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Abstract. The genus *Neoglyptatelus* Carlini, Vizcaíno and Scillato-Yané has been considered a member of Glyptatelinae, a group encompassing the purportedly basal-most glyptodonts. It is up to now represented by two species from Colombia: *Neoglyptatelus originalis* Carlini, Vizcaíno and Scillato-Yané, from the middle Miocene (a carapace fragment, isolated osteoderms and postcranial bones), and *Neoglyptatelus sincelejanus* Villarroel and Clavijo, from the middle or late Miocene (a partial carapace and a caudal armor). More scarce material assigned to this genus was recovered from the late Miocene of Uruguay and Brazil. In this article, we describe a new species, *Neoglyptatelus uruguayensis*, from the late Miocene Camacho Formation, Uruguay, based on an almost complete carapace and several postcranial bones. We conducted a phylogenetic analysis based on 167 morphological characters (23 new ones and 144 from previous analysis) scored for 19 taxa, encompassing some of the best known glyptodontid genera, one pampathere and four armadillos (including the enigmatic genus *Pachyarmatherium* Downing and White). In the most parsimonious tree that was obtained, *Neoglyptatelus* forms a clade with *Pachyarmatherium* (Pachyarmatheriidae), which is the sister group of the glyptodonts + pampatheres clade; consequently, it is not a glyptodont, as previously believed. This result, together with the known stratigraphic and geographic distribution of *Neoglyptatelus* and *Pachyarmatherium*, suggests that this new cingulate clade originated in South America and that *Pachyarmatherium* reached North America during the Plio–Pleistocene. The carapace of *Neoglyptatelus* and *Pachyarmatherium* comprises pelvic and scapular shields overlapping each other without separate intervening transverse mobile bands, an arrangement that differentiates both genera from the remaining cingulates.

Key words. Carapace. Movement. Pachyarmatheriidae. Glyptatelinae. Phylogeny.

Resumen. UNA NUEVA ESPECIE DE *NEOGLYPTATELUS* (MAMMALIA, XENARTHRA, CINGULATA) DEL MIOCENO TARDÍO DE URUGUAY PROPORCIONA NUEVAS PERSPECTIVAS SOBRE LA EVOLUCIÓN DEL CAPARAZÓN DORSAL EN LOS CINGULADOS. El género *Neoglyptatelus* Carlini, Vizcaíno and Scillato-Yané ha sido considerado un miembro de los Glyptatelinae, un grupo que supuestamente incluye a los gliptodontes basales. Actualmente, está representado por dos especies halladas en Colombia: *Neoglyptatelus originalis* Carlini, Vizcaíno and Scillato-Yané, del Mioceno medio (fragmento de caparazón, osteodermos aislados y elementos postcraneanos) y *Neoglyptatelus sincelejanus* Villarroel y Clavijo del Mioceno medio o tardío (parte de un caparazón y coraza caudal). Osteodermos aislados asignados a este género fueron recuperados en el Mioceno tardío de Uruguay y Brasil. En este trabajo, nosotros describimos una nueva especie, *Neoglyptatelus uruguayensis*, del Mioceno tardío de la Formación Camacho, Uruguay, a base de una coraza casi completa y distintos elementos postcraneanos. Nuestro estudio filogenético se sustenta en 167 caracteres óseos (23 nuevos y 144 utilizados previamente) relevados en 19 taxones, que incluyen los géneros de gliptodontes mejor conocidos, un pampaterio y cuatro armadillos, incluyendo *Pachyarmatherium* Downing y White. En el árbol más parsimonioso obtenido *Neoglyptatelus* forma con *Pachyarmatherium* un clado (Pachyarmatheriidae) hermano del grupo formado por pampaterios + gliptodontes, por lo cual no es un gliptodonte como se sostenía previamente. Este resultado, junto al conocimiento estratigráfico y geográfico de *Neoglyptatelus* y *Pachyarmatherium*, sugiere que los Pachyarmatheriidae se habrían originado en América del Sur y que durante el Plio–Pleistoceno *Pachyarmatherium* arribó a América del Norte. El caparazón de *Neoglyptatelus* y *Pachyarmatherium* contiene un escudo escapular y otro pélvico que solapan directamente entre sí, sin mediar bandas movibles transversas; este arreglo morfológico es único entre los cingulados.

Palabras clave. Caparazón. Movimiento. Pachyarmatheriidae. Glyptatelinae. Filogenia.

THE genus *Neoglyptatelus* and its type species *Neoglyptatelus originalis* were established on a small fragment of dorsal carapace, isolated osteoderms and various postcranial bones (Carlini *et al.*, 1997) from the middle Miocene of the La Venta Formation in Colombia (Madden *et al.*, 1997). A small maxilla and mandible were included, with doubt, in the hypodigm because there was no clear association between these specimens and the diagnostic carapace material; unfortunately, these specimens were not described (Carlini *et al.*, 1997).

Vizcaíno *et al.* (2003) assigned several isolated osteoderms from the late Miocene of Uruguay to this genus. Later, Villarroel and Clavijo (2005) founded a new species, *Neoglyptatelus sincelejanus*, from the middle or late Miocene of Colombia, on a partial carapace and a fragment of caudal armor. The genus was also recorded in the late Miocene age from Acre, Brazil (Cozzuol, 2006).

Neoglyptatelus was assigned by Carlini *et al.* (1997) to the Glyptatelinae, a poorly defined group widely believed to include the basalmost glyptodonts (Hoffstetter, 1958). It was characterized by showing, on the external surface of the osteoderms, the main figure displaced towards the posterior edge and the presence of lobulated teeth, similar to those of other glyptodonts, but without central hard osteodentine crests. The type genus of Glyptatelinae is the poorly known *Glyptatelus* Ameghino, 1897, from the late Eocene to late Oligocene of Bolivia and Argentina (McKenna and Bell, 1997). According to Ameghino (1902), the type specimen (MACN-A 52-356) of *Glyptatelus* included osteoderms and teeth. However, the teeth were consistently reassigned to *Pseudoglyptodon* Engelmann, 1987, an unusual Folivora (sloth) with glyptodont-like teeth (Wyss *et al.*, 1994; McKenna *et al.*, 2006). Other taxa recognized by McKenna and Bell (1997) as belonging to Glyptatelinae are *Clypeotherium* Scillato-Yané, 1977, from the late Eocene to late Oligocene of Bolivia and Argentina; *Lomaphorelus* Ameghino, 1902, from the Eocene of Patagonia (considered *nomen dubium* by Vizcaíno *et al.*, 2003); and the late Pliocene−late Pleistocene *Pachyarmatherium* Downing and White, 1995, from USA (Downing and White 1995), Brazil (Porpino *et al.*, 2009), Perú, (Martinez *et al.*, 2008; Martinez and Rincón, 2010), Uruguay (Bostelmann *et al.*, 2008), and Venezuela (Rincón and White, 2007). *Pachyarmatherium*, which is quite similar to *Neoglyptatelus*, was recently positioned by Por-

pino *et al.* (2009, 2010) out of glyptodonts, as the sister group of Pampatheriidae + Glyptodontia.

Considering the material so far described, the principal feature that *Neoglyptatelus* shares with the remaining Glyptatelinae is the posterior displacement of the main figure on the external surface of the carapace osteoderms. However, this feature is also present in the other glyptodonts, such as *Parapropalaehoplophorus* Croft *et al.*, 2007 and *Paraeucinepeltus* González-Ruiz *et al.*, 2011, and some portions of the carapace of *Propalaehoplophorus* Ameghino, 1887a. All this casts doubts on the assignment of *Neoglyptatelus* to the Glyptatelinae and on the validity of this subfamily.

Herein, we describe a new specimen belonging to a new species of *Neoglyptatelus* from the Miocene of Uruguay. The excellently preserved exoskeleton and some associated postcranial elements assignable to this taxon shed new light on the affinities of *Neoglyptatelus* and on the evolution of the pattern of carapace mobility among cingulates.

GEOLOGICAL SETTING

The fossil-bearing strata are located in southwestern Uruguay (San José Department; 34° 34' S; 56° 58' W) in exposures located on the coastal cliffs and littoral platform of Río de La Plata (Fig. 1). There, the lithostratigraphic units recognized from the base to the top are the Camacho (late Miocene), the Raigón (Pliocene and Pleistocene) and the Libertad (Pleistocene) Formations (Bossi and Navarro 1991; Tófalo *et al.*, 2009). The first two units yield many vertebrate fossils, including a variety of cingulates, ground sloths, rodents and notoungulates. The remains hereby described were found in sediments of the Camacho Formation. This Formation is the representation, in Uruguay, of an extended, late Miocene, eustatic event regionally known as the Paranean transgression or Paranean Sea. In the San José Department, this includes facies related to the regressive phase characterized as estuarine and/or paralic environments. The fossil assemblage of the unit comprises terrestrial and fresh-water vertebrates in association with marine invertebrates and ichnofossils (Ubilla *et al.*, 1990; Perea *et al.*, 1996; Sprechmann *et al.*, 2000; Perea 2005). The sediments of the Camacho Formation are formed by greenish-grey friable and medium compressed pelite that becomes greenish-brownish toward the top of the formation. The
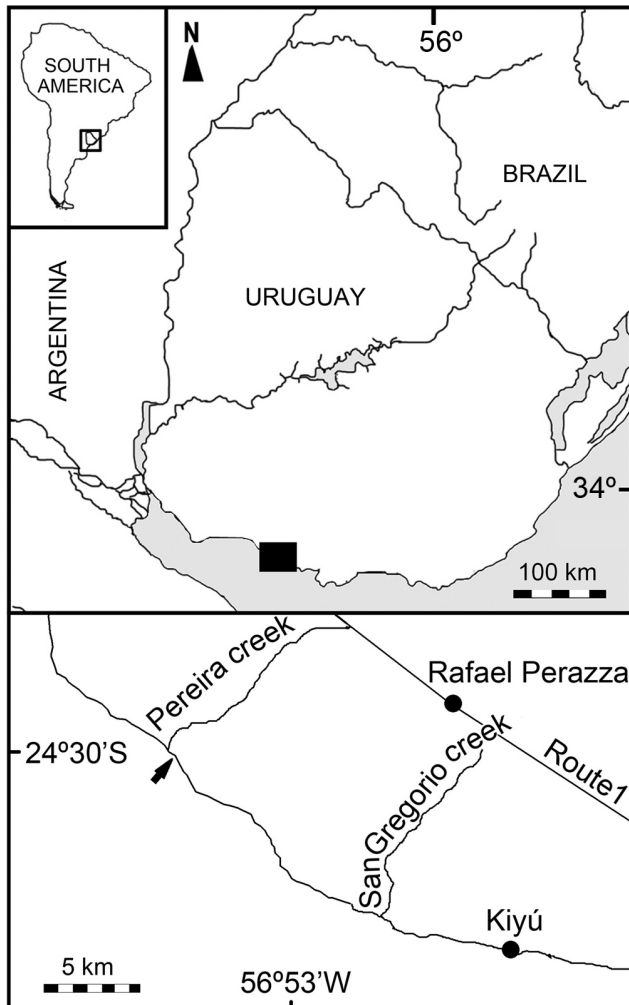
Figure 1. Map of the region where the holotype of *Neoglyptatelus uruguayensis* was collected. The arrow indicates the precise geographic location where MNHN 1642 was found.

