

AN ENIGMATIC CINGULATA (MAMMALIA: XENARTHRA) FROM THE LATE MIOCENE OF URUGUAY

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Cingulates, the armadillos (Dasypodidae), glyptodonts (Glyptodontidae) and pampatheres (Pampatheriidae), are perhaps the most distinctive xenarthrans, as their bony carapaces make them easily recognizable. Dasypodids are known from the late Paleocene to the Recent and glyptodonts and pampatheres from the late Eocene (following Kay et al., 1999) and Miocene (Carlini et al., 1989; Carlini and Scillato-Yané, 1993) to the Pleistocene–early Holocene of South America (Scillato-Yané, 1995). They were abundant, and in the Pliocene all three families dispersed into North America as part of the Great American Biotic Interchange (Stehli and Webb, 1985). They are taxonomically diverse; systematically complex, and distinguished mainly on characters of ornamentation of the carapace and caudal tube. Herein we report the presence of an enigmatic cingulate from the late Miocene of Uruguay (collected in late 1988 by Luis R. Castiglioni) that we tentatively consider as a glyptodont belonging to the genus *Neoglyptatelus*, of the poorly known subfamily Glyptatelineae.

Paula Couto (1979) recognized only four subfamilies within the Glyptodontidae, Propalaeohoplophorinae, Hoplophorinae, Doedicurinae and Glyptodontinae. However, a fifth, the Glyptatelineae, which includes the earliest and most primitive glyptodonts, is also generally recognized (Castellanos, 1932; Hoffstetter, 1958; Scillato-Yané, 1977; Carlini et al., 1997; McKenna and Bell, 1997). Glyptatelines are known from a minimum of three genera, *Glyptatelus* (late Eocene to late Oligocene; Mustersan and Deseadan LMAs, following Kay et al., 1999), *Clypeotherium* (late Oligocene; Deseadan LMA), and *Neoglyptatelus* (middle to late Miocene; Laventan and Huayquerian LMAs).

Abbreviations—LMA, Land Mammal Age; \bar{x} , average; s , standard deviation; n , sample size; OR, observed range; MNHN, Museo Nacional de Historia Natural de Montevideo, Uruguay.

SYSTEMATIC PALEONTOLOGY

Superorder XENARTHRA Cope, 1889

Order CINGULATA Illiger, 1811

Family GLYPTODONTIDAE Gray, 1869

Subfamily GLYPTATELINEAE Castellanos, 1932

NEOGLYPTATELUS Carlini, Vizcaíno, and Scillato-Yané, 1997

NEOGLYPTATELUS sp.

Referred Specimen—MNHN 1483, 45 complete and 12 broken isolated osteoderms belonging to the same individual (Fig. 1).

Locality and Horizon—Uruguay, San José Department, erosional surface of Puerto Arazatí Beach, 3 to 4 km east of El Sauce Creek (Fig. 2); greenish sandy basal mudstone of the upper Miocene Camacho Formation (Ubilla et al., 1990; Perea et al., 1994, 1996).

Measurements (mm)—Length: \bar{x} = 13.98, s = 2.49, n = 38, OR = 10.6–19.7. Width: \bar{x} = 12.76, s = 1.71, n = 37, OR = 9.2–16.4. Thickness: \bar{x} = 6.81, s = 0.84; n = 39, OR = 5.4–8.2.

Description—Most of the osteoderms are pentagonal or hexagonal in outline (Fig. 1). Their size is within the range of *Neoglyptatelus originalis*, and much smaller (approximately one third to one half in length) than the older glyptatelines, *Glyptatelus* and *Clypeotherium*. The surface is smooth as in *Glyptatelus* and *N. originalis*. They have a straight-sided principal figure that frequently reaches the posterior margin, as in *N. originalis*. The principal figure is separated from three to six peripheral figures by the principal sulcus. The peripheral figures are well developed on the anterior and lateral sides and less developed or

absent along the posterior margin (Fig. 1). The peripheral figures are separated by radial sulci. As in *N. originalis*, foramina are located in the intersection of the principal and the radial sulci. They are interpreted as hair follicles as in living armadillos. The number of foramina correlates with the number of peripheral figures. The most conspicuous difference from *N. originalis* is that the foramina are more numerous and smaller.

DISCUSSION

In addition to *Glyptatelus*, *Clypeotherium*, and *Neoglyptatelus*, two other taxa have tentatively been included in the Glyptatelineae: the poorly known Eocene *Lomaphorelus depstus* Ameghino by Mones (1986) and the late Pliocene–early Pleistocene (Blancan and Irvingtonian LMA) *Pachyarmatherium leiseyi* Downing and White by McKenna and Bell (1997). *L. depstus* is based on a very poorly preserved osteoderm without diagnostic features (Scillato-Yané, 1977), so it is regarded here as a nomen dubium.

