

A new species of *Scirrotherium* Edmund & Theodor, 1997 (Xenarthra, Cingulata, Pampatheriidae) from the late Miocene of South America

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A new species of *Scirrotherium* Edmund & Theodor (Pampatheriidae) is described: *S. carinatum*. This genus was previously represented by a single species, *S. hondaensis* Edmund & Theodor, 1997, recorded from the middle Miocene (Laventan) of Colombia. Pampathere remains are common in the 'Conglomerado osífero' (late Miocene) of the Ituzaingó Formation in the Paraná River cliffs of Entre Ríos, Chubut (Argentina) and Acre (Brazil). All of them were referred to *Kraglievichia paranense*, and they are mostly osteoderms. However, only a few of these specimens are strictly consistent with that species. The new species described herein differs from *S. hondaensis* in having very thin osteoderms with more elaborate ornamentation. The movable band (or imbricate) osteoderms have a sculptured exposed surface and a single transverse row of anterior foramina; the lateral margins are wider and also bear foramina, and the longitudinal central elevation is long and proximally wide, and forms a posteriorly raised crest. This elevation is delimited by a fairly broad and shallow depression on each side, separating the marginal elevation from the longitudinal central one. The exposed surfaces of fixed (or fused) osteoderms bear large and deep anterior foramina, the longitudinal central elevation and delimiting depressions are very pronounced. This new species increases the known diversity of the pampathere from the 'Conglomerado osífero'. Additionally, a new nomenclatural scheme for Pampatheriidae osteoderms is proposed.

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THE CINGULATA comprises the families Dasypodidae, Peltephilidae, Pampatheriidae, Glyptodontidae and Palaeopeltidae (Carlini *et al.* 2008). Most authors consider that Pampatheriidae are phylogenetically related to Glyptodontidae (Ameghino 1889, Bordas 1939, Patterson & Pascual 1968, Engelmann 1985, Carlini & Scillato-Yané 1993, McKenna & Bell 1997, Vizcaino *et al.* 1998, De Iuliis *et al.* 2000, Gaudin & Wible 2006, Porpino *et al.* 2009, Vizcaino 2009). However, Abrantes & Bergqvist (2006) considered Pampatheriidae to be within the tribe Tolypeutinae (Dasypodidae).

The first genus established for the family was the enigmatic pampathere *Machlydotherium* Ameghino, 1902, from the Casamayoran (late Eocene; Kay *et al.* 1999) and Mustersan (latest Eocene) of Patagonia, Argentina. Scillato-Yané (1980) followed Ameghino (1902) when he referred *Machlydotherium* to Pampatheriidae, but this proposition was questioned by Hoffstetter (1956, 1958). With the status of *Machlydotherium*

being equivocal, the oldest record of an undoubted pampathere is *Scirrotherium hondaensis* Edmund & Theodor, 1997, from La Venta, Colombia (see Edmund & Theodor 1997, Scillato-Yané *et al.* 2005, Ciancio *et al.* in press). Until the present study, *S. hondaensis* was the only known species of this genus.

The pampathere are recorded from the middle Miocene (Edmund & Theodor 1997) to the early Holocene (Cartelle & Bohórquez 1985, Cartelle 1999, Scillato-Yané *et al.* 2005, Góis & Scillato-Yané 2008, 2010, Góis *et al.* 2012) in South America. They reached Central and North America from South America in several waves of migration during the Great American Biotic Interchange (Marshall *et al.* 1984, Morgan & Hulbert 1995, Scillato-Yané *et al.* 2005, Carlini & Zurita 2010, Woodburne 2010). Subsequently, they diversified between the Pliocene and late Pleistocene (Edmund 1996, Carlini & Zurita 2010, Woodburne 2010).

Four genera of pampathere were described from the Neogene of South America: *Scirrotherium* Edmund & Theodor, 1997, *Vassallia* Castellanos, 1927, *Kraglievichia* Castellanos, 1927 and *Plaina* Castellanos, 1937. The validity of the last genus is questioned (De Iuliis &

Edmund 2002). Two lineages were recognized in the Pliocene–early Holocene: *Pampatherium* Gervais & Ameghino, 1880 and *Holmesina* Simpson, 1930 (see Scillato-Yané *et al.* 1995, Edmund 1996, Scillato-Yané *et al.* 2005, Góis & Scillato-Yané 2008). The most recent North American records of these genera come from the late Pleistocene of Mexico (*Pampatherium*) and the United States of America (*Holmesina*) (Edmund 1985, 1996, Scillato-Yané *et al.* 2005, Carlini & Zurita 2010, Woodburne 2010).

All the pampatherine remains recorded from the Miocene of South America were assigned to *Kraglievichia paranense* (Ameghino, 1883) Castellanos, 1927, including those from the ‘Conglomerado osífero’ of the Ituzaingó Formation, Paraná, Entre Ríos (Fig. 1A–C). Cione *et al.* (2000), Góis & Scillato-Yané (2010) and Scillato-Yané *et al.* (in press) proposed that some of these

osteoderms might belong to *Scirrotherium*, and constitute a new species.

The goal of this contribution is to provide a comparative description of material from the ‘Conglomerado osífero’ and evaluate its status as a distinct taxon. Additionally, a new nomenclatural scheme for Pampatheriidae osteoderms is proposed. This scheme facilitates description of the new material and is applicable to other taxa within the family. We also assess the palaeozoogeography of the Mio–Pliocene Pampatheriidae and provide more information on published and unpublished records.

