. tropicorum* from lower lying regions of Ecuador and Peru. The phylogenetic arrangement of the *Glossotherium* species analyzed here is (*G. robustum* + ((*G. wegneri* + G. tropicorum) + (*G. phoenesis*+*G. tarijense*))). Given the phylogenetic position of *G. wegneri*, there would seem to be little, if any, support for recognizing generic distinction (*Oreomylodon*) for this species.

REFERENCES

AMEGHINO F. 1902. — Notas sobre algunos mamíferos fósiles, nuevos ó poco conocidos del valle de Tarija. *Anales del Museo Nacional de Buenos Aires* 8: 225-261.

BARGO M. S. & VIZCAÍNO S. F. 2008. — Paleobiology of Pleistocene ground sloths (Xenarthra, Tardigrada): biomechanics, morphogeometry and ecomorphology applied to the masticatory apparatus. *Ameghiniana* 45: 175-196.

BOSCAINI A., GAUDIN T. J., MAMANI QUISPE B., MÜNCH P., ANTOINE P.-O. & PUJOS F. 2019a. — New well-preserved craniodental remains of *Simomylodon uccasamamensis* (Xenarthra: Mylodontidae) from the Pliocene of the Bolivian Altiplano: phylogenetic, chronostratigraphic and palaeobiogeographical implications. *Zoological Journal of the Linnean Society of London* 185: 459-486. https://doi.org/10.1093/zoolinnean/zly075

BOSCAINI A., GAUDIN T. J., TOLEDO N., MAMANI QUISPE B., ANTOINE P.-O. & PUJOS F. 2019b. — The earliest well-documented occurrence of sexual dimorphism in extinct sloths: evolutionary and palaeoecological insights. *Zoological Journal of the Linnean Society of London* 187: 229-239. https://doi.org/10.1093/zoolinnean/zlz011

BOSCAINI A., PUJOS F. & GAUDIN T. J. 2019c. — A reappraisal of the phylogeny of Mylodontidae (Mammalia, Xenarthra) and the divergence of mylodontine and lestodontine sloths. *Zoologica Scripta* 48: 691-710. https://doi.org/10.1111/zsc.12376

BOSCAINI A., IURINO D. A., SARDELLA R., TIRAO G., GAUDIN T. J. & PUJOS F. 2020. — Digital cranial endocasts of the extinct sloth *Glossotherium robustum* (Xenarthra, Mylodontidae) from the Late Pleistocene of Argentina: Description and comparison with the extant sloths. *Journal of Mammalian Evolution* 27: 55-71. https://doi.org/10.1007/s10914-018-9441-1

BRAMBILLA L. & IBARRA D. A. 2018. — The occipital region of late Pleistocene Mylodontidae of Argentina. *Boletín del Instituto de Fisiografía y Geología* 88: 1-9.

CARTELLE C. & DE IULIIS G. 2006. — *Eremotherium laurillardi* (Lund) (Xenarthra, Megatheriidae), the Panamerican giant ground sloth: taxonomic aspects of the ontogeny of skull and dentition. *Journal of Systematic Palaeontology* 4: 199-209. https://doi.org/10.1017/S1477201905001781

CARTELLE C., DE IULIIS G. & PUJOS F. 2014. — *Eremotherium laurillardi* (Lund, 1842) (Xenarthra, Megatheriinae) is the only valid megatheriine sloth species in the Pleistocene of intertropical Brazil: a response to Faure *et al.*, 2014. *Comptes Rendus Palevol* 14: 15-23. https://doi.org/10.1016/j.crpv.2014.09.002

CARTELLE C., DE IULIIS G., BOSCAINI A. & PUJOS F. 2019. — Anatomy, possible sexual dimorphism, and phylogenetic affinities of a new mylodontine ground sloth from the late Pleistocene of intertropical Brazil. *Journal of Systematic Palaeontology* 19: 1957-1988. https://doi.org/10.1080/14772019.2019.1574406

CLAPPERTON C. M. & VERA R. 1986. — The Quaternary glacial sequence in Ecuador: a reinterpretation of the work of Walter Sauer. *Journal of Quaternary Science* 1: 45-56. https://doi.org/10.1002/jqs.3390010106

Coltorti M., Ficcarelli G., Jahren H., Moreno Espinosa D., Rook L. & Torre D. 1998. — The last occurrence of Pleistocene megafauna in the Ecuadorian Andes. *Journal of South American Earth Sciences* 11: 581-586. https://doi.org/10.1016/S0895-9811(98)00037-6

Cope E. D. 1889. — The Edentata of North America. *The American Naturalist* 23: 657-664. https://doi.org/10.1086/274985

Cuvier G. 1796. — Notice sur le squelette d'une très grande espèce de quadrupède inconnue jusqu'à présent, trouvée au Paraguay, et déposé au cabinet d'histoire naturelle de Madrid. *Magasin Encyclopédique ou Journal des Sciences, des Lettres et des Arts* 1: 303-310.

