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A new elasmotheriine (Mammalia, Rhinocerotidae) from the Early Miocene of Spain

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Abstract – A new species of *Hispanotherium* from the Early Miocene of Spain is named. Its phylogenetic relationships within Elasmotheriina are discussed owing to a cladistic analysis. *H. grimmi* Heissig, 1974 and *H. beonense* Antoine, 1997 are consequently reintegrated in the genus *Hispanotherium*, together with the type species *H. matritense* and the new species, which differs from other ones by several dental and postcranial features. The westward dispersal of the Elasmotheriina from Asia toward Western Europe during the Early Miocene is hypothesized. To cite this article: P.-O. Antoine, C. R. Palevol 0 (2002) 1–8. © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Rhinocerotidae / Elasmotheriina / Hispanotherium / Early Miocene / Spain / Corcoles / phylogeny

Résumé – Un nouvel élasmothériiné (Mammalia, Rhinocerotidae) du Miocène inférieur d'Espagne. Une nouvelle espèce de *Hispanotherium*, du Miocène inférieur d'Espagne, est nommée. Ses relations phylogénétiques parmi les Elasmotheriina sont discutées à l'aide d'une analyse cladistique. *H. grimmi* Heissig, 1974 et *H. beonense* Antoine, 1997 sont réattribuées au genre *Hispanotherium*, avec l'espèce type *H. matritense* et la nouvelle espèce. Celle-ci diffère des autres par plusieurs caractères dentaires et postcrâniens. L'hypothèse de dispersion vers l'ouest des Elasmotheriina depuis l'Asie jusqu'en Europe occidentale au cours du Miocène inférieur est privilégiée. Pour citer cet article : P.-O. Antoine, C. R. Palevol 0 (2002) 1–8. © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Rhinocerotidae / Elasmotheriina / Hispanotherium / Miocène inférieur / Espagne / Córcoles / phylogénie

Version abrégée

1. Introduction

Le gisement de Córcoles (Guadalajara, Espagne) a livré une faune abondante et diversifiée de mammifères [1] datée du Miocène inférieur (Zone C ; MN 4a). Cette faune inclut deux espèces de rhinocérotidés, dont un élasmothériiné, initialement décrit sous le nom d'*Hispanotherium matritense* [19, 21]. Toutefois, les 700 spécimens dentaires et postcrâniens concernés présentaient certaines différences morphologiques avec l'hypodigme d'*H. matritense sensu stricto*. De ce fait, «*H. matritense* de Córcoles» et *H. matritense s. s.* ont été traitées séparément dans l'analyse cla-

distique des Elasmotheriina [3]. Cette analyse, détaillée ci-dessous, confirme la particularité de l'élasmothériiné de Córcoles et permet de lui conférer un statut spécifique au sein du genre *Hispanotherium*.

2. Systématique

Ordre Perissodactyla Owen, 1848
Famille Rhinocerotidae Owen, 1845
Sous-tribu Elasmotheriina Bonaparte, 1845
Hispanotherium Crusafont et Villalta, 1947

Espèce type. *H. matritense* (Lartet in Prado, 1864).

Autres espèces. *H. grimmi* Heissig, 1974 ; *H. beonense* (Antoine, 1997) ; *H. corcolense* n. sp.

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Diagnose. Elasmotheriiné avec un hypocône étranglé sur M1, un protocône étranglé sur P3-4, une diaphyse au bord médial rectiligne sur le radius, des facettes proximales radio-ulnaires généralement isolées, une petite facette pour le trapèze sur le scaphoïde, une tubérosité postérieure rectiligne sur le magnum, une facette 1 pour le calcaneum généralement basse et large sur l'astragale et des reliefs intermédiaires bas sur les métapodes centraux.

***Hispanotherium corcolense* n. sp.**

Holotype. Série supérieure d'un individu, avec P1-P4 et M2-M3 gauches et droites (Co-4934 à Co-4945). Tous les spécimens sont conservés au laboratoire de paléontologie de l'Universidad Complutense de Madrid (LPUCM), Espagne.

Paratype. Série inférieure droite, avec p2-m1 : Co-212, conservée au LPUCM.

Hypodigme. Principalement constitué des 654 spécimens listés par Iñigo [19] et conservés au LPUCM. Quelques restes supplémentaires au Museo Geominero de España et au Museo Nacional de Ciencias Naturales, à Madrid.

Locus typicus. Córcoles (Guadalajara, Espagne).

Stratum typicum. Miocène inférieur, Aragonien inférieur, Zone C et MN 4a [21, 23].

Distribution spatio-temporelle. Restreinte à la localité type.

Étymologie. De Córcoles, nom du gisement type.

Diagnose. *Hispanotherium* avec un cingulum labial généralement présent sur les prémolaires supérieures; antécrochet généralement présent sur P4; vallée postérieure parfois fermée sur d2; fosse glénoïde présentant un bord médial droit sur l'omoplate; échancrure médiale généralement superficielle sur le magnum; expansion de la facette pour le pyramidal généralement absente sur l'unciforme.

3. Relations phylogénétiques

Celles-ci sont hypothésées à l'aide d'une analyse cladistique portant sur 282 caractères anatomiques [3], contrôlés notamment chez l'ensemble des *Elasmotheriina*.

