

Paleobiogeography of the late Pleistocene pampatheres of South America

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Abstract

This paper deals mainly with the paleobiogeography of the South American Pampatheriidae of the late Pleistocene. Through analysis, we conclude that (1) the species of Quaternary pampatheres may be distinguished clearly by their carapace scutes and craniodental characters; (2) there are two pampathere genera in the South American Quaternary, *Pampatherium* and *Holmesina*; (3) no more than one species of each genus occurs in association at a single locality or site; (4) *Holmesina* differentiated in North America, entered South America during the Late Pleistocene, and later experienced speciation probably related to Late Pleistocene and Holocene climate changes; (5) *Pampatherium* differentiated in South America, and its speciation process produced a second immigration of pampatheres to North America; and (6) the use of contrasting environments may be observed among the Quaternary pampatheres.

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1. Introduction

The Pampatheriidae, along with the families Dasypodidae, Peltephilidae, Glyptodontidae, and the more problematic Palaeopeltidae (=Pseudorhynchodontidae? see Hoffstetter, 1956; Scillato-Yané, 1977), comprise the cingulate xenarthrans (Cingulata, Xenarthra). For several decades, large cingulates that we include in Pampatheriidae were regarded as a subfamily within Dasypodidae (Hoffstetter, 1958; Scillato-Yané, 1980). More recently, a family-level assignment has become more accepted (Edmund, 1985, 1987), related to the gradual replacement of typological classification for phylogenetics. Long before the advent of phylogenetics, the close relationship of Pampatheriidae with Glyptodontidae had been recognized (Ameghino, 1889). Currently, there are two views about the proximity of this relationship. One view asserts that

Pampatheriidae are the sister-group of Glyptodontidae (Carlini and Scillato-Yané, 1993), whereas the other claims they are more phylogenetically distant, with Eutatini the sister-group to Glyptodontidae (Engelmann, 1985).

The oldest genus proposed as a pampatherid is *Machlydotherium* Ameghino, 1902, from the Casamayoran 'Barrancan' (Late Eocene) (Kay et al., 1999) and Mustersan (top of Late Eocene) of Patagonia, Argentina. Ameghino (1902) assigned them to the 'Chlamydotheriidae' (=Pampatheriidae). Scillato-Yané (1980) followed Ameghino and referred *Machlydotherium* to the Pampatheriidae (=Chlamydotheriidae), but this reference was questioned by Hoffstetter (1956) and again later by Carlini and Scillato-Yané (1993). With the status of *Machlydotherium* in question, the oldest record of an undoubted pampathere is *Scirrotherium* Edmund and Theodor, 1997, from the middle Miocene of La Venta, Colombia. The pampatheres, or giant armadillos, are recorded in South America up to the Late Pleistocene or perhaps even into the early Holocene (Cartelle Guerra and Bohorquez Mahecha, 1985) and entered North America as immigrants during the Great American Biotic Interchange (Stehli and Webb, 1985). Pampatheres are recorded in North America beginning in

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the Late Blancan (Late Pliocene) until the Rancholabrean (Late Pleistocene) (Edmund, 1996).

From a historical standpoint, the pampatheres are among the first fossil mammals reported from South America, as Lund identified the genus *Chlamytherium* (lapsus for *Chlamydothorium*, corrected by Lund in 1841) in 1839. This name was preoccupied by *Chlamydothorium* Bronn, 1838; Ameghino erected the genus *Pampatherium*, the type of the family group name.

This article deals mainly with the paleobiogeography of the South American Pampatheriidae of the Late Pleistocene, involving species of two genera: *Pampatherium* Ameghino, 1891 and *Holmesina* Simpson, 1930. We also relate the distribution of these species to climate and environmental factors that may have influenced their differentiation and dispersal.

2. Systematics, evolution, and distribution

2.1. Osteoderm morphology and systematics

The type species of the family Pampatheriidae is *Pampatherium humboldti* (Lund, 1841) from the Late Pleistocene of Brazil.

