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Hermann Karsten (1817–1908): a German naturalist in the Neotropics and the significance of his paleovertebrate collection

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Abstract. During the mid-19th century, the German naturalist Hermann Karsten conducted a 12-year exploration (1844–1856) in the territories of Ecuador, New Granada (now Colombia) and Venezuela, allowing him to produce important botanic, geographic and geologic descriptions with valuable information that permits us to refer to him as a pioneer in many of these topics. With his return to Europe, abundant geological, paleontological and living plant specimens were brought and housed in European museums and botanical gardens. The Karsten collection included an important invertebrate collection from the Cretaceous of the Andes of Colombia and Venezuela, which was studied and published by himself and the renowned German paleontologist Leopold von Buch, filling a large void in the knowledge about ancient faunas. H. Karsten's vertebrate collection was never illustrated or subjected to a detailed taxonomic study, being mentioned in scientific publications in a repetitive manner and with incorrect taxonomic and provenance information. More than 160 years after they were collected, we carried out a taxonomic revision of all H. Karsten's vertebrate specimens from Colombia and Venezuela, which are housed in the Museum of Natural History in Berlin. These specimens are represented by cranial and postcranial elements of megafauna, which include Megatheriidae, Mylodontidae and Glyptodontidae (Xenarthra), Toxodontidae (Notoungulata), Gomphotheriidae (Proboscidea), and many other indeterminate mammal remains. This revision is intended to clarify the taxonomy and provenance of the specimens, emphasizing the historical importance of this fossil collection and its significance for the paleontology of the region.

1 Introduction

Dr. Karl Hermann Gustav Wilhelm Karsten (1817–1908) (Fig. 1) was a Prussian naturalist from Stralsund (northern Germany), who, using his own economic resources, conducted a 12-year long exploration in the Neotropical territories of Venezuela (1844–1847 and 1848–1852) and the Republic of New Granada (now Colombia) and Ecuador (1852–1856) (Röhl, 1944; Alert, 1999). Alexander von Humboldt provided H. Karsten with a letter of introduction to the Venezuelan president, requesting collaboration for the trips and intellectual aim of the young scientist (Röhl, 1944). The previous training of H. Karsten as an apprentice in pharmacy and natural sciences was useful during his explorations in South America, which resulted in detailed descriptions of botany, entomology, geography and geology (Karsten, 1886; Röhl, 1944; Hedberg, 1974; Alert, 1999; Aalto, 2015). During his travels through Venezuela, New Granada and Ecuador, H. Karsten met well-known figures of the political, medical and the natural sciences, including Agustín Codazzi, Alexander Benitz, Karl Moritz, August Gottfried Knoche and Francisco José de Caldas; some of them shared long days of exploration and collection of specimens (Röhl, 1944; Tryon, 1963; Alert, 1999).

Hermann Karsten was engaged mainly in the study of tropical plants, which resulted in many publications, his best known work being *Florae Columbiae Terrarumque Adiacentium Specimina Selecta in Peregrinatione Duodecim Annorum Observata Delineavit et Descripsit*, published in two volumes from 1858 to 1869 (Tryon, 1963). Additionally,

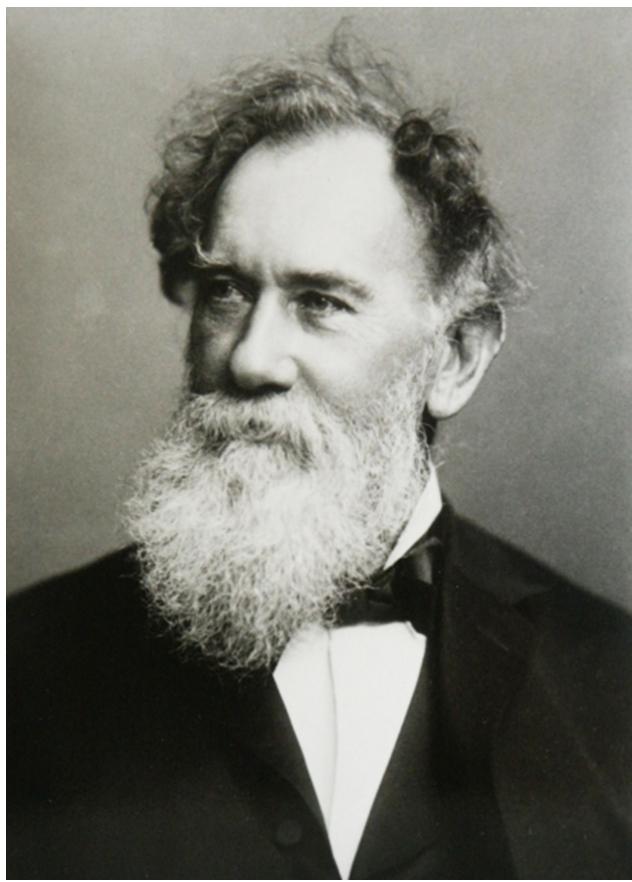


Figure 1. Portrait of Hermann Karsten. Picture courtesy of Stadtarchiv Schaffhausen (Biographien Sammlung der Naturforschenden Gesellschaft Schaffhausen), Switzerland.

H. Karsten was acquiring much geological information during his travels, especially about Cretaceous and Cenozoic rocks, observations and descriptions that are all the more remarkable because it is considered that he was primarily a botanist (Hedberg, 1974). His geological contributions (Venezuela, New Granada and Ecuador) included about 21 publications (summarized in Hedberg, 1974, 36–43), with valuable contributions on geomorphology, geological cartography, mineralogy, orogeny, paleontology, petrography and volcanology, among others subjects, Karsten being a regional pioneer in many of these topics. He published comments about the geology of the Island of Curaçao (Karsten, 1853), which he visited in the middle of his journey from Venezuela to New Granada in 1852. Thirty years after his return from South America, H. Karsten (1886) published his best-known geological contribution *Géologie de l'ancienne Colombie bolivarienne: Vénézuela, Nouvelle-Grenade et Ecuador*, a comprehensive summary of his geological results of 12 years of exploration. In this contribution, written in a diary style, H. Karsten reviewed previous geological, climatic, topographic/vegetation and soil observations, including many references to fossil finds (Karsten, 1886). In these and other

publications (e.g., Karsten, 1849, 1858, 1886), Karsten also included many references to botanical and animal fossils. These fossils, especially invertebrates such as Cretaceous bivalves, echinoids and ammonites, were brought to and deposited in European museums, where some of them were studied by himself and by the renowned paleontologists Leopold von Buch and Charles Louis Perceval de Loriol (von Buch, 1850; Karsten, 1858, 1886; De Loriol, 1876). Using H. Karsten's specimens from the Andes of Lara, von Buch described for the first time a fossil species from Venezuela: *Ammonites* (= *Anapuzosia*) *tucuyensis* (von Buch, 1850). Karsten (1851, pp. 445, 465) also mentioned the finding of amber in Venezuela, specifically from the states of Falcón and Lara; in the latter, he found abundant well-preserved fragments with embedded wasps and bees.

With regard to the fossil vertebrates, only allusive references were made by H. Karsten to mammal remains from different locations in Venezuela, New Granada and Ecuador (e.g., Karsten, 1849, pp. 197, 199; 1851, pp. 465, 467, 479; 1859b, p. 292; 1886, pp. 11, 14, 20, 29, 32, 44–45). According to H. Karsten, the mammalian fossils from Ecuador (Karsten, 1886, pp. 44–45) and some from New Granada (Karsten, 1886, pp. 32, 49) were found by other naturalists (e.g., Alexander von Humboldt, Andrés Posada-Arango and Theodor Wolf) prior to his expeditions. In H. Karsten's publication, there is also an enigmatic reference (without illustration or detailed stratigraphy and location) to the possible presence of *Chirotherium*, tracks in clay shales (ichnofossil) from the Cojedes and Guárico states, as well from the region between Mérida and Barinas (Andean region), all in Venezuela (Karsten, 1862, p. 286; 1886, pp. 13, 17). The H. Karsten vertebrate collection was never illustrated or subjected to a detailed taxonomic study. Moreover, many of H. Karsten's original fossil vertebrate specimens have been mentioned in scientific publications (especially in relation to Venezuelan paleontology) in a repetitive manner and sometimes with incorrect taxonomic and provenance information (e.g., Jahn, 1921, p. 39; Liddle, 1928, p. 351; Schaub, 1935, p. 1; Von der Osten, 1947, p. 161; Takacs et al., 1967, p. 32; Linares, 1983, p. 1; Ochsenius, 1980, p. 21; Rincón et al., 2006, p. 530, 2008, p. 197; Rincón and White, 2007, p. 2; Carrillo-Briceño et al., 2008, p. 242; Rincón, 2011, p. 894). More than 160 years after they were collected, we conducted a taxonomic revision of all H. Karsten vertebrate fossils, also clarifying the provenance of specimens and discussing the historical importance of this collection.