Scirrotherium background

Savage (1951) and Stirton (1953) were the first to publish lists of the Colombian palaeofauna from the Honda Group (Laventan Age; middle Miocene), although

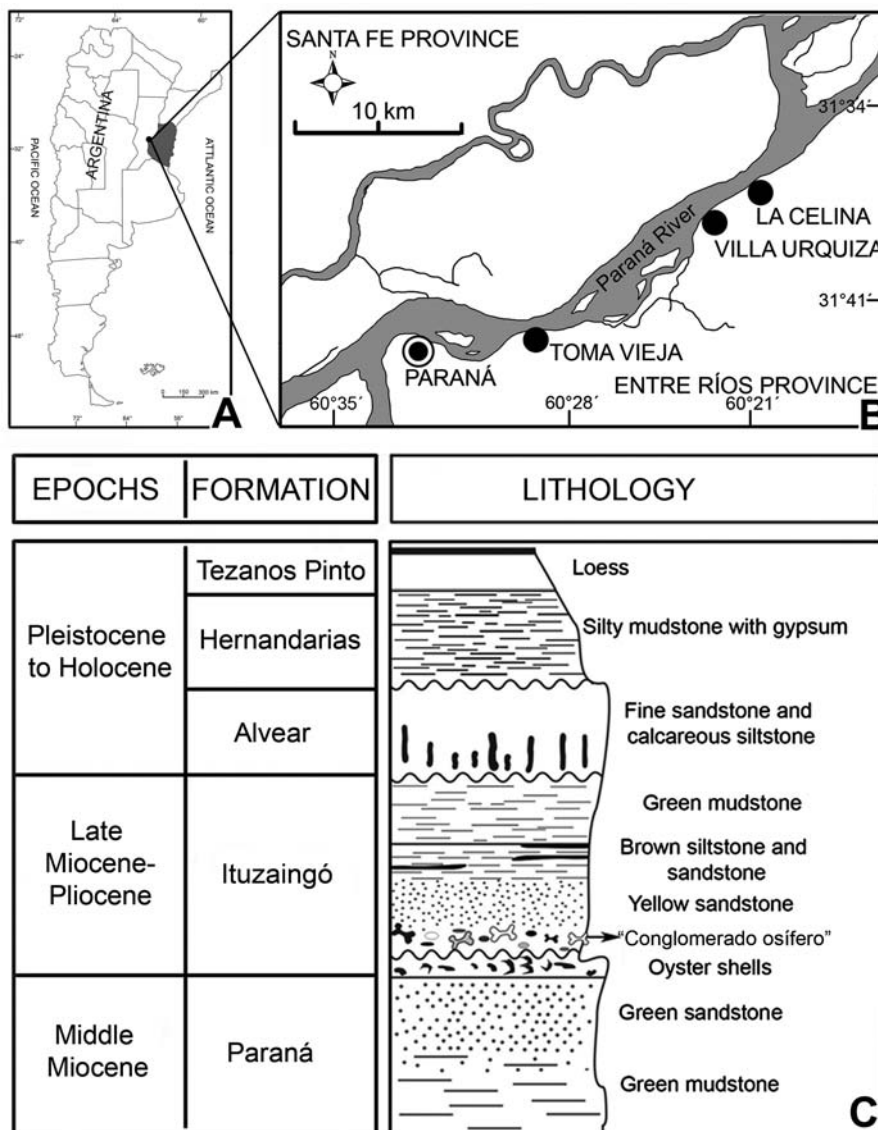


Fig. 1. Locality maps. A, Map of the studied area; B, Map showing the principal fossiliferous localities of the ‘Conglomerado osífero’ (late Miocene) Ituzaingó Formation, Entre Ríos, Argentina (modified from Brandoni and Scillato-Yané 2007); C, Stratigraphic section of the cliffs along the Paraná River near Paraná city, Entre Ríos, Argentina (modified from Aceñolaza 1976).

pampatheres were not included. Porta (1962) described osteoderms from the Honda Group and assigned them to *Kraglievichia paranense*, *Kraglievichia* cf. *paranense* and *Kraglievichia* sp. (see Edmund & Theodor 1997). These osteoderms were assigned to *Vassallia* by Robertson (1976) without any justification. Consequently, the identification of *Kraglievichia* from Colombia has been widely accepted by other workers (Hirschfeld & Marshall 1976, Scillato-Yané 1982, Marshall *et al.* 1984).

Later, Edmund & Theodor (1997, p. 227) recognized a new genus and species of pampatheres from the Honda Group, *Scirrotherium hondaensis*, based on cranial elements; all remains previously referred to *Kraglievichia* (see Porta 1962) they reassigned to *Scirrotherium hondaensis*. Cione *et al.* (2000), Góis & Scillato-Yané (2010) and Scillato-Yané *et al.* (in press) briefly postulated the presence of a new species of *Scirrotherium* in the ‘Conglomerado osífero’, Ituzaingó Formation, Paraná, Entre Ríos (Fig. 1A–C).

The ‘Conglomerado osífero’ of the Ituzaingó Formation

The Pampatheriidae remains from the Ituzaingó Formation, Entre Ríos Province, are abundant and consist mainly of isolated osteoderms. According to the depositional characteristics of the formation (Cione *et al.* 2000), the osteoderms usually occur isolated, making it impossible to determine whether they belong to the same specimen.

The ‘Conglomerado osífero’ (De Alba 1953) constitutes the basal unit of the Ituzaingó Formation. During the 19th century and the first half of the 20th century, the name ‘mesopotamiense’ (first used by Doering 1882) or ‘piso mesopotamiense’ was used to refer to the outcrops along the Paraná River with continental and marine mammals.

Frenguelli (1920) used ‘mesopotamiense’ or ‘piso mesopotamiense’ to designate only the ‘Conglomerado osífero’, and in general, this use of the terms has been adopted since then. Cozzuol (1993) proposed defining ‘Mesopotamiense’ as a formal chronostratigraphic/geochronologic unit (stage/age) of the late Miocene and he used the Paraná River exposures as the type area, a proposal that has not been widely adopted.

The ‘Conglomerado osífero’ crops out discontinuously along the cliffs of the Parana River in the Entre Ríos Province, from the surroundings of Paraná city to the Hernandarias locality to the north, the most studied localities (Fig. 1B) are: La Celina (31°37'37"S, 60°20'04"W), Toma Vieja (31°42'11"S, 60°28'06"W) and Villa Urquiza (31°38'42.5"S, 60°22'50.5"W). The discordance between the underlying Paraná Formation, of marine origin (Bravard 1858), and the sandy to clayey and conglomeratic beds of the Ituzaingó Formation is well defined. The Ituzaingó Formation is of variable thickness and is characterized by beds with chalcedony clasts

and fine quartz gravel in clay. It hosts abundant bones and other fossils, commonly disassociated, together with teeth from continental and marine vertebrates (see Fig. 1C; Brandoni & Scillato-Yané 2007, Brandoni 2010).