Webb et al. (1989:96) noted the presence of “a new small glyptodont” in the early Pleistocene of Florida. However, in the formal description of *Pachyarmatherium leiseyi*, Downing and White (1995) provisionally regarded it as a dasypodoid with a combination of features associated with armadillos and glyptodonts. While the characters that would indicate dasypodoid rather than glyptodontoid affinity were based primarily on features not related to the carapace, they noted that its osteoderms resembled those of *Glyptatelus*. While there is much more to be learned about this animal, especially its cranial features, it was tentatively listed by McKenna and Bell (1997) as a glyptateline glyptodontid. Much of the evidence that *P. leiseyi* was a dasypodoid and not a glyptodont was based on a “poorly restored and mounted specimen under less than ideal conditions” (Downing and White, 1995:384) that belonged in a private collection and was not figured in the paper.

Pachyarmatherium leiseyi has a glyptodont-like carapace, but it differs from those of classic glyptodonts in being divided into two parts with a movable “hinge” between them. However, the presence of movable bands represents the primitive condition for glyptodonts, as they are present in the early Miocene Propalaeohoplophorinae (Scott, 1903–1904). The osteoderms of *Pachyarmatherium* are very similar to those of *Neoglyptatelus* (SFV, pers. obs.), and the large foramina make them more similar to *N. originalis* than those of MNHN 1483. Thus, *Neoglyptatelus* could be a junior synonym of *Pachyarmatherium*. Nevertheless, the available information on other parts of the skeleton is not definitive enough to demonstrate conclusively this synonymy.

The description of the postcrania of *P. leiseyi* by Downing and White (1995) would indicate an armadillo-like form. Nevertheless, most of the characters, such as the presence of claws instead of hooves and free dorsal vertebrae, are primitive features of cingulates. Free dorsal vertebrae were also reported with material of *Neoglyptatelus* from Colombia (Carlini et al., 1997). It is noteworthy that glyptatelines are one of the oldest groups recognized as glyptodonts and that their postcrania are almost unknown. Therefore, they could have retained many plesiomorphic features. On the other hand, Carlini et al. (1997) tentatively attributed a very glyptodont-like mandible with teeth to *Neoglyptatelus*, as is that of *Glyptatelus* (Simpson, 1948).

Several questions remain to be addressed. First, the similarity of osteoderm morphology suggests that *Neoglyptatelus* and *Pachyarmatherium* are the same genus, and the latter should be the valid name. But

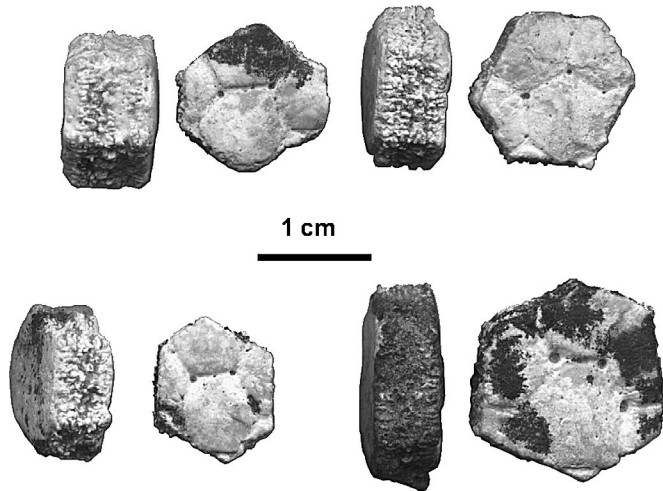


FIGURE 1. Dorsal and lateral views of MNHN 1483, osteoderms of *Neoglyptatelus* sp. from Puerto Arazatí Beach, 3 to 4 km east of El Sauce Creek, San José Department, Uruguay (Fig. 2).

the crania and postcrania of the type species of both genera, *N. originalis* and *P. leiseyi*, remain poorly known and a better understanding of the skeleton is necessary to make an informed taxonomic decision. Additionally, the great difference in geologic age and geographic distance separating them makes it currently more acceptable to remain conservative and keep them separated. Hence, we refrain from synonymizing them and refer the specimen from Uruguay to *Neoglyptatelus*.