Despite recent efforts by Cartelle Guerra and Bohorquez Mahecha (1985), Edmund (1985, 1987, 1996), and Cartelle Guerra (1999), there is still much work to do regarding the systematics of the Quaternary pampatheres of South America, their origin, and their evolutionary history. Edmund (1996) pampatheres revision clarified the validity of the two Quaternary genera *Holmesina* and *Pampatherium*, as well as the general characters of the osteoderms that allow distinguishing, for South America, three species for the first genus and two species for the latter.

The osteoderms of species of *Holmesina* always have a conspicuous central figure, delimited by two lateral furrows, a primitive or plesiomorphic condition for all Cingulata (Scillato-Yané, 1982). Such primitive disposition is maintained but with an even better defined central figure in *Scirrotherium* (Edmund and Theodor, 1997) and *Kraglievichia* Castellanos, 1927.

With regard to the species of *Holmesina*, different species may be characterized by osteoderm morphology and general dimensions, as follows: *Holmesina occidentalis* (Hoffstetter, 1952) is somewhat smaller than the other two species. The osteoderms are large but proportionally thin, with a more uniformly even surface than that of other species. The depressed marginal area, a synapomorphy of *Holmesina*, is not as well developed as in the other two species. The central figure is narrow and well defined (Fig. 1A,A').

According to the linear measurements of the long bones, *H. majus* (Lund, 1842) is the largest Pampatheriidae but not the most robust. The scutes, on average, are somewhat smaller than those of *H. paulacoutoi*. The surface of the osteoderms has delicate punctuation but is more rugose than in *H. occidentalis*, though less than in *H. paulacoutoi*. The

marginal area is wide and the central figure narrow, defined, and somewhat depressed (Fig. 1B,B').

H. paulacoutoi (Cartelle Guerra and Bohorquez Mahecha, 1985) is the most robust Pampatheriidae. This species was described on the basis of Late Pleistocene–Holocene remains from the caves of Bahía, Brazil (Fig. 1C,C'). Later it was transferred to the genus *Holmesina* Simpson by Cartelle Guerra et al. (1989). The carapace scutes are very large, the surface very rugose, and the marginal area wide and low around an elevated central area. Sometimes this convexity continues backward, a unique character among the Pampatheriidae. In turn, Edmund (1996) suggested the putative conspecificity of *H. majus* and *H. paulacoutoi*. We believe that the comparison of both holotypes (Winge, 1915; Cartelle Guerra and Bohorquez Mahecha, 1985) supports two valid species; to the differences observed in the morphology of the carapace scutes, it may be added, for example, that the first upper molars are strongly imbricate in *H. paulacoutoi* but not in *H. majus*, which represents an unlikely intrapopulation variation.

The external surface of the osteoderms of *Pampatherium* are almost even, as in *P. typum* (Gervais and Ameghino, 1880) or slightly sculpted as in *P. humboldti* (Lund, 1841). The same is true for species of *Vassallia* Castellanos, 1927, from the Late Miocene–Pliocene of northwestern Argentina and Bolivia. This character is considered relatively derived, a synapomorphy of *Pampatherium* and *Vassallia*. This sister-group relationship is also supported by significant similarities in the masticatory apparatus (Vizcaíno et al., 1998; De Iuliis et al., 2000). Scillato-Yané (1982: 67) concluded that ‘*Vassallia* may be regarded as the structural ancestor of *Pampatherium*.’

With regard to the species of *Pampatherium*, *P. typum* is the smallest and least robust of the Quaternary Pampatheriidae of South America. The surface of the scutes is very even, and the central area is flat and lacking a central figure (Fig. 1D, D').

The scutes of *P. humboldti* (Lund, 1841) are somewhat more rugose than those of *P. typum* and have a defined central figure (Fig. 1E, E').