2 Materials and methods

The H. Karsten vertebrate collection studied here is represented by a total of 60 cranial and postcranial elements of mammals (Table 1). All these specimens are housed at the Museum für Naturkunde in Berlin (MB.MA.). In H. Karsten's publications, few fossil vertebrate remains corresponding to

Table 1. Taxonomy of the fossil mammal specimens collected by H. Karsten.

Superorder	Order	Family	Subfamily	Genus	Species	Specimen number	Element	Figure
Xenarthra	Pilosa	Megatheriidae	Megatheriinae	<i>Eremotherium</i>	<i>Eremotherium laurillardi</i>	MB.Ma. 42937	Right unciform	Fig. 3a–b
				cf. <i>Eremotherium</i>	cf. <i>Eremotherium laurillardi</i>	MB.Ma. 33534	Five molariforms + four fragments (indet. position)	Fig. 3c–m
				cf. <i>Eremotherium</i>	cf. <i>Eremotherium laurillardi</i>	MB.Ma. 48085	Left humerus, distal section	Fig. 3n
				cf. <i>Eremotherium</i>	cf. <i>Eremotherium laurillardi</i>	MB.Ma. 42903	Left tibia, distal fragment	Fig. 3o–p
				cf. <i>Eremotherium</i>	cf. <i>Eremotherium laurillardi</i>	MB.Ma. 42936	Humeral head (indet. laterality)	Fig. 3q
				cf. <i>Eremotherium</i>	cf. <i>Eremotherium laurillardi</i>	MB.Ma. 42935	Right ulna, distal fragment	Fig. 3r–s
		Mylodontidae	Mylodontinae	Indet.	Indet.	MB.Ma. 33535	Tooth (upper left MF2)	Fig. 4a–b
				Indet.	Indet.	MB.Ma. 42896	Left femur, distal fragment	Fig. 4c–d
				Indet.	Indet.	MB.Ma. 42897	Right tibia, distal fragment	Fig. 4e–f
				Indet.	Indet.	MB.Ma. 42905	Metapodial fragment (indet. position)	Fig. 4g–h
				Indet.	Indet.	MB.Ma. 42902	Right ulna, proximal fragment	Fig. 4i–j
				Indet.	Indet.	MB.Ma. 42901	Humeral head (indet. laterality)	Fig. 4k
				Indet.	Indet.	MB.Ma. 33541	Ungual phalanx, proximal fragment (indet. position)	Fig. 4l–n
				Indet.	Indet.	MB.Ma. 17151	Left glenoid fossa, scapula	Fig. 4o–p
				Indet.	Indet.	MB.Ma. 33536	Proximal phalanx (indet. position)	Fig. 4q–r
				Indet.	Indet.	MB.Ma. 42900	Glenoid fossa, scapula (indet. laterality)	Fig. 5a–b
				Indet.	Indet.	MB.Ma. 33540	Left ? Magnum	Fig. 5c–d
				Indet.	Indet.	MB.Ma. 42904	Right astragalus	Fig. 5e–f
				Indet.	Indet.	MB.Ma. 42907	Metatarsal V (indet. laterality)	Fig. 5g–h
				Indet.	Indet.	MB.Ma. 42906	Left metatarsal V	Fig. 5i–j
				Indet.	Indet.	MB.Ma. 33537	Second phalanx (indet. position)	Fig. 5k–l
				Indet.	Indet.	MB.Ma. 33538	Metapodial, distal fragment (indet. position)	Fig. 5m–n
				Indet.	Indet.	MB.Ma. 17154	Centrum, thoracic vertebra	Fig. 6a–b
				Indet.	Indet.	MB.Ma. 17153	Centrum, thoracic vertebra	Fig. 6c–d
				Indet.	Indet.	MB.Ma. 17156	Centrum, thoracic vertebra	Fig. 6e–f
				Indet.	Indet.	MB.Ma. 17155	Centrum, thoracic vertebra	Fig. 6g–h
				Indet.	Indet.	MB.Ma. 33543	Centrum, caudal vertebra	Fig. 6i–k

Table 1. Continued.

Superorder	Order	Family	Subfamily	Genus	Species	Specimen number	Element	Figure
Cingulata	Glyptodontidae			Glyptotherium	Glyptotherium cf. <i>G. cylindricum</i>	MB.Ma. 33532	Right hemimandible, and two upper molariforms	Fig. 6l–r
				Indet.	Indet.	MB.Ma. 33533-1	Osteoderm	Fig. 6s–t
				Indet.	Indet.	MB.Ma. 33533-2-6	Four carpal-metacarpal elements (indet. laterality)	Fig. 6u–z
Meridiungulata	Notoungulata	Toxodontidae	Indet.	Indet.	Indet.	MB.Ma. 33517	Tooth fragment? (specimen not found in the collection)	Not figured
Proboscidea	Gomphotheriidae	Cuvieroninae		Indet.	Indet.	MB.Ma. 33542	Pisiform bone (indet. laterality)	Fig. 7a–d
				Indet.	Indet.	MB.Ma. 17152	Thoracic vertebra	Fig. 7e–g
				Indet.	Indet.	MB.Ma. 17146	Left metacarpal II	Fig. 7h–j
				Indet.	Indet.	MB.Ma. 17147	Right unciform	Fig. 7k–m
				Indet.	Indet.	MB.Ma. 17148	Right astragalus	Fig. 7n–o
Mammalia Indet.	Indet.	Indet.	Indet.	Indet.	MB.Ma. 17150	Left humeral ? head	Fig. 7p–q	
	Indet.	Indet.	Indet.	Indet.	MB.Ma. 14109	Femoral head	Fig. 7r–s	
	Indet.	Indet.	Indet.	Indet.	MB.Ma. 42899	Occipital condyle	Fig. 8a–b	
	Indet.	Indet.	Indet.	Indet.	MB.Ma. 42908	Centrum, sacrum	Fig. 8c	
	Indet.	Indet.	Indet.	Indet.	MB.Ma. 33539	Indet. fragmentary postcranial element	Fig. 8d–f	
	Indet.	Indet.	Indet.	Indet.	MB.Ma. 17145	Dorsal rib fragments	Fig. 8g–h	
	Indet.	Indet.	Indet.	Indet.	MB.Ma. 17149	Dorsal rib fragments	Fig. 8i	
	Indet.	Indet.	Indet.	Indet.	MB.Ma. 42911	Indet. fragmentary postcranial element	Fig. 8j–k	
	Indet.	Indet.	Indet.	Indet.	MB.Ma. 42910	Indet. fragmentary postcranial element	Fig. 8l	
	Indet.	Indet.	Indet.	Indet.	MB.Ma. 42909	Indet. fragmentary postcranial element	Fig. 8m–n	

his own find (among which are some references to the giant sloth *Megatherium*) were mentioned from different locations in Venezuela (Karsten, 1849, pp. 197, 199; 1851, pp. 465, 467, 479; 1859b, p. 292; 1886, pp. 11, 14, 20, 49) and Colombia (Karsten, 1851, p. 467; 1886, p. 49). In contrast, information mentioned in the MB.Ma. catalog about the H. Karsten vertebrate collection, which lacks a clear stratigraphic context, serves to identify only three localities in Venezuelan territory (Barbacoas, San Juan de Los Morros and Paraguaná Peninsula) and one in Colom-

bia (Barbacoas-Candelillas District, Colombia) (Fig. 2, Table 2). Using H. Karsten's publications (1849, 1850a, b, 1851, 1886) as a geographical reference, the Venezuelan localities (Table 2) are "Barbacoas town" (9°49'34" N, 70°3' 12" W), Morán Municipality, Lara State; "San Juan de Los Morros" (9°54'05" N, 67° 21'15" W), Juan Germán Roscio Municipality, Guárico State; and "Paraguaná Peninsula" (11°56'41" N, 69°55'23" W), Falcón Municipality, Falcón State. The Colombian locality referred in the MB.Ma. catalog as "Barbacoas-Candelillas District, Kolumbien" is