Second, we believe that the thickness of the osteoderms and the lack of any movable bands of osteoderms such as those present on pampatheres and dasypodids is indicative that both *Neoglyptatelus* and *Pachyarmatherium* are glyptodontoids. Nevertheless, their phylogenetic position within the cingulates, in particular, and the glyptatelines, in general, remains uncertain. Third, if the phylogenetic hypothesis that *P. leiseyi* is a glyptateline glyptodontid (as suggested by McKenna and Bell, 1997) is followed, it would represent a significant extension of the geographic and chronologic distribution of the subfamily. Finally, if either *Pachyarmatherium* or *Neoglyptatelus* were not glyptodontoids, then they would represent a peculiar example of convergence within the cingulates. The thickening of the osteoderms observed in *Pachyarmatherium* would have been derived separately from that of the glyptodontoids, as originally proposed by Downing and White (1995).

The Uruguayan specimen of *Neoglyptatelus* was collected from the erosional surface of Puerto Arazatí Beach on the east margin of the La Plata River (Fig. 2). The sediments were originally described as the Kiyú Formation (Francis and Mones, 1965), but are now considered a paralic facies of the Camacho Formation (da Silva, 1990). They have also been included in the Raigón Formation (Preciozzi et al., 1985; Bossi and Navarro, 1991).

Previously, the Glyptatelineae were restricted to the late Eocene (Mustersan LMA) to late Oligocene (Deseadan LMA) of Argentina, late Oligocene (Deseadan LMA) of Bolivia, and middle Miocene (Laventan LMA) of Colombia. Faunistic analyses by Perea et al. (1989, 1994, 1996) strongly suggest correlation between the sediments where the osteoderms were found and the Ituzaingó Formation in Argentina. The "Mesopotamian" mammal fauna from the Ituzaingó Formation is composed of taxa from the Huayquerian LMA (Cione et al., 2000). Following Flynn and Swisher (1995), the Huayquerian is late Miocene, 6.8 to 9.0 Ma, and significantly younger than the Laventan, 11.8 to 13.8 Ma, which produced the previously youngest known South American glyptateline, *N. originalis* (Carlini et al., 1997). Therefore, the new find extends the known temporal range of the subfamily in South America and may represent either a geographic re-expansion into southern latitudes or the persistence of a widely distributed group.

Kay and Madden (1997) proposed a heterogeneous habitat and discontinuous forest canopy extending into interfluvial areas for La Venta, and an estimated annual rainfall between 1,500 and 2,000 mm. It seems plausible that *Neoglyptatelus* was associated with relatively humid and warm environments and such conditions might have favored its south-

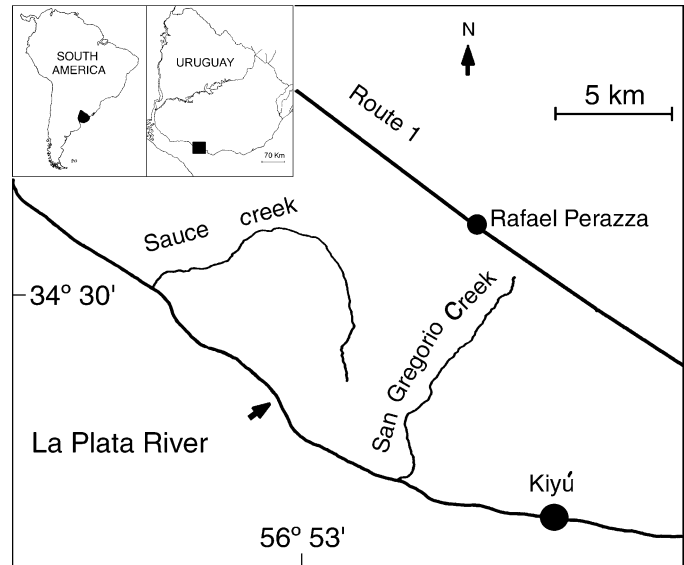


FIGURE 2. Map of the region where *Neoglyptatelus* sp. was collected on the east margin of the La Plata River. The arrow indicates the precise geographic location where MNHN 1483 was found.

ern expansion. Perhaps the smaller size and number of foramina (hair follicles?) indicates warmer conditions at the Uruguay site than in La Venta. The southern record of this tropical genus might correlate with the contemporaneous southernmost range extension of the turtle *Phrynosops geoffroanus* (De la Fuente, 1992). Living representatives of *Phrynosops* inhabit freshwater lowlands in tropical to humid temperate climates. According to Perea et al. (1996), the record of *P. geoffroanus* in the Camacho Formation is in agreement with estuarine, fluvio-deltaic, or coastal environments.

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