2.2. Records of Quaternary pampatherids in South America

H. occidentalis is known from the Pleistocene of Colombia and Venezuela and the Late Pleistocene of Ecuador and Peru. In Colombia, it is reported from Huila Department (near Villavieja; Edmund, 1996), in Venezuela from Falcón (at Muaco; Royo and Gómez, 1960) and Carabobo (near Valencia Lake; Marshall et al., 1984) states, in Ecuador from Guayas province (Santa Elena Peninsula; Hoffstetter, 1952, 1968b), and in Peru near Cuspinique and the Talara Desert (Hoffstetter, 1968c; Marshall et al., 1984).

Definite records of *H. majus* are reported from the Late Pleistocene of Brazil at localities in Minas Gerais, Rio Grande do Sul, and Ceará (Edmund, 1996). Ubilla and Perea

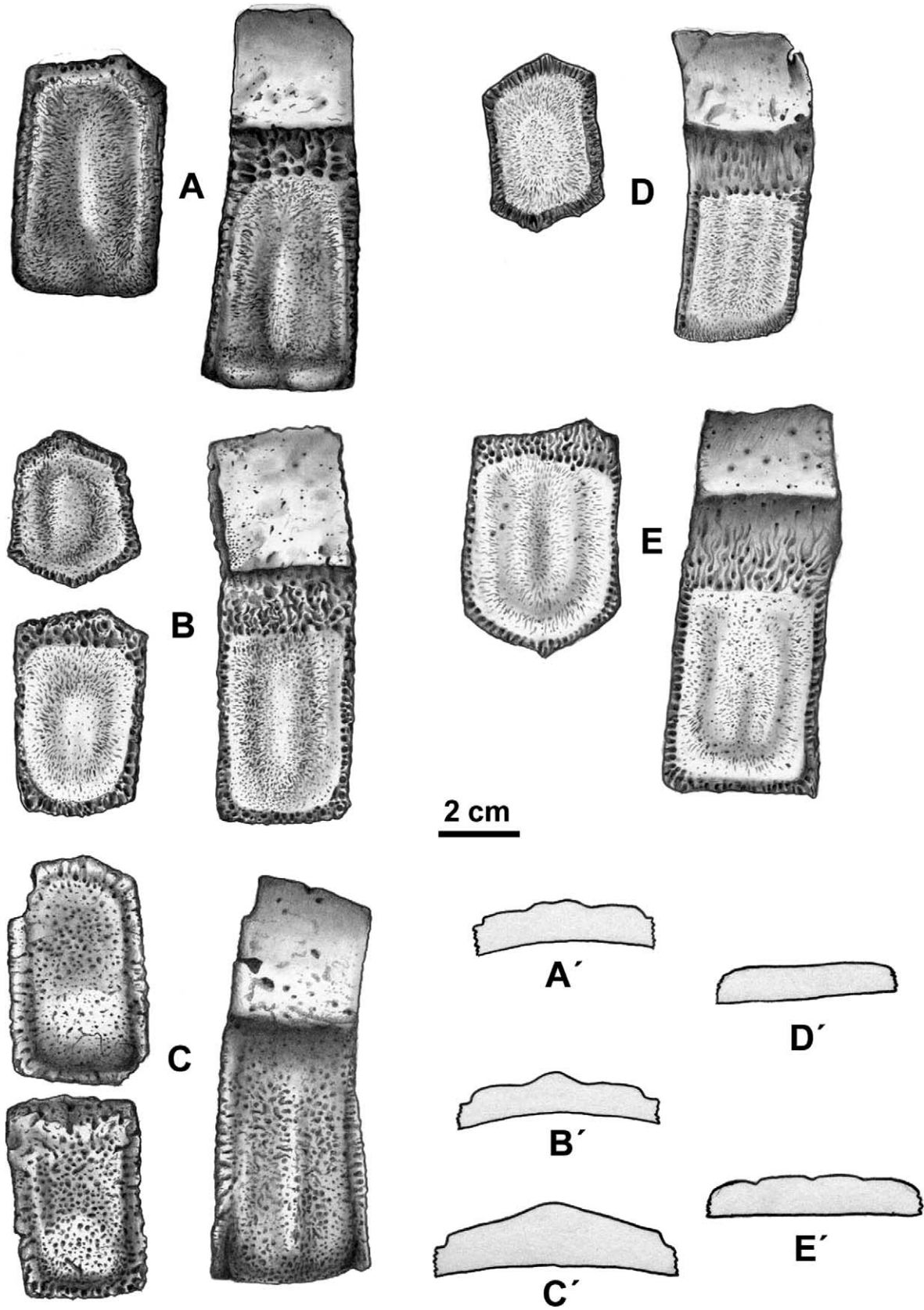


Fig. 1. (A–E) Fixed and mobile scutes of the dorsal shield of South American Quaternary Pampatheres; (A'–E') cross-section of the scutes. (A–A') *Holmesina occidentalis*; (B–B') *H. majus*; (C–C') *H. paulacoutoi*; (D–D') *Pampatherium typum*; and (E–E') *P. humboldti*.

(1999) could not verify the occurrence of this species in Uruguay, as reported by Edmund (1996).

Hdmesina paulacoutoi is known from the Upper Pleistocene of Brazil and Argentina. In Brazil, Cartelle Guerra (1999) reports this species from Bahia state. Material from the Arroyo Chuí local fauna has been assigned to *Holmesina* cf. *paulacoutoi* by Oliveira (1996, 1999). In Argentina, there are records from Corrientes (Late Pleistocene at Arroyo Toropi; Scillato-Yané et al., 1998), Santa Fe (Late Lujanian along the Salado River), Buenos Aires (Middle–Late Pleistocene ‘Pampeano Superior’ at Arrecifes), and Entre Roís (Lujanian Arroyo Feliciano Formation at Diamante; Scillato-Yané et al., 2002). Edmund (1996) has assigned material from Buenos Aires and Santa Fe provinces to *H. majus*, but restudy of this material instead suggests *H. paulacoutoi*.

P. humboldti is known from the Late Pleistocene of Brazil and Uruguay. Records in Brazil include localities in Minas Gerais, Rio Grande do Sul, Ceará, Bahía, and Matto Grosso states (Edmund, 1996; Cartelle Guerra, 1999). According to Cartelle Guerra (1999), the material from Minas Gerais and Bahía come from deposits no older than 13,000 years BP. In Uruguay, material of *P. humboldti* is

reported from the Sopas Formation and assigned to the base of the Lujanian (Ubilla and Perea, 1999).

P. typum is known from the Late Pleistocene of Bolivia, Brazil, Paraguay, and Argentina. In Bolivia, there are records from Nuapúa (Hoffstetter, 1968a) and Tarija (Hoffstetter, 1963). In Brazil, there is a record from Santa Catarina (Paula Couto, 1980). In Paraguay, the record comes from near Asunción (Carlini and Tonni, 2000). Argentine records include the Buenos Aires (Ensenadan north of the city of Buenos Aires, both the Ensenadan and Lujanian at Centinela del Mar, and the Lujanian along the Quequén Grande and Quequén Salado rivers; Bargo et al., 1986; Tonni et al., 1987; Prado et al., 1987; Pardiñas et al., 1996), Formosa (Lujanian along the Pilcomayo River; Tonni and Scillato-Yané, 1997), and Corrientes (the Bonaerian-Lujanian, Yupoí Formation) provinces. These occurrences are depicted as species range maps in Fig. 2.