mammalian fossil assemblage includes marsupial carnivores, xenarthrans, notoungulates, litopterns, hystricognath rodents and cetaceans, thus showing affinities with the late Miocene Chasicoan and Huayquerian Ages/Stages of Argentina, especially with the one informally known as the *"Mesopotamiense"* (formerly considered a Huayquerian age local fossil fauna) of the Entre Ríos Province (Bostelmann and Rinderknecht, 2010; Brandoni 2013; Perea *et al.*, 1994; Perea 2005; Perea *et al.*, 2013; Rinderknecht *et al.*, 2011; Vizcaíno *et al.*, 2003). ^{40}Sr/^{39}Sr dated levels of the Paraná Formation and its southern correlative, the Puerto Madryn Formation, render a late Miocene 9.5 Ma – 10 Ma (Tortonian) age for the top of the Paranean Sea in Argentina (Scasso *et al.*, 2001).

MATERIAL AND METHODS

A cladistic analysis was conducted using TNT 1.5 (Goloboff and Catalano, 2016) to assess the phylogenetic relationships of *Neoglyptatelus* within Glyptodontia (*sensu* Fernicola, 2008), taking into consideration that this taxon had been previously assigned to this group (Carlini *et al.*, 1997; McKenna and Bell, 1997). The data matrix includes 19 taxa and 167 morphological characters (Supplementary appendix 1, 2, and 3). These latter correspond to 84 craniodental characters from Fernicola (2008), three of which were originally proposed by Gaudin and Wible (2006); 83 postcranial characters, 60 of which based on three previous studies (Porpino *et al.*, 2009, 2010; Fernicola and Porpino, 2012) on the systematic of glyptodonts; and 23 new characters (see Appendix I for descriptions and sources of each). The postcranial characters were derived and scored via the direct observation of the specimens and the descriptions and figures in the literature. Forty-eight multistate characters were treated as ordered in the analysis based on numerical and structural morphoclines following the 'method of intermediates' (Wilkinson, 1992). All the characters were equally weighted. From the 19 taxa included in this analysis, 14 correspond to the ingroup: *Neoglyptatelus* (Glyptatelidae); *Propalaehoplophorus* and *Eucinepeltus* Ameghino, 1891 (Propalaehophoridae); *Panochthus* Burmeister, 1866, *Neosclerocalyptus* Paula Couto, 1957 and *Hoplophorus* Lund, 1839 (Panochthidae); *Plohophorus* Ameghino, 1887b, *Doedicurus* Burmeister, 1874 and *Glyptodon* Owen, 1839 (Glyptodontidae)*; Pseudoplohophorus* Engelmann, 1987, *Stromaphorus* Castellanos, 1926, *Hoplophractus* Cabrera, 1939 and *Eosclerocalyptus* Ameghino, 1919 (Glyptodontoinei); and *Urotherium* Castellanos, 1926 (Glyptodontoidea). Recently, Zurita *et al.* (2017) synonimized *Urotherium antiquum* Ameghino, 1888 with *Plohophorus figuratus* Ameghino, 1887b based, among others, on the study of MACN-A 229-231 and MLP 16-153 (holotype), specimens which were assigned to both taxa, respectively. However, both specimens had been included in previous phylogenetic studies (Fernicola, 2008; Porpino *et al.*, 2010; Fernicola and Porpino, 2012) and the taxa that these specimens represent do not form a natural group. Consequently, this synonymy proposal has not been considered in this study. The outgroups include four dasypodids (*Eutatus* Gervais, 1867, *Dasypus* Linnaeus, 1758, *Pachyarmatherium* and *Euphractus*

Wagler, 1830) and one pampathere (*Pampatherium* Gervais and Ameghino, 1880).

With respect to the taxonomy of *Pachyarmatherium,* we follow Oliveira *et al.* (2013), who claim that an exhaustive review of the species *P. tenebris* and *P. brasiliensis* is necessary before definitively accepting the synonymy proposed by Martinez and Rincón (2010) and Valerio and Laurito (2011). As noted by Oliveira *et al.* (2013), the type specimens of both species show some differences, as evidenced by a superficial comparison of their respective diagnoses; yet, the available samples for South American species of *Pachyarmatherium* are small so the discovery of more complete and abundant material would be crucial for a better assessment of their potential synonymy.

All measurements were taken to the nearest 0.1 mm using a digital calliper. Unless otherwise indicated, we use the term osteoderm to denote the bony components of the carapace, and the term scale for the keratinous portion of such components (Krmpotic *et al.*, 2009; Vickaryous and Hall, 2006; Hill, 2006). With respect to the ornamentation pattern, we follow Fernicola and Porpino (2012).

Institutional abbreviations. **AMNH,** American Museum of Natural History, New York, USA; **FC-DPV,** Colección de Vertebrados Fósiles, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; **MACN-A,** Colección Ameghino, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; **MACN-Ma,** Colección Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciudad Autónoma de Buenos Aires, Argentina; **MACN-Pv,** Colección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciudad Autónoma de Buenos Aires, Argentina; **MCC,** Museu Câmara Cascudo, Natal/RN, Brazil; **MNHN,** Museo Nacional de Historia Natural, Montevideo, Uruguay, **MPEF-PV,** Colección Paleontología de Vertebrados, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; **MLP,** Museo de La Plata, La Plata, Argentina; **PV UNS,** Colección Paleontología de Vertebrados, Universidad Nacional del Sur, Bahía Blanca, Buenos Aires, Argentina.

SYSTEMATIC PALEONTOLOGY

Order CINGULATA Illiger, 1811

Family PACHYARMATHERIIDAE new rank

Type genus. *Pachyarmatherium* Downing and White, 1995.
Diagnosis. The carapace of this group differs from that of the known remaining Cingulata in having scapular and pelvic shields articulated without intermediating mobile bands among them.

Geographic and temporal occurrence. In North America, from the late Pliocene to the Early Pleistocene of Florida and in the late Pliocene of South Carolina (Downing and White, 1995 and Hulbert, 2001); in Central America, in the late Blancan–early Irvingtonian of Costa Rica (Laurito *et al.*, 2005, Laurito and Valerio 2012); in South America, in the Plio–Pleistocene of Venezuela (Rincón *et al.*, 2009, Solórzano *et al.* 2015), in the late Pleistocene of Venezuela and Perú (Rincón and White, 2007; Martinez *et al.*, 2008; Martinez and Rincón, 2010), in the middle–late? Miocene of Colombia (Madden *et al.*, 1997), in the late Pleistocene to early Holocene of Brazil (Porpino *et al.*, 2009; Oliveira *et al.*, 2009), in the late Miocene of Brazil (Cozzuol (2006), and in the late Miocene (Vizcaíno *et al.*, 2003) and the Quaternary of Uruguay (Bostelmann *et al.*, 2008).

Genus *NEOGLYPTATELUS* Carlini, Vizcaíno,
and Scillato-Yané, 1997

Type species. *Neoglyptatelus originalis* Carlini, Vizcaíno, and Scillato-Yané, 1997

Emended diagnosis. The osteoderms of this genus differ from those of *Pachyarmatherium* in having narrow and shallow sulci (instead of wide and deep), and smaller foramina. They differ further from those of *Pachyarmatherium* in having each anterior caudal ring formed by two rows of osteoderms instead of three, and in having the articulation zone of the carapace formed by the two posteriormost transversal rows of the scapular shield and the two anteriormost transversal rows of the pelvic shield (instead of by single posteriormost and anteriormost transversal rows of the scapular and pelvic shields, respectively). It differs from *Glyptatelus* and *Clypeotherium* in the following features: it is smaller, its main figure is polygonal (instead of rounded). It differs further from *Clypeotherium* in having its external surface moderately wrinkled (instead of strongly wrinkled and punctuated).

Geographic and temporal occurrence. Middle–late? Miocene of Colombia (Madden *et al.*, 1997), and late Miocene (Vizcaíno *et al.*, 2003) and Quaternary of Uruguay (Bostelmann *et al.*, 2008), South America.

Neoglyptatelus uruguayensis sp. nov.
Figures 2.1–3, 3.1–6, 4.1–2, 5.1–2, 6.1–5

Derivation of name. *uruguayensis;* from Uruguay, to emphasize its geographic provenance.

Type material. MNHN 1642, partial skeleton including: the right portion of the pelvic shield; a nearly complete pectoral shield; tail armor with vertebrae; three thoracic vertebrae fused, complete right hindlimb, and proximal half of the left femur.

Referred Specimen. MNHN 1483, 45 complete and 12 broken isolated osteoderms belonging to the same individual.

Geographic occurrence. Uruguay, San José Department, erosional surface of Puerto Arazatí Beach, 3 to 4 km east of El Sauce Creek (Fig. 1).

Stratigraphic occurrence. Camacho Formation, Uruguay, late Miocene age.

Diagnosis. The osteoderms of *Neoglyptatelus uruguayensis* differ from those of *Neoglyptatelus originalis* in having smaller foramina and narrower sulci. The species differs from *Neoglyptatelus sincelejanus* in having the osteoderms of the dorsal region of the pelvic and scapular shields with six or seven peripheral figures (instead of five as maximum) and a convex external surface (instead of a plane one).