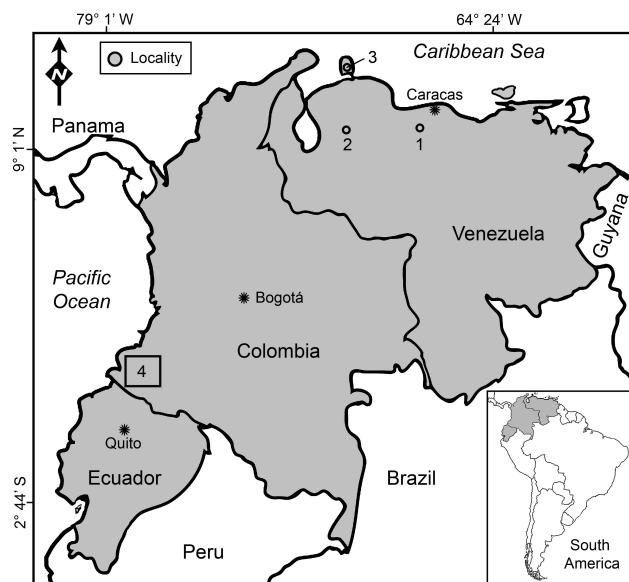


Figure 2. Map of the territories of Venezuela, Colombia (formerly, New Granada) and Ecuador visited by Hermann Karsten during his 12 years of explorations. The provenances of the fossil vertebrates discussed in this work are (1) San Juan de Los Morros; (2) Barbacoas; (3) Paraguaná Peninsula; (4) “Barbacoas-Candelillas District” locality (map shows possible location).

not referred to in any of the relevant publications (e.g., Karsten, 1853, 1858, 1859a, 1886). The most plausible explanation is that the “Barbacoas-Candelillas District” belonged to the ex-province of Barbacoas, which was founded in 1846 and ended in 1855, in the Republic of New Granada. Nowadays Barbacoas is a town on the banks of the Telembí River ($1^{\circ}40'22''$ N, $78^{\circ}8'21''$ W), in the Barbacoas Municipality, and Candelillas is a town on the banks of the Mira River ($1^{\circ}28'32.51''$ N, $78^{\circ}41'8.57''$ W), in the Tumaco Municipality; both belong to Nariño Department (southern Colombia). Although it is unknown if H. Karsten was in any of these locations, it is well known that on his trip he visited many places in the current Nariño Department (e.g., Karsten, 1886, pp. 1–2, 22–35).

Taxonomic identification involved an extensive bibliographical review and comparative studies with collections such as the Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas of the Universidad Experimental Francisco de Miranda (CIAAP, UNEFM-PF); the Museo de Ciencias de Caracas (MCNC) and the Universidad Central de Venezuela (UCV-VF), all in Venezuela; the Fossil Vertebrate Section of the Museum für Naturkunde, Berlin, Germany (MB.Ma.); the Palaeontological Institute and Museum at the University of Zurich (PIMUZ) and the Natural History Museum of Basel (NMB), Switzerland; the Museo de La Plata (MLP), Argentina; and the Muséum national d’Histoire naturelle, Paris, France.

3 Hermann Karsten’s fossil mammals

The taxonomic composition of H. Karsten’s fossil specimens includes 60 cranial and postcranial remains attributed to “ground sloths”, large glyptodonts (close relatives of armadillos), “South American native ungulates”, proboscideans and other indeterminate mammalian remains.

3.1 “Ground sloths” (Xenarthra: Tardigrada Latham and Davies in Forster, 1795)

The specimens ascribed to sloths (Tardigrada) are for the most part isolated and fragmentary elements (Tables 1–2), making precise taxonomic attributions difficult. It is noteworthy that all specimens represent large-sized taxa. At least two taxa belonging to two families, the Megatheriidae and the Mylodontidae, are represented (Table 1). One unciform (Fig. 3a–b) is characteristic of the megatheriid *Eremotherium laurillardi* (Lund, 1842) (see Cartelle and De Iuliis 1995). Various other postcranial and dental elements can safely be ascribed to a Megatheriinae, and we hence assign them to cf. *Eremotherium laurillardi* (Fig. 3c–s). A fragmentary isolated tooth (MB.Ma. 33535; Fig. 4a–b) is the only specimen safely ascribable to a Mylodontinae (likely cf. *Mylodon*). Numerous other postcranial fragments are referred to Tardigrada indet. (Figs. 4c–r, 5a–n, 6a–k).

3.2 Glyptodonts (Xenarthra: Cingulata Illiger 1811)

The specimens are represented by a few cranial and postcranial elements (Fig. 6l–z), all found in the San Juan de Los Morros locality (Tables 1–2). Cranial elements are represented by an anterior fragment of a right hemimandible (MB.Ma. 33532) preserving the molariforms 1–3 (Fig. 6l–n), and two upper isolated molariforms (MB.Ma. 33532) corresponding to the two first (Mfs 1 and 2) (Fig. 6o–r). A comparison with complete material (e.g., MCNC s/n; see Carlini et al., 2008; Oliveira et al., 2010) shows that these remains from San Juan de Los Morros belong to *Glyptotherium* cf. *G. cylindricum* Brown, 1912. The mandible of *G. cf. cylindricum* is slender and morphologically similar to that of *Glyptotherium texanum* Osborn, 1903. It differs clearly from that of *Glyptodon* Owen, 1839, which has a greater robustness in this taxon. In turn, the preserved upper and lower molariforms are trilobate (Fig. 6o–r), as observed in the genus *Glyptodon*, and morphologically similar to that of *Glyptotherium cylindricum*. As in *Glyptodon* the molariforms show an asymmetric development of the three lobes, being more developed labially than lingually. With regard to the isolated postcranial elements, the osteoderm (MB.Ma. 3353-1) could correspond to an accessory osteoderm of the caudal border of the dorsal carapace or, alternatively, to the caudal rings of the caudal armor (Fig. 6s–t). Specimens MB.Ma. 3353-2–6 (Fig. 6u–z) correspond to carpal–metacarpal elements. However, the absence of diag-