2.3. Paleocology of the pampatherids

It may be inferred that *P. typum* was a grazing herbivore with secondary specialization for hard object feeding (De Iuliis et al., 2000). During the long interval

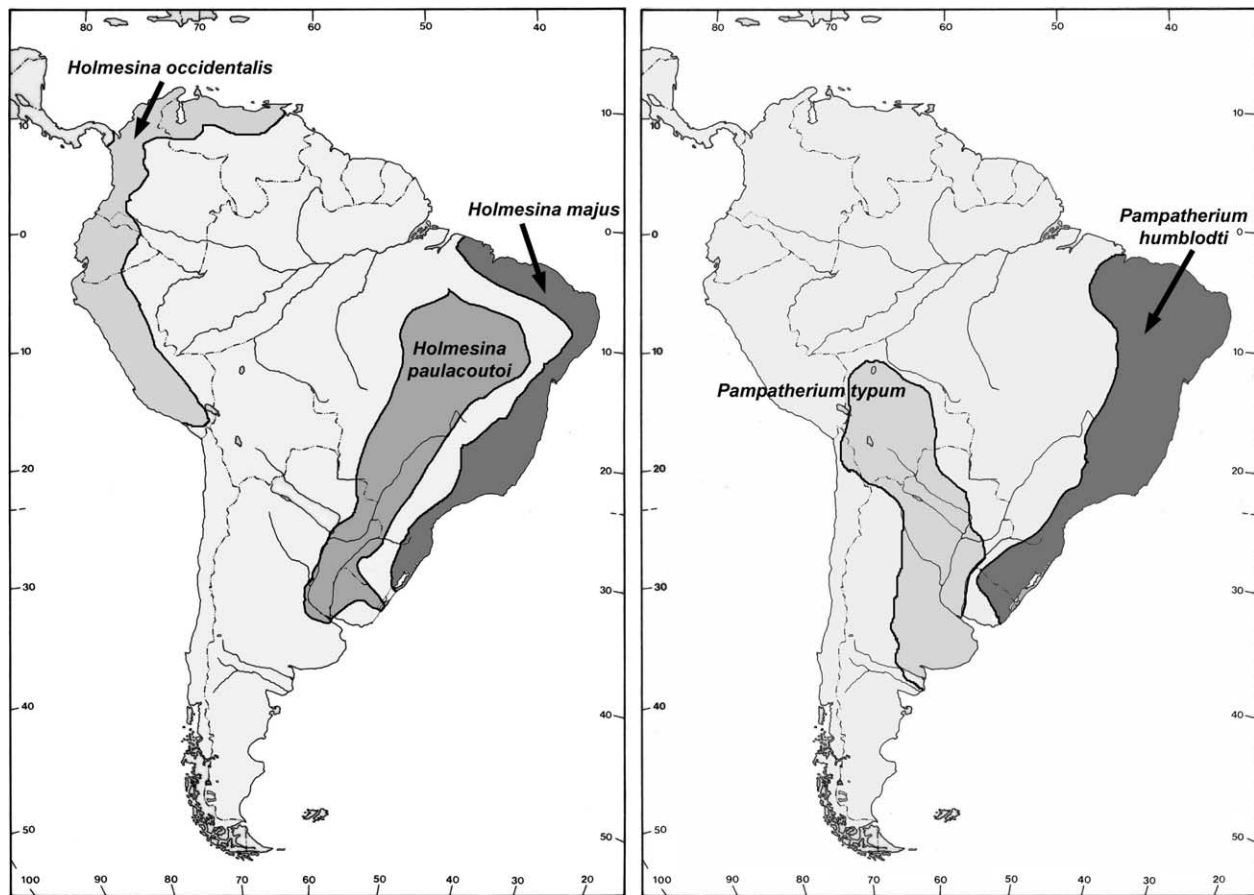


Fig. 2. Reconstructed distributional areas of South American Quaternary Pampatheres, *Holmesina occidentalis*, *H. majus*, *H. paulacoutoi*, *Pampatherium typum*, and *P. humboldti*.