Descriptions and comparisons. The long bones described below show fused epiphyses indicating that the studied specimen is an adult individual. Its carapace is somewhat transversally flattened so that its measurements can be somewhat overestimated although not as much as to prevent a reliable description of its shape.

Carapace. The carapace of *Neoglyptatelus uruguayensis* presents a convex profile with an approximate anteroposterior longitude of 550 mm. The maximum height of approximately 300 mm is in the region where both the scapular and the pelvic shields articulate. The height in the anterior portion is of approximately 140 mm and, in the posterior portion, of approximately 120 mm (Fig. 2.1–2).

Scapular shield. In lateral view, the scapular shield is nearly rectangular. Its anterior border is slightly concave while the posterior one is slightly convex. They are approximately of 140 and 300 mm in height, respectively. The ventral border is straight whereas the dorsal border is slightly convex (Fig. 2.1–2). They both have an anteroposterior length of 350 mm. The osteoderms in the dorsal and lateral region are mostly hexagonal; a few are pentagonal (Fig. 3. 4–5). A narrow band comprising nearly two transversal rows anteriorly positioned and four sagital rows lateroventrally positioned present rectangular to subpentagonal ostoderms. The largest osteoderms occur on the dorsal region. They have an average anteroposterior length of 15 mm and mediolateral length of 13 mm. In contrast, the osteoderms of the lateral region are 12.5 x 11mm in average. This size pattern is inversely correlated with the thickness of the osteoderms. Thus, in the dorsal region, the average thickness is of 6.5 mm whereas, in the lateral region, the average is of 8.5 mm. The figures in the external surface of the osteoderms are smooth and flat to slightly convex. The main and radial sulci are straight, narrow and shallow (in contrast with *Pachyarmatherium*). Small hair follicle pits are located at the intersection of the main and radial sulci. In the dorsal region, they range from three to four, or exceptionally five, whereas, in lateral region, they range from two to three, or exceptionally four. The main figure is hexagonal and displaced posteriorly, and occasionally reaches the posterior border. Excepting the two anteriormost transversal rows, which form the scapular portion of the articulation area of the carapace (see below), the variation in the number of peripheral figures has a concentric pattern: in most dorsal and lateral regions, nearly 85% of the osteoderms present six peripheral figures whereas the remaining 15% bear five, or exceptionally four, peripheral figures. This large area is surrounded by a narrow zone formed by osteoderms bearing two to four peripheral figures. On the other hand, in the anteroventral section, the osteoderms lack clearly discernible peripheral or main figures (Fig. 3.5). In the anterior and ventral borders, the ostoderms have an irregular shape. The osteoderms of the ventral border are pentagonal with a convex free border and a straight dorsal border, and their external surface is somewhat rough and lacks figures. The osteoderms of the anterior border are not preserved.

Pelvic shield. In lateral view, the pelvic shield is trapezoid. Its dorsal and ventral borders are both convex and of 300 mm and 220 mm in anteriorposterior length, respectively (Fig.
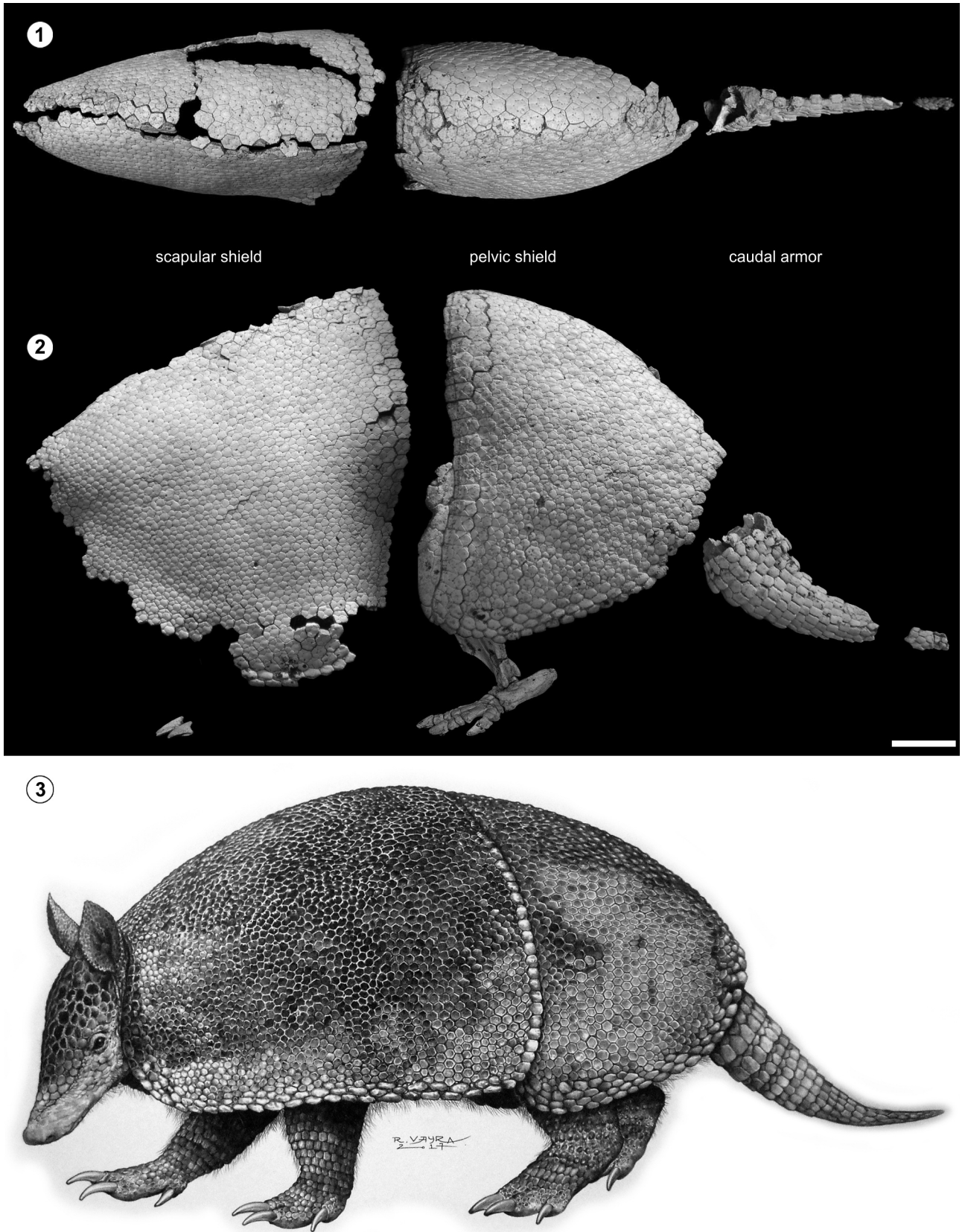
Figure 2. Complete specimen of the holotype of *Neoglyptatelus uruguayensis* (**MHNM** 1642). **1,** dorsal view; **2,** lateral view; **3,** life reconstruction. Scale bar= 50 mm.

2.1–2, 3.1). The anterior border is slightly sigmoid while the posterior one is slightly concave. They are 280 and 150 mm high, respectively. Mostly, the osteoderms in the dorsal and lateral region are hexagonal, and a few ones are pentagonal. Excepting the osteoderms of the ventral border, the size of the osteoderms varies according to their topographic location along the pelvic shield. Thus, in the lateral region, the osteoderms have an average anteroposterior length of 11 mm and a mediolateral length of 8 mm. In the dorsal region, the average anteroposterior length is of 12, 5 mm and the average mediolateral length is of 8 mm. Unfortunately, during preparation, it was necessary to apply a consolidant on the internal surface of the pelvic shield so that the thickness measurements were compromised. Except for a small area, in which they are strongly convex, the figures in the external surface of the osteoderms are smooth and mostly flat to slightly convex (Fig. 3.1–3). As in the scapular shield, the sulci that delineate these figures are straight, narrow and shallow. There are two to five small hair follicle pits at the intersection of the main and radial sulci. Laterally, these pits range from two to three, or exceptionally there is only one, whereas, in the dorsal region, they range from three to four, or exceptionally five. Posterior to the two transversal rows involved in the articulation area between the scapular and the pelvic shields (see below), the variation in size of the peripheral figures forming the pelvic shield follows a distribution pattern that is more complex than that of the scapular one. In the dorsal and the dorsolateral sections, nearly 90% of the osteoderms have six peripheral figures, whereas the remaining 10% have five to seven. Around this most central area, there is a band of osteoderms among which 90% present five peripheral figures whereas 10% show three to four. Finally, in the two ventralmost sagittal rows and the posteriormost row, peripheral figures range from one to two, or are entirely absent. The osteoderms of the ventral border are pentagonal with a convex ventral border and a straight dorsal one. Their external surface is rough and lacks figures. The few preserved osteoderms of the posterior border show a main figure with a very rough surface, and displaced posteriorly, occupying the posterior half of the osteoderm, the anterior half presents two to three peripheral figures.

Articulation area. This area is formed by the two posteriormost transverse rows of osteoderms of the scapular shield

that overlap the first two anteriormost transverse rows of the pelvic shield. Regarding the scapular shield (Fig. 3.5–6), the penultimate row is almost complete whereas the last row is represented by three osteoderms only (Fig. 3.5). In internal view (Fig. 3.6), the posterior third of the osteoderms of the penultimate row and the anterior half of the osteoderms of the last row thin towards their contact zone and delineate a concave area (Fig. 3.6). The posterior half of the osteoderms of the last row is convex so that their anteroposterior axis shows a concavo-convex profile. With respect to the pelvic shield, only the left side of the first row is preserved; the second row is almost complete (Fig. 3.1–2). The preserved portion of the first row is formed by two elements: one is a single osteoderm of nearly 10 mm in dorsoventral length and 12 mm in anteroposterior length, which comprises part of the ventral border of the carapace; the other is a larger structure of 114 mm in dorsoventral length, which may have reached 150 mm taking into consideration that its dorsal portion is missing, and of nearly 20 mm in anteroposterior length. The external surface of this latter element is smooth and presents irregular sutures indicating that it was formed by the fusion of separate smaller osteoderms; it becomes thinner anteriorly. The posterior portion of this large element articulates with 12 osteoderms of the second transversal row of osteoderms. Dorsally, this second row presents nine additional osteoderms besides those articulating with the preserved portion of the large element of the first row. Among these, two osteoderms of more ventral position would have articulated with the missing portion of the large element while the remaining ones become slightly thinner anteriorly, indicating the absence of any anterior articulation area. Except for those closer to the ventral border, each preserved osteoderm of the second row of the pelvic shield presents a transversal depression on its anterior third that is contiguous with those in adjacent osteoderms, forming a sort of transverse canal (Fig. 3.2). Anterior to this canal, there is a convex small area with a smooth surface perforated by small foramina; posteriorly, there is a flat area presenting one main figure displaced posteriorly, as in other osteoderms of the scapular and pelvic shields, which are surrounded by three to five peripheral figures of varied size. All these figures are separated by narrow and shallow sulci. Small hair follicle pits are located at the intersection of these sulci.

