The first complete skull of Hispanotherium matritense (Prado,) (Perissodactyla, Rhinocerotidae) from the middle Miocene of the Iberian Peninsula

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PLEASE SCROLL DOWN FOR ARTICLE

THE FIRST COMPLETE SKULL OF *HISPANOTHERIUM MATRITENSE* (PRADO, 1864) (PERISSODACTYLA, RHINOCEROTIDAE) FROM THE MIDDLE MIOCENE OF THE IBERIAN PENINSULA

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ABSTRACT—New rhinocerotid remains from the early middle Miocene site of Príncipe Pío-2, Madrid Basin (Madrid, Spain), are described and identified as belonging to *Hispanotherium matritense*. They constitute the first complete cranial remains recorded for this species, permitting the description of its cranial morphology and updating the species diagnosis. New remains show *H. matritense* as a middle-sized hornless elasmotheriine rhinoceros, contrary to previous studies. Phylogenetic analysis places the Western European *Hispanotherium matritense* close to the coeval Spanish species *Hispanotherium corcolense* and more distantly related to the French species *Hispanotherium beonense*. The late middle Miocene “*H.*” *tungurense* from Inner Mongolia is placed near later diverging elasmotheres, and its belonging to the genus *Hispanotherium* is questioned.

INTRODUCTION

Hispanotherium matritense is a medium-sized rhinoceros species known from the early Aragonian (MN4) of Western Europe to the MN6 of Asia. It was firstly defined by Prado in 1864 as *Rhinoceros matritensis* based on a few dental remains from the locality of Puente de Toledo in Madrid, Spain. Almost a century later, Crusafont and Villalta (1947) found enough differences to place this species in its own genus, naming it *Hispanotherium*. Thereafter many Iberian remains of *H. matritense* have been described (Hernández-Pacheco and Crusafont, 1960; Antunes, 1979; Aguirre et al., 1982; Antunes and Ginsburg, 1983; Cerdeño and Alberdi, 1983; Ginsburg et al., 1987; Cerdeño, 1992; Cerdeño and Iñigo, 1997). Its appearance in the Iberian central basins was interpreted as being related to an aridity increase (Cerdeño and Nieto, 1995). *H. matritense* was so abundant in these basins that led M. T. Antunes to refer their typical Aragonian species assemblage as 'Hispanotherium faunas' (Antunes, 1979). In addition to the Iberian specimens, remains attributed to *H. matritense* have been reported from the French locality of Faluns d'Anjou (Ginsburg et al., 1987) and the Chinese site of Laogou (Deng, 2003), extending its paleobiogeographic range beyond the Iberian Peninsula.

The material described in this paper was recovered in 2007 during the construction of the Príncipe Pío transport interchange inside the city of Madrid (Fig. 1). The site is next to Príncipe Pío-1, where several giant tortoise remains were previously found (unpubl. data). Príncipe Pío-2 site (formerly known as Intercambiador Príncipe Pío; Roca et al., 2009) revealed a rich accumulation of over a thousand remains of *H. matritense*, constituting the bulk of the fossil association. Príncipe Pío-2 is stratigraphically and geographically close to Puente de Toledo, the type locality of *H. matritense*. The fossil beds pertain to the geological Intermediate Unit of the Madrid Basin. The available data indicate a middle Aragonian age (MN5), local zone Dc, 15 Ma (Roca et al., 2009).

The taxonomic status of some species attributed to the genus *Hispanotherium* has been a cause of debate. Our phylogenetic hypothesis is based on the data matrix made by Antoine (2000, 2003), but we are aware that other previous phylogenies have provided very different scenarios depending on the taxonomic samples used, so phylogenetic relationships within Elasmotheriina are still far from been completely settled.

The first well-preserved skulls of *H. matritense* provide not only the first cranial information on the type species, but more importantly shed light on our understanding of the genus diversification during the first half of the Miocene.

MATERIALS AND METHODS

The Príncipe Pío-2 faunal assemblage contains a vast array of vertebrate remains ranging from articulated limbs to undetermined fragments. Most of them show several taphonomical modifications such as abrasion (eroded articular angles), pitting surfaces, and weathering (superficial cracking in long bone diaphysis). The material includes cranial remains, mandibles, isolated dentition, numerous limb-bone elements, vertebrae, and ribs. The great amount of recovered postcranial remains of *H. matritense* is currently under study, falling beyond the scope of the present work. The fossils studied in this paper are housed at the Museo Nacional de Ciencias Naturales (MNCN), Madrid. Measurements were taken with a digital caliper and a measuring tape for elements larger than 150 mm. They are given in millimeters with an accuracy of one decimal digit. Approximate measurements are given in parentheses. The terminology applied in the description of the anatomical characters generally follows Guérin (1980), but that used by other authors has also been taken into consideration (Heissig, 1972, 1999; Antoine, 2002).

Phylogenetic analyses were carried out with the software TNT: Tree Analysis Using New Technology (Goloboff et al., 2008). The character-taxon matrix has been obtained from bibliographic sources (Antoine, 2002, 2003; Deng, 2008), completed with *H. matritense* remains from the Príncipe Pío-2 site and included the absence of nasal horn in *H. grimmi* as
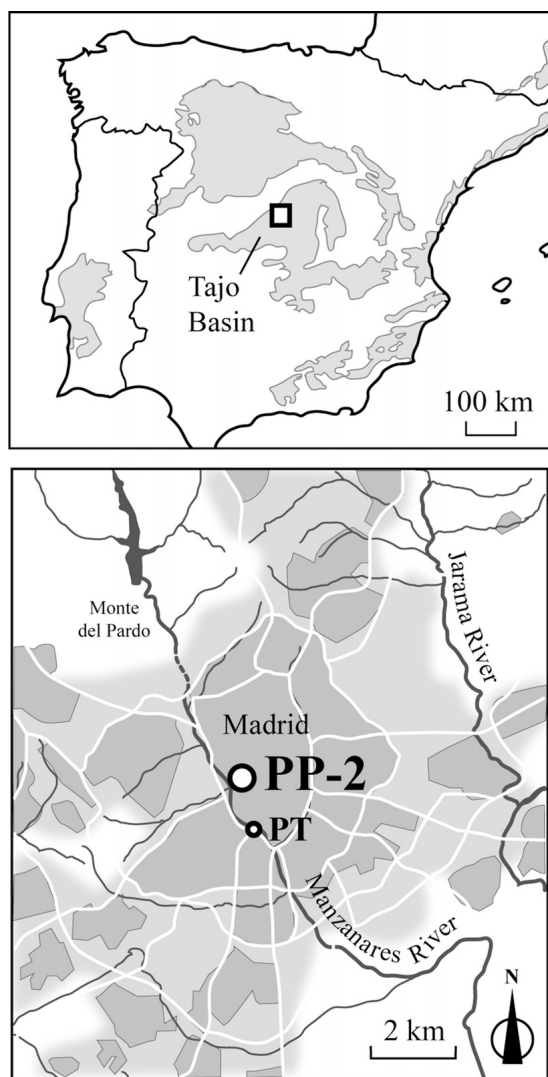
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FIGURE 1. Geographic location of the Miocene Iberian continental basins and the Príncipe Pío-2 site (PP-2) and the type locality of *Hispanotherium matritense* Puente de Toledo (PT).