Cione *et al.* (2000) proposed correlating the ‘Conglomerado osífero’ and the Huayquerian (late Miocene) of the Pampean Region and northwestern Argentina based on the recorded taxa and the stratigraphic relationships between the fossil beds. The age of these units corresponds to the Tortonian Stage of the international scale (Pascual & Odreman Rivas 1971, Cione *et al.* 2000).

Materials and methods

Methods

As in extant dasypodids, the individual dermal plates of pampatheres consist of an underlying osteoderm and a superficial keratinous scute. Unfortunately, the osteoderms are usually referred to as scutes in the palaeontological literature. To avoid confusion with the keratinous true scute, Edmund (1985) proposed to use the term osteoderm only for the bony part, which is usually preserved in the fossil record.

The term ‘fixed’ refers to those osteoderms located in the anterior and posterior regions (scapular and pelvic bucklers). ‘Semi-movable’ osteoderms occur on the last row of the scapular buckler and the first row of the pelvic buckler (term used by Carlini *et al.* 2009, Krmptotic *et al.* 2009, Ciancio *et al.* in press, González Ruiz *et al.* 2012). ‘Movable’ (or imbricating) osteoderms occur in three rows between the scapular and pelvic bucklers and are separated by flexible mid-section transverse rows.

Pampatheriidae osteoderms have a very distinctive morphology within the Cingulata. This means that they can not be fully described using the standard terminology for the ornamentation of the Dasypodidae or Glyptodontidae. Hence, a new descriptive nomenclature for Pampatheriidae (Scillato-Yané *et al.* in press) is required (Fig. 2A–C). This nomenclature employs some of the traditional terms such as: anterior portion, anterior articular surface, edge, sutural surface and anterior and lateral foramina (Ameghino 1889, Scillato-Yané 1975, 1982, Edmund 1985, 1987, 1996, Edmund & Theodor 1997, Hill 2006, González & Scillato-Yané 2008, González Ruiz & Scillato-Yané 2009, Krmptotic *et al.* 2009, Góis & Scillato-Yané 2010, Wolf *et al.* 2011). However, the exposed surface ornamentation of the osteoderms is described using the following terms:

- (a). The lateral margin [to replace the name of marginal band (see Edmund 1985, 1987, 1996, Edmund & Theodor 1997, Rincón & White 2007)]. The lateral margin can be wide or narrow, and where there are large foramina some of

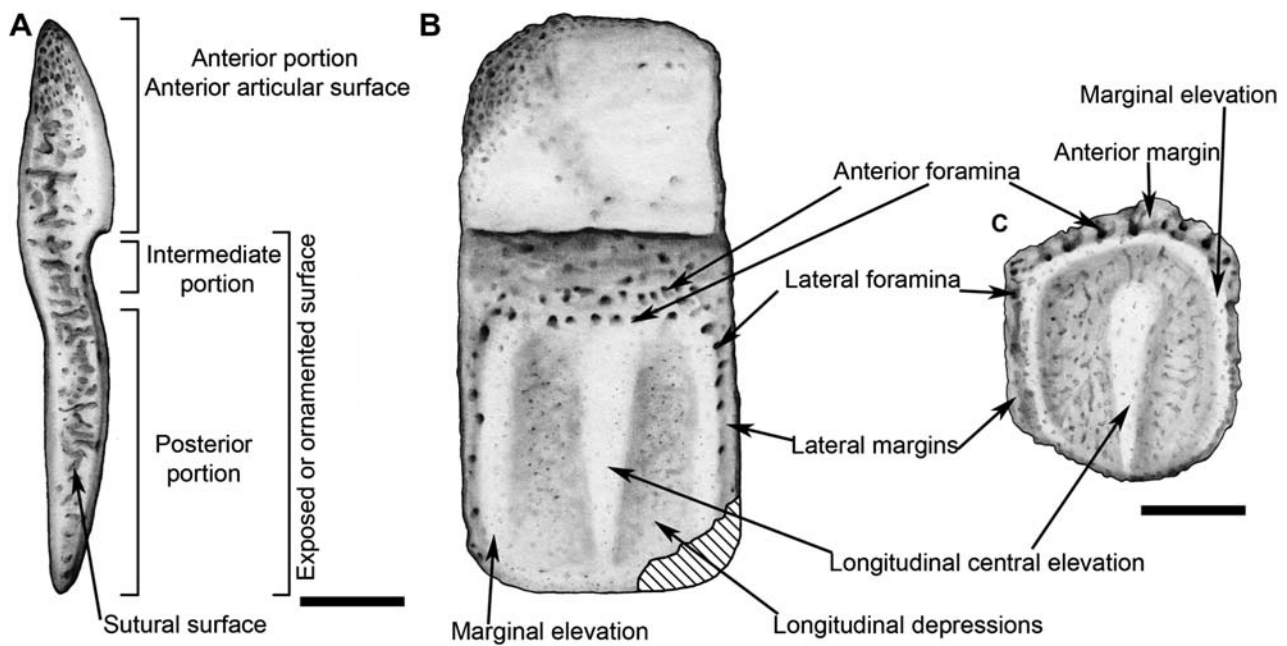


Fig. 2. Proposed terminology for Pampatheriidae osteoderms based on the new species, *S. carinatum* from the 'Conglomerado osífero'. **A** and **B**, movable osteoderm; **C**, fixed osteoderm of the scapular buckler, illustrations of the holotype (MLP 69-IX-8-13AB) and paratype (MLP 69-IX-8-13AC) respectively (modified from Scillato-Yané *et al.* in press). Scale bars = 10 mm.

the rectangular fixed osteoderms can develop a posterior margin.

- (b). The marginal elevation [to replace the names 'marco' and submarginal band (see Porta 1962, Edmund 1985, 1987, 1996, Edmund & Theodor 1997, Rincón & White 2007, Wolf *et al.* 2011)], which delimits the ornamented or exposed (external) surface. This feature is very high in *Scirrotherium*, *Kraglievichia* and *Holmesina* but only slightly pronounced or absent in *Pampatherium* and *Vassallia*.
- (c). The longitudinal depression (instead of sulcus), between the marginal elevation and the longitudinal central elevation, can be either shallow or deep; this feature laterally delimits the longitudinal central elevation.
- (d). The longitudinal central elevation (to replace the term central figure), located in the central line of the exposed surface; it is the most visible structure in many Pampatheriidae species. Unlike the Dasypodidae and Glyptodontidae, Pampatheriidae osteoderms do not have peripheral figures around the 'central figure'. Furthermore, the Pampatheriidae osteoderms were probably covered by just a single keratinous surface (Edmund 1985, 1987).