Caudal armor. The caudal armor (Fig. 2.1–2) is divided into an anterior and a posterior portion measuring approximately 160 mm and 110 mm in length, respectively. The anterior portion comprises six mobile rings of imbricating osteoderms. Each ring covers a caudal vertebra and is formed by two rows of osteoderms whose size decreases from the anteriormost rings to the posteriormost ones. The posterior portion is formed by imbricating osteoderms that, unlike those of the anterior portion, do not form discernible rings. All osteoderms in anterior and posterior portions present smooth external surfaces without any discernible figures.

Dorsal vertebrae. The preserved fragment of the vertebral column comprises three fused vertebrae, four free thoracic and four free lumbar vertebrae. With respect to the fused vertebrae, the vertebral body becomes thicker but narrower towards the posterior portion of the fragment. The contacts between each vertebra present an articular facet for the ribs. There is no sign of supplementary intervertebral articulations (*i.e.* xenarthrous articulations). Therefore, these vertebrae correspond to the fused anteriormost thoracic vertebrae, a condition similar to that of glyptodonts but contrasting with *Pachyarmatherium* (see Downing and White, 1995), armadillos and pampatheres.

Caudal vertebrae. Most of the caudal vertebrae are preserved inside the caudal armor, which precludes their description. The only element preserved out of this structure corresponds to one anterior caudal vertebra. The vertebral centrum is oval and the neural canal is rounded in cranial view and triangular in caudal view.

Femur. The femur (Fig. 4.1–2) is slenderer than that of
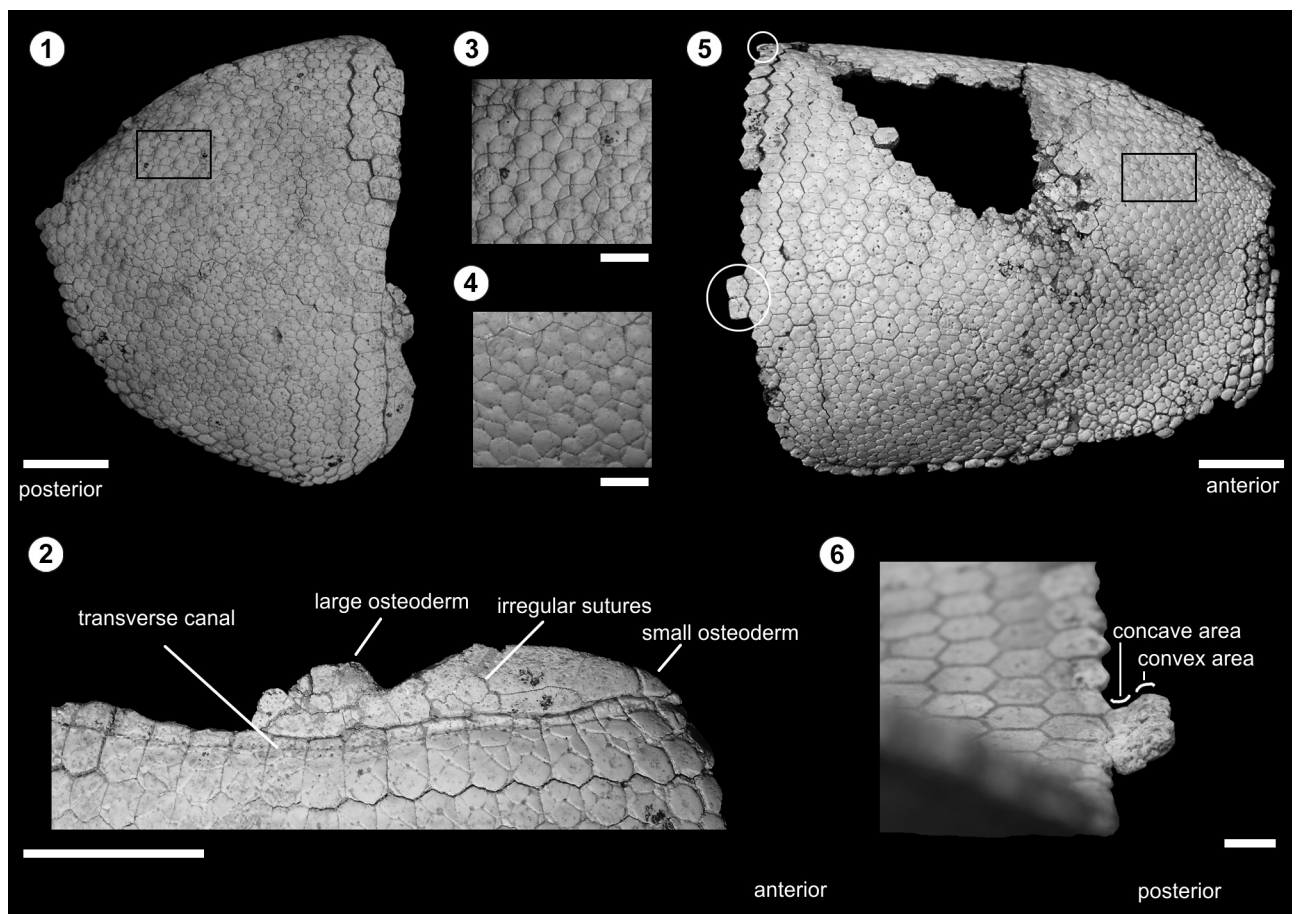
Figure 3. 1, Mirror image of the left pelvic shield (**MNHN** 1642) in lateral view; **2,** mirror image of the part of the pelvic shield (**MNHN** 1642) in lateral view, detail of the preserved articulation area; **3,** detail of the osteoderms of the pelvic shield, the rectangle in 3.1 marks the enlarged region; **4,** detail of the osteoderms of the scapular shield, the rectangle in 3.5 marks the enlarged region; **5,** right scapular shield (**MNHN** 1642) in lateral view; the circle identifies the three osteoderms from the last row; **6,** preserved articulation area of the right scapular shield (**MNHN** 1642) in internal view. Scale bar= 50 mm (1,2, 5 and 6) and 10 mm (3 and 4).

glyptodonts, *Pachyarmatherium* and pampatheres, but more massive than that of armadillos. The femoral head is angled craniomedially. The neck is poorly developed and laterally oriented. The greater trochanter is strongly built, lateromedially compressed and laterally projected, but less so than in late-diverging glyptodonts and *Pachyarmatherium*. Like in armadillos, pampatheres and propalaeohoplophorine glyptodonts, it is clearly projected above the femoral head. The trochanteric fossa is wide and shallow. The intertrochanteric line is poorly marked as in pampatheres and propalaeohoplophorine glyptodonts. The third trochanter is rectangular, strongly laterally projected and positioned at midshaft, as in armadillos. The distal epiphysis is not laterally expanded as in pampatheres and glyptodonts. The lateral and medial epicondyles are slightly marked. The intercondyloid fossa is deeper cranially than it is caudally. The articular surface of both condyles is contiguous to the surface of the patellar trochlea.

Patella. The patella is oval, with the proximodistal axis larger than the lateromedial one, as in armadillos and pampatheres, and it is unlike late-diverging glyptodonts, in which both axes have a similar length. The cranial surface is convex. In the posterior surface, the oval facet for the medial condyle is wider than the oval facet for the lateral condyle.

Tibia-fibula. The tibial shaft is wider than the fibular shaft (Fig. 5.1–2). The distal epiphysis is more transversely extended than the proximal one, like in armadillos and *Pachyarmatherium* and unlike what occurs in glyptodonts. The medial condyle is oval, slightly elongated craniocaudally and mildly concave. The lateral condyle is roughly circular and slightly convex. The medial intercondylar eminence is more proximally projected than the medial one. The tibial tuberosity is stronger than in *Eutatus* but less prominent than in *Dasypus*. The tibial crest is well developed, as in most cingulates, and ends at the distal third of the tibial shaft, as in *Pachyarmatherium* and *Euphractu*s. In this regard, it differs from *Dasypus*, in which the tibial ends in the proximal half, and from glyptodonts, in which it ends at the distal border of the tibial shaft. In anterior view, the tibial crest bends toward the lateral edge while its distal edge is strongly concave, as in *Dasypus* and *Pachyarmatherium*; it differs from glyptodonts and *Euphractus*, in which it is almost straight and gently convex. The fibular crest is well developed and

ends at the proximal half, as in *Dasypus*, *Pachyarmatherium* and glyptodonts. As in other cingulates, a massive and strongly projected lateral malleolus is present; the medial malleolus is not as prominent. As in *Dasypus* and *Pachyarmatherium,* a caudally facing calcaneal facet is present. It has a convex surface unlike that of *Dasypus* and *Pachyarmatherium*, in which it is concave and flat, respectively. This facet, which is absent in glyptodonts, lies in a massive tubercle lateral to the tibial astragalar facets, as in *Pachyarmatherium*. As in this latter, a deep notch separates this tubercle from the lateral malleolus. The orientation and morphology of the tibial astragalar facets concurs with those of the homologous area in *Pachyarmatherium*: the facets are obliquely oriented relative to the long axis of the tibia-fibula, and the medial facet is smaller than the lateral one.