De Iuliis G. 1996. — A systematic review of the Megatheriinae (Mammalia: Xenarthra: Megatheriidae). University of Toronto (Unpublished PhD thesis), 781 p.

De Iuliis G., Cartelle C., McDonald H. G. & Pujos F. 2017. — The mylodontine ground sloth *Glossotherium tropicorum* from the Late Pleistocene of Ecuador and Peru. *Papers in Palaeontology* 3: 613-636. https://doi.org/10.1002/spp2.1088

Dechaseaux C. 1971. — *Oreomylodon wegneri*, édenté gravigrade du Pléistocène de l'Équateur. Crâne et moulage endocrânien. *Annales de Paléontologie* 57: 243-285.

Delsuc F., Catzeflis F. M., Stanhope M. J. & Douzery E. J. P. 2001. — The evolution of armadillos, anteaters and sloths depicted by nuclear and mitochondrial phylogenies: implications for the status of the enigmatic fossil *Eurotamandua*. *Proceedings of the Royal Society B: Biological Sciences* 268: 1605-1615. https://doi.org/10.1098%2Frspb.2001.1702

Delsuc F., Kuch M., Gibb G. C., Karpinsky E., Hackenberger D., Szpak P., Martínez J. G., Mead J. I., McDonald H. G., MacPhee R. D. E., Billet G., Hautier L. & Poinar H. N. 2019. — Ancient mitogenomes reveal the evolutionary history and biogeography of sloths. *Current Biology* 29: 2031-2042. https://doi.org/10.1016/j.cub.2019.05.043

Esteban G. I. 1996. — Revisión de los Mylodontinae cuaternarios (Edentata-Tardigrada) de Argentina, Bolivia y Uruguay. Sistemática, filogenia, paleobiología, paleozoogeografía y paleoecología. Universidad Nacional de Tucumán e Instituto Miguel Lillo (Unpublished PhD thesis), 314 p.

Fariña R. A. & Vizcaíno S. F. 2003. — Slow moving or browsers? A note on nomenclature. *Senckenbergiana Biologica* 83: 3-4.

Ferretti M. P. 2010. — Anatomy of *Haplomastodon chimborazi* (Mammalia, Proboscidea) from the late Pleistocene of Ecuador and its bearing on the phylogeny and systematics of South American gomphotheres. *Geodiversitas* 32: 663-721. https://doi.org/10.5252/g2010n4a3

Ficcarelli G., Azzaroli A., Borselli V., Coltorti M., Dramis F., Fejfar O., Hirtz A. & Torre D. 1992. — Stratigraphy and paleontology of upper Pleistocene deposits in the interandean depression, northern Ecuador. *Journal of South American Earth Sciences* 6: 145-150. https://doi.org/10.1016/0895-9811(92)90004-I

Ficcarelli G., Borselli V., Moreno-Espinosa M. & Torre D. 1993. — New *Haplomastodon* finds from the Late Pleistocene of northern Ecuador. *Geobios* 26: 231-240. https://doi.org/10.1016/S0016-6995(93)80017-L

Flower W. 1883. — On the arrangement of the orders and families of existing Mammalia. *Proceedings of the Zoological Society of London* 51: 178-186.

Gaudin T. J. 2004. — Phylogenetic relationships among sloths (Mammalia, Xenarthra, Tardigrada): the craniodental evidence. *Zoological Journal of the Linnean Society of London* 140: 255-305. https://doi.org/10.1111/j.1096-3642.2003.00100.x

Gaudin T. J. & Croft D. 2015. — Paleogene Xenarthra and the evolution of South American mammals. *Journal of Mammalogy* 96: 622-634. https://doi.org/10.1093/jmammal/gyv073

Gill T. 1872. — Arrangements of the families of mammals. With analytical tables. *Smithsonian Miscellaneous Collections* 11: 1-98. https://doi.org/10.5962/bhl.title.14607

Goloboff P. A. & Catalano S. A. 2016. — TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221-238. https://doi.org/10.1111/cla.12160 Retrieved from http://www.lillo.org.ar/phylogeny/tnt/

Hoffstetter R. 1948. — Nota preliminar sobre los Edentata Xenarthra del Pleistoceno Ecuatoriano. II: Mylodontidae. *Boletín de Informaciones Científicas Nacionales de Quito* 2: 19-42.

Hoffstetter R. 1949. — Nuevas observaciones sobre los Edentata del Pleistoceno superior de la Sierra ecuatoriana. *Boletín de Informaciones Científicas Nacionales de Quito* 3: 67-99.

Hoffstetter R. 1952. — Les mammifères pléistocènes de la République de l'Équateur. *Mémoires de la Société Géologique de France* (66): 1-391.

Hoffstetter R. 1958. — Édentés Xénarthres, *in* Piveteau J. (ed.), *Traité de Paléontologie* 6. Masson, Paris: 535-626.