discussed ahead (detailed in Appendix 1S; available online at www.tandfonline.com/UJVP). Twenty-four terminal taxa were included. The outgroup is *Tapirus terrestris* (Linnaeus, 1758). All the characters were equally weighted and unordered. Parsimony analysis was performed with 1000 starting addition sequences and a tree-bisection-reconnection (TBR) swapping algorithm. No more than 10 trees from each replication were retained.

Anatomical Abbreviations—**H**, height; **L**, length; **P**, upper premolar; **M**, upper molar; **W**, width.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Owen, 1845
SubFamily ELASMOTHERIINAE Bonaparte, 1845
Tribe ELASMOTHERIINI Dollo, 1885
Genus *HISPANOTHERIUM* Crusafont and Villalta, 1947

Type Species—*Hispanotherium matritense* (Prado, 1864).
Emended Diagnosis—As for the type species.

HISPANOTHERIUM MATRITENSE (Prado, 1864)

(Figs. 2–5, Tables 1 and 2)

Rhinoceros matritensis Prado, 1864:152 (pl. 3, figs. 5–9) (original description).
Hispanotherium matritensis Crusafont and Villalta, 1947: 869–883 (figs. 2, 4) (new combination).
Chilotherium quintanelensis, Zbyszewsky, 1952:67–75 (pl. 2–5).
Hispanotherium matritense Antunes, 1960:table 1 (emended spelling).
Hispanotherium alpani, Saraç, 1978:90–96 (figs. 1–3).
aff. *Aceratherium platyodon*, Boné et al., 1980:233–247 (figs. 1–3).

Holotype—Right M2 (unlabeled) figured in Prado (1864:fig. 5) and Crusafont and Villalta (1947:fig. 1). The type series include a left m1 figured in Prado (1864:fig. 6) and Crusafont and Villalta (1947:fig. 3). They are stored in the Museo del Instituto Geológico y Minero de España (IGME), Madrid, Spain.

Emended Diagnosis—Small-sized elasmothere without nasal or frontal horns on the available sample. Nasals elongate, with the nasal notch reaching the level of the P4, a straight upper border, and a concave lower profile. Anterior orbital margin above M3. Subhypsodont cheek teeth with very thick cement cover, deeply constricted protocone and slightly constricted metaconid. Upper premolars with closed median valley. Secondary folds of the enamel developed. The i2-like small tusks, with sexual dimorphism in shape and size. Postcranial skeleton slender, with a reduced non-functional McV.

Referred Material—MNCN-05/101/2/7000, MNCN-05/101/2/7001, and MNCN-05/101/2/7002. Museo Nacional de Ciencias Naturales from Madrid, Spain.

Studied Locality—Príncipe Pío-2, Madrid city, Madrid Province, Spain; early middle Miocene (middle Aragonian, MN5 zone, local zone D, 14–16 Ma).

Description

MNCN-05/101/2/7000 is a dorsoventrally compressed skull with an incomplete left zygomatic arch, both P4–M3 series, a damaged premaxillary bone, and nasals displaced inside the nasal incision (Fig. 2). MNCN-05/101/2/7001 and MNCN-05/101/2/7002 are two partial skulls, laterally twisted and compressed, broken off behind the orbit, and not preserving the premaxillary bone (Fig. 3). MNCN-05/101/2/7001 has both P1–M1 series and MNCN-05/101/2/7002 has both P3–M1. The nasal bones are laterally rotated and have their anterior tips broken. Descriptions are mainly based on MNCN-05/101/2/7000, although comparisons with the other two specimens are detailed when necessary.