Calcaneum. The tuber is mediolaterally compressed (Fig. 6.1–3), as in *Dasypus*, *Pachyarmatherium* and *Euphractus,* with a slightly transversely expanded apex clearly contrasting with the massive tuber calcanei of glyptodonts. Its plantar side is slightly convex. Like in *Pachyarmatherium*, the groove for the calcaneal tendon is wide, elongated and deep, and somewhat displaced medially in relation with the median plane of the calcaneum. The groove for the tendon of the peroneus brevis is very deep and elongated, like in *Pachyarmatherium*, Propalaeohoplophoridae, *Pampatherium* and *Glyptodon*, contrasting with *Dasypus* and *Euphractu*s, in which it is shallow, and with *Doedicurus* and *Panochthus,* in which it is rudimentary. Plantar to this groove is the peroneus tubercle and plantar to this, there is a wide and deep groove for the tendon of the peroneus longus. The sustentacular process is triangular in plantar view. It is thin, like in *Dasypus* and *Pachyarmatherium*, and in contrast with *Pampatherium* and, especially, glyptodonts. Unlike that which happens in *Pampatherium* and *Dasypus,* a peroneal tubercle at the distolateral end of the calcaneum is present, as in *Euphractus*, *Pachyarmatherium* and *Propalaeohoplophorus*. The ectal facet is oblong and weakly convex. The sustentacular facet is roughly triangular, convex and much shorter than the ectal one. These two facets are separated by a shallow interarticular sulcus, as in *Dasypus*, *Euphractu*s and *Pachyarmatherium*, and in contrast with glyptodonts, in which this sulcus is deep, and, to a lesser extent, with *Pampatherium*, in which it is moderately deep. As in *Pachyarmatherium*, there is a flat and rounded fibular facet at the

lateralmost border of the ectal facet, which is positioned in a much less developed fibular tubercle than that of *Dasypus*. A massive plantar tubercle lies on the plantar surface of the calcaneum. In the central portion of this tubercle, there is a narrow and deep groove for the calcaneocuboid ligament. The cuboid facet is broken in its cranial third. The preserved
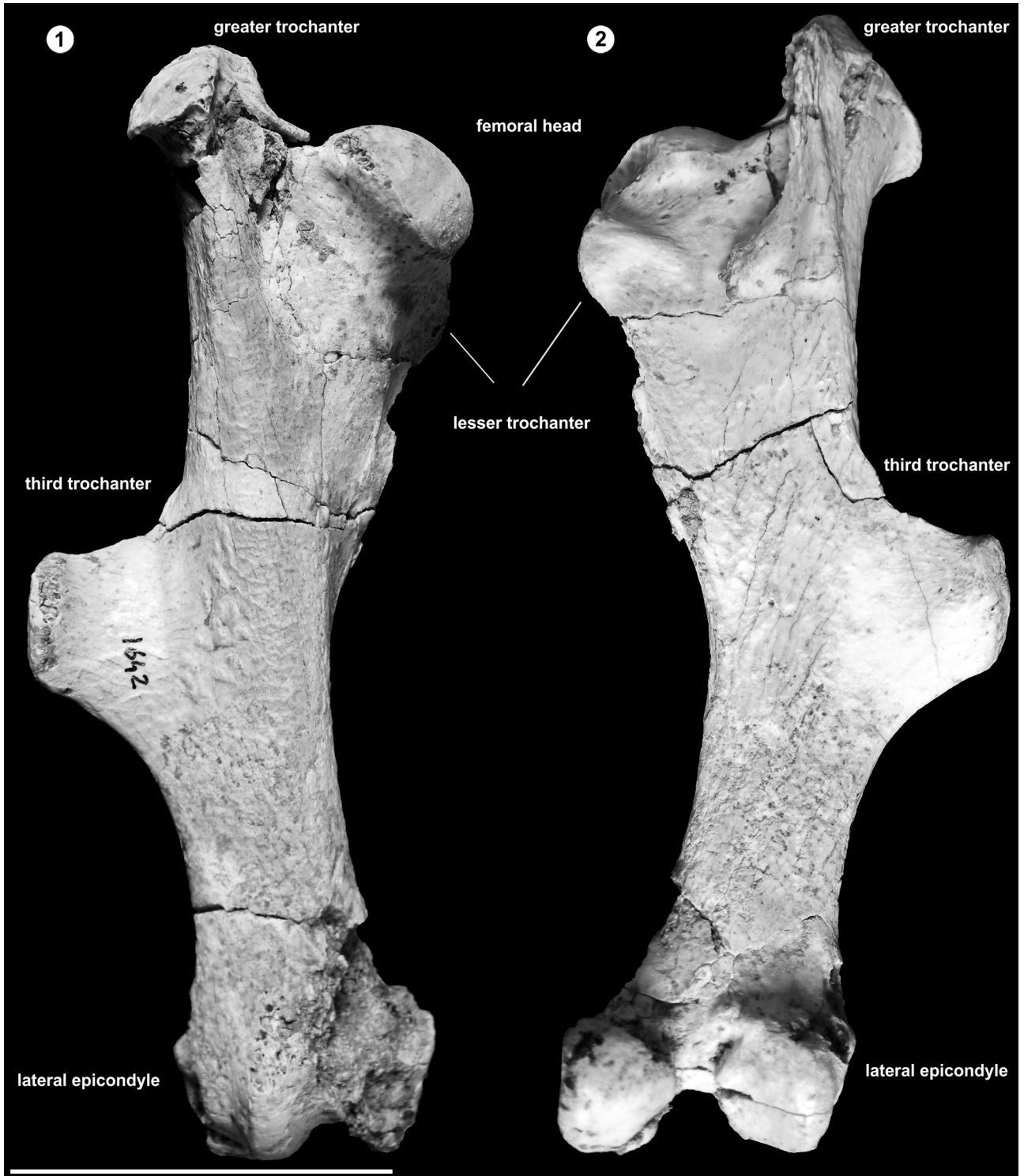

Figure 4. Right femur of the holotype (**MNHN** 1642). **1,** cranial view; **2,** caudal view. Scale bar= 50 mm.

part is rectangular, concave, and with its major axis oriented dorsoventrally. As in *Pachyarmatherium* and glyptodonts, the neck of the calcaneum is relatively short compared to that of armadillos and pampatheres.

Astragalus. The astragalus (Fig. 6. 1,4–5), as in other cingulates, has a strongly asymmetrical trochlea due to the greater development of its lateral crest, and the groove between the crests of the astragalar trochlea is wide and deep. As in *Dasypus* and *Euphractu*s, the ectal facet is distinctly concave and triangular, in contrast with some glyptodonts, in which it is triangular and slightly concave

(*e.g.*, *Propalaehoplophorus*, *Panochthus*, *Neosclerocalyptus*) or flat and rectangular (*e.g.*, *Glyptodon*, *Doedicurus*). The sustentacular facet is oblong and shorter than the ectal facet. The sulcus tali is wide and shallow in contrast with that of late-diverging glyptodonts. The tuberosity for the medial collateral ligament is as developed as in *Euphractus*, more so than in *Dasypu*s, but less than in glyptodonts. In distal view, the facet for the navicular is roughly rectangular and oblique, with its lateromedial axis longer than the craniocaudal, as in *Dasypus*, *Euphractus* and *Eutatus*, and unlike *Pampatherium*, in which it is subrounded, and glyptodonts, in
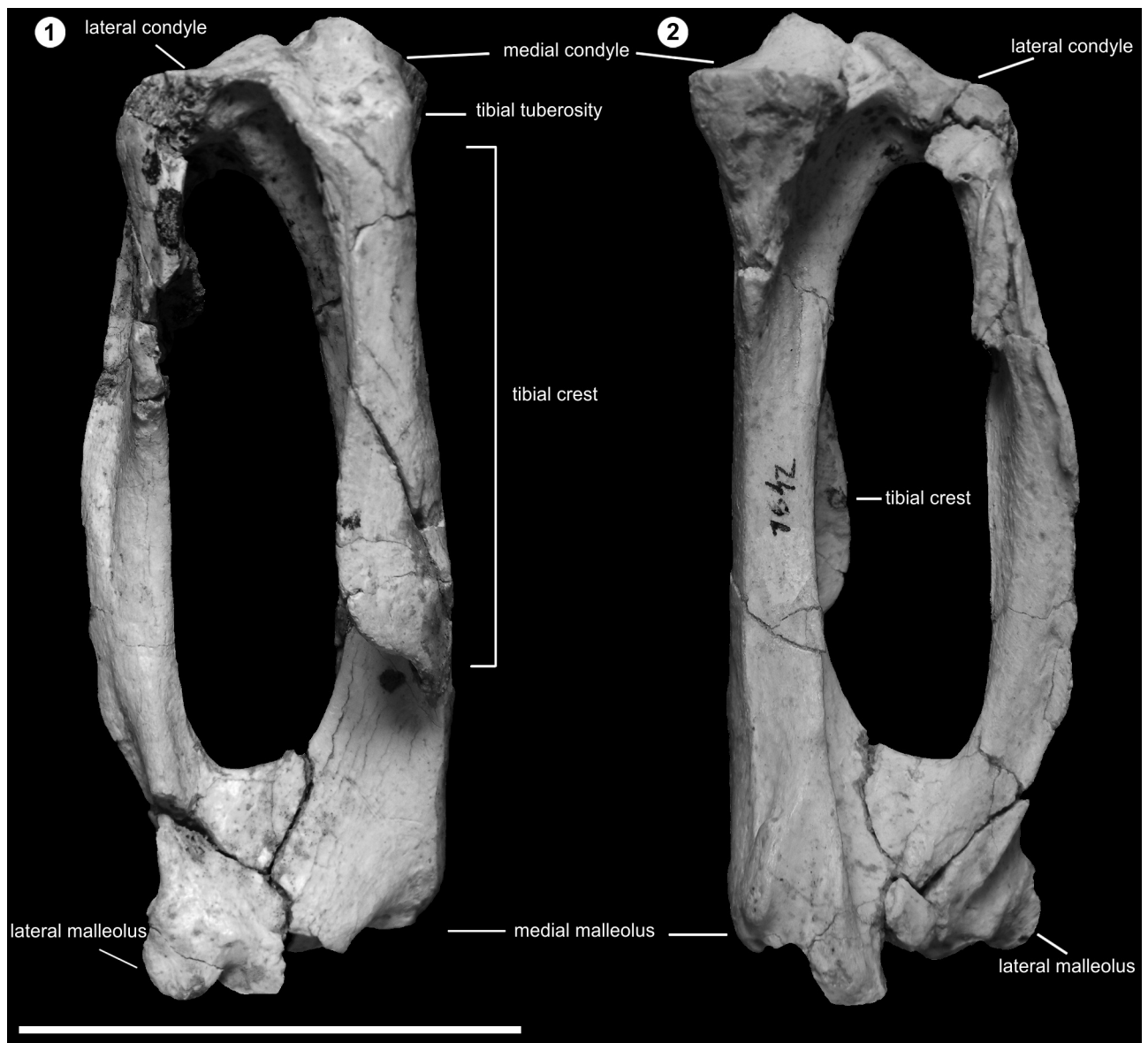

Figure 5. Right tibia-fibula of the holotype (**MNHN** 1642). **1,** cranial view; **2,** caudal view. Scale bar= 50 mm.

which it is roughly triangular. A poorly delimited navicular tuberosity occurs just proximal to the dorsal border of the navicular facet; it is similar to that of *Euphractus* and much less developed than in glyptodonts.

