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# Osteoderm morphology and taxonomy of Pampatheriidae (Cingulata, Xenarthra) from the Quaternary of the Neotropical region

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## ABSTRACT

This study analyses Neotropical Quaternary pampatheriids' osteoderm morphology and reviews their taxonomic history since the first publications accounting for dermal plates. The main objectives are to illustrate and describe for the first time the first osteoderms attributed to *Pampatherium humboldtii* and the lectotype of *Holmesina major*, both from Lund's publications; as much as the neotype of *P. typum* from Ameghino's first records, and the hypodigms designated in this paper; and also, to re-evaluate the taxonomy and redescribe in greater detail the osteoderms from the hypodigm of *P. mexicanum*, *H. paulacoutoi*, and *H. occidentalis*. The taxa *Tonnincinctus mirus*, *H. cryptae*, *H. floridana*, *H. septentrionalis*, *Plaina intermedia*, *Pl. subintermedia*, and *Pl. brocherense* are used solely for comparative analysis. The results allowed the definition of morphological patterns. All taxa are considered to be valid, except for the synonymy herein proposed between *H. major* and *H. paulacoutoi*, based on morphological, geographical, and historical data, with *H. major* taking precedence. Furthermore, the morphological pattern of the osteoderms of *H. cryptae* is considered equivalent to that of the genus *Pampatherium*. It is suggested that future studies should be carried out using cranial and other skeletal elements to further evaluate the taxonomic status of *H. cryptae*.

## ARTICLE HISTORY

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## KEYWORDS

Armadillo; Megafauna;  
Argentina; Brazil; Ecuador;  
Mexico

## Introduction

Cingulata Illiger, 1811 (early Eocene-Recent) is today the most geographically widespread and taxonomically diverse clade within Xenarthra Cope 1889 (McKenna and Bell 1997), being also quite diverse in body size, locomotion, and feeding habits (Gaudin and Croft 2015). Cingulates are characterised by having several osteoderms on legs and feet, and mainly composing cephalic, dorsal, and caudal external armours, except for the genus *Cabassous* McMurtrei 1831, which has the tail naked with only sparsely distributed individual osteoderms (Hill 2006; Góis et al. 2015; Fernicola et al. 2017; Moura et al. 2019; Feijó and Anacleto 2021). The different sizes, morphologies, and arrangements of the osteoderms forming the dorsal carapace are reliable evidence for identifying cingulate taxa (Fernicola and Porpino 2012; Góis et al. 2013; Rodriguez-Bualó et al. 2014). Evolutionary relationships within Cingulata are represented in the most recent view by two major clades: Dasypodidae Gray, 1821, and Chlamyphoroidea (Bonaparte, 1850) (Gaudin and Lyon 2017, based on; Gibb et al. 2016 phylogeny), both comprising extant and extinct armadillos.

The clade Pampatheriidae Paula Couto 1954 (Middle Miocene-Early Holocene) is monophyletic, comprising seven genera and 20 species, and nests within Chlamyphoroidea as the clade sister to Glyptodontidae (Gaudin and Wible 2006; Góis 2013; Gaudin and Lyon 2017; Moura et al. 2019; Jiménez-Lara 2020; Tejada et al. 2023), as suggested by older morphological studies (e.g. Ameghino 1889; Perea et al. 1894; Carlini and Scillato-Yané 1993; McKenna and Bell 1997; Gaudin and Croft 2015; Góis et al. 2015). Pampatheriidae taxa present a dorsal carapace formed by scapular and pelvic shields (= bucklers), separated by two rows of semimovable osteoderms

delimiting three rows of movable ones, forming three articulated bands (Paula Couto 1980; Engelmann 1985; Edmund 1985a, 1985b, 1987; Góis et al. 2013; Moura et al. 2019). Osteoderms also occur on the head, tail, legs, and feet of pampatheriids (Edmund 1985a), but these are not as useful for defining taxa as those of the dorsal carapace. In turn, osteoderms of the dorsal carapace present polygonal shapes with four, five, six, and even seven sides on fixed osteoderms, and rectangular shapes on semimovable and movable ones (Edmund 1985a; Góis et al. 2013).

Osteoderms are known from all pampatheriid species except for *Holmesina rondoniensis* Góis, Scillato-Yané, Carlini and Ubilla, 2012, represented only by an isolated skull from Northern Brazil (Late Pleistocene) (Góis et al. 2012). Several Pampatheriidae species were originally described on the basis of osteoderms, namely *Kraglievichia carinatum* (Góis et al. 2013), *Scirrotherium antelucanus* Laurito and Valerio, 2013, *K. paranense* (Ameghino 1883), *Plaina intermedia* (Ameghino 1888), *Pl. subintermedia* (Rovereto 1914), and *Pl. brocherense* Castellanos, 1956 occurring in the Neogene period, and also *Pampatherium mexicanum* Edmund 1996, *P. typum* (Gervais and Ameghino 1880), and *H. major* (Lund 1842) occurring in the Quaternary period. The osteoderm morphology is, therefore, of paramount importance and largely accepted as a trustful source of evidence to propose and revise species of Pampatheriidae (e.g. Góis et al. 2013; Laurito and Valerio 2013; Jiménez-Lara 2020).

Quaternary taxa present uncertain characteristics since the first designated species (Scillato-Yané et al. 2005; Ferreira et al. 2018), rendering their identification difficult. The morphological information available in the scientific literature regarding the original osteoderms associated with *P. humboldtii* (Lund 1839), *P. mexicanum*, *P. typum*,

*H. major* (Lund 1842), *H. paulacoutoi* (Cartelle and Bohórquez 1985) and *H. occidentalis* (Hoffstetter 1952) is incomplete, leading to a convoluted taxonomy due to the lack of detailed comparisons and figures. These, when available, are mostly restricted to simple drawings, or not illustrated at all. These issues are further aggravated by the loss or uncertain publication status of a few older studies (Paula Couto 1954; Mones 1994; Edmund 1996; Scillato-Yané et al. 2005; Ferreira et al. 2018), rendering taxonomic identification even more challenging. The aim of this paper is to provide a revised morphological and taxonomic account of Neotropical Quaternary Pampatheriidae based on osteoderms, to serve as a reference for their identification, mostly focusing on the firstly described osteoderm specimens for each studied taxon.

### Taxonomic history of neotropical Quaternary pampatheriids

The taxon *Pampatherium humboldtii*, originally named *Chlamytherium humboldtii* (Lund 1839), was the first designated pampatheriid to be discovered in the fossil record, with the lectotype consisting of a left mandible (Ferreira et al. 2018) from the same type locality as the batch of osteoderms presented here below as *P. humboldtii*. Subsequently, *Holmesina major*, originally named *Chlamydothierium majus* (Lund 1842), was proposed in a brief description, which stated that its osteoderms were larger than those of *P. humboldtii*, without determining the holotype, figuring it, or properly describing its morphology (Lund 1842). Together, these two species represent the first known pampatheriids, based on the fossils found in the karsts of the City of Lagoa Santa, State of Minas Gerais, Brazil (Late Pleistocene-Early Holocene) (Lund 1839–1843). The localities listed by Lund (1843) and Winge (1915) allowed the correlation of these two taxa with the material deposited in the P. W. Lund Collection (ZMK), identified on the labels attached to the boxes of Pampatheriidae (Ferreira et al. 2018). These labels allow the identification of the material, even in the absence of type specimens, which were not proposed by Lund (1839–1843), by indicating the fossil locality and the taxonomic accounts. Thus, we can confirm that *P. humboldtii* was recorded for Lapa do Bahú, Lapa do Periperi, Lapa da Escrivania, Fordkellige Huller, Lapa da Lagoa do Sumidouro and Lapa Vermelha, while *H. major* was recorded together with *P. humboldtii* for Lapa da Lagoa do Sumidouro and Lapa Vermelha.

The validity of *Holmesina major* has been disregarded by many authors, which interpreted it as a synonym of *Pampatherium humboldtii* (e.g. Cartelle and Bohórquez 1985; Edmund 1996; Ferreira et al. 2018 and references therein). Winge (1915) also considered these two taxa as one, but he incorrectly accepted the name *Chlamydothierium majus*, ignoring the priority of *C. humboldtii*. However, later, Edmund (1996) reviewed the P. W. Lund Collection, ZMK, and determined a batch with 10 osteoderms from Lapa da Lagoa do Sumidouro as the lectotype for *H. major* (ZMK 1/1845:1807), revalidating the species and including it in the generic lineage *Holmesina* Simpson 1930. Therefore, Edmund (1996) recognised two species (*P. humboldtii* and *H. major*) to the Lagoa Santa locality, as originally proposed by Lund (1842, 1843), also postulating a major morphological similarity between *H. major* and *H. paulacoutoi*, the latter from the State of Bahia, Brazil (Cartelle and Bohórquez 1985), discerning them only by a small difference in size (Edmund 1996). However, the figuration of the lectotype of *H. major* was not presented by Edmund (1996), further

contributing to morphological and taxonomic issues regarding the diagnosis of these species (e.g. Scillato-Yané et al. 2005; Góis et al. 2012; Góis 2013).

The taxon *Holmesina occidentalis*, originally named *Chlamytherium occidentale* (Hoffstetter 1952), was first described by Hoffstetter (1948) as *Chlamydothierium* sp. on the basis of similarities with Lund's material from the Lagoa Santa karsts of Brazil and Ameghino's material from the Pampean Region of Argentina (Hoffstetter 1952). However, the formal description was only made in 1952, as a new high-altitude pampatheriid (Hoffstetter 1952), being transferred to the genus *Holmesina* (Hoffstetter 1953) due to the similarities with Simpson's material from the State of Texas, U.S.A., *H. septentrionalis* (Simpson 1930). Despite being a well-known taxon from the late Pleistocene of the Province of Guayas, Ecuador (Hoffstetter 1968), the morphology of the original specimens of *H. occidentalis* is not well characterised and access to it by the scientific community at large is limited. The only reference in Brazil, for instance, comparing it with *H. paulacoutoi* and *Pampatherium humboldtii*, is an unpublished thesis in Portuguese (Cartelle 1992).

In turn, the taxon *Holmesina paulacoutoi*, originally named *Pampatherium paulacoutoi*, was described on the basis of a complete unarticulated skeleton from the Late Pleistocene-Early Holocene of Gruta das Onças, City of Jacobina, State of Bahia, Brazil (MCL 501/01-336; Cartelle and Bohórquez 1985). It preceded the revalidation of *H. major* (Edmund 1996) and therefore disregards its existence, without access to materials of this taxon to include in the comparative description (Cartelle and Bohórquez 1985). Subsequently, based on a study of postcranial elements (only available in Portuguese and, therefore, of limited accessibility), this species was attributed to the genus *Holmesina* (Cartelle et al. 1991). The most important comparisons with *H. paulacoutoi*, considering the species valid at that time, were with *P. humboldtii* from Gruta dos Brejões, State of Bahia, Brazil, and *H. occidentalis* from El Coralito, Ecuador, cited above (Cartelle 1992). The taxon *H. paulacoutoi* is frequently reported from Brazil but is often confused with *H. major* (e.g. Mello 1990; Cartelle 1992; Edmund 1996; Oliveira and Pereira 2009), as discussed later in the text.

The taxon *Pampatherium mexicanum* was proposed based on osteoderms from the Pleistocene of Mexico (INAH 6201 D.P.) in the same publication in which the validity of *Holmesina major* was reconsidered (Edmund 1996), representing the only *Pampatherium* Gervais and Ameghino, 1880 in North America, and restricted to Mexico (McDonald 2002; Mead et al. 2007). Although *P. mexicanum* clearly belongs to this genus, there is currently no published account for characteristics that would render it distinct from *P. humboldtii* and *P. typum*, leaving some aspects of its anatomy and taxonomy uncertain (Scillato-Yané et al. 2005). Only a drawing of a single osteoderm was made on the lateral view of *P. humboldtii* and *P. typum* (Edmund 1996, p. 303, figure 1), which does not make it possible to distinguish one from the other in detail, thus necessitating an illustration of the type material. As *P. mexicanum* still needs to be compared with other species of *Pampatherium* to review its validity, the holotype of *P. mexicanum* is presented in this paper to complement information to the work of Edmund (1996).