in which this species is recorded in the Pampean region, it is associated with faunas that suggest varied environmental conditions, not necessarily coincident with the production of ‘hard vegetables.’ The oldest records are those from the Ensenadan around the city of Buenos Aires, where the associated fauna include Tapiridae and Procyonidae, which suggests warm and humid conditions. Such conditions are likely to have prevailed during high temperature events between the Jaramillo and Olduvai events coincident with isotopic stages 35–37 and 41–45, as well as the Interensenanadan transgression (Cione et al., in press). Another association between *P. typum* and a warm and humid climate episode occurred at the base of the Lujanian during isotopic stage 5e. In contrast, in the late Lujanian, *P. typum* occurs in association with fauna from the late glacial maximum or isotopic stage 2. This fauna suggests arid, cold conditions (Tonni et al., 1987). These contrasting environmental associations for *P. typum* imply either two different species (a possibility entertained by De Iuliis et al., 2000) or a single species more flexible in its requirements than has been deduced through the masticatory apparatus.

P. humboldti is mostly associated with faunas that are not as eremic as those of the Late Pleistocene (Late Lujanian) of the Argentine Pampean region. In at least one case (Sopas Formation, Uruguay; see Ubilla and Perea, 1999), it has been associated with fauna that may be correlated with the last Interglacial (isotopic stage 5e). De Iuliis et al. (2000) suggest that this species was adapted for grazing on less abrasive substances than those thought for *P. typum*.

According to De Iuliis et al. (2000), *H. occidentalis* would be a grazer of softer vegetation. This species is associated in Ecuador with faunas of relatively open areas (Hoffstetter, 1952), including *Equus (Amerhippus) santaelenae*, *Palaeolama aequatorialis*, *Odocoileus salinae*, *Neochoerus sirasakae*, and Echimyidae.

H. paulacoutoi would also be a grazer of soft vegetation but probably somewhat more abrasive than that eaten by *H. occidentalis* (De Iuliis et al., 2000). No morphofunctional studies have been carried out on *H. majus*.

In summary, the *Pampatherium* species would be adapted to more extreme conditions (arid or semiarid) than would *Holmesina*. However, the evidence supplied by vegetation during glacial cycles may suggest other alternatives.

During glacial periods, the biomas related to open areas of grasslands, steppes, and savannas advanced over the Amazonian rainforest (Clapperton, 1993; Van der Hammen and Absy, 1994), with consequent movements of faunas that were adapted to each environment (e.g., De Iuliis et al., 2000). These climatic changes may have originated the modern distribution pattern of seasonally dry tropical forest (Pennington et al., 2000), vegetation formations typical of a mean annual precipitation around 1600 mm, and dry periods

with mean monthly rainfall <100 mm that do not exceed five to six months. These formations include deciduous forests with abundant shrubs and even Cactaceae but scarce grassland.

If we assume that seasonally dry tropical forests would have experienced greater expansion during glacial periods, whereas interglacials would have been more similar to the present, and that the distribution of pampatheriid species with significant body mass and that are adapted for browsing and/or grazing was linked to environmental conditions characterized by dry seasons, we would expect the following scenario.

The relatively restricted geographic and stratigraphic distribution of *H. occidentalis* appears to have been related to areas of disjunctive distribution of seasonally dry tropical forest. During the glacial maximum, this vegetation formation reached its greatest areal expansion, with which we associate with the relatively continuous geographic records of *H. occidentalis*, including the most southerly and westerly occurrences in Colombia and Venezuela.

Similarly, the southernmost records of *H. paulacoutoi* from Bahía, Brazil, may have resulted from a broader expansion of seasonally dry tropical forest during the glacial maxima. The paleontological records of *H. paulacoutoi* agree with two distinct areas of seasonally dry tropical forest, the Caatinga of northern Bahia and the Núcleo Misiones in Argentinean Mesopotamia, which may have been contiguous during the glacial maxima.