Navicular. The articular facet for the astragalus is lageniform and strongly concave, as in *Dasypus*, *Pachyarmatherium*, propalaehoplophorids and pampatheres, and unlike late-diverging glyptodonts, in which it is subcircular and slightly concave. At the lateral side, the cuboid facet is oblong with its major axis dorsoplantarly. The facet for the plantar sesamoid is slightly oblong, as in *Pachyarmatherium*, *Dasy-*

pus and propalaehoplophorids, and unlike late-diverging glyptodonts (*e.g.*, *Neosclerocalyptus*), *Holmesina* and *Euphractus* in which it is strongly oblong. Like in *Pachyarmatherium*, *Euphractus*, pampatheres and Propalaehoplophoridae, the medial cuneiform facet is subtriangular in shape and oriented at an angle of nearly 90° with respect to the lateral cuneiform facet.

Cuboid. In proximal view, the articular surface for the calcaneum is rectangular and convex. In plantar view, the plantar tubercle bears a subrounded articular facet for the sesamoid, like in *Dasypus* and *Euphractus*, instead of a triangular one,
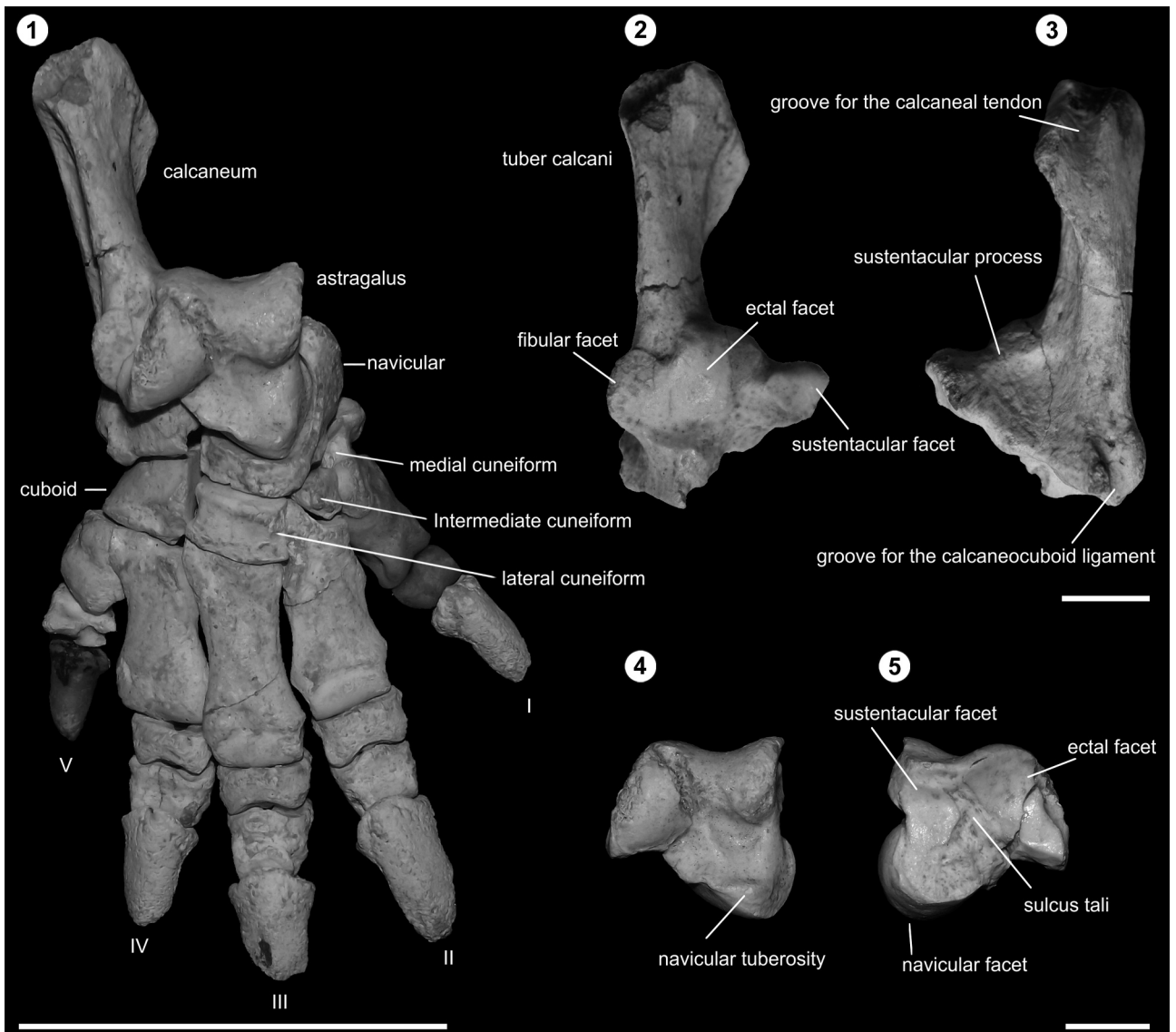

Figure 6. Right foot of the holotype (**MNHN** 1642). **1,** articulated foot in cranial view; **2,** right calcaneum in cranial view; **3,** right calcaneum in caudal view; **4,** right astragalus in cranial view; **5,** right astragalus in caudal view. Scale bar= 50 mm (1) and 10 mm (2–5).

as in glyptodonts. In distal view, there is a wide canal for the tendon of peroneus longus and two articular facets to metatarsals IV and V. This latter facet is more distally positioned than the former. In medial view, the facet for the navicular is rectangular and slightly concave. Next to it, there is a subtriangular and concave facet for the lateral cuneiform. **Cuneiforms.** The medial cuneiform presents, cranially, a wide and deep sulcus for the tendon of peroneus longus. Distally, the articular facet for metatarsal I is strongly concave. Proximally, the facet for the navicular is notched; medial to it, there is a circular facet for metatarsal II. The intermediate cuneiform is elongated dorsoplantarly, with a concave facet for the navicular and a convex facet for metatarsal II. The lateral cuneiform bears a triangular proximal facet for the navicular. Its distal facet for metatarsal III is T-shaped with the transversal segment cranially positioned. **Metatarsals.** The metatarsals (Fig. 6.1) do not present significant differences in relation to the homologous elements in armadillos, *Pachyarmatherium* and pampatheres. Among them, metatarsals I and V are the shortest while metatarsals II and III the longest. Metatarsal IV is of intermediate size. All metatarsals present a concave proximal articular surface and a convex distal articular surface with a well-developed median keel. As in pampatheres, armadillos and *Propalaehoplophorus,* this keel is more salient in such a way that its dorsoplantar extension is visible in distal view; in contrast with late-diverging glyptodonts, it reaches the distal articular surface whereas, in late-diverging glyptodonts, it is limited to the plantar side. The articular surfaces to the plantar sesamoids, like in armadillos, pampatheres and *Pachyarmatherium*, are remarkably shorter in proximodistal length than they are in late-diverging glyptodonts. **Phalanges.** Digits I and II present two phalanges (proximal and ungual) whereas digits II, III and IV present three phalanges (proximal, middle and ungual) (Fig. 6.1). The ungual phalanges are proximodistally elongated. All phalanges present concave proximal articular surfaces and convex distal ones with a small median keel. The distal end of the ungual phalanges is blunt, like in *Euphractus* and *Eutatus* and unlike that of *Dasypus*, which is sharp.

Phylogenetic Analysis

One single most parsimonious tree was obtained by the maximum parsimony analysis (Tree Length=367; CI=0.62;

RI=0.74; Fig. 7). According to this hypothesis, the phylogenetic relationships among the glyptodonts are the same as those obtained by Fernicola (2008), Porpino *et al.*, (2009, 2010) and Fernicola and Porpino (2012); however, in some nodes, new synapomorphies are recorded, whereas in others some previous unambiguoussynapomorphies become ambiguous.

In the obtained topology, node A represents the clade formed by *Neoglyptatelus* + *Pachyarmatherium* and its sister group formed by *Pampatherium* + Glyptodontia. The last group is supported by four unambiguous synapomorphies, two of which were found by Porpino *et al.* (2010; 84:1 and 86:1) and two of which are new: the greater trochanter of the femur lateral to the patellar trochlea (103:1) and an angle between the caudal border of the lesser trochanter and the transverse axis of the proximal epiphysis ≤ 40° (106:0).

A new clade, herein denominated Pachyarmatheriidae, is formed by *Neoglyptatelus* and *Pachyarmatherium* (node B). This clade is supported by six unambiguous synapomorphies and has high bootstrap frequencies and Bremer support values (81 and 4, respectively): a cranial border of the tibial crest straight along its entire length (121:1), the ratio between the dorsoplantar length/transversal length of the sustentaculum of calcaneum > 2 (133:2), the presence of a groove for the fascia ligament in the lower plantar tubercle (136:1), the anterior border of the sustentacular facet in line or posterior to the anterior border of the ectal facet (137:0), the medial border of the ectal facet in line or slightly laterally relative to the lateral border for the sustentacular facet (138:0), and a dorsal carapace formed by anterior and posterior shields without transverse mobile band(s) between them (166:2).