In another historical turn, the species *Pampatherium typum* was probably defined on the basis of osteoderms unknown to the scientific literature, since the original description developed by Ameghino in 1875a was not published or is missing (Torcelli 1914; Cartelle 1992; Mones 1994; Edmund 1996; Góis 2013). Part

of Ameghino (1875a) is found in Torcelli (1914, v.II), citing '*P. typus*', which is considered *nomen nudum* by Mones (1994) after having reviewed the primary records written by Ameghino (e.g. Ameghino 1875a, 1875b, 1878, 1886, pp. 203–20). Mones (1994) explained that the first valid publication referring to *P. typum*, as a synonym of *Chlamydotherium typus*, could be Gervais and Ameghino (1880), although due to the superficial description, this author also considered *P. typum* Gervais and Ameghino (1880) as a *nomen nudum*, and regarded Ameghino (1886) as the correct authorship for *P. typum*. Nonetheless, this last position has not been adopted by subsequent reviewers (e.g. Edmund 1996; Góis 2013), which regarded Gervais and Ameghino (1880) as the correct authorship, as we also consider here. Adding to that, the first drawings and general pattern of osteoderms of *P. typum* were not presented until Ameghino (1889), in which the morphology is illustrated, but the material described has not been found in collections (Scillato-Yané 1982). Subsequently, Ameghino (1891) used for the first time the current name combination. However, up to that point, no material had been designated as the type material for the species.

The oldest osteoderms of *Pampatherium typum* identified to date are deposited in a single batch in the Cope Collection (AMNH), which was proposed as the neotype by Edmund (1996) for the species (AMNH 11233), as the holotype of *P. typum* is currently unknown and possibly missing. Edmund (1996) noticed that the material identified by collection number AMNH 11233 is the same material reported by Ameghino (1878), who mentioned this material (then numbered 4762–4778 at the Universal Exposition in Paris) as a new species, distinct from Lund's *P. humboldtii*, recognised by the number 4779 (Mones 1994; Edmund 1996). Although Ameghino (1878) never indicated that this material was in fact *P. typum*, this work was published only three years after the manuscript from 1875a, and also considering that this Argentinean material was passed on by Ameghino to Edward D. Cope and then to the American Museum of Natural History, it could well be the original osteoderms used by Ameghino (1875a) to describe *P. typum*. For this reason, Edmund (1996) proposes this material as the neotype of this taxon. The presumed neotype (Edmund 1996) is included in this paper and morphologically and taxonomically revised to finally fill this gap in taxonomic history, also comparing it to other material from the fossil collections of Argentina.

Completing the currently known taxonomic history of the Quaternary Pampatheriidae of the Neotropics, three recent taxa have been proposed (Góis et al. 2012, 2015; Moura et al. 2019), but only two of them have osteoderms. One is the species *Tonnictus mirus* Góis et al. 2015 assigned to an Early-Middle Pleistocene material from the City of Ensenada, Province of Buenos Aires, Argentina (Góis et al. 2015). Probably due to the lack of information on the first osteoderms of *Pampatherium typum*, the holotype of *T. mirus* was previously assigned to the species (Carlini and Scillato-Yané 1999; Cioni and Tonni 2005; Scillato-Yané et al. 2005; Soibelzon et al. 2010; Góis et al. 2015). The other species is *Holmesina cryptae* Moura et al. 2019, proposed on the basis of two very complete skeletons found in Gruta da Lapinha, City of Iramaia, State of Bahia, Brazil, and described and illustrated in detail (Moura et al. 2019, 2021). In order to contribute to a broader analysis of the morphological patterns of Quaternary pampatheriid osteoderms and to assess the validity of the taxa which they are associated with, the type specimens presented for the first time in this paper

are compared to the osteoderms of *T. mirus* and *H. cryptae*, and the Nearctic representatives *H. floridana* (Robertson 1976) and *H. septentrionalis* (Leidy 1889).

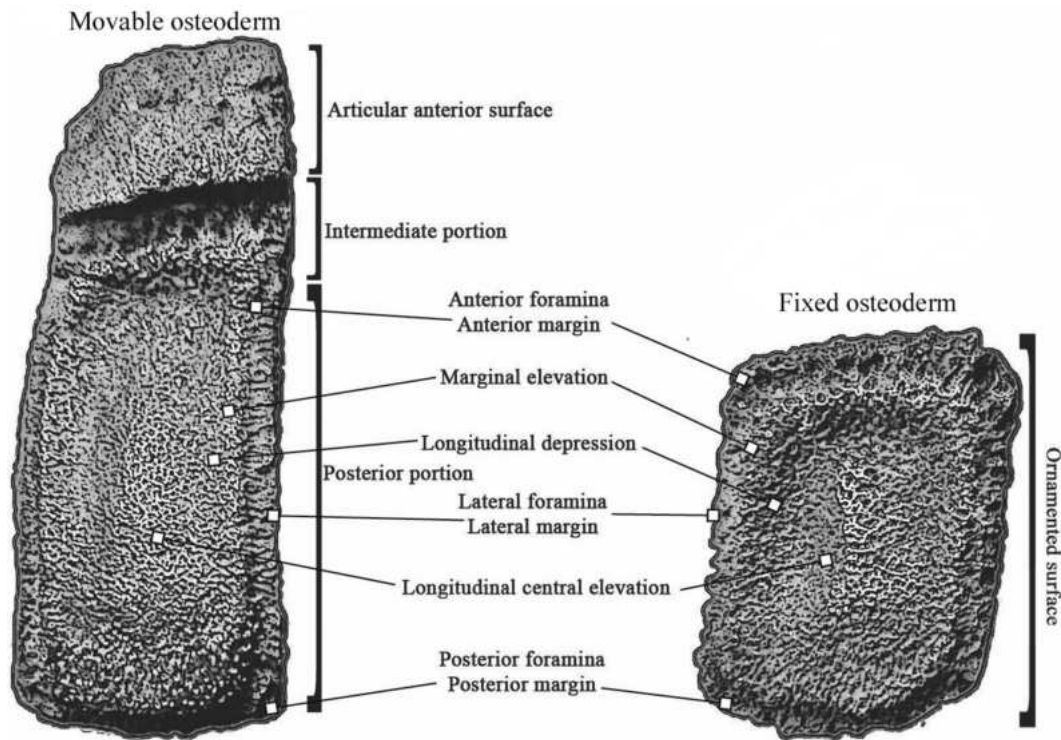
In this paper, we include photographs and updated descriptions for *Holmesina major*, *H. paulacoutoi*, *H. occidentalis*, *Pampatherium humboldtii*, *P. typum*, and *P. mexicanum*, to define species diagnosis through osteoderm morphology and relevant discussions.

## Materials and methods

The evaluated materials are isolated osteoderms from the dorsal carapace, including fixed, semimovable, and movable, that represent the type or the first specimens attributed to each taxon revised in this paper. Both focal taxa as well as those used in comparative analyses are listed below. We present here the first photographs and a full description of the external osteoderm morphology. With the exception of exclusive Miocene pampatheriids (*Kraglievichia* Castellanos, 1927, *Vassalia*; Castellanos, 1927, and *Scirrotherium*; Edmund and Theodor, 1997), which are much distant in time from the taxa that are the main subject of this paper, a comparative analysis of all pampatheriids with known osteoderms has been carried out. The materials were studied mainly by first-hand observations of the specimens housed in museum collections and complemented by descriptions and illustrations available in the literature. Measurements were made using the digital caliper Mitutoyo to the nearest 0.1/0.5 mm and using open-source software ImageJ. The morphological descriptions follow the same terminology as Moura et al. (2021) (Figure 1). Each observed anatomical feature is discussed to define intra- and interspecific morphological variability in Pampatheriidae, which is of paramount importance for establishing a stable taxonomy and characters to be used in future phylogenetic analyses. Taxonomic notes follow updates present in Ferreira et al. (2018), for historical consistency, and adherence to the International Code of Zoological Nomenclature (ICZN). The open-source software QGis 3.28.11 was used to develop the distribution map, with a coordinate reference system SIRGAS 2000, and data source GADM.

**Materials.** *Pampatherium humboldtii* (Lund 1839) (Figure 2(A–D)), ZMK 1/1845:13914/13915, ZMK 1/1845:13911, ZMK 1/1845:216, ZMK 1/1845:1803; *Pampatherium mexicanum* Edmund, 1996 (Figure 2(E)), INAH 6201 D.P., holotype; *Pampatherium typum* (Gervais and Ameghino 1880) (Figure 3(A–C)), AMNH 11233, neotype, MLP 52-IX-28-20, MLP 76-VII-2-6; *Holmesina major* (Lund 1842), ZMK 1/1845:1807, lectotype, ZMK 1/1845:271, ZMK 1/1845:933, ZMK 1/1845:932, ZMK 1/1845:222/1045, ZMK 1/1845:1806 (Figure 4(A–C)); *Holmesina paulacoutoi* (Cartelle and Bohórquez 1985) [junior synonym of *H. major* in this study] (Figure 5(A,B)), MCL 501/112, MCL 501/205, MCL 501/212, MCL 501/205, MCL 501/90, MCL 501/199, MCL 501/128, MCL 501/193, MCL 501/94 and MCL 501/200, holotype, MCL 2870; *Holmesina occidentalis* (Hoffstetter 1952) (Figure 5(C)), MCL 6057, MCL 6058, MCL 6066, MCL 6061, MCL 6065, MCL 6063, MCL 6067, and MCL 6060. References and localities are presented in the Results.

**Comparative materials.** *Pampatherium humboldtii* (Lund 1839), MLP 81-X-31-1 [Provincia de Buenos Aires, Argentina (Lujanian Stage/Age/Late Pleistocene-Early Holocene)]; MCL 900 [Gruta dos Brejões, Bahia State, Brazil (Lujanian Stage/Age/Late Pleistocene-



**Figure 1.** Osteoderm morphology nomenclature according to Moura et al. (2021). Illustration based on osteoderms of *Holmesina occidentalis* Hoffstetter, 1952.

Early Holocene)]; *Pampatherium typum* (Gervais and Ameghino 1880), MLP 80-VIII-13-80 [Paso Otero (Lujanian Stage/Age/Late Pleistocene-Early Holocene)]; MLP 52-X-3-79, MLP 91-III-1-3 [Quenquén Salado (Lujanian Stage/Age/Late Pleistocene-Early Holocene)]; MLP 76-VII-2-7, one fixed osteoderm [Malacara (Ensenadan Stage/Age/Early-Middle Pleistocene)]; MACN 12051; MACN 14737; MACN 12810; MACN 12811; MACN A-1114 [specimens deposited in MACN (Pleistocene)], all from Argentina; MNRJ 3538-V [City of Santa Vitória do Palmar, State of Rio Grande do Sul, Brazil (Late Pleistocene) (Oliveira and Pereira 2009)]; *Holmesina major* (Lund 1842), MACN 12367, MACN 12631, MNRJ 2767 V (Edmund 1996); *Holmesina paulacoutoi* (Cartelle and Bohórquez 1985), MLP 69-XII-26-3 [Alvear, City of Rosario, Provincia of Santa Fé, Argentina (Luanian Stage/Age/Late Pleistocene-Early Holocene)]; MLP 69-VIII-25-13 [City of Arrecifes, Salto, Provincia de Buenos Aires, Argentina (Pampean)]; MLP 34-IV-12-6b [Río Salado, Provincia de Santa Fe, Argentina (Lujanian Stage/Age/Late Pleistocene-Early Holocene)]; MACN 8960; MACN 11681; MACN 12125; MNRJ 3538a, MNRJ 3538b (Oliveira and Pereira 2009); *Holmesina occidentalis* (Hoffstetter 1952), ROM 28393, four osteoderms from La Brea, Talara, Perú (Rancholabrean NALMA/Late Pleistocene), deposited in MLP; *Holmesina floridana* (Robertson 1976), UF 16698 [Haile XV A (Robertson 1976, Plate 10)], UF 10902 [Xaile 15A (Downing and White 1995, p. 394, figure 6 B)], UF 15136 (Edmund 1985a); UF 10431 (Santa Fe); all from Condado de Alachua, Florida, U.S.A. (Blancan NALMA/Late Pliocene-Early Pleistocene) (see Góis 2013), UF 86498 [Leisey 14 (Irvingtonian NALMA/Middle Pleistocene) (Downing and White 1995, p. 394, figure 6 C)], UF 223544, UF 223812, UF 223813, UF 275496 [Haile 7 G, Florida, from Vertebrate Paleontology Database, UF (Blancan NALMA/Early Pleistocene)]; *Holmesina septentrionalis* (Leidy 1889), A.M. 23435 [Saber-tooth Cave, Citrus

County, Florida, U.S.A. (Holmes and Simpson 1931)], A.M. 23587, A.M. 23588, A.M. 23589 [Seminole Field, Pinellas County, Florida, U.S.A. (Holmes and Simpson 1931)], UF 933b [Brandford IA, Suwaneco, Florida (Late Pleistocene), deposited on MLP], UF 9336 [Brandford 14, (Rancholabrean NALMA/Late Pleistocene)] (Downing and White 1995, p. 394, figure 6E), osteoderms from Río Tomayate, San Salvador, El Salvador [Irvingtonian NALMA/Middle Pleistocene (Aguilar and Laurito 2009, Plate I)], UF 260553 [Horse Creek, Florida, from Vertebrate Paleontology Database, UF (Late Pleistocene)]; *Holmesina cryptae* Moura et al. 2019, LPP-PV-001 (holotype), LPP-PV-002 (paratype) [Gruta da Lapinha, City of Iramaia, State of Bahia, Brazil (Late Pleistocene-Early Holocene)]; *Tonnictus mirus* Góis, González Ruiz, Scillato-Yané and Soibelzon, 2015, MLP 54-III-16-1 [City of Ensenada, Province of Buenos Aires, Argentina, holotype (Early-Middle Pleistocene)], MLP 34-IV-12-6 [Salado River, Province of Santa Fe, Argentina, paratype (Late Pleistocene-Early Holocene)]; *Plaina intermedia* (Ameghino 1888), MACN 7799, MLP 69-VIII-25-1, 69-VIII-25-7, 69-VIII-25-11 [Monte Hermoso (Montehermosan, late Pliocene)], Provincia de Buenos Aires]; *Plaina subintermedia* (Rovereto 1914), MACN PV 8473, holotype, MLP 29-IV-15-6 [Formación Tunuyán (Montehermosan Stage/Age, Late Miocene-Early Pliocene)]; *Plaina brocherense* Castellanos, 1958, MUFyCA 769, holotype [Los Reartes, Province of Córdoba, Argentina (Late Miocene-Pliocene) (Cruz 2010; Góis 2013)].