Here we apply the terms: portion (anterior, intermediate and posterior, Fig. 2A) for an area on the osteoderms and region for an area on the carapace (Fig. 3A–I).

A multivariate analysis was performed using two techniques: the principal-component analysis (PCA) and

canonical correlation analysis (MONOVA/CVA). These analyses were performed with the statistical program Palaeontological Statistics—PAST, version 2.14. Six measurements on fixed osteoderms of the scapular buckler from five Mio–Pliocene Pampatheriidae species (*v. infra*). The analyses were performed from the variance-covariance matrix obtained from the measurements. They were first \log_{10} -transformed to decrease the effect of the size factor. The multivariate analysis was used to morphometrically characterize the osteoderm variation of the new taxon in relation to established species. Three principal measures were used for comparison (See online supporting data: Tables 1 and 2).

Materials

The specimens of the new species were compared with all the known species of South American Pampatheriidae from the Miocene, except *Plaina* (see p. 3), *viz.*, *Scirrotherium hondaensis*, *Kraglievichia paranense*, *Vassallia minuta* (Moreno & Mercerat, 1891) and *V. maxima* Castellanos, 1946. The species of *Pampatherium* and *Holmesina* are giant and they hardly share any anatomical feature with the new species, except those characters common to the family. Consequently, only a few comparisons with *P. typum* Gervais & Ameghino, 1880 and *H. paulacoutoi* (Cartelle & Bohórquez, 1985) were included.

The specimens studied were: *Scirrotherium hondaensis*, paratypes UCMP 37924, 38066, 40056 and 88381. *Kraglievichia paranense* MLP 41-XII-13-903, 41-XII-13-912, 41-XII-13-916, 52-IX-1-36, 62-VIII-10-7 and

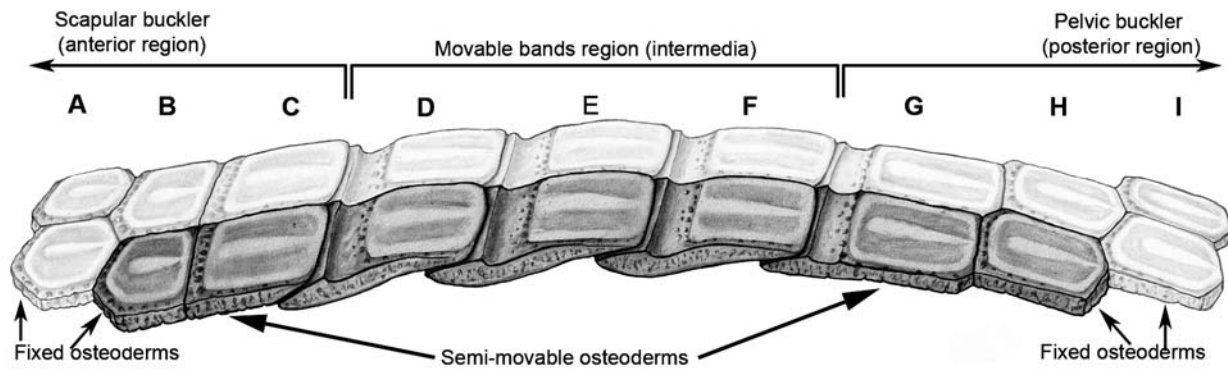


Fig. 3. Typical morphology of the carapace (armour) of pampatheres, model inferred from known carapaces of: *Holmesina*, *Pampatherium* and *Vassallia*. A–B, fixed osteoderms (anterior region) of the scapular buckler; C, semi-movable osteoderms of the scapular buckler; D–F, intermediate region of the movable band osteoderms; G, semi-movable osteoderms of the pelvic buckler; H–I, fixed osteoderms (posterior region) of the pelvic buckler. Not to scale.

69-IX-8-13; MACN Pv 292, 1570, 2684 and 2473; *V. maxima*, holotype MUFyCA 500; MLP 29-X-10-12, 29-X-10-65, 52-IX-30-21 and 96-XII-10-1; *V. minuta* MLP 29-IV-15-6, 29-X-8-39, 69-XII-26-17 and 95-VIII-1-1; *P. typum* MLP 52-IX-28-20, 80-VIII-13-80; *H. paulacoutoi*, holotype MCL-501/01; MLP 34-IV-12-6, 69-VIII-29-13 and 69-XII-26-3.

In the diagnosis, we considered only characters of the osteoderms, since no other assignable material is known. Consequently, osteoderm features (i.e., piliferous sculpturing; vascular and glandular foramina; roughness) have a high diagnostic value for differentiating taxa (Scillato-Yané 1975, 1982, González & Scillato-Yané 2008, González Ruiz & Scillato-Yané 2009, Carlini *et al.* 2009, González Ruiz *et al.* 2012).

Institutional abbreviations

MLP: División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina. MACN: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina. MUFyCA: Museo Universitario Florentino y Carlos Ameghino, Rosario, Santa Fe, Argentina. MPEF-PV: Museo Paleontológico 'Egidio Feruglio', Trelew, Chubut, Argentina. AC: Museo Paleontológico de Real de San Carlos, Departamento de Colonia, República Oriental de Uruguay. LPP/UFAC: Laboratório de Pesquisas paleontológicas, Universidade Federal do Acre, Brazil. MNHN-Bol: Museo Nacional de Historia Natural, La Paz, Bolivia. MCL-PUC/MG: Museu de Ciências Biológicas da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil. FMNH: Field Museum Natural History, Chicago, United States of America. HMNS: Houston Museum of Natural Science, Houston, Texas, United States of America. LACM: Natural History Museum Los Angeles, Los Angeles, United States of America. UCMP: University of California Museum of Paleontology, California, United States of America.