This clade is the sister group of the clade formed by *Pampatherium* + Glyptodontia (node C), which is supported by ten unambiguous synapomorphies and has high bootstrap frequencies and Bremer support values (92 and 5, respectively). Six of these synapomorphies were previously found by Porpino *et al.* (2010; 85:1, 87:1, 97:1, 109:1, 110:1, and 143:1), whereas four represent new postcranial unambiguous synapomorphies: a lateral crest of the trochlea lateromedially oriented (118:1), the ratio between the dorsoplantar length/transversal length of the sustentaculum of calcaneum <1 (133:0), the lateral crest of the astragalar

trochlea nearly at the same level than the medial one (140:1), and the medial portion of the astragalus between <90%, >80% of the maximum width of the astragalus (146:1). The last three characters were modified from Porpino *et al.* (2010).

The Glyptodontia (*sensu* Fernicola 2008; node D) is strongly supported by 42 unambiguous synapomorphies and has good bootstrap frequencies and Bremer support values (99 and 28, respectively). Of these 42 synapomorphies, 29 has been previously found by Fernicola (2008; 3:2, 5:1, 6:0, 8:1, 9:1, 14:2, 15:1, 18:0, 23:2, 25:1, 30: 1, 39:2, 41:1, 45:1, 47:1, 54:1, 56:1, 5:2, 60:1, 62:1, 64:2, 66:2, 67:1, 69:1, 71:2, 71:2, 78:1, 81:1, and 83:1), four by Porpino *et al.* (2010; 100:1, 128:1, 131:1, and 139.1), one by Fernicola and Porpino (2012; 166.1), and eight represent new postcranial synapomorphies: an absent or poorly defined cranial depression between the head and the greater trochanter of the femur (107:0), the length between the proximal border of the third trochanter and the proximal border of the greater trochanter being greater than 50% of the maximum
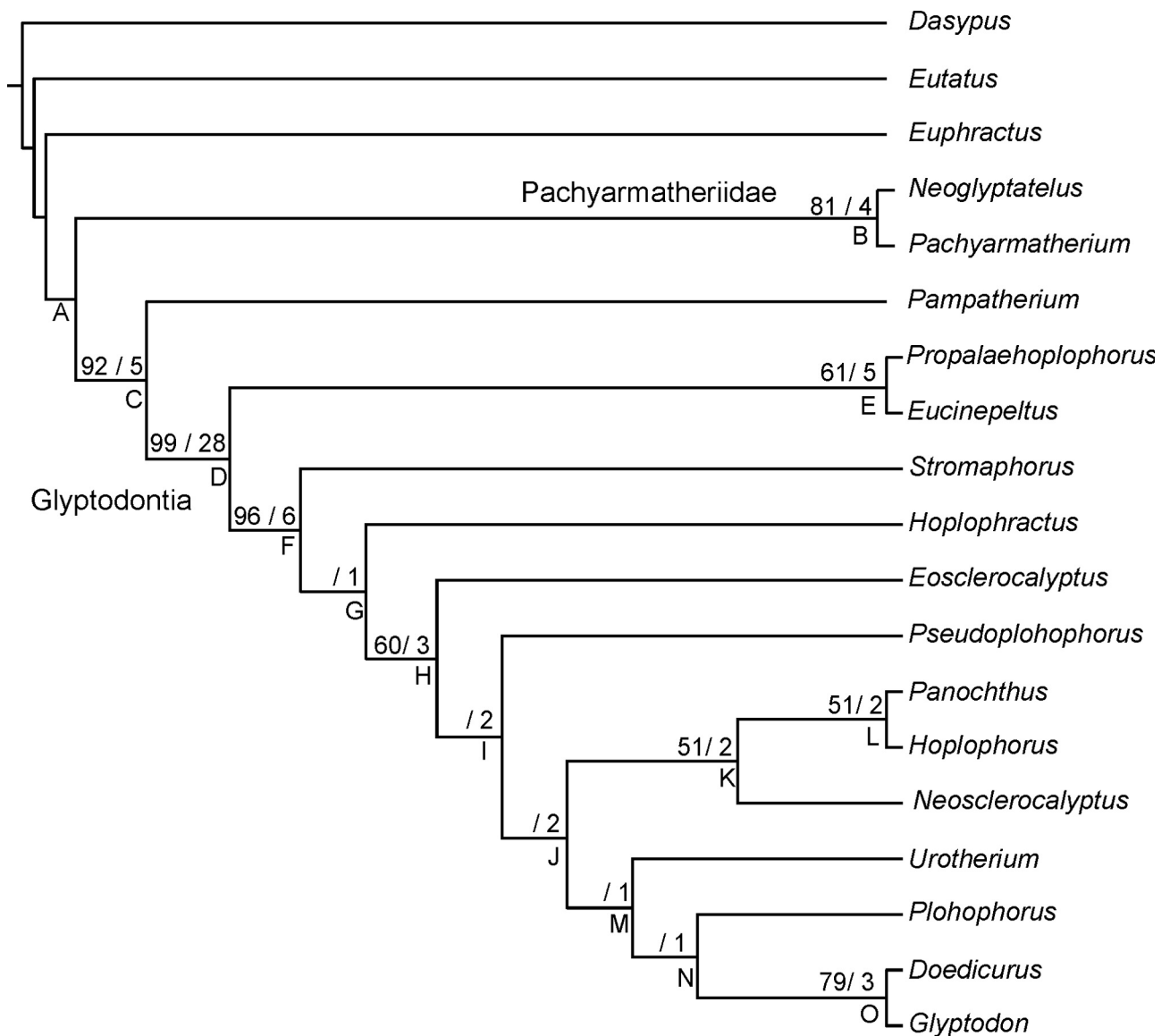

Figure 7. Most parsimonious tree resulting from the cladistic analysis. Capital letters represent the nodes discussed in the text. The number immediately above and to the left of each node represents a bootstrap value, and the second one and at the right, the Bremer support.

length of the femur (108:2), the length of the medial margin of the femoral neck being smaller than the length of its lateral margin (112:2), absent or poorly developed trochanteric fossa (116:0), the smooth surface of the ectal facet of calcaneum (125:1), a deep interarticular sulcus between the astragalar facets of the calcaneum (126:2), the ratio between the length of the ectal facet of calcaneum and the length of the neck of calcaneum > 2 (129:2), and transverse width of calcaneum at the level of very wide astragalar facets (130:1).

The internal relationships within Glyptodontia show a basal dichotomy between Propalaehoplophoridae (*sensu* Fernicola, 2008; node E) and the remaining glyptodonts (Glyptodontoinei *sensu* Fernicola, 2008; node F). Node E is supported by two unambiguous synapomorphies previously found by Fernicola (2008; 29.2 and 49.3). Node F is a well-supported clade (bootstrap= 96%; Bremer= 6) diagnosed by seven unambiguous synapomorphies. Six of these had been previously found by Fernicola (2008: 20:2, 35:1, 36:1; 64:3, 80:0, and 82:2) whereas one, by Porpino *et al.* (2010; 157:2).

The following clades, represented by the nodes G, H and I, have the same synapomorphies than those observed in the previous analysis. Node G is supported by one unambiguous synapomorphy previously found by Fernicola (2008; 2:3). Node H is supported by six unambiguous synapomorphies, two of which were found by Fernicola (2008; 41:0 and 43:1) while the remaining ones were found by Porpino *et al.* (2009: 86:2, 88:2, 89:1, and 90:1). Node I is supported by two unambiguous synapomorphies previously found by Fernicola (2008; 45:2 and 46:2).

The Glyptodontoidea (node J) is supported by three synapomorphies. Two of these were previously found by Fernicola (2008; 15:0 and 25:0), and one was previously found Porpino *et al.* (2010; 93:1). The Glyptodontoidea are composed of two clades: the Panochthidae (node K) and one group (node M) formed by *Urotherium* as a sister group of Glyptodontidae (Node M). In the first, *Neosclerocalyptus* is placed as the sister group to *Hoplophorus + Panochthus* in node L (Panochthidae *sensu* Fernicola, 2008), which is supported by 14 unambiguous synapomorphies of which eleven were found by Fernicola (2008: (2:3, 29:2, 31:2, 45:1, 46:3, 53:1, 54:1, 55:2, 58:1, 73:1 and 77:1) and three were found by Porpino *et al.* (2009: 85:1, 87:1, and 116:1). Three characters were resolved as synapomorphies of this clade

in Porpino *et al.* (2010); yet, in this study, they do not present such status: character 117 from Porpino *et al.* (2010)—angle between the major axis of the ectal facet and the long axis of the calcaneum—has a greater variability than that which had been previously found and has thus become non-informative. Character 135 corresponds with the character 129 from Porpino *et al.* (2010). In this case, the character is solved as an ambiguous synapomorphy. Finally, character 140 corresponds to a modification of character 131 from Porpino *et al.* (2010), which included a new state and reformulation of the previous ones. In this new scheme, the assigned states are not resolved as a synapomorphy of this node.

The second group (node M), formed by *Urotherium* as sister group of Glyptodontidae (Node N), is supported by one unambiguous synapomorphy found by Fernicola (2008; 74:2). *Urotherium* is characterized by two synapomorphies found by Fernicola (2008: 26:4 and 70:0), and one found by Fernicola and Porpino (2012; 163:3). The Glyptodontidae is supported by two unambiguous synapomorphies found by Fernicola (2008; 81:3 and 83:0); within this clade, *Plohophorus* is characterized by one apomorphy found by Fernicola and Porpino (164:2), and the monophyletic group *Doedicurus + Glyptodon* (node O) is supported by four unambiguous synapomorphies found by Fernicola (2008: 41:1, 77:1, 79:2, and 80:0).

