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**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
INTRODUCTION

Sloths (Folivora synonym of Tardigrada synonym of Phyllophaga; Delsuc et al. 2001; Farinha & 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 monogenetic 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, andOctomylodontinae (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 further 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 was 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 Pintud 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 Pintud 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).

INSTITUTIONAL ABBREVIATIONS

| Institution     | Location                      | City           | Country  |
|-----------------|-------------------------------|----------------|----------|
| AMNH            | American Museum of Natural History | New York, United States |
| AMNH F:AM       | American Museum of Natural History, Frick Collection | New York, United States |
| EPN             | Collezione di Paleontologia della Escuadra Politecnica Nacional | Quito, Ecuador |
| MECN            | Museo Ecuatoriano de Ciencias Naturales | Quito, Ecuador |
| MNHN            | Museu national d’Histoire naturelle | París, France |

ANATOMICAL ABBREVIATIONS

- Cf/cf: upper/lower caniniform tooth
- L: left
- Mf/mf: upper/lower molariform tooth
- R: right

OTHER ABBREVIATIONS

- NALMA: North American Land Mammal Age

GEOGRAPHIC AND STRATIGRAPHIC CONTEXT

The physiographic and stratigraphic setting of the fossiliferous localities Quebrada Pintud 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 Pintud (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 16670 ± 80 years BP (Coltorti et al. 1998). The sequence at Quebrada Pintud 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 14450 ± 70 and 12350 ± 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 Alangası (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 & Faríña (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 Alangası, late Pleistocene (Montellano-Ballesteros & Román-Carrión 2011: fig. 2) (Fig. 1).

**Referenced 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 antero-posteriorly 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 sub-circular 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. phoenicis* (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 darwini* 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.
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. *Simomyodon uccasamamensis* Saint-André, Pujos, Cartelle, De Iuliiis, 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 Iuliiis 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 Iuliiis 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 Iuliiis 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 Iuliiis 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
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.
Portions of the dentary are approximately of the same height (Fig. 3I–K). In *M. darwini*, 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).
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; Boscaiini 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 been documented among fossil and living sloth species, including G. robustum (for a review, see Boscaiini et al. 2019b). Among the remains on which such intraspecific variation has been recognized include specimens, from the same or similar localities, that span the range of proportioned 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 Spellmann’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 Alangasi, 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 darwini. Among them, are the presence of an internasal element (although considerably smaller than that of M. darwini), 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. 3-K); a transversely expanded mandibular spur (Fig. 3D); and upper tooth rows that diverge markedly (Fig. 2C, E), particularly due to the lateral position of the Cฟ‌s (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. wege‌ri 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 Alangasi, 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. wege‌ri 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. wege‌ri. 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. wege‌ri is distinct and easily distinguishable from other Glossotherium species, as well as from other mylodontines (for a detailed review, see Boscaiini 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. wege‌ri (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. wege‌ri 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. wege‌ri (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
(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 megatherine Eremothereium laurillardi (Lund 1842), but not in its close relative Megatherium americanum Cuvier, 1796. In megatherines 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 → 3), 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 CFI from the anterior edge of maxilla (21: 0 → 1), a short mandibular symphysis (62: 2 → 1) ending anteriorly to cfi (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 expanded posteriorly (124: 1 → 0), zygomatic process of the squamosal greatly elongated (168: 2 → 3), relatively enlarged size of the hypoglossal foramen (187: 1 → 2), circumpalatal expansion of the rostral 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. phoenicis+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.

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On the status of the giant mylodontine sloth *Glossotherium wegneri*
APPENDICES

APPENDIX 1. — List of specimens assigned to Glossotherium wegneri (Spillmann, 1931) (MECN specimens include those that we were able to examine directly).

AMNH 1758  
R dentary, preserving cf1-mf3, missing tip of mandibular condyle and of coronoid process and symphysis, Punin, Quebrada Chalán, Riobamba, Ecuador;

AMNH 9971  
anterior portion of L and R dentaries (mandibular spout), preserving R cf1-mf1, Punin, 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, Alangasi, Ecuador;

AMNH 96220  
mandibular symphysis region of L dentary, preserving cf1-mf1, Alangasi (?), Ecuador;

AMNH FAM 95808  
neotyp, 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  
neotyp, nearly complete skull, La Cocha, Alangasi, 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  
unqua phalax, Quebrada Pistud, Bolivar, Ecuador;

MECN 354  
unqua phalax, 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  
L 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, Punin, Ecuador.


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.

APPENDIX 6. — The complete most parsimonious tree recovered from the phylogenetic analysis (length: 1167 steps; consistency index: 0.545; retention index: 0.887).