Abbreviations for osteoderm and structures

APL: antero-posterior length; LCEW: longitudinal central elevation width; LMW: lateral margin width; MEW: marginal elevation width; TS: thickness; TW: Transverse width; ME: marginal elevation; LCE: longitudinal central elevation; LDs: longitudinal depressions; LMs: lateral margins; PM: posterior margin; PC: principal components; CVA: correlation canonical analysis.

Systematic palaeontology

XENARTHRA Cope, 1889

CINGULATA Illiger, 1811

PAMPATHERIIDAE Paula Couto, 1954

Scirrotherium Edmund & Theodor, 1997

Type species. Scirrotherium hondaensis Edmund & Theodor, 1997.

Scirrotherium carinatum sp. nov. (Fig. 4A–R)

Etymology. From Latin carina, in relation to the form of the exposed central elevation area in the osteoderms.

Holotype. MLP 69-IX-8-13AB, Roth Collection: an almost complete movable osteoderm with the right posterior angle broken.

Paratypes. MLP 69-IX-8-13AC, Roth Collection, one fixed osteoderm of the scapular buckler. MLP 69-IX-8-13AD, Roth Collection, one semi-movable osteoderm of last row of the scapular buckler. MLP 52-X-1-35, Roth Collection, one movable osteoderm. MLP 69-IX-8-13AE, Roth Collection, one semi-movable osteoderm of the first row of the pelvic buckler. MLP 70-XII-29-1, Roth Collection, one fixed osteoderm of the pelvic buckler.

Hypodigm. The holotype, the paratypes, and M 227, one movable osteoderm; MLP 41-XII-12-920, one fixed osteoderm of the scapular buckler; MLP 41-XII-13-407, one movable osteoderm; MLP 41-XII-13-414,



Fig. 4. *Scirrotherium carinatum* sp. nov. Osteoderms from different regions of the carapace; A, MLP 69-IX-8-13AB; B, MLP 69-IX-8-13AC; C, MLP 69-IX-8-13AD; D, 52-X-1-36, E, MLP 69-IX-8-13AE; F, MLP 70-XII-29-1; G, MLP 41-XII-13-905; H, MLP 41-XII-13-414A; I, MLP 69-IX-8-13AN; J, MLP MLP 69-IX-8-13AF; K, MLP 69-IX-8-13AL; L, MLP 69-IX-8-13AG; M, LPP/UFAC 5393; N, MLP 69-IX-8-13AW; O, MLP 69-IX-8-13AY; P, MLP 69-IX-8-13AS; Q, MLP MLP 41-XII-13-414B; R, MLP 69-IX-8-13AK. Scale bar = 30 mm.

one fixed osteoderm of the scapular buckler; MLP 41-XII-13-924, one fixed osteoderm of the pelvic buckler; MLP 41-XII-13-905, one fixed osteoderm of the scapular buckler; MLP 41-XII-13-909, one movable osteoderm; MLP 41-XII-13-916, one movable osteoderm; MLP 41-XII-13-920, one fixed osteoderm of the scapular buckler; MLP 41-XII-13-923, one fixed osteoderm of the scapular buckler; MLP 41-XII-13-924, one fixed osteoderm of the scapular buckler; MLP 52-X-1-36, one movable osteoderm; MLP 69-IX-8-13AF-Z, 22 osteoderms, 10 fixed, six movable and semi-movable; MACN Pv 1297, one fixed osteoderm of the pelvic buckler; MACN Pv 3951, one movable osteoderm; MACN Pv 4016, two movable osteoderms; MACN Pv 4705, three fixed, one fixed osteoderm of the scapular buckler and two of the pelvic buckler; MACN Pv 5053, one fixed osteoderm; MACN Pv 6599, one fixed pelvic buckler and two movable osteoderms; MPEF-PV 2529/1–11, eight fixed and three movable osteoderms; LPP/UFAC 4803, one semi-movable osteoderm of the first row of the pelvic buckler; LPP/UFAC 4804, one fixed osteoderm of the pelvic buckler; and LPP/UFAC 5393, one semi-movable osteoderm of the last row of the scapular buckler.

Stratigraphical, chronological and geographical origin. All specimens were recovered from the 'Conglomerado osífero' (Huayquerian Age, late Miocene) of the Ituzatingó Formation, Paraná River cliffs, between Paraná and Villa Urquiza, Entre Ríos Province (Argentina) with

the exceptions of: MPEF-PV 2529/1–11, Puerto Madryn Formation (Huayquerian Age, late Miocene), Rincón Chico (42°47.503'S, 63°41.005'W), Península Valdes, Chubut (Argentina); LPP/UFAC 4803 and 4804, Solimões Formation (Huayquerian Age, late Miocene), Acre River, locality Cachoeira do Bandeira (10°56'21"S, 69°20'37"W), Brasília Municipality, Acre state (Brazil). LPP/UFAC 5393, Solimões Formation (Huayquerian Age, late Miocene) and Patos (10°55'31"S, 69°48'35" W), Assis Brasil Municipality, Acre state (Brazil).

Differential diagnosis. The middle portion of the movable osteoderms is rougher than in *S. hondaensis* and *V. minuta* and less rough than in *K. paranense* and *V. maxima*; with two rows of large and deep anterior foramina. The foramina are irregularly arranged in the first row and linearly arranged in the second row (two rows in *S. hondaensis* and *V. minuta*), versus more than two rows in *K. paranense* and *V. maxima* and with more pronounced lateral margins than in *S. hondaensis*, *K. paranense*, *V. maxima* and *V. minuta* (in decreasing order of width). Foramina on the lateral margins of larger diameter and deeper than the anterior foramina from the intermediate portion, as in *V. maxima*, unlike in *S. hondaensis*, *V. minuta* and *K. paranense*. Marginal elevation laterally raised, but anteriorly and posteriorly absent; more pronounced than in *S. hondaensis* and even more elevated than in *Vassallia*, but less convex and narrower than in *K. paranense*. The longitudinal central elevation begins far anteriorly (near the anterior foramina),

is wider anteriorly than posteriorly and is raised and sharp, whereas this feature is flattened, shorter and rounded in *S. hondaensis*, more elevated and convex in *K. paranense* and reduced or slightly sculpted in *Vassallia* species. Fixed osteoderm surfaces (scapular and pelvic) rougher than in *S. hondaensis*, the lateral margins are more reduced than in the movable osteoderms and with fewer foramina, wider than in *S. hondaensis*, *K. paranense*, *V. minuta* and *V. maxima*; marginal elevation laterally more elevated than in *S. hondaensis*, *V. minuta* and *V. maxima*, but less than in *K. paranense*; longitudinal central elevation extended to the posterior edge, more elevated and narrower than in *S. hondaensis*, much more than in *V. minuta* and *V. maxima* and less than in *K. paranense*; delimited by deep longitudinal and anterior depressions as in *K. paranense*.