**Institutional abbreviations.** AMNH, American Museum of Natural History, U.S.A.; EPN, Escuela Politécnica Nacional, Museo de Historia Natural ‘Gustavo Orcés V.’, Ecuador; INAH, Instituto Nacional de Antropología y Historia, Mexico; LPP, Laboratório de Paleocologia e Paleoicnologia, Departamento de

Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos, Brazil; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Argentina; MCL, Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais, Brazil; MCN-PV, Museu de Ciências Naturais, Secretaria do Meio Ambiente e Infraestrutura do Rio Grande do Sul, Brazil; MG-PV, Museo Provincial de Ciencias Naturales Ángel Gallardo, Argentina; MLP, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Museo de La Plata, Argentina; MNRJ, Museu Nacional do Rio de Janeiro, Brazil; MUFyCA, Museo Florentino y Carlos Ameghino (Instituto de Fisiografía y Geología), Argentina; ROM, Royal Ontario Museum, Canada; UF, Florida Museum of Natural History, U.S.A.; ZMK, Universitets Zoologisk Museums Kvartærzoologiske Samlinger, Denmark.

## Results

### Systematic palaeontology

Superorder Xenarthra Cope, 1889

Order Cingulata Illiger, 1811

Family Pampatheriidae Paula Couto, 1954

### Genus *Pampatherium* Gervais and Ameghino, 1880

= *Chlamydotherium* Lund, 1839:69; non Bronn, 1838:1258

= *Chlamytherium* Lund in Örsted, 1839; *lapsus pro* Lund, 1839:69

= *Pampatherium* Ameghino, 1875b:528; *nomen nudum*

= *Pampatherium* Gervais and Ameghino, 1880:210

= *Pampatherium* Ameghino, 1891:252–253

= *Pampatherium* Ameghino 1875a in Torcelli, 1914:16–17

**Type species.** *Chlamydotherium humboldtii* Lund, 1839; by subsequent designation (Ameghino, 1891:252–253)

### *Pampatherium humboldtii* (Lund, 1839) Ameghino, 1891

= *Chlamytherium humboldtii* Lund, 1839:69

= *Chlamytherium humboldtii* Lund in Örsted, 1839, *lapsus pro* Lund, 1839:69

= *Pampatherium humboldtii* Ameghino, 1891:253; first use of current name combination

= *Chlamydotherium majus* Winge, 1915:270, *partim*

= *Holmesina humboldtii* Edmund, 1987:2

**Lectotype.** ZMK 1/1845:618, left mandible from Lapa do Bahú, Lagoa Santa, State of Minas Gerais, Brazil (Lund 1840, plate 14, figure 1; Lund 1842, plate 34, figure 9; Winge 1915, plate X; Cartelle 1992, p. 138; Ferreira et al. 2018, p. 170, figure 4).

**Referred material.** ZMK 1/1845:13914/13915, six fixed osteoderms (Figure 2(A)) [Lapa do Bahú, same locality of the lectotype (Ferreira et al. 2018, p. 170, figure 4)]; ZMK 1/1845:1391, six osteoderms (Figure 2(B)) [Lapa da Escrivania Nr.11, same locality of the osteoderms figured on plate VIII by Winge (1915)]; ZMK 1/1845:216, six fixed osteoderms (Figure 2(C)) (Lapa do Periperi Nr.1); ZMK 1/1845:1803, six movable osteoderms (Figure 2(D)) (Fordkellige Huller). The entire material of ZMK is from the Late Pleistocene–Early Holocene of the karsts of the City of Lagoa Santa, State of Minas Gerais (MG), Brazil.

**Diagnosis.** The area of fixed and semimovable osteoderms varies from 10.12 cm<sup>2</sup> to 19.43 cm<sup>2</sup>, with a median of 14.50 cm<sup>2</sup>, including the greatest and smallest specimens within the lots (Figure 2(A,B,C)), and that of movable osteoderms is approximately 23.0 cm<sup>2</sup>, considering the Fordkellige Huller fossils (Figure 2(D)). The anterior margin varies from intermediate to wide (4.0–7.0 mm). The posterior and lateral margins are thin (2.0–3.0 mm); the marginal elevation is presented well-defined all around the ornamented surface, as in the specimens of Lapa do Bahú (Figure 2(A)), or less marked, as in those of Lapa da Escrivania (Figure 2(B)) and Lapa do Periperi (Figure 2(D)). The longitudinal depressions are shallow and vary in position from closer to the marginal elevation to closer to the longitudinal central elevation, defining it. In turn, the longitudinal central elevation is mostly imperceptible and smooth, but in some osteoderms it can be defined, together with the longitudinal depressions, by U- or V-shaped contours, presenting low or no elevation. The general relief is flat, with few or no irregularities. The ornamented surface is straight at the level of the margin or lower. The thickness varies from thin to intermediate (6.0–8.0 mm). The osteoderm foramina of *Pampatherium humboldtii* are numerous and vary in size from small to large in the same batch, with a pattern observed in the anterior foramina in which they are parallel to each other, both with and without spaces between them.

**Comparative description.** The osteoderms of the taxon *Pampatherium humboldtii* have a greater surface area than those of *Plaina intermedia* (Figure 6(C,D)), *Pl. subintermedia* (Figure 6(B)), *Holmesina floridana*, *P. typum*, as represented by its neotype (Figure 3(A)), *P. mexicanum* (Figure 2(C)), and *Tonnincinctus mirus* (Figure 6(G)). On the other hand, *P. humboldtii* has a similar or smaller surface area than *P. typum*, as represented by the largest osteoderms in Argentinean collections (see Discussion), and those of *H. cryptae* (Figure 6(E,F)) as well. Moreover, *P. humboldtii* is smaller than *Pl. brocherense* (Figure 6(A)), *H. occidentalis* (Figure 5(C)), *H. septentrionalis*, and *H. major* (Figures 4 and 5(A,B)). Therefore, *P. humboldtii* exhibits intermediate dimensions within the family Pampatheriidae. Their margins are marked and wider than *Pl. intermedia*, *Pl. subintermedia*, *P. typum*, *P. mexicanum*, and *H. cryptae*, but thinner in relation to the size of the osteoderms than *Pl. brocherense*, *H. floridana*, *T. mirus*, *H. occidentalis*, *H. septentrionalis*, and *H. major*. Like *Pl. intermedia*, *P. mexicanum*, *P. typum*, and *H. cryptae*, the *P. humboldtii* osteoderms are usually devoid of marginal elevations, as in Lapa do Periperi and Fordkellige Huller (Figure 2(C,D)), but in some cases, these elevations are as marked as those observed in *Pl. subintermedia*, *Pl. brocherense*, *H. floridana*, *T. mirus*, *H. occidentalis*, and *H. septentrionalis*, albeit less high, as in Lapa do Bahú and Lapa da Escrivania specimens (Figure 2(A,B)) (Winge 1915, pl. VIII). Longitudinal depressions could be absent, as in *P. mexicanum*, or be located very close to the marginal elevations, being low and almost imperceptible, like in *Pl. intermedia*, *P. typum*, and *H. cryptae*, and different from the deep and well-defined ones of *Pl. subintermedia* and *H. occidentalis*, or from those irregulars of *Pl. brocherense*, *T. mirus*, and *H. major*. Moreover, in other cases, a depression may be present in the middle part of the osteoderm surface, similarly to a few osteoderms of *H. cryptae*, as noted by Moura et al. (2019, 2021). Therefore, the marginal elevation and longitudinal depressions cannot be relied upon to define this taxon. The longitudinal central elevation is often either low or absent, as in *Pl. intermedia*, *P. mexicanum*, *P. typum*, and *H. cryptae*. In some specimens, it has a distinctive V-shaped feature unique to the taxon,

which differs from the long and deep V-shape of *T. mirus*. The longitudinal central elevation of *P. humboldtii* differs from the long one observed in *Pl. subintermedia*, *H. septentrionalis*, and *H. occidentalis*, from the irregular one of *Pl. brocherense*, and from those irregular and near to the posterior margin of *H. major*, which may or may not be present in these species (see Diagnosis). The ornamented surface relief is flat with little or no ornamentation, similar to *Pl. intermedia*, *P. mexicanum*, *P. typum*, and *H. cryptae*, different from the flat relief with irregular ornamentation, as in *P. subintermedia*, *Pl. brocherense*, *H. floridana*, *H. septentrionalis*, and *H. occidentalis*, and distinguishable from *H. major*, which have the ornamented surface irregular and raised relative to the level of the margins. The thickness of *P. humboldtii* is intermediate among the *Pampatherium* genus, in which *P. mexicanum* is the thickest. Among other pampatheriids, the thickness is closer to that of *Pl. intermedia*, *Pl. subintermedia*, *H. floridana*, *H. cryptae*, and *T. mirus*. In contrast, specimens of *Pl. brocherense*, *H. occidentalis*, *H. septentrionalis*, or *H. major* are thicker. The foramina are most similar to *P. typum* and *H. cryptae* in their variation, equal to or larger than those in *Pl. intermedia*, *Pl. subintermedia*, *H. floridana*, and *P. mexicanum*, and slightly smaller than some foramina of *Pl. brocherense*, *T. mirus*, *H. septentrionalis*, *H. major*, and *H. occidentalis*.

**Comments.** Illustrations of *Pampatherium humboldtii* osteoderms were drawn in Lund (1839) followed by a photographed material in Winge (1915, pl. VIII), equivocally identified as ‘*Chlamydotherium majus*’ (Ferreira et al. 2018 and references therein). In this study, the morphology of the osteoderms belonging to the hypodigm of *P. humboldtii* (Lund 1839) from the type locality Lapa do Bahú is illustrated in order to add to previous efforts to characterise cranial (ZMK 1/1845:2314/2318, skull) and mandibular (ZMK1/1845:618, left dentary) elements revised by Ferreira et al. (2018), and complementing the studies of Lund (1839–1843) and Winge (1915) about the species. The material from Lapa do Periperi (Figure 2(B)), Lapa da Escrivania (Figure 2(C)), and Fordkellige Huller (Figure 2(D)), presented here, also extends our knowledge of the osteoderm morphology of *P. humboldtii*.

### ***Pampatherium mexicanum* Edmund, 1996**

**Holotype.** INAH 6201 D.P., 10 osteoderms of the same individual from Valsequillo Reservoir, State of Puebla, Mexico (Rancholabrean NALMA/Late Pleistocene) (Edmund 1996).

**Referred material.** INAH 6201 D.P., the holotype, four fixed, one semimovable, and one movable osteoderm from the same batch as the holotype (Edmund 1996), which contains 22 osteoderms in total (Figure 2(E)).

**Diagnosis.** The area of fixed osteoderms varies from 9.06 cm<sup>2</sup> to 12.60 cm<sup>2</sup>, with a median of 11.12 cm<sup>2</sup>, while the average area of movable osteoderms is 23.40 cm<sup>2</sup>, and of the semimovable ones is 16.01 cm<sup>2</sup>. Anterior, posterior, and lateral margins are thin, approximately 1.0 mm wide, with the anterior margin achieving 3.0 mm wide. The marginal elevation is absent or inconspicuous, not delimited, continuous throughout the ornamented surface, and straight in relation to the margins, forming a flat relief. In some osteoderms, the ornamented surface is lower than the level of the lateral margins, but still flat. The longitudinal depressions and the longitudinal central elevation are absent or imperceptible. The thickness is intermediate (8.5 mm). The osteoderm foramina are

numerous and small, with anterior foramina being parallel and close to each other.