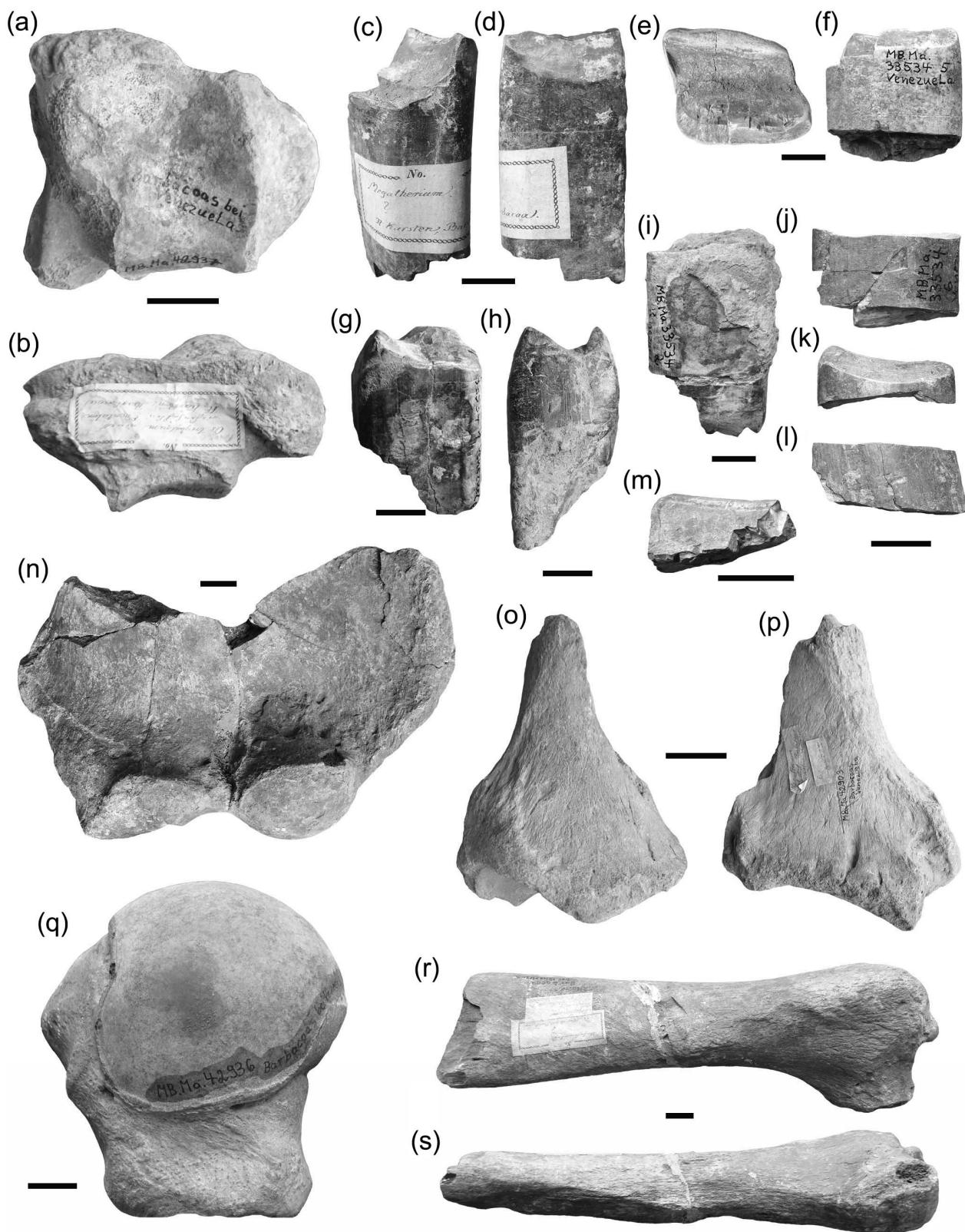


Figure 3. “Ground sloth” specimens. (a–b) *Eremotherium laurillardi* right unciform (MB.Ma. 42937) and (c–s) cf. *Eremotherium laurillardi* (c–m) Five fragmentary molariforms (MB.Ma. 33534); (n) distal fragment of left humerus, (MB.Ma. 48085); (o–p) distal fragment of left tibia (MB.Ma. 42903); (q) humeral head of indet. laterality (MB.Ma. 42936); (r–s) distal fragment of right ulna (MB.Ma. 42935). Scale bar equals 2 cm.

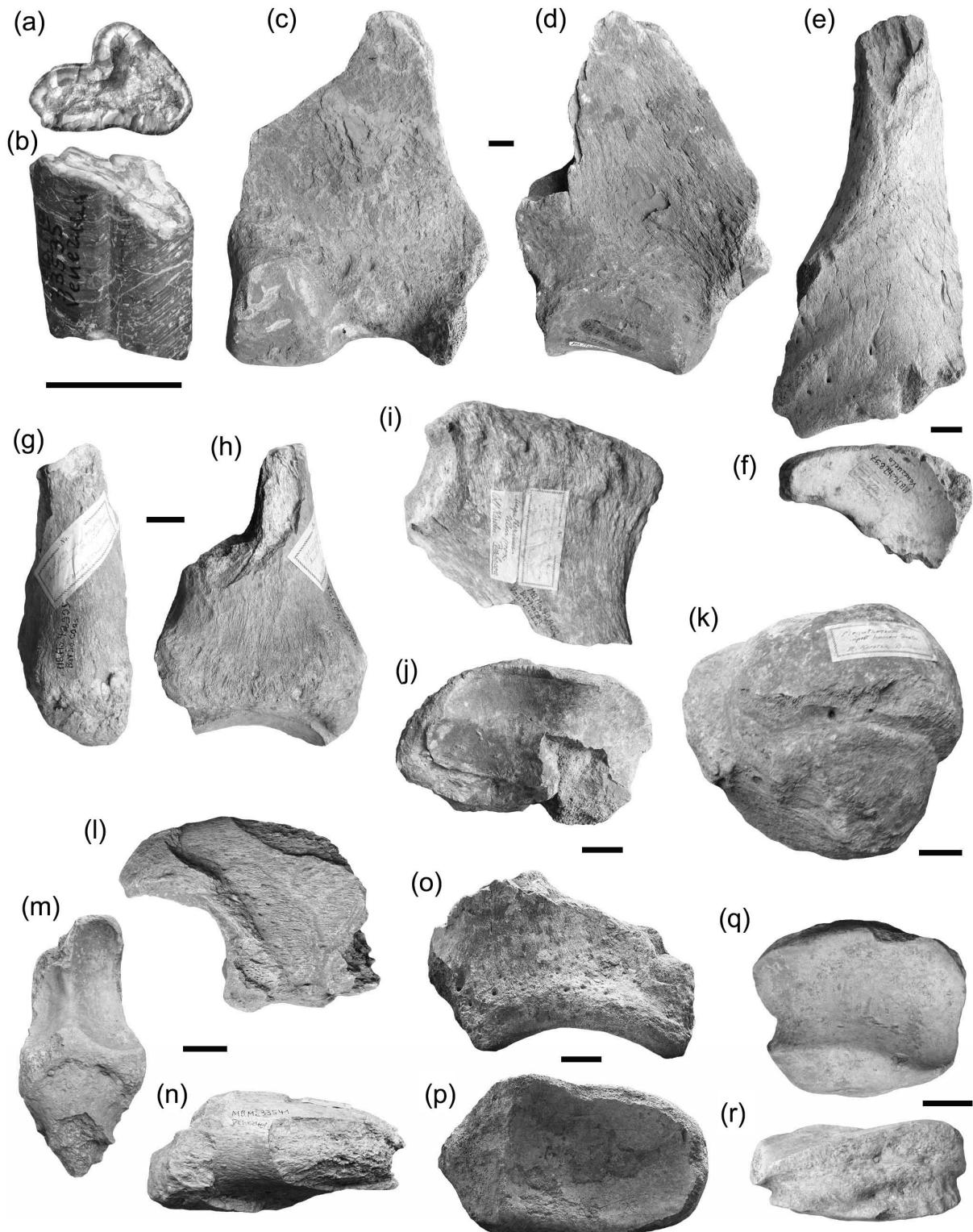


Figure 4. “Ground sloth” specimens. (a–b) Tooth of Mylodontinae indet. (MB.Ma. 33535) and (c–r) Tardigrada indet. (c–d) Distal fragment of left femur (MB.Ma. 42896); (e–f) distal fragment of right tibia (MB.Ma. 42897); (g–h) distal fragment of metapodial of indet. position (MB.Ma. 42905); (i–j) proximal fragment of right ulna (MB.Ma. 42902); (k) humeral head of indet. laterality (MB.Ma. 42901); (l–n) fragment of ungual phalanx (MB.Ma. 33541); (o–p) left glenoid fossa of scapula (MB.Ma. 17151); (q–r) proximal phalanx of indet. Position (MB.Ma. 33536). Scale bar equals 3 cm.