Comparative description

Though the osteoderms of the Cingulata vary in size and shape in the different regions of the carapace, they always retain, within each region, a basic morphology and consistent ornamentation diagnostic of each species.

As in living dasypodids, the carapace of the pampatheres consists of the three regions: an anterior (scapular, Fig. 3A–C) and posterior (pelvic, Fig. 3G–I) rigid buckler, separated by a flexible mid-section consisting of the three transverse rows of movable band osteoderms (Fig. 3D–F).

The fixed osteoderms forming the rigid buckler were solidly fused along all sutural surfaces (Fig. 3A–B, H–I). The flexible region in pampatheres consists of the three transverse bands (Fig. 3D–F) plus the last row of the scapular buckler and the first row of the pelvic buckler (Fig. 3C, G). The number of movable bands (three) is known in four species. One, figured by James (1957), is referred to *H. septentrionalis* (HMNS 173); the others are *Plaina subintermedia* (Ameghino, 1888) (MNHN-Bol-V 003418; Anaya & MacFadden 1995), *P. humboldtii* (MCL 900) and a Pampatheriidae indet. (AC 1050; Bostelmann & Carlini 2010, Bostelmann *et al.* 2010). Due to the conservation of other features in the Pampatheriidae, and that the three articulated specimens represent different lineages (*Plaina*, *Pampatherium* and *Holmesina*), it seems that all the pampatheres had only three movable bands (Edmund 1985). All the osteoderms of *S. carinatum* are similar to *V. minuta* in thickness, but are notably thinner than in *S. hondaensis*, *K. paranense* and *V. maxima* (Online supporting data: Tables 1–4).

Fixed osteoderms of the scapular buckler. These osteoderms, as in the dasypodids, have a polygonal (pentagonal or hexagonal) shape (Fig. 3A–B). In *S. carinatum*, the anterior margin has numerous, deep and closely spaced foramina, as in *K. paranense* although in greater numbers. For the scapular buckler of *S. hondaensis*, Edmund & Theodor (1997, p. 229, fig. 14.3A, B)

commented: ‘osteoderms has small number of well-spaced follicular pits connected by distinct channel’. This characteristic is also present in *V. minuta*. On the other hand, *V. maxima* has foramina that are more widely spaced and are shallower than in *S. carinatum* and *K. paranense*.

The LMs are wider in *S. carinatum* than in any other Mio–Pliocene species: *S. hondaensis*, *V. minuta*, *V. maxima* and *K. paranense* (in decreasing order). In *S. carinatum*, the LMs of the foramina are more numerous and their diameter less than in *S. hondaensis*, *V. minuta*, *V. maxima* and *K. paranensis*.

In *S. carinatum*, the MEs (Fig. 4B–C) of some osteoderms are positioned slightly below the longitudinal central elevation. Therefore, the MEs of these osteoderms have the same height around the osteoderm perimeter (Fig. 4G, J) and in others the height decreases in the anterior portion and the ME disappears in the posterior portion (Fig. 4F, H).

The width of the ME varies greatly depending on the species: *K. paranense* has the greatest values (between 4.5 and 5 mm), and these values decline in *S. carinatum* (3–4.1 mm), *S. hondaensis* (2.5–3 mm) and *V. minuta* (2.5 and 3.1 mm). The ME of *S. carinatum* is more convex than in *K. paranense*.

Within the ME, there are two LDs, that are deeper in *S. carinatum* than in *S. hondaensis*. In *V. minuta*, the ME is more flattened than in both species of *Scirrotherium*. In *K. paranense* it is deeper (Ameghino 1883), more so than in *S. carinatum* and even more so than in *S. hondaensis* and *V. minuta*. In *V. maxima*, most fixed osteoderms are practically smooth, similar to the Pleistocene species *P. typum*.

In *S. carinatum*, the LCE begins anteriorly (near the anterior foramina) and reaches the posterior edge; this elevation is anteriorly wide and distally narrow, unlike in *S. hondaensis*, where it is short, low and rounded. In *K. paranense*, the LCE is even more depressed in the anterior region than in *S. carinatum*, and it extends towards the posterior edge where it is convex. In *V. maxima*, the LCE is almost imperceptible or diffuse because most of the osteoderms do not have deep LDs. *Vassallia minuta* has a more pronounced LCE than in *V. maxima*, but less than in *Scirrotherium* and *K. paranense*.

The osteoderms of the scapular buckler have numerous pits over their surface, especially gathered laterally in front of the LCE. These foramina are smaller in *S. carinatum* than in *S. hondaensis*, very similar to those of *K. paranense*. The *Vassallia* species have a less rough surface.

Semi-movable osteoderms of the scapular buckler. The osteoderms of the last row of the scapular buckler have almost the same shape as those of the movable osteoderms, except that they are shorter and well sutured to the adjacent osteoderms of the buckler (Fig. 3C). Unlike the movable osteoderms, these osteoderms do not develop an anterior articulated surface, but have a fixed articulation

(Fig. 4C). Semi-movable osteoderms have fewer foramina than the fixed osteoderms in the anterior portion; they are smaller and generally arranged in one row.

In *S. carinatum*, the LMs are narrower than in the fixed scapular osteoderms, whereas they are wider in *K. paranense* and very reduced in *V. maxima* and *V. minuta*. In *S. carinatum*, the ME is laterally narrow and narrower in the anterior portion.