Skull—The dorsal profile of the skull is almost flat, partially due to its strong dorsoventral compression. The postorbital region is slightly raised, indicating a probable original dolichocephalic skull roof. The frontal bone is flat. The braincase is wide and low, with the maximum width located between the posterior half of the zygomatic arches. The nasals are long and unfused, anteriorly pointed. Their dorsal surface is smooth and has a soft concave profile, lacking any signal of horn boss. Their ventral surface is concave, with a soft ridge flanking the internasal suture. The anterior half of the nasals is narrow, expanding at about the middle of their total length. The nasal incision reaches the level of P4, but has been displaced because of the general backward slanting suffered by the skull. Its profile is dorsally straight and ventrally concave. Fragments of the posterior part of the premaxilla are preserved, but badly crushed. Orbits are situated just under the skull roof, with their anterior borders reaching the level of the M3; they are not laterally projected. Badly preserved oval infraorbital foramina can be observed on each side of the skull at the level of the anterior border of the P4 in
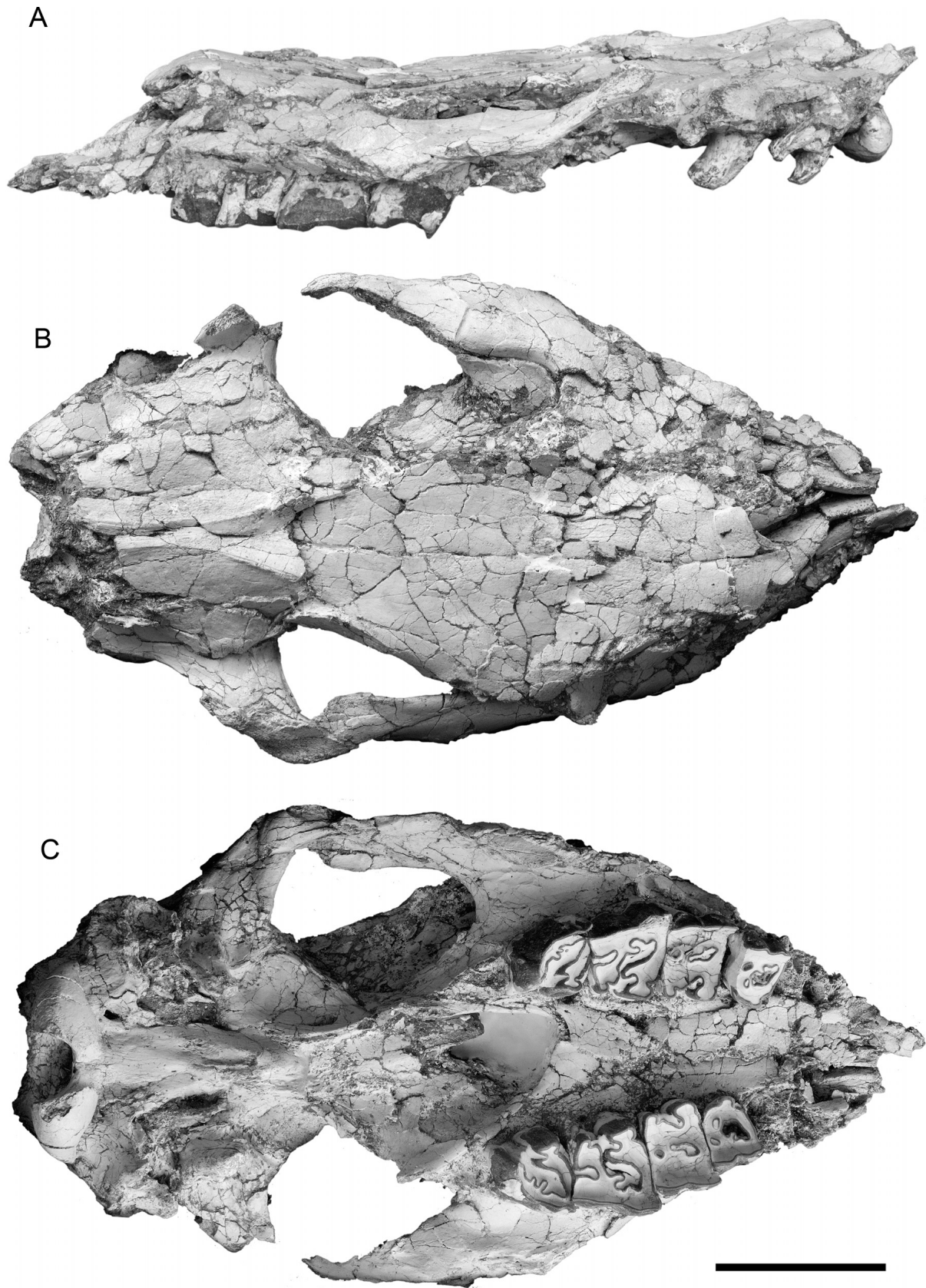
FIGURE 2. Skull of the elasmotheriine rhinocerotid *Hispanotherium matritense* from the early middle Miocene of Príncipe Pío-2 (Madrid Basin, Spain), MNCN-05/101/2/7000. **A**, left view; **B**, dorsal view; **C**, occlusal view. Scale bars equals 10 cm.
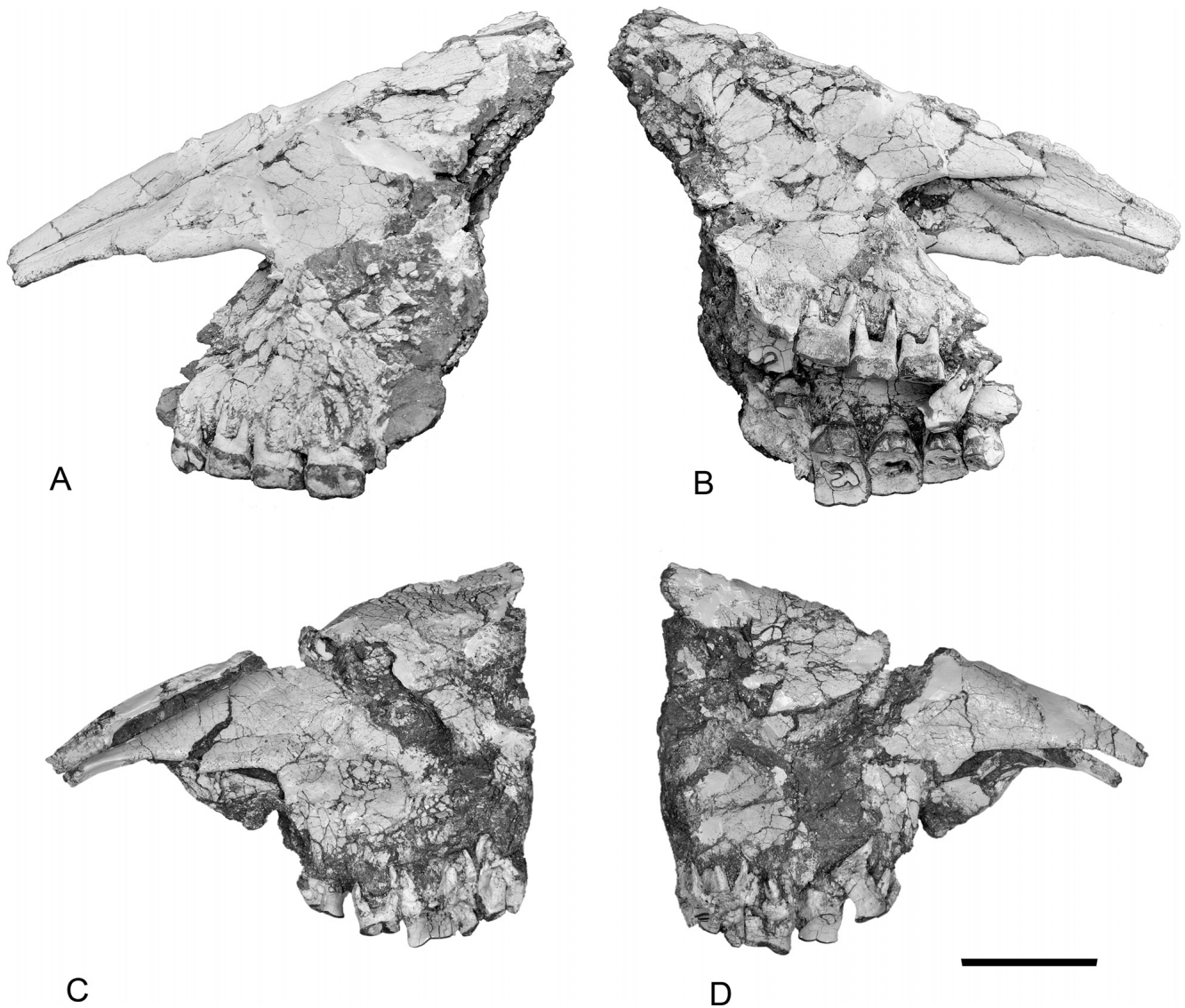
FIGURE 3. Fragmentary skulls of the elasmotheriine rhinocerotid *Hispanotherium matritense* from the early middle Miocene of Príncipe Pío-2 (Madrid Basin, Spain) in lateral view. **A**, **B**, MNCN-05/101/2/7001; **C**, **D**, MNCN-05/101/2/7002. Scale bars equals 10 cm.