**Comparative description.** In terms of size, *Pampatherium mexicanum* osteoderms are greater than those of *Platina subintermedia* (Figure 6(B)), *Pl. intermedia* (Figure 6(C,D)), and *P. typum*, as represented by its neotype (Figure 3A), and smaller than *Pl. brocherense* (Figure 6(A)), *P. humboldtii* (Figure 2(A-D)), larger plates of *P. typum* (see Discussion), *Tonnictus mirus* (Figure 6(G)), and those of members of the genus *Holmesina*. The osteoderms of *P. mexicanum* have the thinnest margins among Quaternary pampatheriids, even thinner than those of *P. typum* and *H. cryptae* (Figure 6(E,F)). The margins are similar to those of *Pl. intermedia*. Following this increase in marginal width, *H. floridana*, *Pl. brocherense*, and *P. humboldtii* width ranges from thin to intermediate, and *T. mirus*, *H. septentrionalis*, *H. occidentalis*, and *H. major* have margins ranging from intermediate to the widest among pampatheriids. As in most specimens of *Pl. intermedia*, *P. typum* and *H. cryptae*, and some particular osteoderms of *P. humboldtii* (Figure 2(C,D)), the marginal elevation, longitudinal depressions, and longitudinal central elevation are not visible, and the entire surface is plane and at the same level, creating a flat relief of the ornamented surface. The general flatness of the ornamented surface of *P. mexicanum* differs from *Pl. brocherense*, *T. mirus*, and *Holmesina* taxa (except *H. cryptae*), and is similar to *Pl. intermedia*, *P. typum*, *H. cryptae*, and some osteoderms of *P. humboldtii*. Even though *P. mexicanum* has more gracile structures as described above, it has a thick osteoderm that is thicker than *Pl. intermedia*, *Pl. subintermedia*, *P. typum*, *H. floridana*, and *P. humboldtii*, but thinner than any other Quaternary pampatheriids compared in this analysis. The foramina are smaller or similar in size to those of *P. humboldtii*, *P. typum*, and *H. floridana*, and smaller than the greatest foramina of all the other taxa compared here.

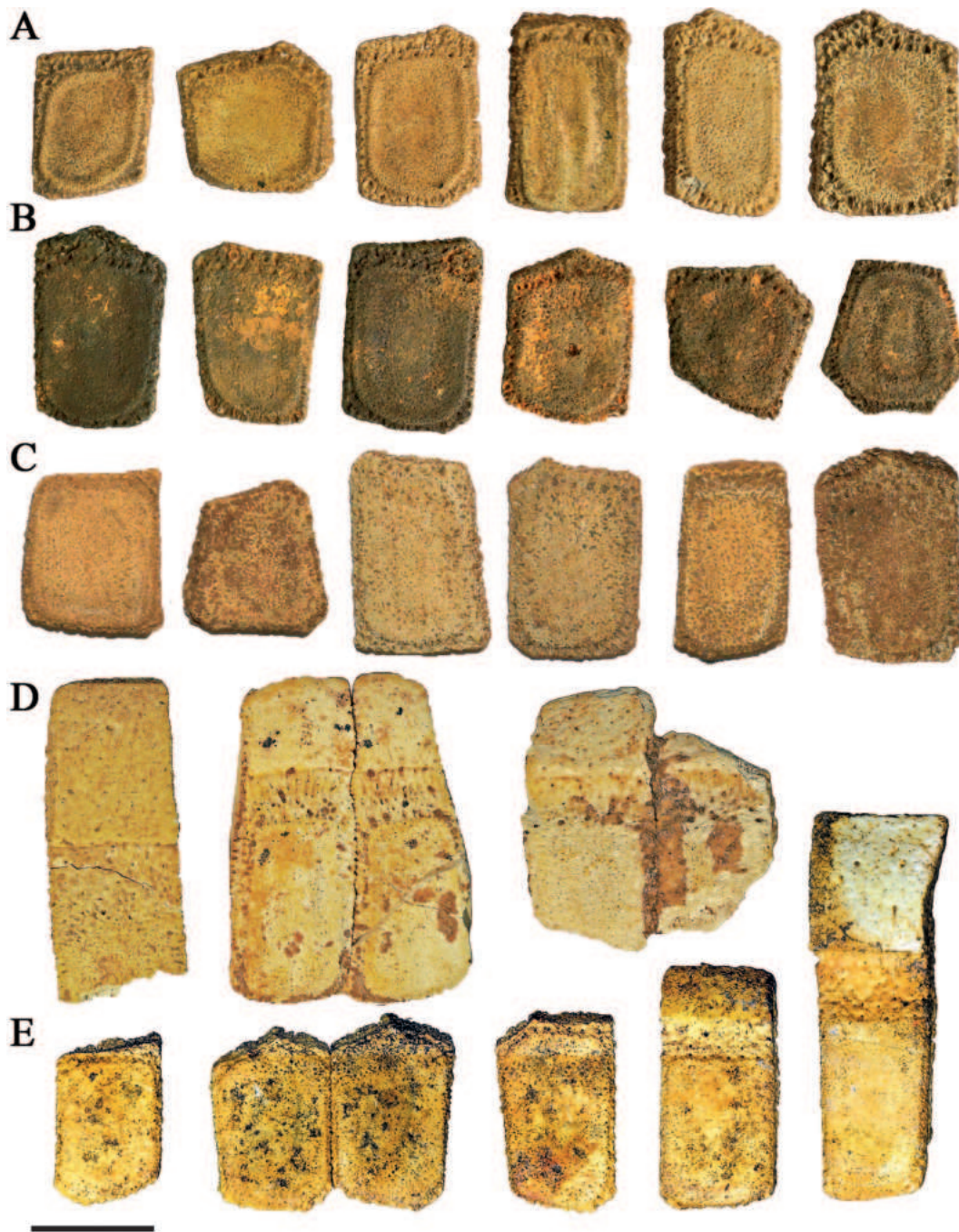
### ***Pampatherium typum* (Gervais and Ameghino, 1880) Ameghino, 1891**

= *Pampatherium typus* Ameghino 1875b:528, *nomen nudum*  
= *Chlamydotherium typus* Gervais and Ameghino, 1880:210:211  
= *Chlamydotherium typum* Ameghino, 1886:203–205  
= *Pampatherium typum* Simpson, 1930:8; first use of the current name combination  
= *Chlamytherium typum* Bordas 1939:449  
= *Pampatherium validum* Cartelle et al. 1991:662, *lapsus pro P. typum*

**Neotype.** AMNH 11233, 16 isolated osteoderms from the same individual – two movables, one semimovable, nine fixed, and four fragments of osteoderms, in which two of them are articulated portions – unknown locality from the ‘Pampean Formation’ (Edmund 1996). The most probable locality is the City of Ensenada, Province of Buenos Aires, Argentina (Ensenadan Stage/Age, Early-Middle Pleistocene) (see Discussion).

**Referred material.** AMNH 11233, the neotype (Figure 3(A)); MLP 52-IX-28-20, three osteoderms from a batch of five (Figure 3(B)); MLP 76-VII-2-6, two fixed and one movable osteoderm from a batch of four (Figure 3(C)); all proposed here as the hypodigm of *P. typum*.

**Diagnosis.** The areas of most of the fixed osteoderms of the neotype vary approximately from 6.72 cm<sup>2</sup> to 8.37 cm<sup>2</sup>, with an average of 7.66 cm<sup>2</sup>. The exception is a single greater plate with 13.72 cm<sup>2</sup>,



**Figure 2.** Fixed, semimovable, and movable osteoderms of the genus *Pampatherium*. (A). *P. humboldtii* (ZMK 1/1845:13914/13915) from Lapa do Bahú (type locality); (B). *P. humboldtii* (ZMK 1/1845:13911) from Lapa da Escrivania Nr.11; (C). *P. humboldtii* (ZMK 1/1845:216) from Lapa do Periperi; (D). *P. humboldtii* (ZMK 1/1845:1803) from Fordkellige Huller; all from Lagoa Santa, MG, Brazil; (E). *P. mexicanum* (INAH 6201 D.P.) from Valsequillo Reservoir, Puebla State, Mexico. Scale: 30 mm.

and also the movable and semimovable osteoderms, which have an average area of about 16.48 cm<sup>2</sup> (Figure 3(A)). Fixed osteoderms of the hypodigm assigned here present an average area of 9.85 cm<sup>2</sup> (MLP 52-IX-28-20), and 11.56 cm<sup>2</sup> (MLP 76-VII-2-6), and the movable specimens are about 13.56 cm<sup>2</sup> (MLP 52-IX-28-20) and 20.44 cm<sup>2</sup> (MLP 76-VII-2-6). The anterior, posterior, and lateral margins are thin, from 1.0–2.6 mm overall, with the anterior margin reaching 7.0 mm in movable osteoderms. The marginal elevation appears slightly raised or even absent. A depression of the

entire ornamented surface is observed as in MLP 52-IX-28-20 (Figure 3(B)) and, more commonly, it is levelled with the margins, although this can be variable among specimens (Figure 3(A,B,C)). Longitudinal depressions are also absent or imperceptible in most osteoderms. When noticeable, the longitudinal depressions are located parallel and close to the marginal elevation on all sides of the osteoderm. The longitudinal central elevation is absent. The thickness is thin to intermediate, varying from 5.0 mm to 8.0 mm. The osteoderm foramina are numerous and small, with some

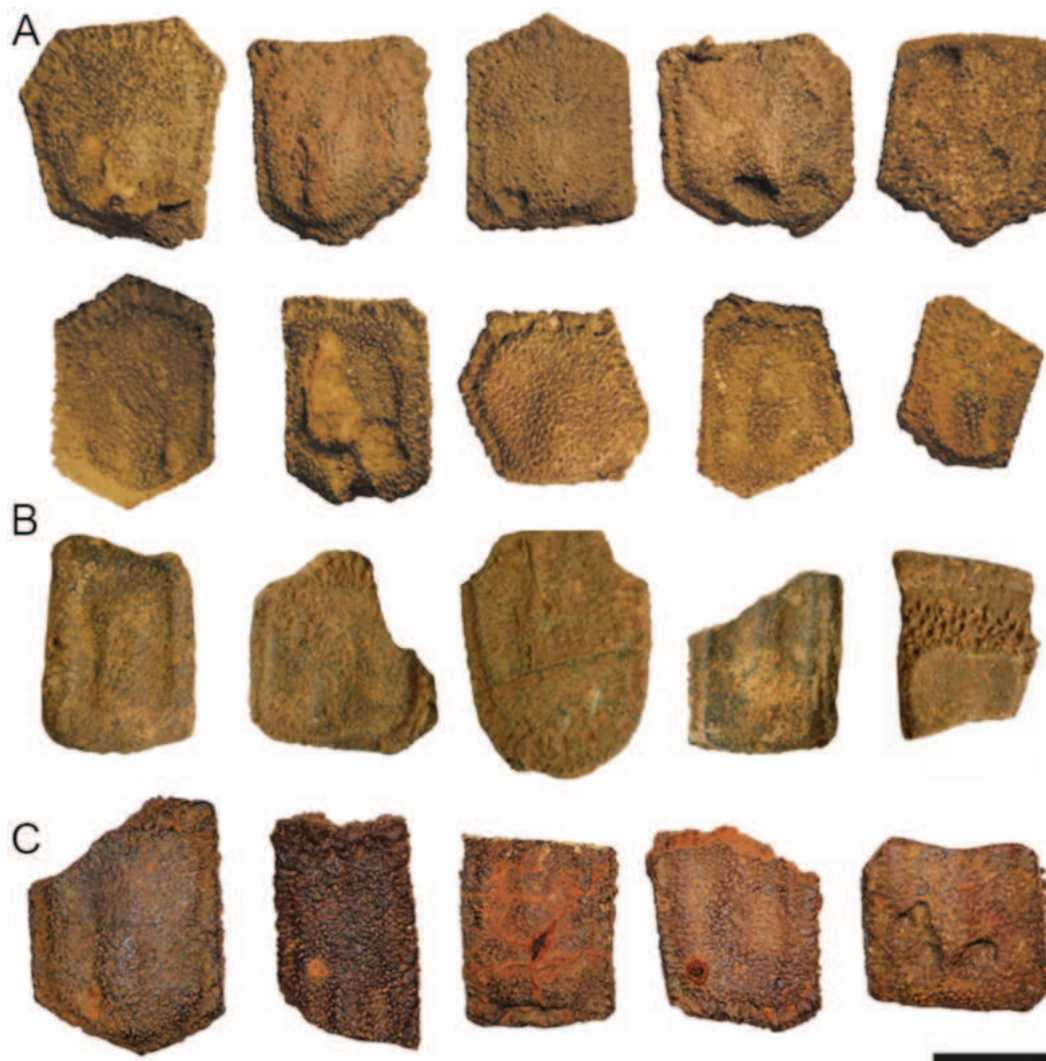


**Figure 3.** Fixed, semimovable, and movable osteoderms of *Pampatherium typum*. (A). AMNH 11,233, neotype, probably from the City of Ensenada, Argentina, Ensenadan/Early-Middle Pleistocene, Pampean Formation; (B). MLP 52-IX-28-20; (C). MLP 76-VII-2-6, both from Centinela del Mar, Argentina (Ensenadan/Early-Middle Pleistocene). Scale: 30 mm.

greater in the anterior margin, with or without a space between them.