Kraglievichia paranense has osteoderms with a very wide ME the same height around the osteoderm perimeter but in *V. maxima* and *V. minuta* the ME can hardly be seen. In the semi-movable osteoderms from the scapular buckler of *S. carinatum*, the LCE is less pointed than in the fixed osteoderms of this buckler and begins posteriorly, flanked by more shallow LDs. In *K. paranense*, the LCE is longer and wider than in *S. carinatum* and is delimited by deeper LDs. In the *Vassallia* species, the LCE is flattened, and the LDs are shallow.

Osteoderms of the movable bands and semi-movable osteoderms of the pelvic buckler. These osteoderms have an anterior articular surface (Fig. 2A) and they are very similar to each other (Fig. 3D–F, respectively). The semi-movable osteoderms differ from the movable ones in that the posterior edge is not articulated (Figs 3G, 4M–O), the articular surface and the middle portion are generally smaller, and the latter has a constant thickness. The LMs are more reduced, and the ME is less elevated.

Therefore, between the articular surface and the exposed or ornamented surface in the movable and semi-movable osteoderms, there are several foramina, and the surface is rough. These osteoderms have two different portions: (a) the most anterior portion (immediately posterior to the articular surface), which is less rough and has few foramina; and (b) the posterior portion, with more foramina, which are usually arranged in transverse rectilinear rows.

In *S. carinatum*, those foramina of the anterior portion are not aligned in two regular rows (as in *S. hondaensis* and *V. minuta*, see Edmund & Theodor 1997, fig. 14.3), but are so aligned only in the posterior row. *Kraglievichia paranense* and *V. maxima* have more than two rows of foramina with an irregular distribution. The LMs are wider in *S. carinatum* than in *S. hondaensis*. They have great foramina with more space between them than the anterior foramina, as in *V. maxima*. In *S. carinatum*, the lateral ME is high, slightly more elevated than the LCE, whereas the ME is lower in *S. hondaensis*. In *K. paranense*, the ME is generally wider and more elevated than in *S. carinatum* and *S. hondaensis*. The posterior ME has a tendency to disappear in all the species.

Fixed osteoderms of the pelvic buckler. These osteoderms are rectangular (Fig. 3H–I). The LMs are narrower than in the fixed osteoderms from the scapular buckler. The LMs are wider than in *S. hondaensis*, *V.*

minuta and *V. minima* but narrower than in *K. paranense*.

In *S. carinatum*, the ME is laterally wide and anteriorly reduced, very similar to *V. minuta* and wider than in *S. hondaensis* and *V. maxima*. The ME of *Kraglievichia paranense* is well developed laterally but anteriorly reduced.

The LDs are deeper in *S. carinatum* than in *S. hondaensis*, *V. minuta* and *V. maxima*, and much shallower than in *K. paranense*. In *S. carinatum*, the LCE has a similar shape to that of the fixed osteoderms of the scapular buckler, movable and semi-movable osteoderms, and it is posteriorly more expanded than in *S. hondaensis*, *V. minuta*, *V. maxima* and *K. paranense*.

Statistical analysis

The statistical analysis reinforces the diagnostic value of osteoderms within the Cingulata, especially for the taxa studied here. In the principal-components analysis, the first two components explain more than 87% (65% and 22.1% respectively; Fig. 5A and values in Tables 3 and 4: online supporting data) of the total variation.

The first component (PC1) separates species by size (e.g., larger—*K. paranense* and *V. maxima*); and smaller—*S. carinatum*, *S. hondaensis* and *V. minuta*). This first axis is influenced by LCE width. The second component (PC2) separates *S. carinatum* from *S. hondaensis* and *V. minuta*, but there is some overlap between the fields of the last two. This axis was most influenced by the width of the LMs and the width of the ME. *Scirrotherium carinatum* is distinctly separated from *S. hondaensis* and *V. minuta* due to the narrower shape of its LCE. *Kraglievichia paranense* and *V. maxima* have narrow LMs. The ME is very wide in the former and more reduced in the latter. In *S. carinatum*, the ME is more pointed than in *S. hondaensis* and *V. minuta*, the ME width in *S. carinatum* and *V. minuta* are practically the same.

The results of the canonical correlation (MANOVA/CVA) provide a clearer differentiation of the species in the morphospace, with no overlap between taxa (Fig. 5B). The first canonical correlation axis (CV1) accounts for more than the 75% of the total explained variance, and indicates a significant difference ($p < 0.01$) between *S. carinatum* and the others species.

Geographical distribution of Miocene pampatheres

Neogene pampatheres are abundant in Argentina (Fig. 6); the most abundant species being *K. paranense* ('Conglomerado osífero', late Miocene) represented by osteoderms, skulls and postcranial elements. The distribution of *Kraglievichia* includes the Arroyo Chasicó Formation (Chasicóan Age, late Miocene) from the homonymous area in Buenos Aires Province (see Scillato-Yané 1979). The pampatheres recorded in the El Palo

Formation (Huayquerian Age) from the north of Río Negro (Cerro Vaca Mahuida, Departamento General Roca; Scillato-Yané 1982, Góis & Scillato-Yané 2010) may also correspond to *K. paranense*. Ciancio *et al.* (2006) cited *K. paranense* from Departamento Ullum, San Juan. Perea (1993) mentioned *K. paranense* from coastal cliffs of La Plata River (Kiyú Formation: late Miocene), Puerto Arazití, Departamento San José, Uruguay. Marshall & Sempere (1991) mentioned cf. *Kraglievichia* from three localities in Bolivia: Jankoqui, Rosario and Camacho (Camacho Formation) from the Huayquerian (late Miocene).

Scirrotherium hondaensis is known exclusively from the middle Miocene of the Honda Group (Levantán Age,

Colombia). *Scirrotherium carinatum* n. sp. is present in the ‘Conglomerado osífero’ (late Miocene) of the Entre Ríos (in the same levels of *K. paranense*), but the number of specimens is very low, and cranial or postcranial elements are still unknown. *Scirrotherium carinatum* has an extensive distribution and has been found in north Patagonia, between Punta Delgada and Pico Lobo (Dozo *et al.* 2002, 2010, Fig. 4A–H), in the late Miocene Puerto Madryn Formation (Península Valdés, Chubut) and also in the late Miocene Solimões Formation (Acre, Brazil). Material from the last locality was erroneously described as *Kraglievichia* sp. (see Góis *et al.* 2004, Góis 2005, Cozzuol 2006, Latrubesse *et al.* 2010).