MNCN-05/101/2/7000 and above the P3 level in MNCN-05/101/2/7001 and MNCN-05/101/2/7002. The supraorbital apophyses are triangular, small, pointed, laterally projected, and individualized from the orbital margins. The anterior part of each zygomatic arch constitutes a laterally developed facial crest, beginning above the anterior border of the M3. Zygomatic arches are high and fairly well developed, becoming narrower posteriorly, and bending upwards at their final extreme. Frontoparietal crests are sharp and converge backward, without forming a single sagittal crest. The minimal distance between them is 11.6 mm. The occipital face is damaged, preventing its description.

The posterior border of the palate is rounded and their pterygoidean crests are straight, partially broken, and diverge, forming an acute angle. The basicranium has the postglenoid and posttympanic processes clearly separated. The postglenoid process is short, oval in section, and anteriorly curved at the tip. The posttympanic process is short, oblique, and anteriorly curved. The paraoccipital process is also oblique and oriented forwards, having the same length as the posttympanic one.

Paraoccipital and posttympanic processes are basally fused and placed forming a 'C.' The external auditory meatus is partially closed by a lateral flange of the posttympanic process, and is placed at the level of the dorsal border of the occipital condyles. The occipital foramen is oval and has the same width as each occipital condyle. These are subtriangular, with the wider surface flat and oriented downward.

Upper Dentition—The fragmented premaxillary bone of MNCN-05/101/2/7000 (Fig. 4A) is badly dorsoventrally crushed, so no upper incisor insertions are preserved. The premolars of the three specimens have closed median valleys. In MNCN-05/101/2/7001 and MNCN-05/101/2/7002 (Fig. 4B), remains of cement cover the ectoloph of the premolars and fill the valleys. Cheek teeth are subhypsodont, with a softly undulated ectoloph. The protocones of M2–M3 are more constricted than that of M1; the parastyle is short and wide except on the M3, where it is very narrow and sharp; cement is present in their median valley and the postfossette of the M2. All of them belong to adult individuals, as judged from their wear degree.
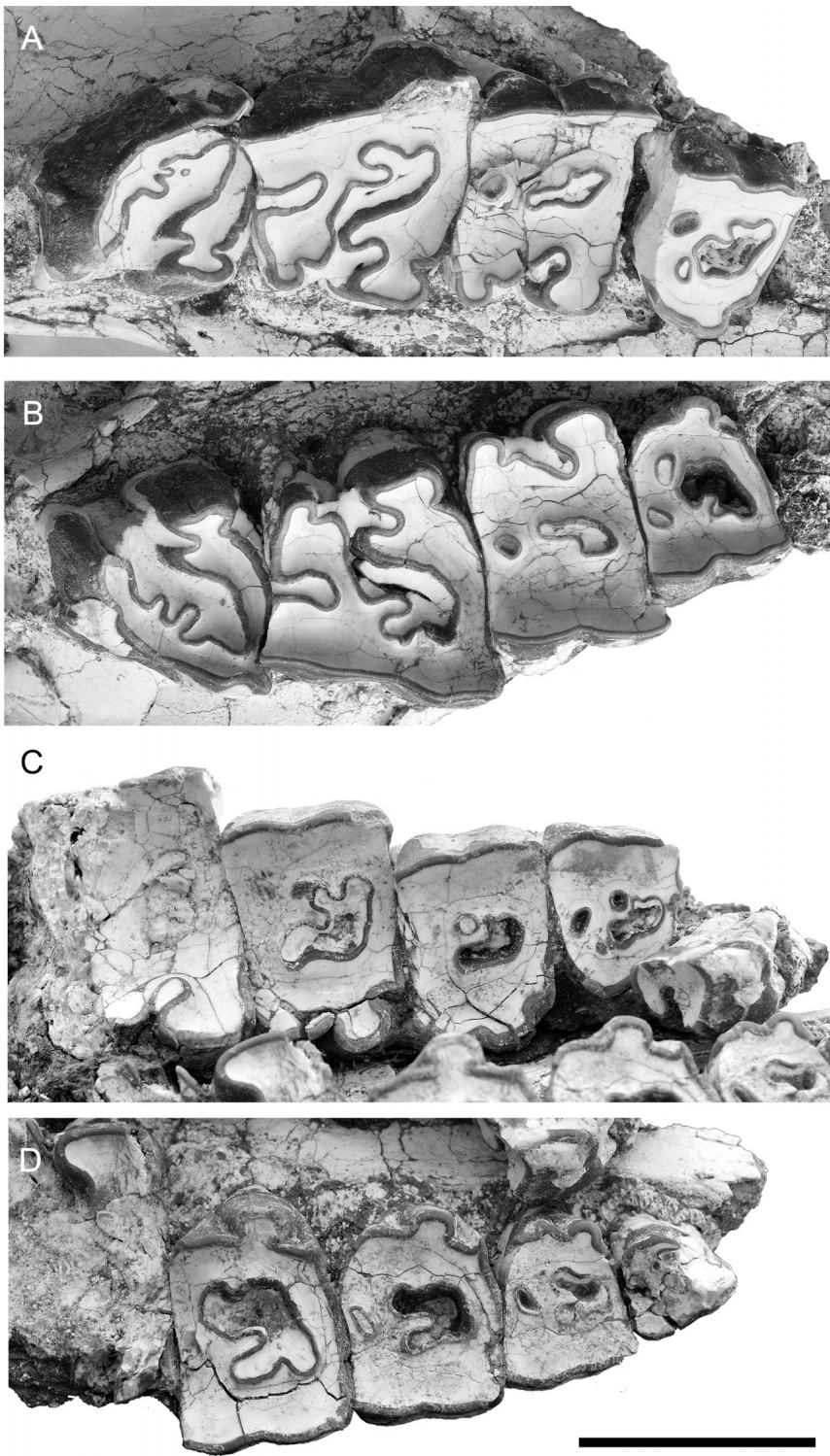
FIGURE 4. Upper teeth of the elasmotheriine rhinocerotid *Hispanotherium matritense* from the early middle Miocene of Príncipe Pío-2 (Madrid Basin, Spain) in occlusal view. MNCN-05/101/2/7000 **A**, right P4–M3; **B**, left P4–M3. MNCN-05/101/2/7001 **C**, right P1–M1; **D**, left P1–M1. Scale bar equals 5 cm.