Hoffstetter R. 1970. — Radiation initiale des mammifères placentaires et biogéographie. *Comptes Rendus de l'Académie des sciences de Paris* 270: 3027-3030.

Hoffstetter R. 1986. — High Andean mammalian faunas during the Plio-Pleistocene, *in* Vuilleumier F. & Monasterio M. (eds), *High Altitude Tropical Biogeography*. Oxford University Press, New York: 219-245.

Lund P. W. 1842. — Blik paa Brasiliens Dyreverden før sidste Jordomvaeltning. Tredie Afhandling: Forsaettelse af Pattedyrene. *Det Kongelige danske Videnskabernes Selskabs Skrifter* 9: 137-208.

Maddison W. P. & Maddison D. R. 2011. — Mesquite: a modular system for evolutionary analysis. Version 3.04. Retrieved from http://mesquiteproject.org/

Marshall L. G., Berta A., Hoffstetter R., Pascual R., Bombin M. & Mones A. 1984. — Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary of South America. *Palaeovertebrata Mémoire Extraordinaire* (13): 1-76. https://doi.org/10.1016/S0016-6995(84)80130-8

McAfee R. K. 2007. — Reassessing the taxonomy and affinities of the Mylodontid sloths, *Glossotherium* and *Paramylodon* (Mammalia: Xenarthra: Tardigrada). Northern Illinois University (Unpublished PhD thesis), 177 p.

McAfee R. K. 2009. — Reassessment of the cranial characters of *Glossotherium* and *Paramylodon* (Mammalia: Xenarthra: Mylodontidae). *Zoological Journal of the Linnean Society of London* 155: 885-903. https://doi.org/10.1111/j.1096-3642.2008.00468.x

McAfee R. K. 2015. — Dental anomalies within extant members of the mammalian Order Pilosa. *Acta Zoologica* 96: 301-311. https://doi.org/10.1111/azo.12077

McDonald H. G. 1995. — Gravigrade xenarthrans from the early Pleistocene Leisey Shell Pit 1A, Hillsborough County, Florida. *Bulletin of the Florida Museum of Natural History* 37: 345-373.

McDonald H. G. & De Iuliis G. 2008. — Fossil history of sloths, *in* Vizcaíno S. F. & Loughry W. J. (eds), *The Biology of the Xenarthra*. University Press of Florida, Gainesville: 39-55.

Montellano-Ballesteros M. & Román-Carrión J. L. 2011. — Redescubrimiento de material tipo depositado en la colección del Museo de Historia Natural "Gustavo Orcés V." del Instituto de Ciencias Biológicas, Escuela Politécnica Nacional, Quito, Ecuador. *Boletín de la Sociedad Geológica Mexicana* 63: 379-392. https://doi.org/10.18268/BSGM2011v63n3a1

Owen R. 1839. — Fossil Mammalia (3), *in* Darwin C. (ed.), *The Zoology of the Voyage of H.M.S. Beagle*. Smith. Elder and Co., London: 65-80.

Owen R. 1842. — Description of the skeleton of an extinct gigantic sloth, *Mylodon robustus*, Owen, with observations on the osteology, natural affinities, and probable habits of the megatheroid quadrupeds in general. *Annals of The Royal College of Surgeons of England, London*: 1-176.

Pitana V. G., Esteban G. I., Ribeiro A. M. & Cartelle C. 2013. — Cranial and dental studies of *Glossotherium robustum* (Owen, 1842) (Xenarthra: Pilosa: Mylodontidae) from the Pleistocene of southern Brazil. *Alcheringa* 37: 147-162. https://doi.org/10.1080/03115518.2012.717463

PRESSLEE S., SLATER G. J., PUJOS F., FORASIEPI A. M., FISCHER R., MOLLOY K., MACKIE M., OLSEN J. V., KRAMARZ A., TAGLIORETTI M., SCAGLIA F., LEZCANO M., LANATA J. L., SOUTHON J., FERANEC R., BLOCH J., HAJDUK A., MARTIN F. M., SALAS GISMONDI R., REGUERO M., MUIZON C. DE, GREENWOOD A., CHAIT B. T., PENKMAN K., COLLINS M. & MACPHEE R. D. E. 2019. — Palaeoproteomics resolves sloth relationships. *Nature Ecology & Evolution* 3: 1121-1130. https://doi.org/10.1038/s41559-019-0909-z

PUJOS F., DE IULIIS G. & CARTELLE C. 2017. — A Paleogeographic Overview of tropical fossil sloths: towards an understanding of the origin of extant suspensory sloths? *in* ANTOINE P.-O. & PUJOS F. (eds), Proceedings of the Symposium Cenozoic Evolution of Tropical-Ecuatorian Mammals, *Journal of Mammalian Evolution* 24: 19-38. https://doi.org/10.1007/s10914-016-9330-4

PÜSCHEL H. P., PÜSCHEL T. A. & RUBILAR-ROGERS D. 2017. — Taxonomic comments of a *Glossotherium* specimen from the Pleistocene of central Chile. *Boletín del Museo Nacional de Historia Natural, Chile* 66: 223-262.