In summary, *Scirrotherium* has a more widespread distribution than *Kraglievichia*, possibly as a consequence of

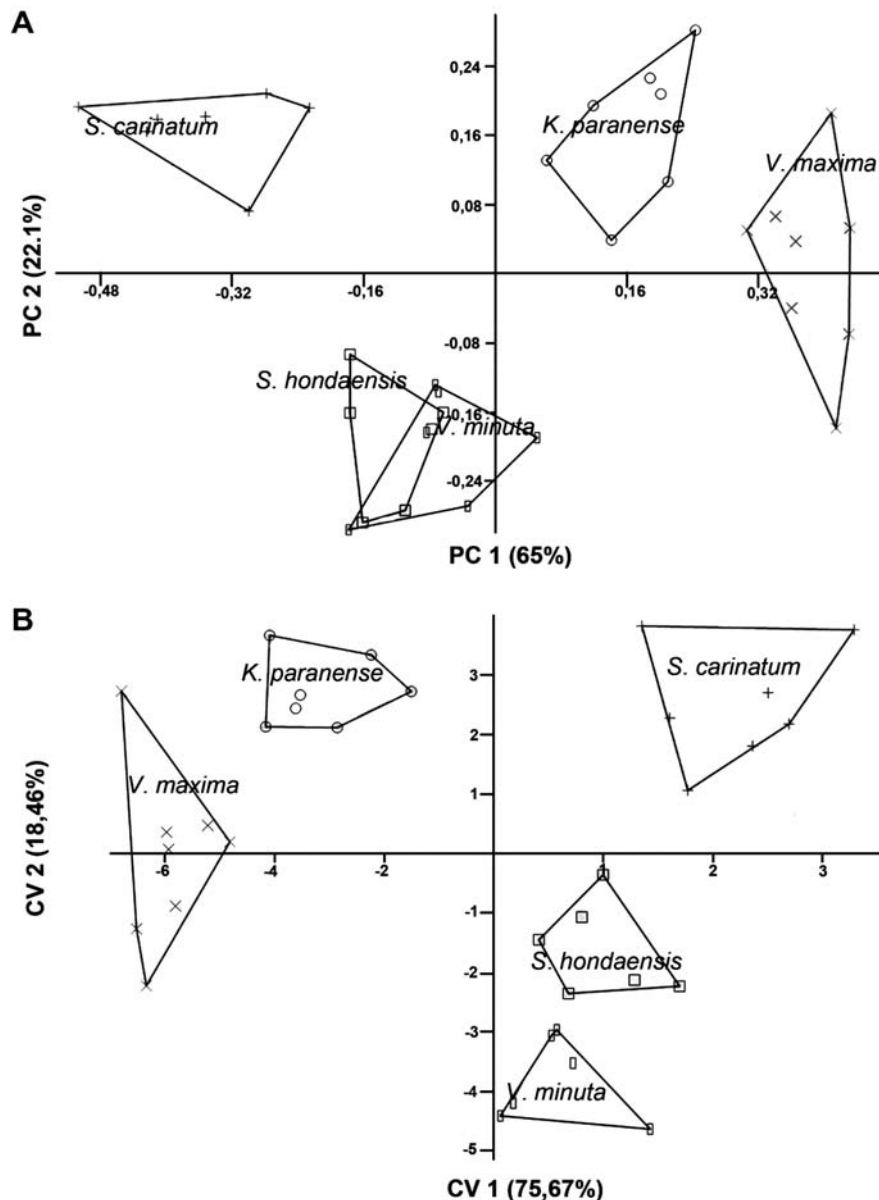


Fig. 5. A, Principal-component analysis and B, Canonical correlation, both measures of the fixed osteoderms of the scapular buckler. PC, principal-component; %, percentage of explained variation.



Fig. 6. Distribution of South American Miocene pampatheriid species. **A**, *Kraglievichia paranense* (Paraná, Entre Ríos); **B**, *K. paranense* (Arroyo Chasicó, Buenos Aires Province); **C**, *Kraglievichia* sp. (Departamento General Roca, Río Negro Province); **D**, *K. paranense* (Departamento Ullum, San Juan Province, Argentina); **E**, *K. paranense* (Departamento of San José, Uruguay); **F–H**, cf. *Kraglievichia* (San Andrés de Machaca, Municipality within Ingavi Province); **I**, *S. carinatum* sp. nov. (Paraná, Entre Ríos); **J–K**, *S. carinatum* sp. nov. (Península Valdes, Argentina); **L**, *S. carinatum* sp. nov. (Assis Brasil Municipality, state of Acre, Brazil); **M–N**, *S. carinatum* sp. nov. (Brasiléia Municipality, state of Acre); **O**, *S. hondaensis* (Villavieja, Departamento Huila, Colombia). See text for references.

its greater ecological flexibility that allowed its presence in more varied environments over a wider latitudinal range.

Discussion

The terminological scheme for Pampatheriidae osteoderms proposed by Scillato-Yané *et al.* (in press) proved to be useful for evaluating these unusual cingulates because the morphological features now have unambiguous names that are more applicable to pampatheres. In this context, Wolf *et al.* (2011) mentioned that the osteoderms of pampatheres have a unique histological pattern and postulated a new synapomorphy for this group. The Peltephilidae have osteoderms with a similar morphology to that described for Pampatheriidae: absence of peripheral figures, ME wider, LDs deep and LCE pointed. Thus, the new terminology may also be applicable to the Peltephilidae.

Conclusions

- (1) The differences in osteoderm ornamentation clearly distinguish *Kraglievichia paranense* and the two *Scirrotherium* species.
- (2) The osteoderms of *S. hondaensis* are proportionally smaller and thicker than those of *S. carinatum*. The new species has more sharply defined features.
- (3) The description of *S. carinatum* sp. nov. increases the known diversity of Pampatheriidae from the Ituzzaingó Formation of Entre Ríos, that previously was limited to one species: *K. paranense*.
- (4) *Scirrotherium carinatum* has a distribution including the Mesopotamian region of northeast Patagonia and northwest Brazil (Acre).

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