**Comparative description.** The taxon *Pampatherium typum* has a variation in size area (from small to intermediate) of fixed osteoderms equivalent to specimens from the taxa *Plaina subintermedia* (~7 cm<sup>2</sup>) (Figure 6(B)), *Pl. intermedia* (~10 cm<sup>2</sup>) (Figure 6(C,D)), *H. floridana* (~8.5 cm<sup>2</sup>), *P. mexicanum* (~11.12 cm<sup>2</sup>) (Figure 2(C)), *P. humboldtii* (~14.50 cm<sup>2</sup>) (Figure 2(A-D)), *Pl. brocherense* (~15 cm<sup>2</sup>) (Figure 6(A)), *Tonnictus mirus* (~12.5 cm<sup>2</sup>) (Figure 6(G)), and *Holmesina cryptae* [(~15.0 cm<sup>2</sup>, the holotype, ~11.25 cm<sup>2</sup>, the paratype)] (Figure 6(E,F)), while it is smaller if compared to the other Quaternary taxa. The margins of *P. typum* are thin, similar to those of *H. cryptae*, wider than those of *Pl. subintermedia*, *Pl. intermedia*, *P. mexicanum*, and thinner than those of *Pl. brocherense*, *H. floridana*, *P. humboldtii*, *H. septentrionalis*, *H. occidentalis*, and *H. major*. The marginal elevation, longitudinal depressions, and longitudinal central elevation of *P. typum* are absent or barely visible in most osteoderms,

such as those of *Pl. intermedia* and *P. mexicanum*, most of *H. cryptae*, and a few of *P. humboldtii* (Figure 2(C,D)). On the other hand, *Pl. subintermedia*, *Pl. brocherense*, and *T. mirus* have a defined and wide margin, more similar to those of the genus *Holmesina* (except for *H. cryptae*), which is a notable difference from *P. typum*. Longitudinal depressions also occur, shallow and closer to the margins than to the central longitudinal elevation, as observed in *H. cryptae* and a few specimens of *P. humboldtii* (Figure 2(C,D)). In other pampatheriids, such as *Pl. subintermedia*, *Pl. brocherense*, *T. mirus*, *H. floridana*, *H. major*, *H. septentrionalis*, and *H. occidentalis*, the longitudinal central elevation is always visible in the ornamented surface interfering in the relief. The osteoderms of the taxon *P. typum* are the thinnest among the Quaternary species, similar to *H. floridana* (4.7–9.7 mm, Jiménez-Lara 2020), *Pl. intermedia* (6.5–8.0 mm), and some osteoderms of *H. cryptae*. Slightly thicker osteoderms are observed in *H. cryptae*, *P. humboldtii*, *P. mexicanum*, *T. mirus*, *Pl. brocherense*, *H. septentrionalis*, *H. occidentalis*, and the thickest ones are those of *H. major*. The foramina present a pattern and size



**Figure 4.** Osteoderms of *Holmesina major* from Lagoa Santa, MG, Brazil: (A). ZMK 1/1845:1807, the lectotype from apa da Lagoa do Sumidouro; (B). ZMK 1/1845:1807, the same lot of the lectotype from Lapa da Lagoa do Sumidouro; (C). ZMK 1/1845:271/933/932/222/1045/1806 from Lapa Vermelha. Scale: 30 mm.

similar to those of *Pl. intermedia*, *Pl. subintermedia*, *Pl. brocherense*, *H. cryptae*, and *P. humboldtii*, being more sparsely distributed than those of *H. floridana* and *P. mexicanum*. The foramina are smaller than the largest ones of *T. mirus*, some of the *H. cryptae* (Figure 6(E)), *H. septentrionalis*, *H. major*, and *H. occidentalis*.

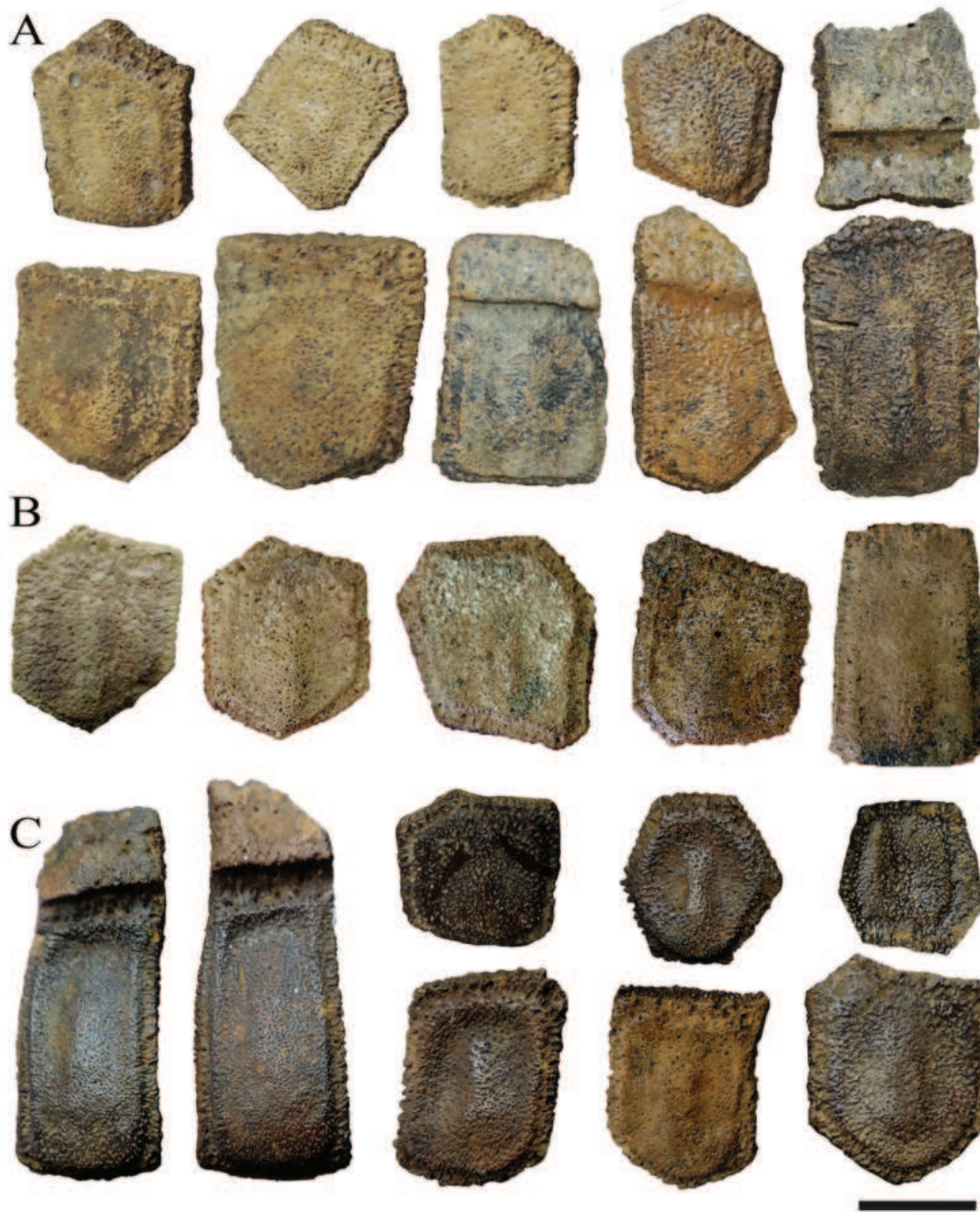
**Comments.** There is a size difference between the osteoderms of the neotype assembled by Ameghino and deposited in the Cope collection, which may or may not be the osteoderms cited in the last publication Ameghino (1875a) (see Introduction). The difference in sizes observed within osteoderms of one individual is not uncommon for pampatheriid carapaces (e.g. *Holmesina cryptae*, Figure 6 (E,F)). Furthermore, MLP 52-IX-28-20 (Figure 3(B)) and MLP 76-VII-2-6 (Figure 3(C)), both from Centinela del Mar, Argentina (Ensenadan Stage/Age/Early-Middle Pleistocene), described and illustrated here, are the most similar to the osteoderms of Ameghino (1899, lám. LXVII) that we identified. The taxon

*Pampatherium typum* is also represented by slightly larger plates deposited in Argentinean museums (e.g. MACN 12811), which are morphologically equivalent to *H. cryptae*, including size, calling for an in-depth revision of the latter taxon, in light of the type and referred material described here (see Discussion).

#### **Genus *Holmesina* Simpson, 1930**

= *Chlamydotherium* Lund, 1839:69, *partim*; non Bronn, 1838:1258  
 = *Chlamytherium* Lund in Örsted, 1839; *lapsus pro* Lund, 1839:69, *partim*  
 = *Glyptodon* Leidy, 1889:97; non Owen, 1839:178  
 = *Hoffstetteria* Castellanos, 1957:5

**Type species.** *Holmesina septentrionalis* (Leidy, 1889) Simpson, 1930, by original designation (Simpson, 1930:3).



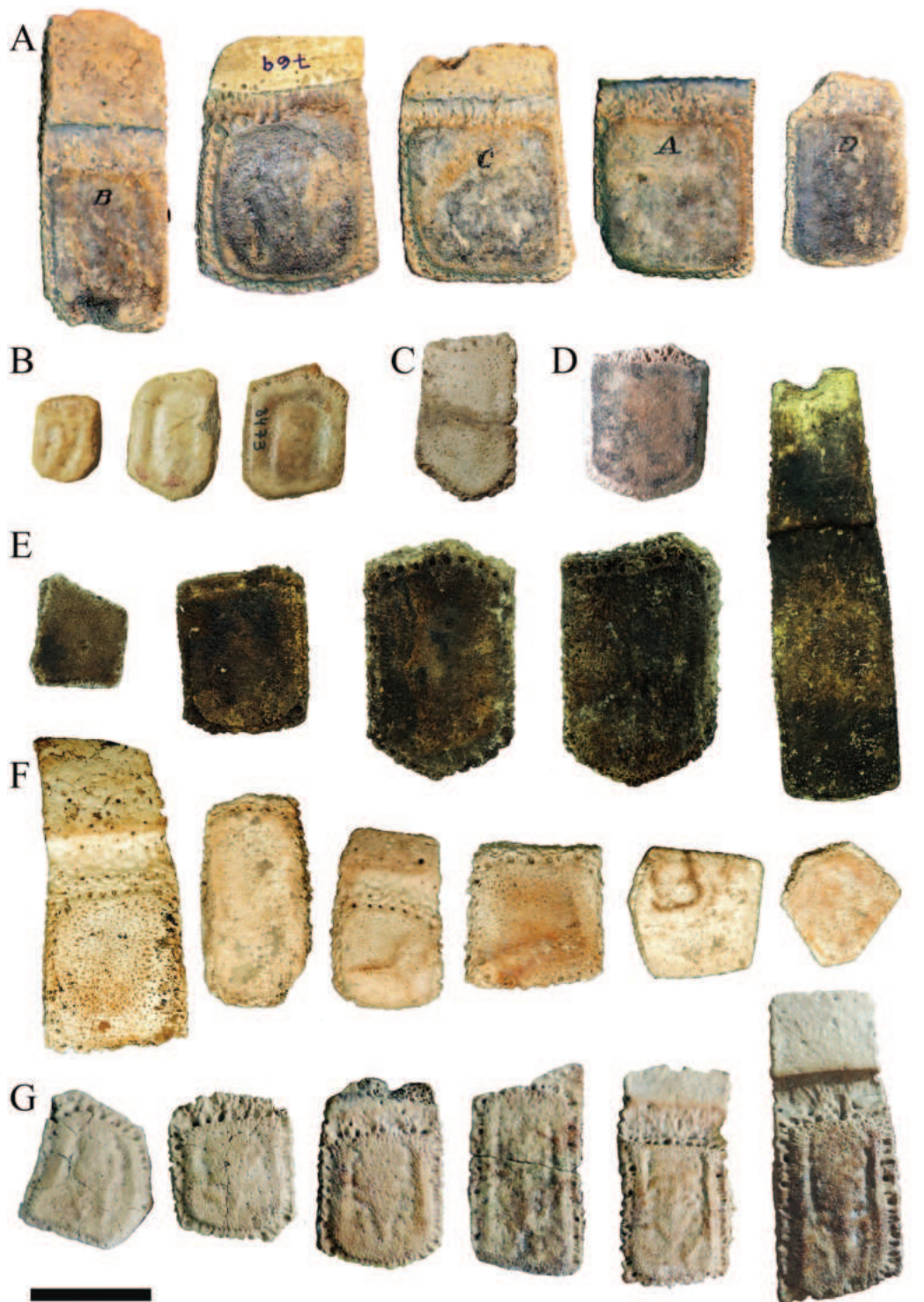
**Figure 5.** Fixed, semimovable, and movable osteoderms of the genus *Holmesina*. (A). MCL501/112, MCL 501/205, MCL 501/212, MCL 501/205, MCL 501/90, MCL 501/199, MCL 501/128, MCL 501/193, MCL 501/94, MCL 501/200, *H. major* from Gruta das Onças, Jacobina, Bahia, Brazil; (B). Osteoderms from the batches MCL 2078, *H. major* from the caves of Bahia, Brazil; (C). MCL 6057, MCL 6058, MCL 6066, MCL 6061, MCL 6065, MCL 6063, MCL 6067, MCL 6060, *Holmesina occidentalis* from El Coralito, Ecuador. Scale: 30 mm.