P1 is oval in occlusal view. The protoloph is absent. Anterior and posterior cingula are present. The ectoloph is wide. Protocone and hypocone are connected by a wide lingual bridge. Crochet and crista are small and narrow.

P2 is square in occlusal view, the protocone is rounded. The hypocone is lingually expanded in the lingual side and is smaller than the protocone. The posterior cingulum is well developed, and encloses a small posterior valley. The anterior and lingual cingulum are absent. Crochet and crista are fused, forming a rounded small medifossette.

The protocone of P3 is rounded, has a flat lingual side, and both anterior and posterior protocone folds well developed. The ectoloph and the lingual bridge are broad and have the same width. The protoloph has a pointed fold on its lingual side that contacts
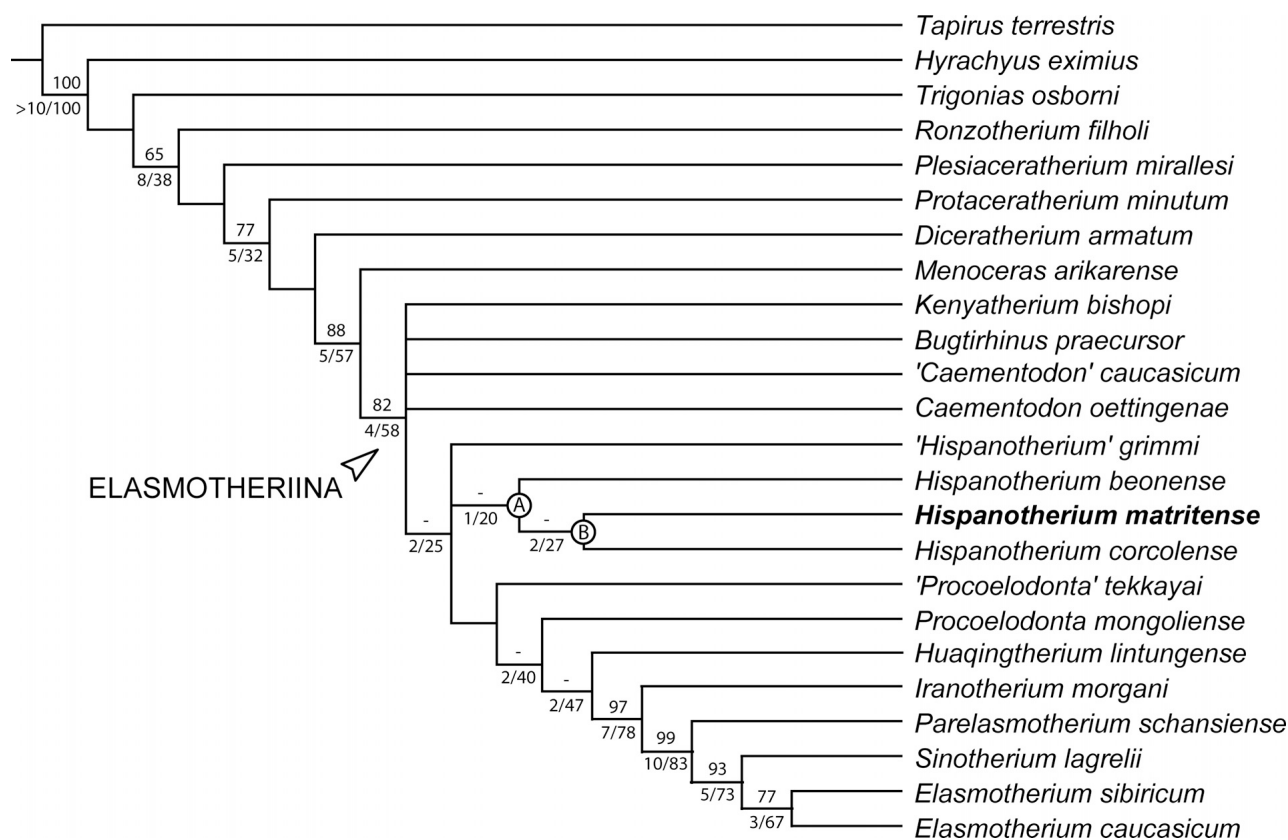
FIGURE 5. Phylogenetic relationships of *Hispanotherium matritense* within Elasmotheriina (Rhinocerotidae). The strict consensus tree (646 steps; CI = 0.52; RI = 0.66) has been obtained from three most parsimonious trees by means of TnT v. 1.1. (Goloboff et al., 2008). The value above each branch represents the bootstrap proportions for clades found in more than 50% of 1000 replicates. The pair of numbers below a branch represents, from left to right, absolute and relative Bremer values respectively (according to Goloboff, 2008). Character/taxa matrix is basically that of Antoine (2002, 2003) and Deng (2008).

with the base of the protocone. As in P2, crista and crochet are united, forming a rounded median valley, filled with cementum.