Alternatively, the fragmentation of areas within seasonally dry tropical forests (Pennington et al., 2000) into areas with ecological peculiarities may have promoted population disjunctions and consequent isolation and speciation among Late Pleistocene pampatheres.

3. Discussion

In the geographic distribution of pampather species (Fig. 2), the species ranges for each genus are not superimposed. It seems likely that this allopatric pattern resulted from speciation processes during the last part of the Pleistocene. During this time, barriers originated through climate changes associated with the transition between the last Interglacial and the Last Glacial Maximum, or isotopic stages 5e and 2 (Clapperton, 1993; Van der Hammen and Absy, 1994; Haberle and Maslin, 1999). One consequence of this recent cladogenesis is that there was little time for subsequent changes in distribution. The last period of transitional climates in the Late Pleistocene and Holocene would have interrupted any developing superposition of species ranges.

We should point out that stratigraphic association does not necessarily imply sympatry. The stratigraphic unit yielding two or more species may represent a temporal

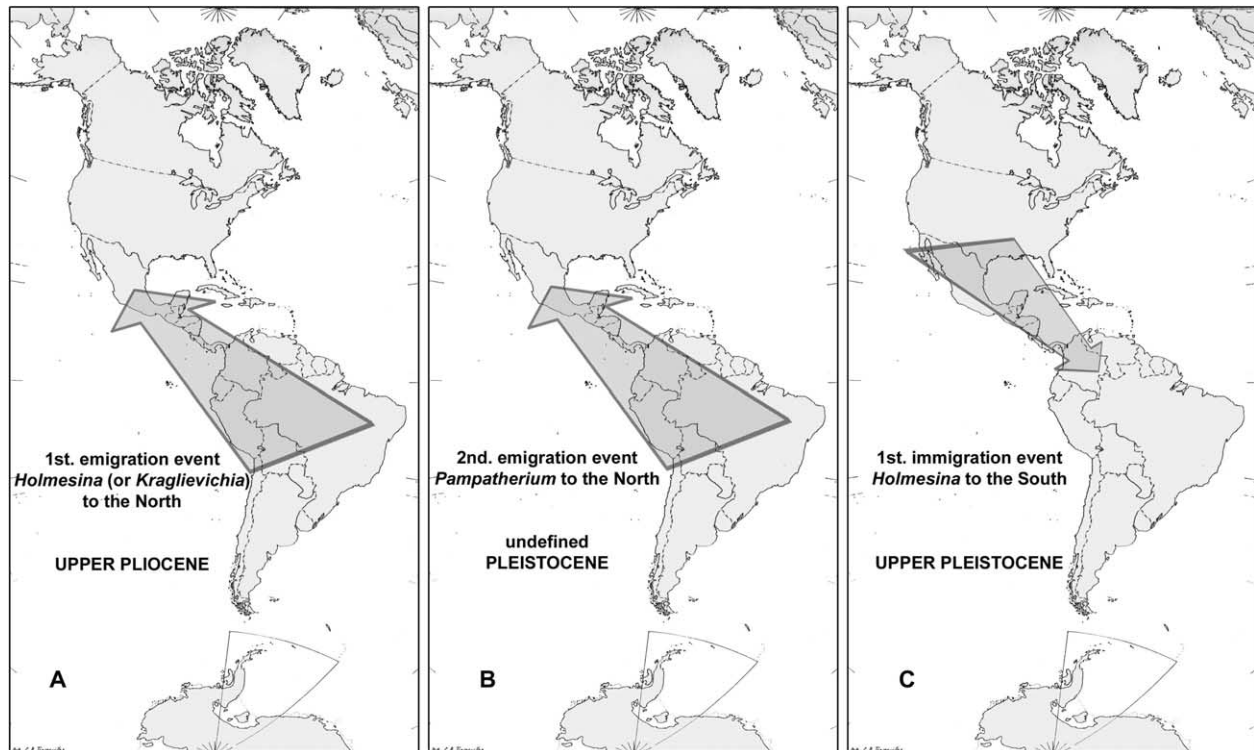


Fig. 3. Main dispersion events of Pampatheres between South America and North America. (A), First immigration event to North America (Upper Pliocene) of a primitive *Holmesina* (or *Kraglievichia*) species and subsequent differentiation of *H. septentrionalis*. (B), Second immigration event to North America (undefined Pleistocene) of a *Pampatherium* species and subsequent differentiation of *P. mexicanum*. (C) First immigration event from North America of a *Holmesina* species and subsequent differentiation of *H. occidentalis*, *H. majus*, and *H. paulacoutoi* in South America.

averaging that includes a complete cycle of alternating conditions. Changes in climate and environmental conditions were frequent and rapid during the Late Pleistocene (Grootes et al., 2001; Scott et al., 2002), which may have produced alternating conditions that promoted the expansion and contraction of species ranges, such as between soft vegetation during temperate and humid periods and hard vegetation during dry and cold periods.

Holmesina is likely to have differentiated in North America from more generalized pampatheres, a primitive species of either *Holmesina* or *Kraglievichia* (Fig. 3A), that originally came from South America. The subsequent reintroduction of the genus along a western coastal corridor is supported by the occurrence of *H. occidentalis*, which presents a series of primitive characters with respect to other South American species (Fig. 3C). Another differentiation may have occurred on the eastern coastal fringe, giving rise to *H. majus* during the Late Pleistocene. The most derived species, *H. paulacoutoi*, probably differentiated during the latest Pleistocene in a more central area, such as the San Francisco and Paraná basins.