***Holmesina major*** (Lund, 1842) **Edmund, 1996**  
 = *Chlamydotherium gigas* Lund, 1842:142, *partim*  
 = *Chlamydotherium majus* Lund, 1842:142  
 = *Chlamydotherium majus* Winge 1915:270, *partim*  
 = *Chlamydotherium giganteum* Lydekker, 1887:136; *non* Lund, 1839:69  
 = *Pampatherium paulacoutoi* Cartelle and Bohórquez, 1985:233  
 = *Holmesina paulacoutoi* Cartelle, Câmara and Prado, 1991:622  
 = *Holmesina majus* Edmund, 1996:314; first use of current name combination

**Lectotype.** ZMK 1/1845:1807, 10 fixed osteoderms from Lapa da Lagoa do Sumidouro, City of Lagoa Santa, State of Minas Gerais, Brazil (referred to as UZM 1807 in Edmund 1996).

**Hypodigm.** MCL 501/01-336, a skeleton from Gruta das Onças, City of Jacobina, State of Bahia, Brazil (Cartelle and Bohórquez 1985), the holotype of *Holmesina paulacoutoi*.

**Referred material.** ZMK 1/1845:1807, the lectotype (Figure 4(A)), 10 osteoderms from a lot of 22 from the same individual, from Lapa da Lagoa do Sumidouro; and more five isolated osteoderms found together named likewise as ZMK 1/1845:1807 (Figure 4(B)); ZMK 1/1845:271; ZMK 1/1845:933; ZMK 1/1845:932; ZMK 1/1845:222; ZMK 1/1845:1045; ZMK 1/1845:1806, five fixed osteoderms and one movable osteoderm from Lapa Vermelha (Figure 4(C)); all from Lagoa Santa, Minas Gerais State, Brazil; MCL 501/112; MCL 501/205; MCL 501/212; MCL 501/205; MCL 501/90; MCL 501/199; MCL 501/128; MCL 501/193; MCL 501/94; MCL 501/200 [(Gruta das Onças, Jacobina City, State of Bahia, Brazil (Figure 5(A))); MCL 2078, State of Bahia, Brazil (Figure 5(B))].



**Figure 6.** Fixed, semimovable, and movable osteoderms of the comparative material from South America. (A). MUFyCA 769, *Plaina brocherense* from río Los Reartes, campo La Isolina; Provincia de Córdoba, Argentina (Cruz 2010); (B). MACN PV 8473, holotype, *Plaina subintermedia* from Formación Tunuyán, Argentina; (C). MACN 799, *Plaina intermedia*; (D). 69-VIII-25-11, *Plaina intermedia*, both from Monte Hermoso, Provincia de Buenos Aires, Argentina; (E). LPP-PV-001, holotype; (F). LPP-PV-002, paratype, *H. cryptae*, both from Gruta da Lapinha, Iramaia Municipality, Bahia, Brazil; (G). MLP 54-III-16-1, holotype, *Tonnincinctus mirus* from the City of Ensenada, Province of Buenos Aires, Argentina. Scale: 30 mm.

**Diagnosis.** The area of fixed and semimovable osteoderms varies from 17.14 cm<sup>2</sup> to 27.94 cm<sup>2</sup>, with an average of 22.74 cm<sup>2</sup>. The anterior, posterior, and lateral margins vary from wide to the widest sizes among pampatheriids (5.0–6.0 mm). In some specimens, the anterior margin is even wider, and the posterior margin is thinner due to the projection of the longitudinal central elevation posteriorly. The marginal elevation extends

through the entire ornamented surface, keeping it raised or appearing wide when bounded by deep longitudinal depressions, although not delimited. The longitudinal depressions vary from a smooth mark to a very deep one around the central longitudinal elevation. The longitudinal central elevation is mostly perceptible, being low or high, and always positioned close to the posterior margin. The general relief is elevated and

irregular. The thickness mostly varies from thick to very thick (~10.0 mm), being even thicker in a few osteoderms (~20.0 mm). The osteoderm foramina are numerous, ranging in size from small to large in comparison to the dimensions of the specimen. It is possible to observe relatively large foramina distributed throughout the margins, with a higher concentration on the anterior margin.

**Comparative description.** The taxon *Holmesina major* has the greatest size among Pampatheriidae, but with irregular size variation, ranging from large to very large even among their congeners or regions of the same carapace. A few fixed osteoderms of *H. occidentalis* (Figure 5(C)) and *H. septentrionalis* observed in this study may also reach sizes similar to those of *H. major*, but are generally smaller. In most of the osteoderms of *H. major*, the posterior margin is thinner than the anterior and lateral margins due to the posterior projection of the central longitudinal elevation over the posterior margin. This is less marked in *H. occidentalis* and absent in *H. septentrionalis*, in which the margins are of similar size on all sides. This pattern is quite different from that observed in *Plaina intermedia* (Figure 6(C,D)), *H. cryptae* (Figure 6(E,F)), and *Pampatherium* species, in which the lateral margins are absent or present only shallow marks. It also differs from *Pl. brocherense* (Figure 6(A)), *T. mirus* (Figure 6(G)), and *H. floridana*, which have intermediate margins. The marginal elevation in *H. major* does not follow a clear pattern (see Diagnosis), but is similar in its variability, whether the marginal elevation is outlined or not, being always high relative to the lateral margins. It can be distinguished from *Pl. brocherense*, *Pl. subintermedia* (Figure 6(B)), *T. mirus*, *H. septentrionalis*, and *H. occidentalis*, which have a well-delineated and always present marginal elevation, in spite of the different width patterns of this structure in each taxon. The longitudinal depressions vary from absent to very deep, in contrast to *Pl. subintermedia*, *H. floridana*, *H. septentrionalis*, and *H. occidentalis*, in which they are always present, and characterise this taxon. The central longitudinal elevation in specimens of *H. major* is indicated from the centre to close to the posterior margin, and it is not always defined. It may vary from a short or almost imperceptible elevation to the highest and most irregular shape among the pampatheriids. The ornamented surface relief of *H. major* is irregular due to the ornamentation described above and is raised relative to the margins, even when deep longitudinal depressions or high central longitudinal elevations are present. Differently from the general gracile and flat relief with irregularities of *Pl. subintermedia*, *Pl. brocherense*, *T. mirus*, *H. septentrionalis*, and *H. occidentalis*, and without irregularities of *Pl. intermedia*, *P. humboldtii*, *P. typum*, *P. mexicanum*, and *H. cryptae*, it is possible to identify *H. major* by the entirely raised and robust relief, unique to the taxon, despite the ornamentation being smooth. The osteoderms of *H. major* reach the maximum thickness among pampatheriids, being considered to vary from thick to very thick. All morphological patterns reported here for *H. major* also apply to osteoderms so far associated with *H. paulacoutoi*, with both taxa being indistinguishable. Concerning the osteoderm foramina, the most similar taxon is *H. occidentalis*, which presents the same pattern of size and distribution of the foramina all over the margins, with the greatest concentration in the anterior margin. The osteoderm foramina of *H. major* are larger than those of the *Plaina* and *Pampatherium*, *H. floridana*, and *H. cryptae*, and slightly smaller than those of *T. mirus* and *H. septentrionalis*. The taxon *T. mirus* has large foramina with regular spaces between them, mostly in the lateral and anterior margins, while

*H. septentrionalis* presents the largest foramina among Pampatheriidae, mostly in the anterior margin, but also on the lateral and posterior margins.

**Comments.** The synonymy of *Holmesina major* and *H. paulacoutoi* is proposed here, since the first specimens used by Lund (1842) to define *H. major* from the karstic region of Lagoa Santa, MG, Brazil, are described here for the first time and are morphologically identical to the dorsal carapace osteoderms first assigned to *H. paulacoutoi* from Gruta das Onças, BA, Brazil (Cartelle and Bohórquez 1985). The diagnosis and comparative description include the character variations observed in all the osteoderms from the batches. It is important to note that *H. paulacoutoi* was described before the revision and revalidation by Edmund (1996), which explains the lack of comparison between materials while describing this taxon (Cartelle and Bohórquez 1985). The name *H. major* should prevail as it was published earlier, thus being the senior synonym.

***Holmesina occidentalis* (Hoffstetter, 1952) Hoffstetter, 1953**  
= *Chlamytherium occidentale* Hoffstetter, 1952:119  
= *Pampatherium occidentale* Paula Couto, 1954:6

**Holotype.** EPN, V. 1117. One maxillary with six teeth from La Carolina, El Coralito, Ecuador (Late Pleistocene-Early Holocene) (Hoffstetter 1952).

**Referred material.** MCL 6057, MCL 6058, MCL 6066, MCL 6061, MCL 6065, MCL 6063, MCL 6067, and MCL 6060, eight osteoderms from El Coralito, Ecuador (Late Pleistocene) (Figure 5(C)).

**Diagnosis.** The average area of fixed and semimovable osteoderms, from the smallest hexagonal (12.53 cm<sup>2</sup>) to the greatest (24.69 cm<sup>2</sup>) rectangular ones, is approximately 20.37 cm<sup>2</sup> (Figure 5(C)). The movable osteoderms have about 39.0 cm<sup>2</sup> of area. The anterior, posterior, and lateral margins are of equal width (intermediate to wide), around 4.0 mm, well-marked, with the posterior margin thinner in some specimens due to the ornamented surface projecting posteriorly. The marginal elevations are delimited and raised on all sides. The longitudinal depressions are present as deep sulci around the longitudinal central elevation, which is centred, extended anteroposteriorly, high, and always conspicuous. The general relief is irregular, but overall, the surface is on the same level as the lateral margins. The thickness is intermediate (6.0–9.0-mm). The osteoderm foramina are numerous, ranging in size from small to large in comparison to the dimensions of the specimen. It is possible to observe relatively large foramina distributed throughout the margins, with a higher concentration on the anterior margin.

**Comparative description.** The osteoderms of *Holmesina occidentalis* are greater in area than the representatives of the genera *Plaina*, *Pampatherium*, and *Tonnictus*, as well as *H. cryptae* (Figure 6(E, F)), and *H. floridana*. On the other hand, the osteoderms of *H. occidentalis* are smaller than or similar in size to those of *H. septentrionalis*, and smaller than those of *H. major* (Figures 4 and 5(A,B)). The margins are intermediate to wide, even on all sides, and thinner than those of *H. major* osteoderms. The marginal elevations are well-defined, similar to those in *Pl. subintermedia* (Figure 6(B)), *Pl. brocherense* (Figure 6(A)), *T. mirus* (Figure 6(G)), *H. floridana*, and *H. septentrionalis*. Margins are also similar to *T. mirus* in their proportion to the size of the osteoderm, although less high, and also similar to those of some *P. humboldtii* osteoderms from Lapa do Bahú (Figure 2(A)) and Lapa da Escrivania (Figure 2(B)). *H. occidentalis* has deep longitudinal depressions on all sides of the ornamented surface, invariably different from the inconsistent or absent longitudinal depressions of *H. major*, and from shallower and more parallel ones observed in *H. septentrionalis*. The longitudinal central elevation is well defined

as in *Pl. subintermedia*, *H. septentrionalis* and some osteoderms of *H. major*. This pattern, unique to the taxon, is consistent in all specimens examined, being smooth and anteroposteriorly long. It differs from the pattern of *H. major*, which in some osteoderms has what Edmund (1996) called a 'grotesque' elevation and a more posterior position of the structure. It also differs from the longer and wider anterior longitudinal central elevation of *H. septentrionalis*, which forms a Y-shape in most specimens. In terms of general relief morphology, it is similar to *Pl. intermedia* and *H. septentrionalis*, with ornaments and irregularities at the level of the lateral margins, which are not raised relative to the margins. Thickness varies from intermediate to thick, with specimens thicker than *P. mexicanum* and *H. cryptae*, but thinner than *H. septentrionalis* and *H. major*. Likewise in *H. major*, the foramina of *H. occidentalis* are larger than those of the *Platina* and *Pampatherium*, *H. floridana*, and *H. cryptae*, and slightly smaller than those of *T. mirus* and *H. septentrionalis*.