RINDERKNECHT A., BOSTELMANN E., PEREA D. & LECUONA G. 2010. — A new genus and species of Mylodontidae (Mammalia: Xenarthra) from the late Miocene of souhern Uruguay, with comments on the systematics of the Mylodontinae. *Journal of Vertebrate Paleontology* 30: 899-910. https://doi.org/10.1080/02724631003757997

ROMÁN-CARRIÓN J. L. 2007. — Nuevos datos sobre la distribución geográfica de los "perezosos gigantes" del Pleistoceno del Ecuador. *Politécnica* 27: 111-124. http://bibdigital.epn.edu.ec/handle/15000/3841

ROMÁN-CARRIÓN J. L. 2012. — Nuevo registro de un mylodonte (*Glossotherium wegneri* Spillmann, 1931) en Conocoto, Quito. *Politécnica* 30: 218-220. http://bibdigital.epn.edu.ec/handle/15000/5246

ROMÁN-CARRIÓN J. L. & BRAMBILLA L. 2019. — Comparative skull osteology of *Oreomylodon wegneri* (Xenarthra, Mylodontinae): defining the taxonomic status of the Ecuadorian endemic mylodontid. *Journal of Vertebrate Paleontology* 39: e1674860. https://doi.org/10.1080/02724634.2019.1674860

SAINT-ANDRÉ P.-A., PUJOS F., CARTELLE C., DE IULIIS G., GAUDIN T. J., MCDONALD H. G. & MAMANI QUISPE B. 2010. — Nouveaux paresseux terrestres (Mammalia, Xenarthra, Mylodontidae) du Néogène de l'Altiplano bolivien. *Geodiversitas* 32: 255-306. https://doi.org/10.5252/g2010n2a4

SIMPSON G. G. & PAULA COUTO C. DE 1981. — Fossil mammals from the Cenozoic of Acre, Brazil III - Pleistocene Edentata Pilosa, Proboscidea, Sirenia, Perissodactyla and Artiodactyla. *Iheringia Séries Geológica* 6: 11-73.

SPILLMANN F. 1931. — *Die Säugetiere Ecuadors im Wandel der zeit (I. Teil).* Universidad Central, Quito, 112 p.

STOCK C. 1925. — *Cenozoic gravigrade Edentates of Western North America with special reference to the Pleistocene Megalonychinae and Mylodontidae of Rancho La Brea.* Carnegie Institution, Washington: 1-206.

TOMIATI C. & ABBAZZI L. 2002. — Deer fauna from Pleistocene and Holocene localities of Ecuador (South America). *Geobios* 35: 631-645. https://doi.org/10.1016/S0016-6995(02)00075-X

VARELA L. & FARIÑA R. A. 2016. — Co-occurrence of mylodontid sloths and insights on their potential distributions during the late Pleistocene. *Quaternary Research* 85: 66-74. https://doi.org/10.1016/j.yqres.2015.11.009

VARELA L., TAMBUSSO P. S., MCDONALD H. G. & FARIÑA R. A. 2019. — Phylogeny, macroevolutionary trends and historical biogeography of sloths: insights from a Bayesian morphological clock analysis. *Systematic Biology* 68: 204-218. https://doi.org/10.1093/sysbio/syy058