DISCUSSION
Carapace structure and movement

The presence in the *Pachyarmatherium + Neoglyptatelus* clade of large pelvic and scapular shields overlapping each other without separate transverse mobile band(s) is unique among cingulates (Figs. 2.1–3, 3.1–4). Excluding the new group, two main types of general arrangements of osteoderms along the middle dorsal line of the dorsal carapace can be recognized (Ameghino, 1889; Scott, 1903–04; Engelmann, 1985). The glyptodont type represents a pattern in which the osteoderms articulate with each other forming an undivided carapace without separate shields or transverse mobile bands crossing the carapace from side to side. The other general morphological type includes the remaining cingulates, characterized by the presence of transverse bands of imbricated osteoderms crossing the carapace from side to side. In some cases, these bands vir-

tually occupy the whole carapace (*e.g.*, *Stegotherium* Ameghino, 1887a, *Peltephilus* Ameghino, 1887a) while, in others, the posterior osteoderms form a pelvic shield and are preceded by transverse mobile bands crossing the carapace from side to side over the lumbar and thoracic regions of the vertebral column (*e.g.*, *Proeutatus*). Finally, there are those in which the cranial osteoderms form a scapular shield separated from the pelvic shield by transverse mobile bands crossing the carapace form side to side (*e.g.*, *Tolypeutes*, *Dasypus*).

In terms of carapace movement, the articular region of *Neoglyptatelus uruguayensis* is clearly defined by the transverse sulci that run through the ventral surface of the last two rows of the scapular shield and the dorsal surface of the second row of the pelvic shield (Fig. 3.1–4). This morphology suggests a movable articulation over one another, like a hinge, although it may have allowed some slide between them with the main movement axis represented by the central region of the articular zone. Considering the length between the transverse sulcus of the first complete row of the pelvic shield and the anterior border of the large lateroventral osteoderm, the maximum relative displacement between the shields of the carapace in the ventrolateral region would be of about 25 mm.

While a comprehensive comparison is not possible and is beyond the scope of this contribution, the range of movements in the carapace of *N. uruguayensis* includes some dorsoventral flexion. This flexion is certainly more restricted than in the remaining cingulates, in which complete transverse bands of imbricated osteoderms are present but less limited than in glyptodonts in which complete transverse bands are absent. In *N. uruguayensis*, this movement is severely compromised by the virtually immobile carapace and the extensive vertebral fusions in the thoracic and lumbar regions of the vertebral column, also present in glyptodonts (Scott 1903–04).

Finally, regarding *Pachyarmatherium,* and according to Downing and White (1995), the scapular shield and the pelvic shield overlap each other by a single immovable transverse row of osteoderms in each shield (instead of two, as in *N. uruguayensis*). This type of articulation is very different from that of *Neoglyptatelus* and, as in *Pachyarmatherium*, the articular surface between both shields is flat. Therefore, it appears that the *Pachyarmatherium* carapace

was more limited in terms of dorsoventral movement than that of *Neoglyptatelus*, at least in comparison with the new species herein described.

From a phylogenetic perspective, both glyptodonts and Pachyarmatheriidae are characterized by a tendency toward limiting carapace mobility, which was attained via distinct trajectories. In glyptodonts, it apparently involved the loss of the imbricated osteoderm bands from the top of the dorsal region towards the lateral border, with a concomitant fusion of the shields and some taxa retaining vestigial imbricating areas in certain zones of the lateral region (*e.g.*, *Propalaeohoplophorus*); in Pachyarmatheriidae, the restriction in mobility was attained by the loss of the complete transverse mobile band(s), with the retention of separate shields, but resulting in distinct articular regions between them in each genera, which also likely allowed the abovementioned distinct grades of mobility. It is curious that this clade, formed by only two genera, presents a greater variation of carapace mobility in comparison with the taxonomically diverse glyptodonts, in which the variation in carapace mobility is solely represented by the presence or absence of a vestigial lateroventral mobile region.

Phylogenetic considerations: are glyptatelines glyptodonts?

The expanded matrix used in this paper not only provides a test for the position of the *Neoglyptatelus* but also allows the reevaluation of the broad phylogenetic relationship of glyptodonts. In this regard, the internal relationships within Glyptodontia are identical to those obtained by Porpino *et al.* (2010) and Fernicola and Porpino (2012) (Fig. 7).

With respect to *Neoglyptatelus*, our phylogenetic analysis shows that this taxon, like *Pachyarmatherium* (see also Porpino *et al.*, 2009), is not a glyptodont (Fig. 7). This raises an important question: are the remaining taxa, which had been previously assigned to Glyptatelinae, glyptodonts? This is quite an elusive problem as these taxa are based on scarce material—the very reason for their exclusion from our matrix and that of previous studies, except for that of Croft *et al.*, (2007). However, these latter authors included only a single external group, Pampatheriidae, which implies the assumption that the Glyptatelinae were glyptodonts. As we claimed earlier, *Lomaphorelus*, which was previously

regarded as a member of Glyptatelinae, is in fact a *nomen dubium* (Vizcaíno *et al.*, 2003), so that the question exclusively concerns *Glyptatelus* and *Clypeotherium*. After McKenna *et al.* (2006) reassigned the teeth Ameghino (1897) had attributed to *Glyptatelus* to *Pseudoglyptodon* (an unusual sloth with glyptodont-like teeth), this genus and *Clypeotherium* are known only from a few osteoderms, which, in the case of *Clypeotherium*, are somewhat damaged.

There are some character states of osteoderms that are shared by *Glyptatelus* and *Clypeotherium*: (i) both have quite thick osteoderms, in contrast with most armadillos or pampatheres; and (ii) they present a posteriorly displaced main figure. Yet, these character states occur in other taxa. Similarly, thick osteoderms, for instance, are typical of glyptodonts and are homoplastic between these latter and *Pachyarmatherium* (Porpino *et al.*, 2009) and, taking into consideration the results of our phylogenetic analysis, *Neoglyptatelus*. A posteriorly displaced main figure is also found in some basal glyptodonts such as *Propalaehoplophorus* (in some osteoderms; see Scott, 1903) and *Parapropalaehoplophorus* (in all known osteoderms; see Croft *et al.*, 2007), as well as in different armadillos (*e.g.*, *Dasypus*), and likely represents a plesiomorphic condition (see also Croft *et al.*, 2007). Therefore, concerning the external morphology of the available osteoderms—the only known elements for *Glyptatelus* and *Clypeotherium*—there is no clear evidence allying these genera with glyptodonts, nor is there a potential synapomorphy to suggest the recognition of Glyptatelinae (minimally represented by *Glyptatelus* + *Clypeotherium*) as a clade. However, there are histological characters in osteoderms of *Glyptatelus* that are more similar to those of glyptodonts (thinner superficial and deep layers of compact bone; Carlini *et al.*, 2008) than to those of *Pachyarmatherium* and *Neoglyptatelus*, which present osteoderms with a dasypodid-like histology (*e.g.*, thicker superficial and deep layers of compact bone; see Carlini *et al.*, 2008 and Da Costa Pereira *et al.*, 2014). These histological features are the best evidence to date, suggesting that at least *Glyptatelus* could represent an earlier glyptodont rather than being a member of another cingulate lineage.

Paleobiogeographic implications

The genus *Pachyarmatherium* is widely represented in America by three species. *Pachyarmatherium leiseyi* Downing and White, 1995, the type species, has been recorded in North America from the late Pliocene to the Early Pleistocene of Florida and in the late Pliocene of South Carolina (Downing and White, 1995 and Hulbert, 2001), in the late Blancan–early Irvingtonian of Central America (Laurito *et al.*, 2005, Laurito and Valerio 2012) and in the Plio–Pleistocene of Venezuela (Rincón *et al.*, 2009, Solórzano *et al.* 2015). In South America, the species *Pachyarmatherium tenebris* has been recorded in the late Pleistocene of Venezuela and Perú (Rincón and White, 2007; Martinez *et al.*, 2008; Martinez and Rincón, 2010) while a different species—*Pachyarmatherium brasiliense* Porpino, Fernicola and Bergqvist, 2009—has been proposed for the late Pleistocene to early Holocene of Brazil (Porpino *et al.*, 2009; Oliveira *et al.*, 2009) although some dispute exists concerning their synonymy (*e.g.*, Oliveira *et al.*, 2013; Solórzano *et al.*, 2015; see Material and Methods). Finally, *Pachyarmatherium* sp. was recorded in the Quaternary of Uruguay and Southern Brazil (Bostelmann *et al.*, 2008). This temporal distribution implies a ghost lineage from the late Miocene on the branch that leads to *Pachyarmatherium* because its sister group, *Neoglyptatelus*, was recorded from the middle–late? Miocene of Colombia and the late Miocene of Uruguay, South America. In this context, this clade would have originated in South America, and the absence of Pachyarmatheriidae in North and Central America before the late Pliocene could be related with the absence of a wide and constant terrestrial connection among the Americas in the late Miocene (Woodburne, 2010, O'Dea *et al.*, 2016). The presence of *Pachyarmatherium leiseyi* in the three subcontinents and the existence of *P. tenebris* and *P. brasiliensis* in South America supported the hypothesis that the first species migrated towards the north during the Plio–Pleistocene, when terrestrial connections were stable and broad (Woodburne, 2010; O'Dea *et al.*, 2016).

CONCLUSIONS

The new species, *Neoglyptatelus uruguayensis*, has osteoderms with smaller foramina and narrower sulci than in *N. originalis*, as well as osteoderms from the dorsal section of the pelvic region with more peripheral figures and more convex surfaces in comparison to those of *N. sincelejanus*. Based on the maximum parsimony analysis, we conclude that *Neoglyptatelus* is not a glyptodont and comprises, together with *Pachyarmatherium*, a new clade herein named

Pachyarmatheriidae and supported by six unambiguous synapomorphies (five from the postcranial skeleton and one from carapace). This clade would have originated in South America and reached Central and North America during the Plio–Pleistocene, in which it is represented by *Pachyarmatherium leiseyi*. The members of Pachyarmatheriidae present a carapace formed by large scapular and pelvic shields, in contrast with the undivided carapace of glyptodonts and more similar to the remaining cingulates but differing from these in not having transverse mobile bands. The articulation zone between the shields shows differences between *Neoglyptatelus* and *Pachyarmatherium* but, based on the available evidences in both genera, would allow some limited dorsoventral flexion (perhaps more limited in the latter) in contrast with glyptodonts (in which this flexion was likely absent) and the remaining cingulates (in which this flexion is/was less limited). This shows that the evolution of the cingulate carapace proved more complex than previously thought.

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