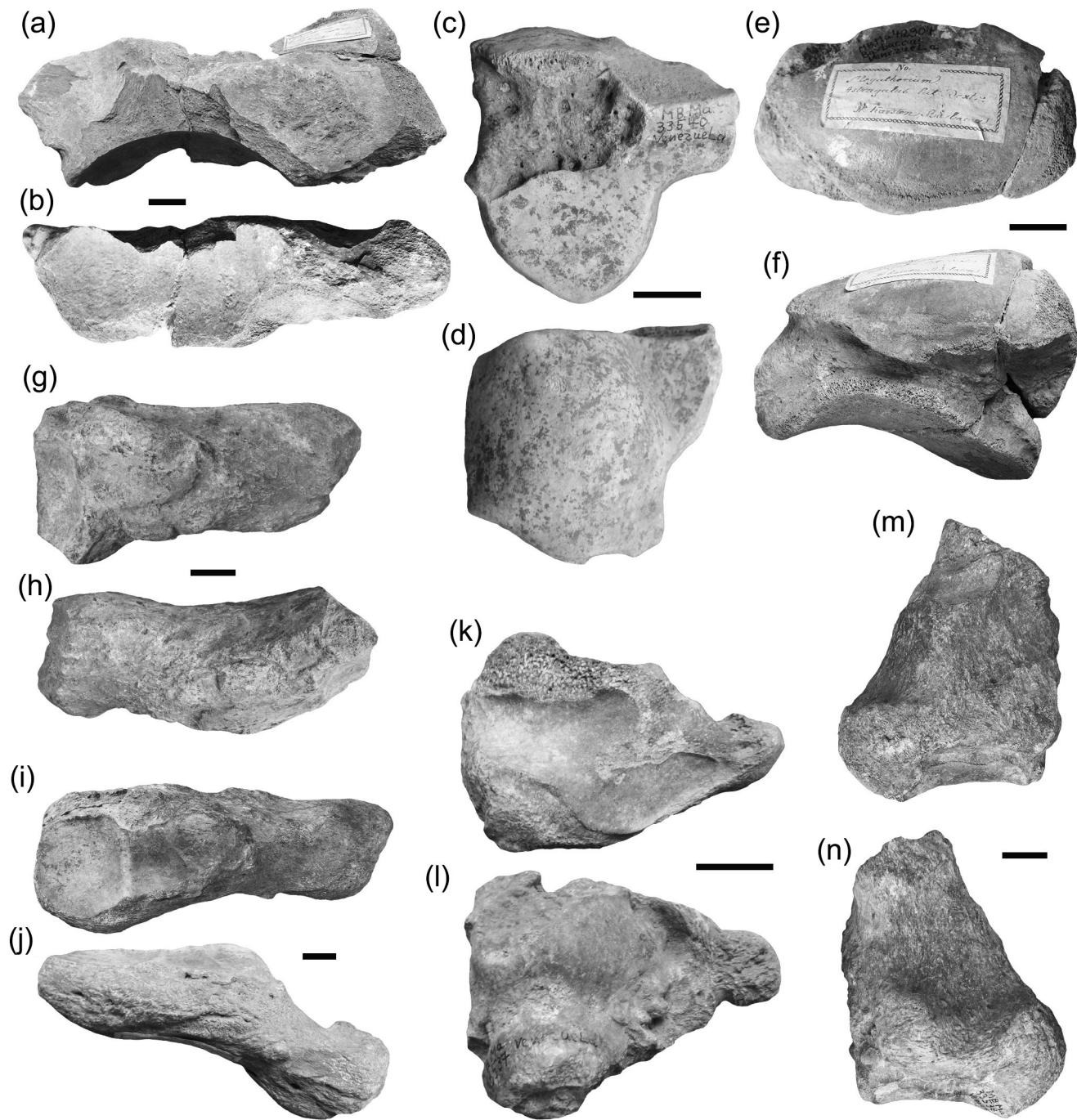


Figure 5. “Ground sloth” specimens. (a–n) Tardigrada indet. (a–b) Glenoid fossa of scapula (MB.Ma. 42900); (c–d) left? magnum (MB.Ma. 33540); (e–f) right astragalus (MB.Ma. 42904); (g–h) metatarsal V of indet. laterality (MB.Ma. 42907); (i–j) left metatarsal V (MB.Ma. 42906); (k–l) second phalanx of indet. laterality (MB.Ma. 33537); (m–n) distal fragment of metapodial of indet. laterality (MB.Ma. 33538). Scale bar equals 2 cm.

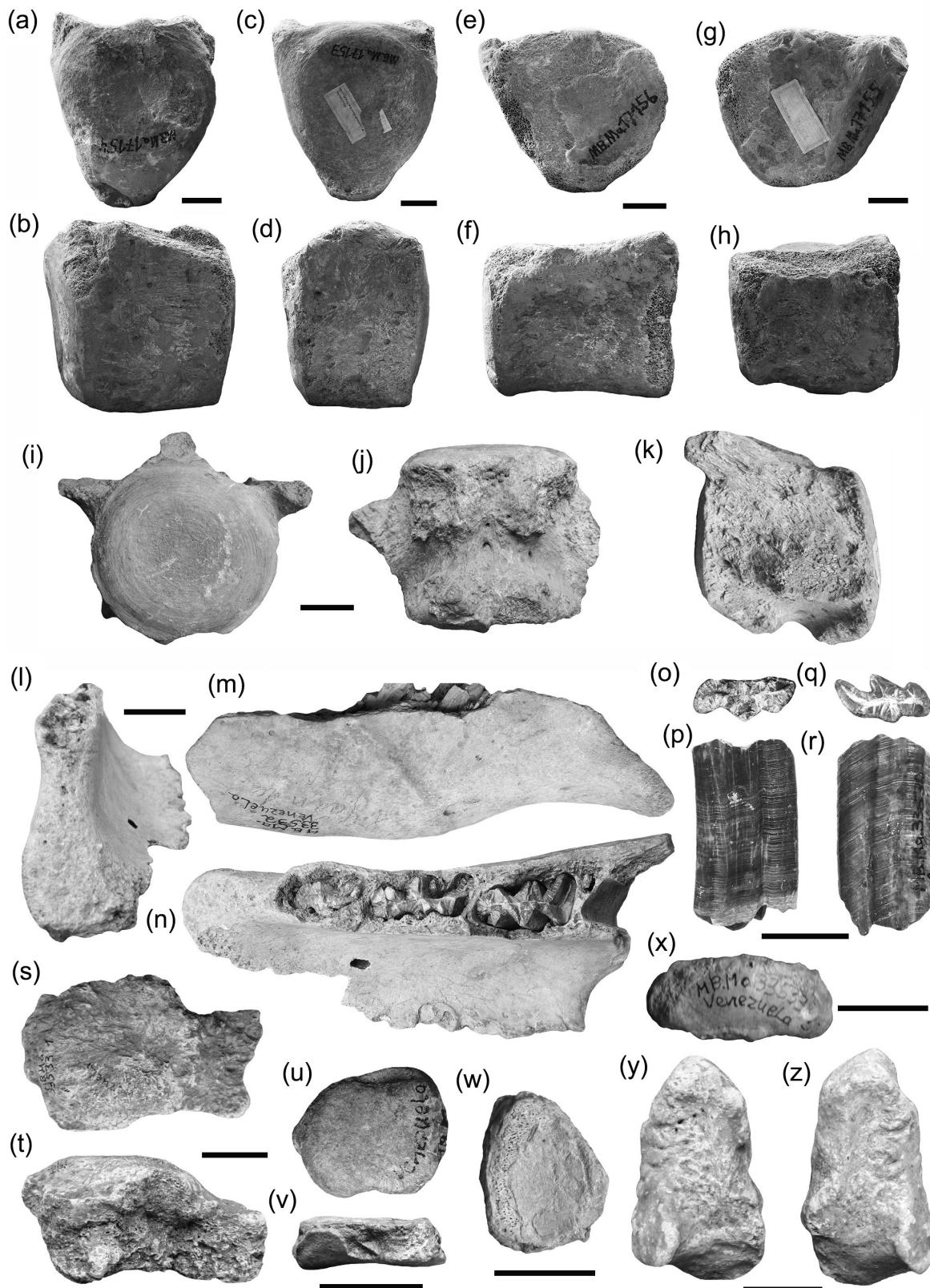


Figure 6. “Ground sloth” and glyptodont specimens. (a–k) Tardigrada indet. (a–h) Centra thoracic vertebrae [(a–b) MB.Ma. 17154; (c–d) MB.Ma. 17153; (e–f) MB.Ma. 17156; (g–h) MB.Ma. 17155]; (i–k) centra of caudal vertebra [MB.Ma. 33543)], (l–r) Right hemimandible and two upper molariforms of *Glyptotherium* cf. *G. cylindricum* (MB.Ma. 33532), and (s–z) Glyptodontidae indet. [(s–t) osteoderm (MB.Ma. 33533-1); (u–z) four carpal-metacarpal elements of indet. laterality (MB.Ma. 33533-2-6)]. Scale bar equals 2 cm.

nostic characters in these elements precludes a more specific identification than Glyptodontidae indet.