In P4, the protocone is smooth and rounded, with the anterior fold slightly more developed than the posterior one; hypocone and protocone are fused, delimiting a close median valley; the ectoloph is much wider than protoloph and metaloph; double crochet present; the labial crochet is blunt and short, the lingual crochet is narrow, very long, lingually oriented, and contacts with the lingual bridge, closing a small oval fossette; the crista is short and smooth; the parastyle is narrow and the mestastyle is wide; there is a shallow, oval postfossette; the lingual cingulum is a low smooth ridge extending posteriorly from the protocone, more developed in the right P4. In MNCN-05/101/2/7001, crista and crochet are rounded and separated.

M1 is square in occlusal view and heavily worn; protocone is rounded and constricted at both sides. Due to its advanced wear, metaloph and protoloph are fused, delimiting a closed median valley. The postfossette is reduced and rounded. The anterior cingulum is absent. The metastyle is wide. The hypocone has a small lingual rounded expansion limited by an anterior groove.

M2 is larger than M1 and has a longer ectoloph that gives a more 'fan'-like shape in occlusal view. The protocone is wide, strongly constricted, and lingually flattened. The antecrochet is strong, extending posteriorly as a hanging expansion into the median valley, but it does not reaches the metaloph at the present stage of wear, leaving a narrow opening of the median valley. The crochet is thick and short; the crista is present but poorly developed. The metastyle is wide and long. The protocone is well developed, expanded, and square and has an expansion similar to that of M1. The posterior cingulum is present, closing a narrow and curved posterior valley filled with cement. Cement also fills the median valley. No anterior cingulum has been observed.

M3 has a typical triangular occlusal surface; the protocone has a flat to slightly concave lingual border, and is wider and more constricted than the M2. The hypocone is less developed than the protocone. Antecrochet and crista are absent. There are two crochets and a third incipient expansion. A tiny fossette is present in the median valley of the right M3, in front of the labialmost crochet. Protoloph is oblique, oriented posteriorly and has a triangular expansion, less developed than the M2. The protoloph-ectometaloph connection is narrow. The ectometaloph is labially convex; it has a constant width and finishes in a sharp hypocone. The parastyle is short, very narrow, sharp, and projected forwards. The paracone fold is not very developed. The posterior cingulum is reduced to a prominent tubercle partially covered by cement. Cement fills completely the median valley and covers the anterolingual side of the tooth.

MORPHOLOGICAL COMPARISON

The dental morphology of the rhinoceros material from Príncipe Pío-2 fits with that of the type series of *Hispanotherium matritense* from Puente de Toledo (Madrid), showing a closed median valley on the premolars and developed secondary enamel folds. Their enamel folding in the median valley and ectoloph undulation fall within the observed variability in the Iberian

TABLE 1. Comparative measurements (mm) of the skulls of *Hispanotherium matritense* from the middle Miocene of Intercambiador Príncipe Pío (Madrid Basin, Spain).

	MNCN-05/101/2/7000	MNCN-05/101/2/7001
5. Minimal width of braincase	105*	
9. Distance between nasal notch and orbit	113	107*
13. Distance between occipital condyle and M3	397*	
16. Width between mastoid processes	190	
17. Minimal width between parietal crests	11	
18. Width between postorbital processes	151*	
20. Width between lachrimal tubercles	165*	
21. Maximal width between zygomatic arches	284*	
22. Width of nasal base	65*	67*
25. Cranial height in front of P2		150*
26. Cranial height in front of M1		189*
31. Width of foramen magnum	40	
32. Width between exterior borders of occipital condyles	118	

*Approximate measurement due to compression.

specimens, being simpler and smoother, respectively, than Asian specimens referred to *H. matritense* by Deng (2003). A preliminary study of the abundant postcranial remains confirms its determination. Postcranial differences between *H. matritense* and some related species are carefully detailed in Antoine (2002), so we will mainly focus on cranial characters in light of the new remains from Príncipe Pío-2.

TABLE 2. Measurements (mm) of upper teeth of *Hispanotherium matritense* (MNCN-05/101/2/7000, 05/101/2/7001, and 05/101/2/7002) from the middle Miocene of Intercambiador Príncipe Pío in the Madrid Basin (Madrid, Spain).

		Intercambiador Príncipe Pío (Spain)				Hommes (France)[1]	Laogou (China)[2]
		MNCN-05/101/2/7000		MNCN-05/101/2/7001			
Upper teeth		Left	Right	Left	Right	Left	
P[1]	L			20.9	—		22.5–24.0
	W			21.2	20.4		23.0
	H			19.4	18.7		25.0
P[2]	L			25.8	25.4		
	W			29.7	30.4		
	H			16.0	14.6		
P[3]	L			27.5	27.2	26	30.0
	W			35.0	37.1	38.9	41.0
	H			15.1	13.1	—	38.0
P[4]	L	29.6	30.4	30.4	30.4		33.5
	W	40.8	40.9	41.0	43.0		45.5
	H	18.7	18.2	19.1	18.2		44.5
M[1]	L	37.7	37.8				44.5
	W	51.7	53.4	—	51.0		52.5
	H	13.4	12.3				44.0
M[2]	L	51.9	52.1				49.0–56.0
	W	57.5	59.4				55.0–57.0
	H	23.9	23.4				44.0–63.6
M[3]	L	56.0	57.7				47.0–49.5
	W	37.5	41.8				49.5–50.5
	H	27.7	28.4				30–70**

**Unworn teeth. Measurements from Laogou (China) and Hommes (France) were obtained from Deng (2003)[1] and Ginsburg et al. (1987),[2] respectively.

The last diagnosis for *H. matritense* was given by Deng as a "small rhinocerotid with one nasal horn, maybe with sexual dimorphism" (Deng, 2003:142). The inclusion of "*H.*" *tungurense* within the genus *Hispanotherium* led us to consider the horn presence as a sexually dimorphic character (Cerdeño, 1995, 1996). If we focus on *H. matritense*, only one nasal bone has been published. The piece, labeled as MNCN-Ac-17, is a well-preserved nasal fragment from the Spanish locality of Paseo de las Acacias (Madrid). It is long, straight, and narrow and does not exhibit any signal of nasal horn boss (Cerdeño and Iñigo, 1997). Its general morphology matches with that of the three nasal bones studied from Príncipe Pío-2 site, pointing to a hornless condition for *H. matritense*.