APPENDICES

|	
AMNH 1758	R dentary, preserving cf1-mf3, missing tip of mandibular condyle and of coronoid process and symphysis, Punín, Quebrada Chalán, Riobamba, Ecuador;
AMNH 9971	anterior portion of L and R dentaries (mandibular spout), preserving R cf1-mf1, Punín, 8 miles SE of Riobamba, Ecuador;
AMNH 96217	R dentary of a juvenile individual, preserving cf1-mf3, missing tip and angular and coronoid processes, Sloth Quarry, Ecuador;
AMNH 96218	posterior fragment of cranium of a juvenile individual, Ecuador;
AMNH 96219	posterior portion of L dentary of a juvenile individual, preserving mf2-mf3, missing most of angular, coronoid, and condyloid processes, Alangasí, Ecuador;
AMNH 96220	mandibular symphysis region of L dentary, preserving cf1-mf1, Alangasí (?), Ecuador;
AMNH 96221	L maxillary fragment, preserving Cf1 and alveoli of Mf1-Mf4, Spring Q., Ecuador;
AMNH FAM 95808	nearly complete R and L humeri and R radius, Ecuador;
AMNH FAM 95816	R ulna, R fourth metacarpal, and R fourth metatarsal, Sloth Quarry, Quebrada Chalán, Ecuador;
AMNH FAM 95817	nearly complete L humerus, Quebrada San Francisco, Ecuador;
AMNH FAM 96216	skull, preserving alveoli of Mf1-Mf4, partially preserving R Cf1-Mf4, missing dorsal roof, zygomatic arches, and portion of L orbital wall, Sloth Quarry, Quebrada Chalán, Ecuador;
EPN V. 120	neotype, nearly complete skull, La Cocha, Alangasí, Ecuador;
MECN 55	R maxillary fragment with Cf1 and alveoli of Mf1-2 of a juvenile individual, Quebrada Cuesaca, Bolivar, Ecuador;
MECN 61	articular surface of R scapula, Quebrada Pistud, Bolivar, Ecuador;
MECN 66	distal fragment of L fibula, Quebrada Pistud, Bolivar, Ecuador;
MECN 67	acetabular cavity of pelvis, Quebrada Pistud, Bolivar, Ecuador;
MECN 125	R maxillary fragment with Cf1-Mf2 of a juvenile individual, Quebrada Pistud, Bolivar, Ecuador;
MECN 190	L humerus, Quebrada Pistud, Bolivar, Ecuador;
MECN 191	second phalanx, Quebrada Pistud, Bolivar, Ecuador;
MECN 261	R tibia, Quebrada Pistud, Bolivar, Ecuador;
MECN 264	axis, Quebrada Pistud, Bolivar, Ecuador;
MECN 265	lumbar vertebra, Quebrada Pistud, Bolivar, Ecuador;
MECN 266	ventral fragment of R scapula, Quebrada Pistud, Bolivar, Ecuador;
MECN 274	L femur, Quebrada Pistud, Bolivar, Ecuador;
MECN 279	distal portion of L tibia, Quebrada Pistud, Bolivar, Ecuador;
MECN 353	ungual phalanx, Quebrada Pistud, Bolivar, Ecuador;
MECN 354	ungual phalanx, Quebrada Pistud, Bolivar, Ecuador;
MECN 355	highly damaged skull, preserving only part of the occipital and the basisphenoid, Quebrada Pistud, Bolivar, Ecuador;
MECN 356	damaged skull, preserving the occipital and the cranial ventral surface, Quebrada Pistud, Bolivar, Ecuador;
MECN 357	complete L mandible without dentition, Quebrada Pistud, Bolivar, Ecuador;
MECN 358	fragment of L mandible with cf1-mf2, Quebrada Pistud, Bolivar, Ecuador;
MECN 359	fragment of atlas, Quebrada Pistud, Bolivar, Ecuador;
MECN 360	R mandibular fragment of a juvenile individual, with mf2-mf3, Quebrada Pistud, Bolivar, Ecuador;
MECN 363	distal portion of R femur, Quebrada Pistud, Bolivar, Ecuador;
MECN 365	complete R humerus, Quebrada Pistud, Bolivar, Ecuador;
MECN 367	complete R humerus, Quebrada Pistud, Bolivar, Ecuador;
MECN 368	complete L humerus, Quebrada Pistud, Bolivar, Ecuador;
MECN 369	L tibia, Quebrada Pistud, Bolivar, Ecuador;
MECN 370	L tibia, Quebrada Pistud, Bolivar, Ecuador;
MECN 371	L fibula, Quebrada Pistud, Bolivar, Ecuador;
MECN 372	R fibula, Quebrada Pistud, Bolivar, Ecuador;
MECN 417	almost complete skull preserving the L jugal, but missing the L side anteriormost portion, Quebrada Pistud, Bolivar, Ecuador;
MECN 487	atlas, Quebrada Pistud, Bolivar, Ecuador;
MECN 488	part of R scapula, Quebrada Pistud, Bolivar, Ecuador;
MECN 489	R astragalus, Quebrada Pistud, Bolivar, Ecuador;
MECN 496	R ulna, Quebrada Pistud, Bolivar, Ecuador;
MECN 505	skull with almost complete dentition, missing R Cf1, Quebrada Pistud, Bolivar, Ecuador;
MNHN.F.PUN220	skull with damaged R side of the skull roof, Punín, Ecuador.