**Comments.** Although initially described based on a partial mandible, the taxon *Holmesina occidentalis* exhibits its osteoderms on a complete skeleton and carapace from the Late Pleistocene of the Province of Guayas, Ecuador (ROMVP 55369, ROM Database; Hoffstetter 1968), which permitted the association of the osteoderms described here to this taxon, in addition to their geographic provenance, which are from the same locality as the lectotype (El Coralito, Ecuador). The osteoderms have been donated to the MCL to facilitate the most comprehensive comparisons with the Brazilian taxa and are here described to contribute to the Pampatheriidae morphological revision.

## Discussion

### Morphological patterns and taxonomic implications

Comparative analyses have highlighted the main features distinguishing the traditional genera *Holmesina* and

*Pampatherium* (Ameghino 1891; Simpson 1930), the recently described genus *Tonnictus* (Góis et al. 2015), and each species studied, allowing the selection of variable or non-variable morphological structures (Table 1). The Neotropical taxa *P. mexicanum*, *T. mirus*, and *H. occidentalis* show little or no variation in morphology within the same individual, as do the Nearctic *H. septentrionalis* (Holmes and Simpson 1931). On the contrary, *P. humboldtii*, *P. typum*, *H. cryptae*, and *H. major* require a more detailed analysis of several osteoderms to make taxonomic identifications due to the lack of concordance between representatives from the same batch, as seen in the results, and we recommend that identifications based solely on isolated osteoderms should be avoided for these taxa. For all taxa, the results showed that the ornamented surface morphology was preserved throughout the dorsal carapace regions (scapular and pelvic shields, and movable bands), regardless of whether the osteoderm is fixed, semimovable, or movable. Moreover, we found that the most consistent variation is observed in lateral margins, thickness, relief, longitudinal central elevations, and size, rendering these regions and their associated properties more reliable candidates for taxonomic diagnosis and proposing characters to be used in phylogenetic inferences of Pampatheriidae.

The monotypic genus *Tonnictus* has large lateral margins in proportion to its small size and a combination of unique features on the osteoderms that distinguish it from the other genera, mainly due to the lateral projections that branch asymmetrically on either side of the ornamental surface, as described by Góis et al. (2015), and in agreement with the results obtained here. Regarding the results based on the Quaternary Neotropical taxa, the genus *Pampatherium* is characterised by a narrow width of the lateral margins, from nearly absent to showing an intermediate width, the thinnest thickness among the Neotropical pampatheriids, and

**Table 1.** Comparative morphology of osteoderms from quaternary pampatheriids, highlighting the qualitative general pattern found within each species. \*refers to *H. cryptae*-like specimens of *P. typum*, discussed in this paper.

Taxon	Average area (fixed/movable)	Margins	Marginal elevation	Longitudinal depressions	Central longitudinal elevation	Relief of the ornamented surface	Thickness	Foramina
<i>P. humboldtii</i>	Intermediate	Intermediate	Inconspicuous or outlined, low, and thin	Inconspicuous, low, centred in U/V-shaped	Inconspicuous, centred, and low	Flat with ornaments or not/lower	Thin	Small to large
<i>P. mexicanum</i>	Small/intermediate	Thinnest	Absent or inconspicuous	Absent	Absent	Flat with few irregular point (no ornaments)	Intermediate	Small
<i>P. typum</i>	Small/intermediate*	Thin	Absent or inconspicuous	Absent/inconspicuous near the edges	Absent	Flat with ornaments or not/lower	Thin/intermediate*	Small to large
<i>T. mirus</i>	Small/intermediate	Wide	Outlined, raised, and intermediate width	Deep, long, and V-shaped with branches	Elevated, long, and irregular with branches	Irregular	Intermediate	Intermediate to large
<i>H. floridana</i>	Small	Thin/intermediate	Outlined, low, and intermediate width	Outlined, and low	Low, centred, and extending posteriorly	Flat with ornaments	Thin	Small
<i>H. septentrionalis</i>	Large	Wide	Outlined, and raised	Outlined/low	Centred, extending anteriorly	Flat with ornaments/irregular	Thick	Small to the largest
<i>H. cryptae</i>	Intermediate	Thin	Absent or inconspicuous	Absent/inconspicuous near the edges	Absent	Flat with ornaments or not/lower	Intermediate	Small to large
<i>H. occidentalis</i>	Intermediate/large	Wide	Outlined and elevated	Deep, and wide	Raised, long, and centred	Flat with ornaments/irregular	Intermediate/thick	Small to large
<i>H. major</i>	large	Wide	Outlined or not, always elevated, and wide	Absent/deep	Inconspicuous/high, extending posteriorly	Irregular, elevated in relation to the margins	Thick/thickest	Small to large

the flat general relief with a smooth ornamented surface. The osteoderms of the genus *Holmesina* show a thickness that varies from intermediate to the largest sizes, with broad and outlined lateral margins, general relief irregular due to the ornamentation and projections slightly or very pronounced, plus an apparent longitudinal central elevation, which is not always well-marked. However, the osteoderms of the recently proposed species *H. cryptae* (Moura et al. 2019) do not conform to this morphological pattern and resemble that of the genus *Pampatherium*, warranting a taxonomic revision, as will be further discussed in the text. Aside from that, our results corroborate the distinction between the three Quaternary pampatheriid genera.

Concerning each species, the osteoderms of *Pampatherium typum* and *P. humboldtii* show some variability within specimens (e.g., outlined versus imperceptible marginal elevation), sometimes very similar to each other in overall morphology. However, *P. humboldtii* is uniform in size, like *P. mexicanum*, and different from *P. typum* when analysing different individuals from the same species. The neotype and the hypodigm proposed in this paper contain small to slightly larger osteoderms. The results presented here elucidated that *P. typum* ranged from a relatively small pampatheriid, as well as *Holmesina floridana*, which is the oldest and also the smallest representative of its respective genera (Ameghino 1889; Robertson 1976; Gaudin and Lyon 2017; Jiménez-Lara 2020), to achieve intermediate sizes among Pampatheriidae, as indicated by measurements of *P. typum* given by Ameghino (1889), which represent specimens as large as *P. humboldtii* and *H. cryptae*. Many other specimens deposited as *P. typum* in Argentinean collections have the largest sizes among *Pampatherium* (e.g. MACN 12051, MLP 76-VII-2-7, MLP 52-IX-28-20). Alternatively, these large osteoderms could represent other species or simply an anagenetic change within the species. In any case, this difference in size compared to the neotype has no effect on the morphological pattern of the specimens, being similar to *H. cryptae*. These large osteoderms are henceforth referred to as ‘*H. cryptae*-like’ specimens, due to the high similarity between both taxa.

Osteoderms of *Holmesina cryptae* were described as ‘more defined and punctate than *Pampatherium*’ (Moura et al. 2019). However, our results indicate that *H. cryptae* and *P. typum* share the same morphological pattern and range of variability, with small and large osteoderms observed in both taxa. Both species present osteoderms with flat ornamented surfaces, absent or weakly indicated ornaments delimited by the longitudinal depressions, and sometimes, with a double elevation on either side of a depression in the centre (e.g. MACN A-11114; Moura et al. 2021, p. 409, figure 4 D). Additionally, in osteoderms of both taxa, marginal elevations are absent or only slightly perceptible, and the narrow margins are relatively thinner than in other pampatheriids. *H. cryptae* also presents smaller sizes than those taxa of the South American species of *Holmesina*, even considering the pronounced size differences observed between the two skeletons of *H. cryptae* found together in the Gruta da Lapinha cave (LPP-PV-001 and LPP-PV-002, Moura et al. 2019). All that considered, we suggest that *H. cryptae* needs a systematic revision, especially of the cranial and dental morphology, reconsidering the possibility of being a *Pampatherium*. This

would also require a detailed reevaluation of the large dermal plates housed in the Argentinean collections. Hypothetically, if these are indeed different species, the larger materials associated with *P. typum* could belong to *H. cryptae*, given its compatible morphology; or maybe *H. cryptae* is, in fact, the taxon *P. typum* subjected to anagenetic changes, and *H. cryptae* a junior synonym.

The large *Holmesina cryptae*-like specimens identified as *Pampatherium typum* quoted above were found not only in the Lujanian Stage/Age but also in the Ensenadan Stage/Age, along with the small specimens of *P. typum*, as observed among the collection specimens. The neotype of *P. typum* is probably from the City of Ensenada, Province of Buenos Aires, Argentina (Ensenadan Stage/Age, Early-Middle Pleistocene), since the fossilisation is consistent with that observed in *Tonnincinctus mirus* from the City of Ensenada (MLP 54-III-16-1), with no further taphonomic similarities with any of the other pampatheriids observed in Argentine collections. Ameghino’s (1889) statements about the time of occurrence of *P. typum*, ‘Pampean region, piso Ensenadense, Belgranense and Bonaerense’ (Ameghino 1889), are congruent to the locality hypothesised here to the neotype. In addition, the hypodigm proposed in this paper (Figure 3(B,C)) is in agreement not only with the morphology of the neotype, described here for the first time (Figure 3(A)), but also with the correspondence with its stratigraphic provenance, the current Ensenadan Stage/Age according to their identifications as *P. typum* from the ‘Prebonaerense’ in old and handwritten museum labellings stored with the osteoderms. Many other specimens in Argentinean museums, from small to large, also belong to this time interval ‘Prebonaerense’, most from Centinela del Mar (Pascual et al. 1965; Cioni and Tonni 2005; Vallone 2015), indicating the presence of *P. typum* in the Early-Middle Pleistocene.

According to palaeoecological studies of mammalian faunas recorded in Argentina related to Stage/Age chronology, *Pampatherium typum* occurs in three different faunas: (I) Ensenadan Stage/Age (Early-Middle Pleistocene), (II) Bonaerian Stage/Age (Middle-Late Pleistocene), and (III) Lujanian Stage/Age (Late Pleistocene-Early Holocene) (Scillato-Yané et al. 2005 and references therein). Similar to the morphological data, which exposes a relatively broad range of sizes, the temporal distribution studies suggest the possibility of more than one species among the current samples of *P. typum*, as anatomical features are not expected to be conserved over a long period under different climatic conditions (e.g. De Iuliis et al. 2000; Scillato-Yané et al. 2005; Mead et al. 2007), although anagenetic changes cannot be disregarded as well. In opposition to this idea, *Tonnincinctus mirus* is a well-established species that occurs in Ensenadan and Lujanian Stages/Ages conserving the same size during a long time interval (Góis et al. 2015). For the time being, and based solely on osteoderm evidence, we accept the three currently recognised *Pampatherium* species, *P. humboldtii*, *P. typum*, and *P. mexicanum* as valid species.

The redescription of the original materials of *Holmesina major* from Lapa da Lagoa do Sumidouro (lectotype) and Lapa Vermelha provided further confirmation and additional details to the general pattern that has been widely accepted since the revalidation of this taxon by Edmund (1996) (e.g. Scillato-Yané et al. 2005). The large variability in the structures, ornamentation, and thickness among *H. major* specimens from the State of Minas Gerais (Lund 1842, 1843; Edmund 1996) is similar to that observed in the specimens assigned to *H. paulacoutoi* from the State of Bahia (Cartelle and

Bohórquez 1985), which have both ‘delicate’ and ‘grotesque’ osteoderms (Cartelle 1992; Edmund 1996). Edmund (1996) points out only a small difference in size between *H. paulacoutoi* and *H. major*, which we confirm here to be restricted to a few individual osteoderms, and that are not considered to be of greater significance. Size could vary between different individuals of the same species, clearly observed in representatives of *Pampatherium typum* discussed in this paper, *H. cryptae*, and *H. floridana* (e.g. Robertson 1976; McDonald 2005; Laurito and Valerio 2013; Moura et al. 2019). The indistinguishable morphology of *H. major* and *H. paulacoutoi*, as observed here, led many collections to identify the material as *Holmesina* sp., a fact observed by the main author of this study during her studies to scientific collections (e.g. MCN-PV). To further illustrate this, osteoderms of *H. major* illustrated in Edmund (1996) from the City of Itapipoca, State of Ceará, Brazil (MNRJ 2767 V, page 304, figure 2 B, C) were previously identified as *H. paulacoutoi* (Mello 1990; Cartelle 1992). Conversely, elements initially associated with *H. major* from the State of Rio Grande do Sul, Brazil, were also considered to be *H. paulacoutoi* (Oliveira and Pereira 2009). From the morphological evidence found described in the comparative description, we propose the synonymy for *H. major* and *H. paulacoutoi*. The senior synonym *H. major* should prevail over the junior synonym *H. paulacoutoi*, according to the International Code of Zoological Nomenclature (ICZN).