In North America, *Holmesina* underwent an increase in body size after the Blancan and especially during the Irvingtonian. All South American species of *Holmesina* are similar in size to the largest North American species *H. septentrionalis*. Moreover, all the South American

species of *Holmesina* of the Late Pleistocene are very similar to one another (morphologically), in support of the hypothesis of a late reentry from North America.

Pampatherium would have become differentiated during the early Pleistocene in southern South America. One species, *P. typum*, inhabited a more central region with presumably dryer conditions throughout the Late Pleistocene. As for *Holmesina*, the pampatheres of the *Vassallia-Pampatherium* lineage underwent an increase in body size during the early Pleistocene.

Edmund (1996) reports records of *P. mexicanum* in the North American Quaternary from Puebla, Hidalgo, and Jalisco in Mexico. Although we believe the chronology and some aspects of the anatomy of this taxon remain uncertain, the records are certainly *Pampatherium*. If we accept that this genus differentiated in South America as the sister-group to *Vassallia*, a second immigration event from south to north may be proposed for the biogeographic history of the Pampatheriidae (Fig. 3B). This event would have been earlier than the reverse migration of *Holmesina* from north to south.

4. Conclusions

First, species of Quaternary pampatheres may be clearly distinguished by the carapace scutes and craniodental

characters. Second, there are two pampatheres genera in the South American Quaternary, *Pampatherium* and *Holmesina*. *Pampatherium* has two species (*P. humboldti* and *P. typum*) and *Holmesina* three (*H. occidentalis*, *H. majus* and *H. paulacoutoi*). Third, no more than one species of each genus occurs in association at a single locality or site.

Fourth, *Holmesina* would have differentiated in North America from South American pampatheres (*Kraglievichia?*), entered South America during the Late Pleistocene, and later experienced speciation probably related to Late Pleistocene and Holocene climate change. Fifth, *Pampatherium* differentiated in South America from other South American pampatheres (*Vassallia?*), then the speciation process produced a second immigration of pampatheres into North America, where a third species became differentiated (*P. mexicanum*).

Sixth and finally, the use of contrasting environments may be observed among the pampatheres. Less humid environments with more fibrous grasses were occupied by species of *Pampatherium*, whereas species of *Holmesina* occupied more humid environments with softer vegetation.

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