A

B

C

APPENDIX 2. — Skull of *Glossotherium wegneri* (Spillmann, 1931) (MECN 417) in dorsal (**A**), lateral (**B**) and ventral (**C**) views. Scale bar: 10 cm.
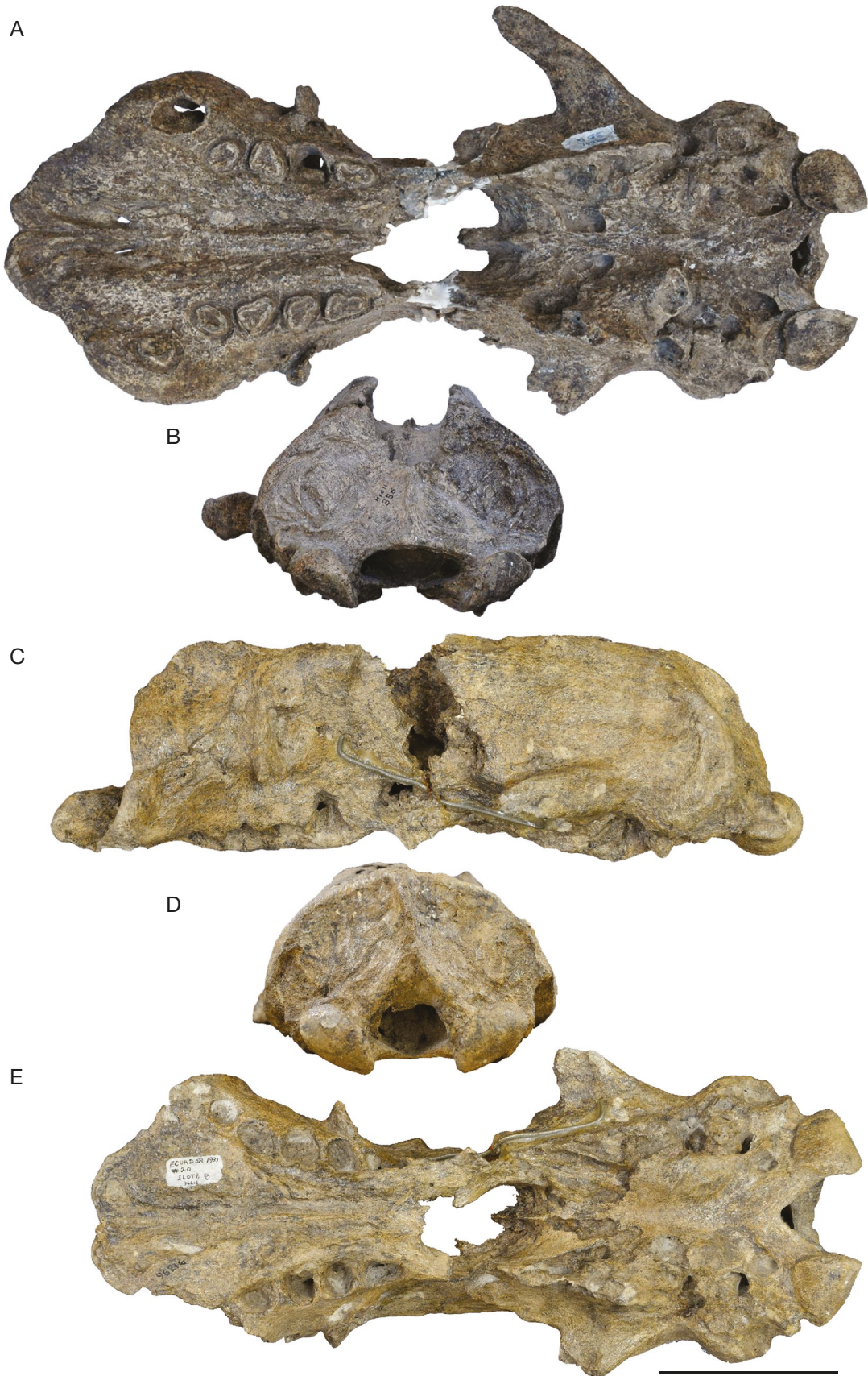
APPENDIX 3. — Skulls of *Glossotherium wegneri* (Spillmann, 1931) representing a robust (**A**, **B**) and a gracile (**C**-**E**) morph, which are suggestive of the presence of sexual dimorphism: **A**, **B**, skull (MECN 356) in ventral (**A**), and posterior (**B**) views; **C**-**E**, skull (AMNH 96216) in lateral (**C**), posterior (**D**) and ventral (**E**) views. Scale bar: 10 cm.
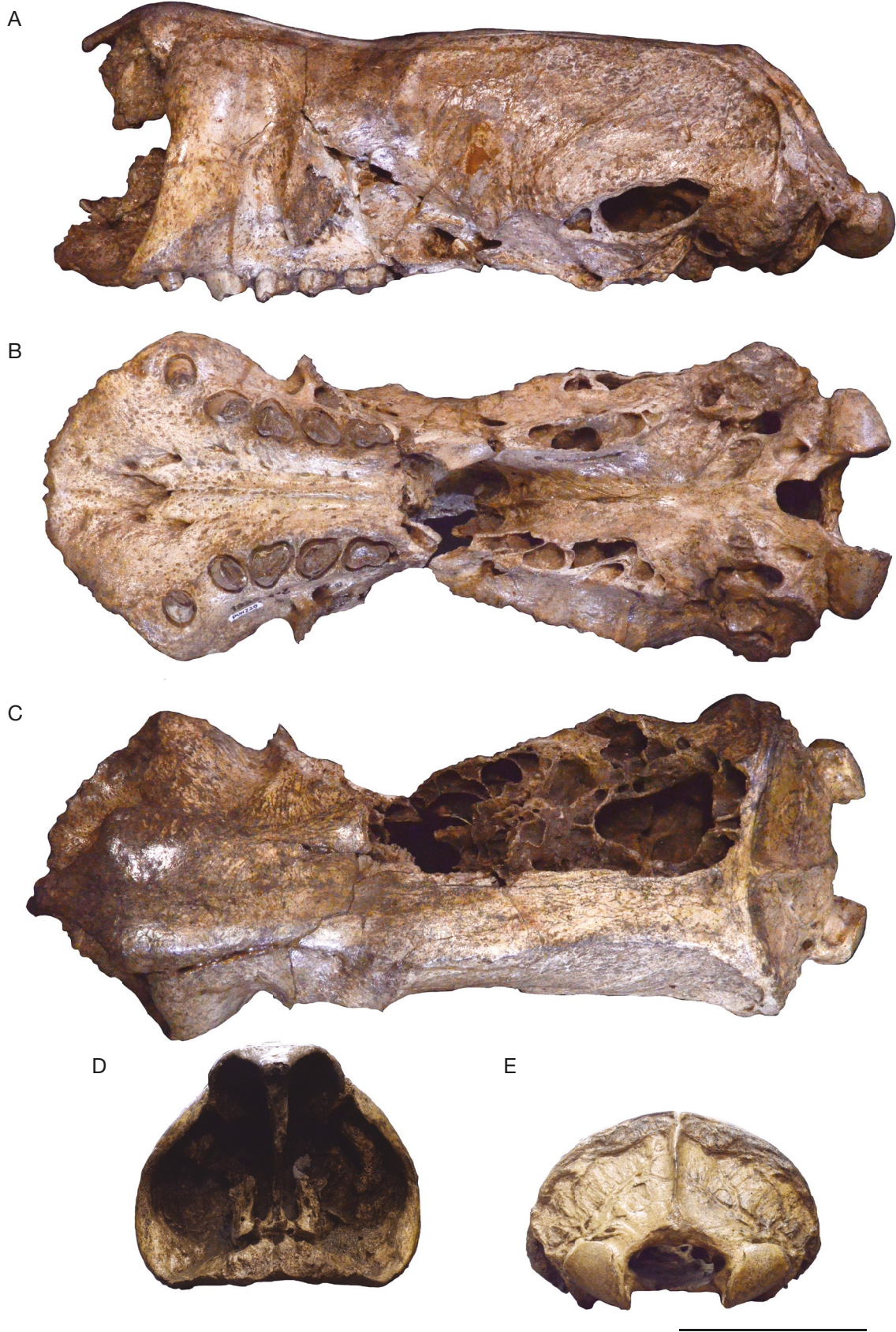
APPENDIX 4. — Skull of *Glossotherium wegneri* (Spillmann, 1931) (MNHN.F.PUN220) in lateral (**A**), ventral (**B**), dorsal (**C**), anterior (**D**) and posterior (**E**) views. Scale bar: 10 cm.