3.3 “South American native ungulates” (Notoungulata: Toxodontidae Gervais 1847)

One possible tooth fragment referred in the MB.Ma. catalog as “Toxodonta” (MB.Ma. 33517) from San Juan de Los Morros (the specimen could not be located in the collection) and a postcranial element assigned to a pisiform (MB.Ma. 33542) of indeterminate laterality (Fig. 7a–d) from the Paraguaná Peninsula (Tables 1–2) are the only specimens assigned to this group in the H. Karsten collection. The articular surfaces of the pisiform (81.6 mm long) are slightly eroded. A comparison with some pisiforms of *Toxodon* Owen, 1837, from Argentina (MLP and PIMUZ) shows that the specimen from Venezuela is apparently much larger and robust. *Mixotoxodon larensis* Van Frank, 1957, is the only species known from the Pleistocene of Venezuela (Rincón, 2011; Carrillo-Briceño, 2015), and its paleogeographic distribution possibly ranges from the United States to the north of Argentina (Carrillo-Briceño, 2015). Although dental characters have been used to distinguish *Toxodon* from *Mixotoxodon* (e.g., Van Frank, 1957; Rincón, 2011), little is known about their postcranial differences, especially for the few remains that have been assigned to *Mixotoxodon*. The absence of a stratigraphic context and of diagnostic characters in the specimen from Paraguaná Peninsula precludes a more specific identification than Toxodontidae indet.

3.4 Proboscideans (Proboscidea: Gomphotheriidae Hay, 1922)

The fossil specimens are represented only by four postcranial elements (Fig. 7e–o, Table 1); all of them were found in the “Barbacoas-Candelillas” locality, Colombia (Table 2). MB.Ma. 17152 corresponds to a thoracic vertebra that lacks the neural arch (Fig. 7e–g). Podial elements are represented by a left metacarpal II (MB.Ma. 17146; Fig. 7h–j), a right unciform (MB.Ma. 17147; Fig. 7k–m) and a right astragalus (MB.Ma. 17148; Fig. 7n–o). Recent taxonomic revisions of the South American gomphotheres, based on well-preserved diagnostic materials (e.g., upper tusks and/or complete skull elements), allowed the recognition of only two species, namely *Cuvieronius hyodon* Fischer, 1814, and *Notiomastodon platensis* Ameghino, 1888, with a distribution encompassing lowland to highland localities (Lucas, 2013; Mothé et al., 2013; Mothé and Avila, 2015). Some morphological distinctions have been observed in postcranial elements among North American and Neotropical gomphotheres (e.g., Ferretti, 2010; Lucas et al., 2011; Lucas, 2013). However, the lack of more detailed studies in postcranial bones of South American gomphotheres makes the identification of diagnostic features at generic or specific level difficult, especially if the specimens are not associated with

other cranial elements such as mandibles, teeth and tusks (e.g., Mothé and Avila, 2015).

3.5 Indeterminate mammalian remains

Some specimens are only ascribed to Mammalia indet. due to their fragmentary nature (Figs. 7p–s, 8). They notably include what seems to be a fragment of the femoral head of a gigantic taxon (MB.Ma. 14109; Fig. 7r–s). While its maximum diameter reaches roughly 20 cm, the proximal surface shows an irregular typical structure denoting an unfused epiphysis, indicating that the individual was not skeletally mature.

4 Discussion

4.1 Implications and significance of Hermann Karsten’s vertebrate collection

According to Röhl (1944, p. 1004), the first mention of fossil vertebrate remains found by H. Karsten dates from his exploration to the provinces of Caracas and Carabobo (trips made during his first journey to Venezuela between 1844 and 1847). Röhl (1944, p. 1004) noted that H. Karsten discovered remains of *Megatherium* in the vicinity of San Juan de Los Morros. In reference to this find, H. Karsten (1849, pp. 198–199) stated “Auf dem Rücken des östlichen Gebirgszuges findet sich eine Gruppe säulenartig hervorgehobener Kalkschichten mit dem darauf liegenden Sandsteine, die mit den in ihnen befindlichen Höhlen sehr an die früher von mir Ihnen beschriebenen und in Gesteinproben vorgelegten Kalkkegel von St. Juan de los Morros erinnern, in deren Umgebung gleichfalls fossile Reste des Megatherium’s [sic] gefunden werden”. Later in another publication (Karsten, 1886, p. 14), he wrote “A St. Juan on a trouvé dans ces marnes des squelettes de Megatherium [sic]”. In both quotations above, H. Karsten does not claim the discovery of the *Megatherium* remains from San Juan de Los Morros; on the contrary, he emphasized that these remains “have been found there”, so it is not clear if he found the fossil himself. The above is not an indication that H. Karsten did not find remains of terrestrial sloths at San Juan de Los Morros; however, the only fossil specimens from this location attributable to the H. Karsten collection that we could trace (fossils without a clear date of collection), are those assigned to *Glyptotherium* cf. *G. cylindricum* and Glyptodontidae indet. (Tables 1–2). Before the visit of H. Karsten to San Juan de Los Morros, remains referred to as *Megatherium* were also mentioned in this location by the naturalist and Venezuelan president José María Vargas Ponce and the renowned English artist and diplomat Sir Robert Ker Porter (Carrillo-Briceño, 2015, pp. 66–67). Fossils of Pleistocene “ground sloths” found in Venezuela during the 19th and the first half of the 20th century were referred to the southern closely related species *Megatherium* (e.g., Karsten, 1849,

Table 2. Geographical context of fossil mammal specimens collected by H. Karsten.

Specimen number	MN.Ma Catalog		Historical provinces during Karsten's travels	Geographical region	Administrative entity
	Locality	Country			
MN.Ma. 14109	Barbacoas	?	?	?	?
MN.Ma. 17145	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17146	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17147	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17148	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17149	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17150	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17151	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17152	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17153	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17154	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17155	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 17156	Barbacoas-Candelillas District	Colombia	Province of Barbacoas ?	Pacific region ?	Nariño Department ?
MN.Ma. 33532	San Juan de Los Morros	Venezuela	Province of Caracas	Orinoquia region	Guárico State
MN.Ma. 33533-1	San Juan de Los Morros	Venezuela	Province of Caracas	Orinoquia region	Guárico State
MN.Ma. 33533-2-6	San Juan de Los Morros	Venezuela	Province of Caracas	Orinoquia region	Guárico State
MB.Ma. 33517	San Juan de Los Morros	Venezuela	Province of Caracas	Orinoquia region	Guárico State
MN.Ma. 33534	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 33535	?	Venezuela	?	?	?
MN.Ma. 33536	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 33537	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 33538	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 33539	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 33540	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 33541	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 33542	Paraguaná Peninsula	Venezuela	Province of Coro	Caribbean region	Falcón State
MN.Ma. 33543	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42896	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42897	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42899	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42900	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42901	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42902	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42903	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42904	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42905	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42906	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42907	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42908	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42909	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42910	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42911	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42935	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42936	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 42937	Barbacoas	Venezuela	Province of Barquisimeto	Andes	Lara State
MN.Ma. 48085	Barbacoas-Candelillas District	Colombia	Province of Barbacoas?	Pacific region ?	Nariño Department ?

1851, 1886; Nectario María, 1937, 1941; Schaub, 1935; Von der Osten, 1951). However, later taxonomic revisions (e.g., Cartelle and Iuliis, 1995) suggest that the previous assignments to *Megatherium* for specimens found in the region are erroneous, ascribing those specimens to *Eremotherium* (Cartelle and De Iuliis, 1995). Our own attributions go in the same direction.