The Spanish site of Córcoles represents the earliest record of the genus *Hispanotherium* (Iñigo, 1993). Firstly recognized as *H. matritense* (Íñigo, 1993; Íñigo and Cerdeño, 1997), their remains were later identified as *Hispanotherium corcolense* (Antoine et al., 2002). An unpublished braincase fragment (IGME 1174M) stored in the Museo del Instituto Geológico y Minero de España is the only known cranial material from Córcoles. Even though it coincides with MNCN-05/101/2/7000 from Príncipe Pío-2 in the rather flat skull roof and their low, sharp, and converging, but separated, frontoparietal crests, these traits are also shared with "*Plesiaceratherium*" *platyodon*, the second rhinoceros identified at Córcoles.

A new species of *Hispanotherium* from the Tung-gur Formation (late Miocene) from Inner Mongolia was described based on both cranial and postcranial remains and erected as *Hispanotherium tungurense* (Cerdeño, 1996). Broadly, *H. tungurense* is larger and has a developed nasal horn boss, contrary to *H. matritense*. It has also stronger enamel folding, more constricted protocone, and more undulated ectoloph. Both have the same nasal incision shape and an elevated posterior end of the zygomatic arch (even though is much more developed in "*H.*" *tungurense*). It is important to mention that other shared characters such as infraorbitalis foramen reaching the level of P4, anterior part of the orbit at the level of the M3, and a flat skull profile can be easily distorted by general slanting and ontogeny (Borsuk-Bialynicka, 1973) and should be compared with caution. The same occurs with some cranial differences such as a deeper nasal incision (above P4) in *H. matritense*, a linking characteristic with more modern elasmotheriines such as *Ningxiatherium*. Dental morphology of both *H. matritense* and "*H.*" *tungurense* are not far from each other. *H. tungurense* show a more undulated ectoloph. This fact is shared by most Miocene elasmotheriines, because they show a rather similar dental pattern quite different from the enamel folding complexity of the derived hypsodont species, such as *Sinotherium*, *Elasmotherium*, or even *Iranotherium*.

Heissig (1974) described the species *Hispanotherium grimmi* according to several remains from the Turkish locality of Sofça 4. The species was synonymized with *H. matritense* by Cerdeño (1989) and posteriorly retained as a distinct species of the genus *Hispanotherium* by several authors (Cerdeño, 1995; Antoine et al., 2002). Our phylogenetic analysis places "*H.*" *grimmi* apart from the genus *Hispanotherium*. 1968 VI 43, the only known nasal bone, lacks any nasal roughness, albeit horn insertion was included as a diagnostic character for the species (Heissig, 1974). The nasal is short, robust, and triangular in lateral view, resembling the nasals of *Hispanotherium beonense* to some degree. Even though we have not directly observed it, Heissig describes some kind of shallow rugosities present on its posterior half (Heissig, 1976). We think that the simple nasal suture and the position of this scars suggest the absence of nasal horn, instead of being a juvenile stage of development as proposed (Heissig, 1974). If horn presence in "*H.*" *grimmi* is not proven to be dimorphic, it could be a linking character with *H. matritense*.

H. beonense was discovered in the late early Miocene (MN4–5) of France and originally named as *Aegyrcitherium beonense*

(Antoine, 1997). Shortly after *Aegyrcitherium* was considered a subgenus of *Hispanotherium* (Antoine et al., 2002; Guérin and Pickford, 2003). Posteriorly, the species was directly included in the genus *Hispanotherium*, even though phylogenetic analysis set it as a distinct taxa (Antoine, 2003). Both *H. matritense* and *H. beonense* share a low anterior end, a high posterior end of the zygomatic arch, and a flat skull profile. In contrast to *H. matritense*, *H. beonense* has a small triangular nasal bone, rostrally broadened nasals, a processus postorbitalis on the zygomatic arch, laterally projected orbits, labial cingulum on upper premolars, and stronger zygomatic arches. Several nasal bones from *H. beonense* have been recorded. Some of them have nasal rugosities confined to the nasal tip (MNHN Béon 1998 E3 3060 and MHNT Béon 1991 G4 64), likewise placed as those found in some Teleoceratina rhinoceroses such as *Brachypotherium* or *Teleoceras*. Others are narrower and have a smooth dorsal surface, so sexual dimorphism could be feasible in this species (Antoine, 2002), a main cranial difference with *H. matritense*. The peculiar horn rugosities of *H. beonense* or the horn absence in *H. matritense*, "*H.*" *grimmi*, and more distantly *Ougandatherium napakense* (Guérin and Pickford, 2003) suggest a diverse nasal horn development within early Elasmotheriini, characterized by a hornless basal condition and a rapid diversification towards well-developed nasal or frontal horns. These data contrast with previous works, which proposed the presence of a nasofrontal horn as a synapomorphy of the whole elasmotheriine group (Fortelius and Heissig, 1989).

CLADISTIC ANALYSIS

The taxonomic status of some species attributed to the genus *Hispanotherium* has been a cause of debate. This problem, widespread among Elasmotheriina, is mainly caused by a limited knowledge of several basal taxa together with common dental morphologies at an intergeneric level. Íñigo and Cerdeño (1997) revisited the Asian *Caementodon oettingenae*, *Beliajevina caucasica*, and *Begertherium borissiaki* and considered them as synonymous with *H. matritense*. Posterior analyses on Elasmotheriina made by Antoine (2002, 2003) kept some of them in their own genus: placing *Caementodon oettingenae* basal to "*Caementodon*" (*Beliajevina*) *caucasicum*, transferring *Begertherium borissiaki* close to the later diverging species *Procoelodonta mongoliense*, and finally considering *Hispanotherium* as a paraphyletic group composed by "*H.*" *grimmi*, *H. matritense*, *H. corcolense*, and "*H.*" *beonense* (Antoine, 2002, 2003). In addition, Deng (2003) assumed a wider intraspecific variability partially coinciding with Íñigo and Cerdeño (1997) and referred some of the elasmotheriine remains from the Chinese locality of Laogou to the type species *H. matritense*. The same analyses considered "*H.*" *tungurense* basal to the later diverging Elasmotheriina, separating it from other *Hispanotherium* species (Antoine et al., 2002; Deng, 2003).