APPENDIX 5. — Phylogeny supplementary information. Character codification of *Glossotherium wegneri* (Spillmann, 1931) (a = 0 & 1; b = 1 & 2), added to the matrix of Boscaini *et al.* 2019c.

	10	**20**	**30**	**40**	**50**
1 2 0 1 1 a 1 0 2	0 2 0 2 0 1 1 0 1 1	1 1 0 0 0 a 1 0 1 0	0 1 3 4 4 7 4 3 a 0	0 2 2 0 1 0 0 1 0 1	1

	60	**70**	**80**	**90**	**100**
1 1 1 0 2 2 2 1 0	1 1 1 0 0 0 1 ? 1 0	0 0 0 1 1 0 0 ? ? ?	? 1 3 0 0 2 3 1 1 1	1 1 1 0 0 ? 0 1 1 1	?

	110	**120**	**130**	**140**	**150**
1 0 1 1 0 1 ? 1 0	1 0 0 0 3 1 0 1 ? ?	1 4 3 1 0 1 1 0 0 0	2 1 0 ? ? ? ? 1 ? 1	? 0 0 0 0 3 1 ? 0 0	?

	160	**170**	**180**	**190**	**200**
? ? ? ? 1 0 1 2 0	1 1 2 ? ? ? ? 0 3 1	1 1 ? 1 3 1 0 0 0 1	0 0 2 0 0 0 0 2 0 0	0 0 1 0 1 0 ? 0 1 ?	?

	210	**220**	**230**	**240**	**250**
? 0 0 0 1 0 0 ? ?	? 1 ? 2 0 ? 0 b 2 0	1 0 0 1 ? ? ? 1 0 1	0 ? 1 1 1 1 1 0 1 1	? 1 1 ? 0 ? ? 1 ? ?	?