In 1847 H. Karsten came back to Germany, and after one year (1848) returned to Venezuela to continue with his explorations; the Academy of Sciences in Berlin provided him with 300 thalers for paleontological excavations (Röhl, 1944). *Megatherium* remains from Barbacoas, Andes of Lara State (Karsten, 1849, p. 197), Carora (La Mesa, south Baragua River), Lara State (Karsten, 1851, p. 465) and the vicinity of Pueblo Nuevo, Paraguaná Peninsula, Fal-

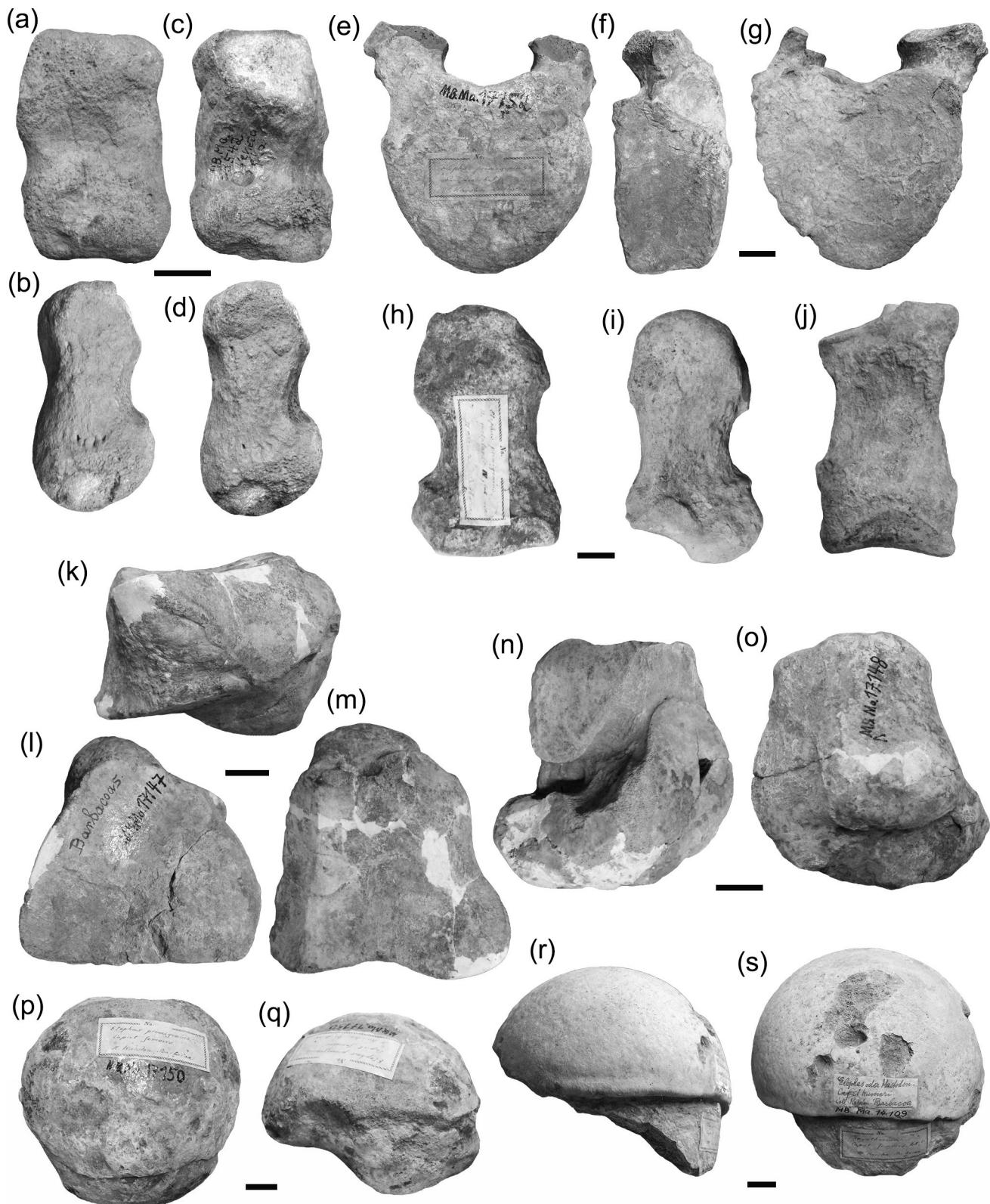


Figure 7. Notoungulata, proboscidean and mammalian indet. specimens. (a–d) Pisiform bone of Toxodontidae indet. (MB.Ma. 33542). (e–g) Gomphotheriidae indet.: (e–g) thoracic vertebra (MB.Ma. 17152); (h–j) left metacarpal II (MB.Ma. 17146); (k–m) right unciform (MB.Ma. 17147); (n–o) right astragalus (MB.Ma. 17148). (p–s) Mammalia indet.: (p–q) left humeral? head (MB.Ma. 17150); (r–s) femoral head (MB.Ma. 14109). Scale bar equals 2 cm.

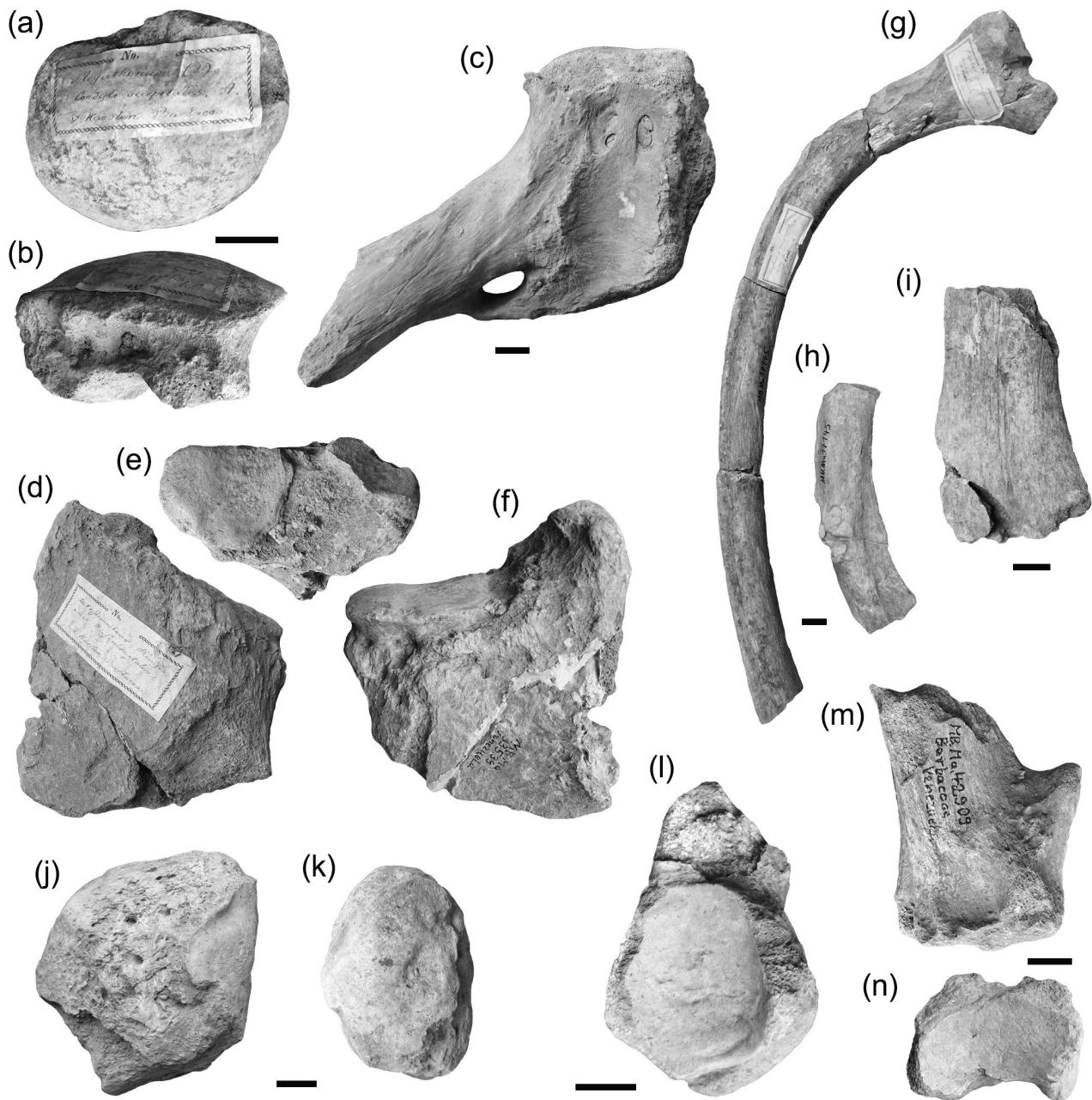


Figure 8. Mammalia indet. specimens. (a–b) Occipital condyle (MB.MA. 42899); (c) fragment of sacral vertebra (MB.MA. 42908); (d–f) indet. fragment of postcranial element (MB.MA. 33539); (g–i) dorsal rib fragments (MB.MA. 17145, MB.MA. 17149); and (j–k) fragments of indet. postcranial elements (MB.MA. 42909, MB.MA. 42910, MB.MA. 42911). Scale bar equals 2 cm.

cón State (Karsten, 1851, p. 467), were referred to. Possible “ground sloth” remains were also found by H. Karsten in Cerro Turimiquire, Sucre State, western Venezuela (Karsten, 1859b, p. 292; 1886, p. 11). H. Karsten (1851, p. 467) stated that years before his visit to Pueblo Nuevo (Paraguaná Peninsula), some locals discovered a complete fossil skeleton of an enormous mammal while drilling a well. According to the locals, the femur was 4.5 feet long (~106 cm) with a head

diameter of 1 foot (~30.4 cm). H. Karsten mentioned that abundant fossil remains of mammals, among which he recognized *Megatherium* (Karsten, 1851, p. 467), were found at San José de Cúcuta (Colombia), close to the Venezuelan border in the Andean region (Táchira State).