Our phylogenetic analysis produced three most parsimonious trees with a length of 646 steps long (CI = 0.52; RI = 0.66). Consistency index are similar to those of previously published phylogenies (Antoine et al., 2002). The strict consensus tree is represented in Figure 5. The tree topology generated in our analysis is broadly consistent with that forwarded by Deng (2008) except for the unsolved polytomy of *Ningxiatherium euryrhinus*, *Ningxiatherium longirhinus*, and the genus *Elasmotherium*. The branching sequence of Elasmotheriina is (*K. bishopi*, *B. praecursor*, "*C.*" *caucasicum*, *C. oettingenae* ("*H.*" *grimmi* (*H. beonense* (*H. matritense, H. corcolense*)) ("*P.*" *tekkayai* (*P. mongoliense* ((*H. lintungense*, "*H.*" *tungurense*) (*I. morgani* (*P. schansiense* (*S. lagrelii* (*E. sibiricum*, *E. caucasicum*)))))))))). Cranial data provided for *H. matritense* clarify the phylogenetic relationships of the genus *Hispanotherium*. Monophyly for a *H. matritense*, *H. corcolense*, and *H. beonense* clade (node A) is weakly supported by the following synapomorphies: close frontoparietal crests, abrupt anterior tip of the zygomatic process of maxillary, lingual groove of the mandibular ramus present, lingual cingulum usually present on P2–P4 and usually absent on M1–M3, and posterior cingulum low and reduced on the M1–M2. The monophyly of the Iberian *Hispanotherium* species, comprising *H. matritense* and *H. corcolense* (node B), has been previously proposed as a feasible alternative for the paraphyletic status of the French and Iberian species (Antoine et al., 2002). In our analysis it is supported by five synapomorphies: developed crown of the i1, weaker protocone than hypocone on the P2, usually present crista on the upper molars, straight posterior part of the ectoloph on the M1–2, and usually absent calcaneus fibula-facet. On the other hand, "*H.*" *tungurense* appears as a more derived representative of the Elasmotheriina. This clade, labeled as node C, strongly sets apart "*H.*" *tungurense* and *H. lintungense*, relying on following synapomorphies: usually simple crochet and usually absent lingual cingulum on P2–P4, protocone less than the hypocone and protoloph joined to the ectoloph on the P2, transverse metaloph on the P3–P4, separated hypocone and metacone on the P4, crista usually absent on the upper molars, glenoid fossa of the scapula with a straight medial border, and always present posterior expansion of the pyramidal-facet of the unciform. The presence of a lingual groove in the mandibular ramus and the low and reduced posterior cingulum on M1–M2 appear also in the genus *Hispanotherium* and are considered as convergent characters. "*H.*" *grimmi* is also excluded and placed as the sister group of the genus *Hispanotherium* and the more evolved Elasmotheriina clade.

Three elasmotheriine species have been recorded from the European early to middle Miocene: *H. corcolense*, *H. beonense*, and *H. matritense*. *H. corcolense* is restricted to the early Miocene of Córcoles (MN4a, zone C), being the first occurrence of the group in the Iberian Peninsula (Antoine et al., 2002). At the same time, *H. beonense* appeared in the early Miocene of Pellecahus, France (MN4a, zone C; Antoine et al., 2000), extending its chronostratigraphic range up to the MN5 of the Aquitaine and Loire Basins (Antoine, 1997). Finally, *H. matritense* appeared in the western European fossil record, becoming a key species in the Iberian middle Miocene macromammal assemblages (from the MN4b to the MN5, zones D and E; Antoine et al., 2002). At least some French assemblages had the greatest diversity of western European Elasmotheriines, because *H. matritense* and *H. beonense* were sympatric on the Loire Basin (Ginsburg et al., 1987; Antoine et al., 2002).

The evolutionary history of the Elasmotheriina is marked by a rapid lower Miocene radiation. This was probably due to a wide early paleobiogeographic distribution and a global polar cooling that progressively substituted moist subtropical forests with open landscapes characterized by drought-adapted vegetation (Axelrod, 1975). The new geographic and climatic conditions favored a major dispersal event between Asia and Europe (named as 'Proboscidean Datum Event'; Madden and Van Couvering, 1976). *H. corcolense* and *H. beonense* appeared in the early Miocene (MN4a, Zone C), being the earliest known elasmotheriine species in the European fossil record. Their common ancestor would have been differentiated in Asia, passed through the Anatolian plate, and dispersed westwards into southwestern Europe (Antoine et al., 2002; Deng, 2003). Our novel phylogenetic hypothesis suggests that the European climatic conditions during the late early Miocene favored a short-termed evolutionary radiation independent from the main Asian elasmotheriine lineage. This diversification has also been observed in other contemporary macromammal groups, such as anchitheriine equids (Sánchez et al., 1998; Salesa et al., 2004) and boselaphine bovids (Gentry et al., 1999). Meanwhile, *H. corcolense* and *H. beonense* remained as endemic species with very restrictive biogeographic and chronostratigraphic ranges; *H. matritense* spread back

eastwards along the Greek-Iranian Province and reached the Chinese basins, where it has been recorded well into the middle Miocene (Deng, 2003), thus increasing the Asian elasmotheriine diversity.

CONCLUSIONS

The analysis of new specimens of *H. matritense* from the middle Miocene of Príncipe Pío-2 (Madrid Basin, Spain) gives a full picture of the species and supplements the previously known material. The probable horn absence in *H. matritense* is shared with other primitive elasmotheriines (such as *O. napakense*), whereas its dental configuration is closer to other derived species such as *Procoelodonta mongoliense*. The hornless nasals of *H. matritense* point out that the presence and shape of nasal horns are homoplastic characters above the genus level in Elasmotheriina. Our phylogenetic analysis places *H. matritense* close to *H. corcolense* and *H. beonense* (*H. beonense* (*H. corcolense*, *H. matritense*)), pointing to a monophyletic *Hispanotherium* genus. The exclusion of "*H.*" *tungurense* and "*H.*" *grimmi* clarifies the previously paraphyletic status of the genus. In addition, the topology of the genus *Hispanotherium* produced by our analysis results in a satisfactory alternative hypothesis to those previously proposed (Antoine, 2002, 2003; Antoine et al., 2002) on the basis of both geographical and chronostratigraphical points of view.

ACKNOWLEDGMENTS

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