	260	**270**	**280**	**290**	**300**
? 2 1 1 0 1 1 2 3	3 0 ? 2 1 1 1 1 0 ?	2 1 ? ? ? ? 0 0 2 1	1 0 1 2 1 0 1 ? ? ?	? ? ? ? 1 1 1 0 0 1	1

	310	**320**	**330**	**340**	**350**
0 0 2 2 1 1 1 2 1	0 0 1 1 1 2 0 1 0 1	1 1 3 1 1 1 1 1 1 ?	1 ? ? ? ? ? ? ? ? ?	? ? ? ? 1 1 1 1 1 1	2

	360	**370**	**380**		
0 1 2 1 1 2 2 2 2	1 1 1 1 1 2 1 ? 1 1	? ? ? ? ? ? ? ? ? ?	1 ? ? ?		
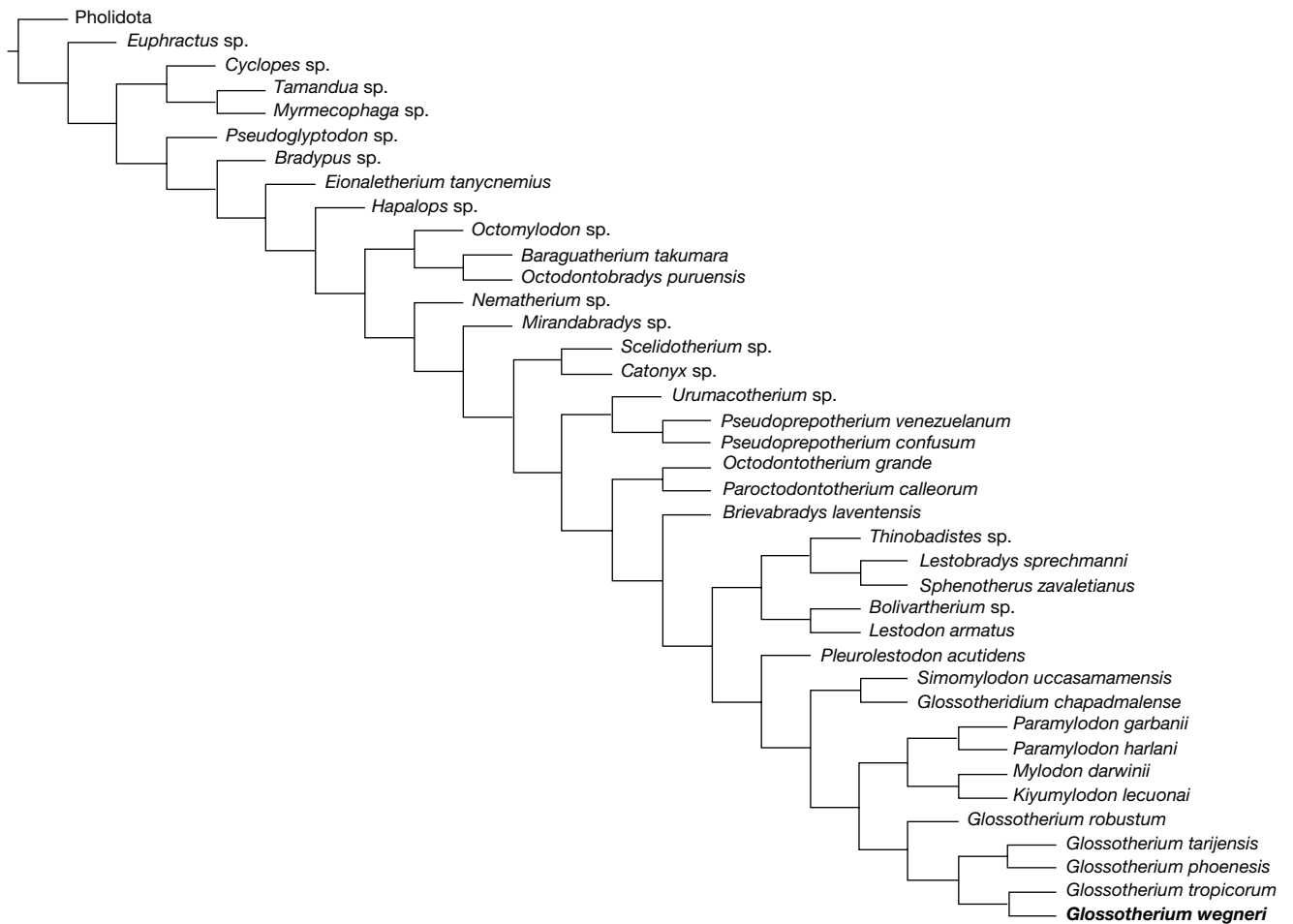
APPENDIX 6. — The complete most parsimonious tree recovered from the phylogenetic analysis (length: 1167 steps; consistency index: 0.545; retention index: 0.887).