The Megatheriidae, Mylodontidae and Tardigrada indet. remains described here from the H. Karsten collection (Tables 1–2) include specimens from just one location in

Venezuela and one in Colombia. The Venezuelan location mentioned on the labels is Barbacoas, and we did not find any specimens from the other Venezuelan locations (Carora, Paraguaná Peninsula and Cerro Turimiquire) mentioned by H. Karsten (Karsten, 1851, pp. 465, 467; 1859b, p. 292; 1886, p. 11). There are no vertebrate specimens labeled as being from the Colombian sites of San José de Cúcuta (Karsten, 1851, p. 467) or El Plato (Karsten, 1886, p. 49). The only specimens from Colombia in the H. Karsten collection are those labeled as from “Barbacoas-Candelillas District, Kolumbien” (Table 2). We did not find a mention of the latter location in any of the relevant publications (Karsten, 1853, 1858, 1859a, 1886), and, as mentioned above, “Barbacoas-Candelillas District” may have been part of the former province of Barbacoas, which existed from 1846 to 1855, in the Republic of New Granada (nowadays Nariño Department, southern Colombia). Although it is unknown whether H. Karsten visited this location, it is recorded that on his trip he visited many places in its vicinity (e.g., Karsten, 1886, pp. 1–2, 22–35). Karsten (1886, p. 49) stated about his fossil vertebrate find from Colombia “toutes les peines que je pris pour en déterrre quelques-uns des mieux conservés, dans un but scientifique, furent rendues vaines par la fragilité des ossements; je ne dressai pas même de liste exacte de ces localités, tant elles étaient nombreuses, de sorte que je ne puis malheureusement donner maintenant qu'une partie de celles que j'ai connues”. Due to the unclear information in H. Karsten's publications and in the catalog data, it is not possible to establish with certainty the provenance of many fossil vertebrates. After more than 160 years, problems associated with labels/classification and/or destruction and damage of collections, especially during the Second World War, could have affected valuable information and even the final whereabouts of some “missing” H. Karsten fossils. It is possible that H. Karsten did not collect all the fossil vertebrates he referred to, as was noted by himself (e.g., Karsten, 1886, p. 49).

Many historical and geological/paleontological publications, especially about Venezuela, have mentioned H. Karsten's fossil vertebrate finds in a repetitive manner and sometimes with incorrect taxonomic and provenance information (e.g., Jahn, 1921, p. 39; Liddle, 1928, p. 351; Schaub, 1935, p. 1; Von der Osten, 1947, p. 161; Takacs et al., 1967 or 1968, p. 32; Linares, 1983, p. 1; Ochsenius, 1980, p. 21; Rincón et al., 2006, p. 530, 2008, p. 197; Rincón and White, 2007, p. 2; Carrillo-Briceño et al., 2008, p. 242; Rincón, 2011, p. 894). In a detailed revision of H. Karsten's bibliography (e.g., Karsten, 1849, 1850a, b, 1851, 1862, 1886), we have not been able to find any mention of or reference to fossil remains of glyptodonts, toxodonts, proboscideans or horses, from Barbacoas (Lara State) or any other locality of Colombia or Venezuela, contrary to reports by Jahn (1921, p. 39), Liddle (1928, p. 351), Schaub (1935, p. 1), Von der Osten (1947, p. 161), Takacs et al. (1967, p. 32), Linares (1983, p. 1), Ochsenius (1980, p. 21), Rincón et al.

(2006, p. 530, 2008, p. 197), Rincón and White (2007, p. 2), Carrillo-Briceño et al. (2008, p. 242), and Rincón (2011, p. 894). For example, Jahn (1921, p. 39) stated “En las arcillas sedimentarias de Barbacoas descubrió Karsten en 1850 restos fósiles de *Taxodon* [sic], *Glyptodon* [sic], *Mastodon* y una especie de equino que se diferencia bastante, en cuanto a su dentadura, del *Equus Andium* [sic] del Ecuador”. The reference of Jahn (1921, p. 39) has possibly given rise to the use of this erroneous information in a repetitive manner by Liddle (1928, p. 351) and other subsequent publications. The new taxonomic list presented herein securely documents the existence of “South American ungulates”, “ground sloths”, glyptodonts and proboscidean remains in the H. Karsten collection (MB.Ma.); however, their provenance is unclear. The H. Karsten vertebrate collection lacks a clear stratigraphic/age context; nevertheless, none of the specimens are well mineralized, having a typical Pleistocene type of preservation. From the overall H. Karsten vertebrate collection, the “ground sloth” remains are the most abundant. As is to be expected, the widely distributed species *Eritherium laurillardii* (Cartelle and De Iuliis, 1995) is represented in the collection. The rest of the “ground sloths,” together with the Toxodontidae and Gomphotheriidae specimens, do not offer significant information regarding biostratigraphy and biogeography, due to the fragmentary nature and scarce diagnostic characters of the specimens. In contrast, the presence of *Glyptotherium* cf. *G. cylindricum* from San Juan de Los Morros (Orinoco River basin) increases the paleobiogeographic range of this taxon because to date *Glyptotherium* remains have only been recorded in South America in a few lowland Late Pleistocene localities of the Caribbean basin in Venezuela (Carlini et al., 2008; Carlini and Zurita, 2010) and the Atlantic coast of Brazil up to 20° S (Oliveira et al., 2010). According to Zurita et al. (2012), *Glyptotherium* records from Venezuela and Brazil suggest that after its entry into South America during the Great American Biotic Interchange (GABI), this taxon could have followed an “eastern corridor” as a migratory route. Below the 20° S, the only recorded Glyptodontinae corresponds to *Glyptodon*, which is also recorded in a strip parallel to the Cordillera de Los Andes (Zurita et al., 2012).

5 Conclusions

Hermann Karsten is well known due to his various contributions to botany in South America during the second part of the 19th Century. His explorations allowed him to produce important geographic and geologic descriptions that make him a pioneer in these topics as well. Although the H. Karsten collections from South America are found in different museums and botanical gardens of Europe (e.g., extant plants and some fossil invertebrates), we have not found references to vertebrate fossil specimens deposited in any other collection apart from the Museum of Natural History

in Berlin. For more than 160 years, this vertebrate collection was practically unknown and subject to incorrect taxonomic and provenance references. Many of H. Karsten's vertebrate fossils are broken and incomplete, which prevented us from undertaking a more accurate taxonomic identification for specimens of Mylodontidae, Toxodontidae and Gomphotheriidae, with the exception of the “ground sloth” *Eremotherium laurillardi*. However, the identification of *Glyptotherium* cf. *G. cylindricum* from San Juan de Los Morros (Orinoco River basin) increases the paleobiogeographic range of this taxon, which has been previously referred to from a few coastal locations in Venezuela and Brazil. Using H. Karsten's publications and his fossil collection, we can suggest that fossil remains attributable to horses were not found by him during his expeditions, contrary to claims in many publications from the 19th and 20th century. The H. Karsten vertebrate collection was one of the first made during a scientific exploration in Venezuela and the Nueva Granada and is thus of historical importance for the paleontology of the region.

6 Data availability

The data presented are based purely on fossil specimens, which are designated by a specific catalog number. All the fossil specimens used here are available in their entirety in a public repository: the fossil vertebrate collection of the Museum für Naturkunde in Berlin (MB.MA.). Access to the collection is obtained by a request directly to the curator of the collection and the relevant authorities. All relevant data necessary to replicate the results presented in our article are available in this paleontological collection.

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