The neotropical taxon *Holmesina occidentalis* presents a conserved morphological pattern in osteoderms, being more gracile than *H. major*, despite the similarities in ornamentation. The material of *H. occidentalis* from Talara, Peru, deposited in the MLP and belonging to the Ontario Museum, Canada (numbered ROM 28393), shows a morphology consistent with the described material from Ecuador, confirming the evidenced morphology described here. It is possible to highlight the longitudinal central elevation elongated in the centre of the ornamented surface, an intermediate thickness, and the always present longitudinal depressions, observed here as a unique character combination for the *H. occidentalis*. We agree, therefore, with the validity of *H. occidentalis*.

### **The palaeogeography of Quaternary neotropical pampatheriids**

Morphological and taxonomic studies of Pampatheriidae are traditionally separated according to the time of occurrence between species reported up to the Pliocene (e.g. Góis et al. 2013; Laurito and Valerio 2013) and those that appeared in the Pleistocene (e.g. Simpson 1930; Cartelle and Bohórquez 1985; Edmund 1996; Góis et al. 2012, 2015; Ferreira et al. 2018; Moura et al. 2019 -, 2021). Nevertheless, the North American species *Holmesina floridana* is recorded for the Plio-Pleistocene, representing the connection between geological time perspectives (Robertson 1976; Edmund 1987; Gaudin and Lyon 2017; Dávila et al. 2019; Jiménez-Lara 2020). Similarly, Pampatheriidae is usually studied in a regionalised way, independently in North, Central, and South America, with few analyses among taxa from distant parts of the entire American continent (e.g. Edmund 1987; Scillato-Yané et al. 2005; Góis 2013; Góis et al. 2015; Jiménez-Lara 2020). However, in Mexico, *Pampatherium mexicanum* occurs throughout the Nearctic, Transitional, and Neotropical regions, following the regional classification of Morrone (2020). The type locality of *P. mexicanum* (Figure 7) is in the Transitional region, close to the Neotropical one (Edmund 1996; Mead et al. 2007). The records of *P. mexicanum* were made mainly by using the geographic limits within Mexico, taking into account the few morphological information in the literature (Edmund 1996; Scillato-Yané et al. 2005).

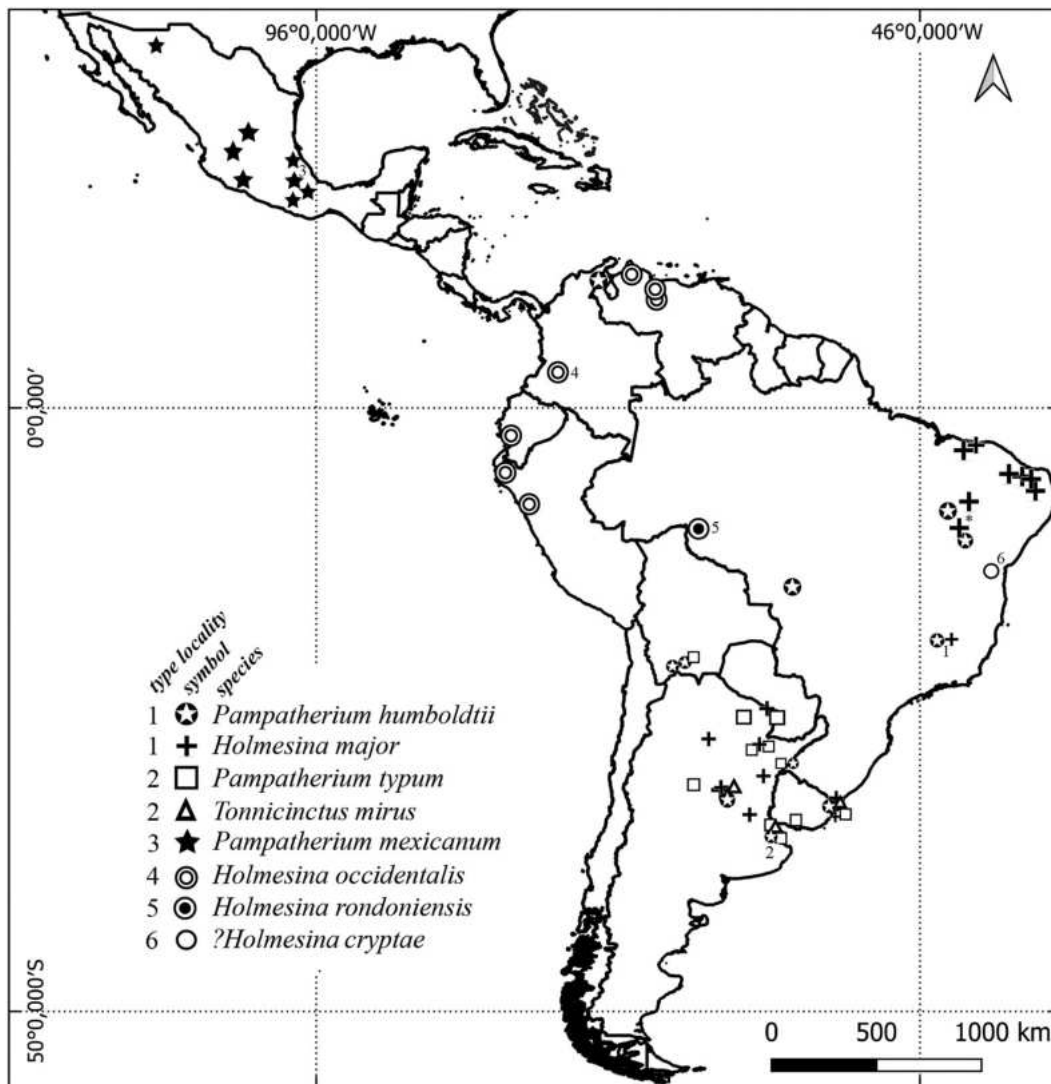
Despite this, the results presented here considered the morphology of the holotype to be unique within Pampatheriidae, in agreement with Edmund (1996) and the validity of its taxonomy.

Also occurring in three major climatic regions (Morrone 2020), the taxon *Holmesina septentrionalis* has been recorded in the Transitional region of Mexico (Laurito and Valerio 2013 and references therein; Morrone 2020) and was recently reported in the Neotropical region in the río Tomayate, El Salvador, Central America (Aguilar and Laurito 2009; Morrone 2020), despite being a Nearctic taxon, occurring largely in North America (Góis 2013 and references therein). The taxon *H. septentrionalis* is the type species for the genus from a type locality far from that of *H. floridana*, in addition to their association with different geological times (e.g. Simpson 1930; Holmes and Simpson 1931; Robertson 1976; Edmund 1985b, 1987). In terms of direction of dispersal and increase in size over time, *H. septentrionalis* is older, more northerly distributed, and slightly smaller than the South American representatives of *Holmesina* (except for *H. cryptae*, pending revision), but quite similar in osteoderm morphology, as seen in the results. All that considered here, *H. septentrionalis* is a good candidate for the common ancestor (or sister taxa) of the Late Pleistocene Neotropical taxa of Central and South America (*H. occidentalis*, *H. rondoniense*, and *H. major*), which is not incompatible with the phylogenetic inferences of Jiménez-Lara (2020).

The inferences obtained by Góis (2013) support an early diverging position for *Holmesina floridana*, but did not recover the genus *Holmesina* as monophyletic, with the genera *Kraglievichia* and *Scirrotherium* being recovered as more closely related to the remainder of *Holmesina*, to the exclusion of *H. floridana* - a less likely result from the stratigraphic perspective. The genus *Holmesina* is thought to have first emerged in North America and diversified into Central and South America (Scillato-Yané et al. 2005; Gaudin & Lyon, 2017). The reconstruction of distribution areas of *H. paulacoutoi* and *H. major* on Scillato-Yané (2005) highlights the geographical proximity of their occurrences, even though this author considered the two taxa as different species. The distribution area of occurrence of *H. major* is expanded here by including both type localities (Figure 7) of the records of *H. major* (Edmund 1996), and those of the junior synonym *H. paulacoutoi* (Cartelle and Bohórquez 1985). Also, more material identified as *Holmesina* sp., following the synonym proposed here, occurring from the north of Brazil to the southeast of Argentina (Figure 7; Ferreira et al. 2018 and references therein; Moura et al. 2019) further expands the distribution area of *H. major*.

The taxon *Holmesina occidentalis* is distributed in the north-western part of South America, where it is associated with high altitudes, being far from the occurrence of the Brazilian species of the genus *Holmesina* (Figure 7). In addition to the morphological evidence, the record of the species also influences the identification of the taxon when only isolated osteoderms are found, because the osteoderms of *H. occidentalis* are very similar to some fixed ones of *H. major*, as discussed in the comparative analysis (Figure 5(A,B,C)) and previously pointed out by Edmund (1987) with reference to the junior synonym *H. paulacoutoi*. In addition to the wide distribution of *H. occidentalis* in northern South America, *Pampatherium humboldtii* is reported from Venezuela (Carlini and Zurita 2010), demonstrating the geographical proximity of the two taxa.

It is worth observing that osteoderms from *Holmesina rondoniense* are currently unknown, with the only record of the species far from the estimated range of *H. major*, being quite isolated



**Figure 7.** Distribution map of the Neotropical Quaternary pampatheriids. Coordinate reference system: SIRGAS 2000. Datasource: GADM. The asterisk (\*) indicates the type locality of the junior synonym of *Holmesina major*, *Holmesina paulacoutoi*.

(Figure 7) (Cartelle 1992; Scillato-Yané et al. 2005; Góis et al. 2012; Ferreira et al. 2018). The distance between distributional areas was used, in addition to the cranial evidence, to set it as a separate species of pampatheriid (Scillato-Yané et al. 2005; Góis et al. 2012).

The taxon *Pampatherium typum* is recorded for a longer interval in the Pampean and Mesopotamian regions of Argentina and southern Brazil (Figure 7) (e.g. Kerber and Oliveira 2008; Oliveira and Pereira 2009; Kerber et al. 2014; Ferreira et al. 2023), associated with different environments, including the smallest to the largest individuals (*Holmesina cryptae*-like specimens), as discussed above. The probable type locality of *P. typum* must be the same as that of *T. mirus* (Góis et al. 2015), as discussed in this paper, and far from those of the Brazilian species *P. humboldtii*, *H. major*, and *H. cryptae* (Figure 7) (Lund 1839, 1843; Cartelle and Bohórquez 1985; Edmund 1996; Góis et al. 2012; Moura et al. 2019).

The taxa *Pampatherium humboldtii* and *Holmesina major* have been reported concomitantly since the first discoveries of pampatheriids (Lund 1842, 1843), even when identified as the junior synonym *H. paulacoutoi* (Scillato-Yané et al. 2005;

Ferreira et al. 2018 and references therein). Furthermore, the high similarity between *H. cryptae* and many specimens of *P. typum* also suggests the necessity of a revision of their geographical distribution, as the recently proposed species has been reported together with *H. major* and *P. humboldtii* in the Brazilian state of Bahia (Figure 7; Moura et al. 2019). An anagenetic change between *P. typum* and *H. cryptae* could also be hypothesised and corroborated in line with the geographical viewpoint, where both share environments with *P. humboldtii* and *H. major*. Lastly, taking the phylogenetic positions of *P. typum* versus *P. humboldtii* plus *P. mexicanum*, as suggested by the results of Góis (2013), the most likely area for the origin of the genus is in the southern portion of South America, possibly expanded by subsequent northward geographic dispersal associated with speciation events (Scillato-Yané et al. 2005). The co-occurrence of *P. typum* and *P. humboldtii* in southern South America could have been achieved ancestrally, with their common ancestor occupying this area, or be derived by dispersal, due to a secondary entrance of the latter taxon in the southern area of the continent. In any case, a formal historical biogeographical

analysis will be necessary to fully disentangle the biogeographical history of the genus *Pampatherium*, and of pampatheriids.

## Conclusion

The purpose of publishing the photographs presented here, together with detailed descriptions of the osteoderms, was to fill taxonomic and morphological gaps in the scientific literature by comparing Pliocene and Pleistocene pampatheriids from different parts of the American continent. A better understanding of all these Neotropical pampatheriids through the first osteoderms, which has been associated with them, is provided by the description, figuration, and comparative analysis of all Quaternary species. The type material presented here not only contributes to our knowledge of the Pampatheriidae but also serves as a reference for the identification of the Quaternary species known to date. It may provide some guidance for collection managers to improve the identification of osteoderm material, which is usually the most common evidence available for pampatheriids and cingulates in general (De Iuliis and Edmund 2002; Ciancio 2016). It is hoped that by filling in the gaps about our knowledge of the original osteoderms mentioned in the first publications of each taxon, as well as in the pioneer studies pioneers of Quaternary pampatheriids, more detailed studies such as biogeographic distribution, palaeoecology and phylogeny will be possible in the future. Since many pampatheriids have been described on the basis of cranial, mandibular, dental, and femoral characters, future efforts should be directed at extending such assessments to the endoskeleton.

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