Deux arbres également parcimonieux sont obtenus (748 pas; IC = 0,47; IR = 0,64), où les *Elasmotheriina* sont monophylétiques (Fig. 1). La seule ambiguïté concerne précisément les relations phylogénétiques entre *H. matritense* et *H. corcolense* n. sp., qui forment un clade dans l'arbre 1 (sélectionné par pondération successive; Fig. 1A) et un ensemble paraphylétique dans l'arbre 2 (Fig. 1A). La séquence de branchement des *Elasmotheriina* est (*K. bishopi* (*B. praecursor* (*C. oettingenae* ((*B. caucasica*, *T. fangxianense*) (*H. grimmi* ((*H. matritense*, *H. corcolense*) («A.» *beonense* (*B. tekkayai* (*B. borissiki* (*P. mongoliense* (*H. lintungense* (*I. morgani* (*P. schansiense* (*S. lagrelii* (*Elasmotherium*)))))))))))).

Les dichotomies au voisinage de *H. corcolense* ne sont pas bien soutenues. En revanche, l'examen de la distri-

bution des caractères dans l'arbre 1 permet d'isoler fiablement les *Elasmotheriina* les plus primitifs (*Kenyatherium*, *Bugtirhinus* et *Caementodon*) et les plus évolués (*Procoelodonta*, *Huaqingtherium*, *Iranotherium*, *Parelasmotherium*, *Sinootherium* et *Elasmotherium*).

4. Comparaison

La comparaison anatomique entre *H. corcolense* n. sp. (Fig. 2) et les taxons morphologiquement proches, *H. matritense*, *H. grimmi* et «*Aegyrcitherium*» *beonense* Antoine, 1997, effectuée en marge de l'analyse cladistique, est synthétisée dans le Tableau. Ainsi, certaines caractéristiques dentaires et postcrâniennes isolent *H. grimmi*, mais sont communes à *H. corcolense*, *H. matritense* et «A.» *beonense*; d'autres isolent seulement *H. matritense* ou encore «A.» *beonense*. Enfin, six caractères sont diagnostiques de *H. corcolense*: le cingulum labial, généralement présent sur les prémolaires supérieures, l'antécrochet, généralement présent sur P4, la vallée postérieure, parfois fermée sur d2, la fosse glénoïde, présentant un bord médial droit sur l'omoplate, l'échancrure médiale, généralement superficielle sur le magnum et l'expansion de la facette pour le pyramidal, généralement absente sur l'unciforme.

5. Discussion et conclusions

De nombreux auteurs [6-10, 21, 24] considèrent que tous les élasmothériinés du Miocène inférieur et moyen d'Eurasie appartiennent à *Hispanotherium*, ce que la présente analyse réfute: outre l'espèce type *H. matritense*, le genre doit être restreint à *H. grimmi*, *H. beonense* (initialement rapporté au genre *Aegyrcitherium* Antoine, 1997) et *H. corcolense* n. sp. Les autres *Elasmotheriina* (*Caementodon oettingenae*, *Beliajevina caucasica*, *Tesselodon fangxianense*, *Kenyatherium bishopi* et *Bugtirhinus praecursor*, primitifs; «B.» *tekkayai*, «B.» *borissiki*, *P. mongoliense*, *H. lintungense*, *I. morgani*, *P. schansiense*, *S. lagrelii* et *Elasmotherium*, évolués) sont rapportés à des genres distincts d'*Hispanotherium*. Ce genre est paraphylétique. Toutefois, la monophylie de (*H. matritense*, *H. corcolense*) ne peut être exclue.

L'élasmothériiné le plus ancien décrit à ce jour provient du Miocène basal du Pakistan [3, 4]. Les dichotomies suivantes (Fig. 1) impliquent successivement des élasmothériinés d'Asie, du Caucase et d'Asie Mineure (Anatolie), puis d'Europe occidentale. Le groupe paraît donc s'être dispersé vers l'ouest pendant le Miocène inférieur, probablement à la faveur de la collision entre les plaques Arabo-Africaine et Eurasiatique [3].

La présence de trois élasmothériinés est avérée en Europe occidentale à la fin du Miocène inférieur: *H. corcolense* et *H. beonense* pendant la MN 4a; *H. beonense* et *H. matritense* pendant la MN 4b et la MN 5.

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1. Introduction

The Elasmotheriina are fossil Rhinocerotidae known from the Early Miocene to the Late Pleistocene in Eurasia [3]. Among them, the genus *Hispanotherium* is widely spread in Spain, Portugal and France during the late Early Miocene [3, 7, 8] and during the Middle Miocene in Anatolia [16, 17]. The type species *H. matritense* (Lartet in Prado, 1864) has the best representation. It has been recognized in about 30 localities, mainly from Iberia [6-8], but also in France [3, 14].

The locality of Córcoles (Guadalajara, Spain) has yielded a diversified mammal fauna [1, 21], which allows to place it within the Lower Aragonian (zone C; MN 4a). The rhinocerotid fauna was supposed to associate '*Plesiaceratherium*' *platyodon* (Mermier, 1895) and *H. matritense* [19-21]. Nevertheless, the latter appeared to bear some distinctive features, once compared with the whole hypodigm of *H. matritense sensu stricto* [3, 21].

A cladistic analysis has been performed recently in order to recover the phylogenetic relationships of Elasmotheriina within Rhinocerotidae [3]. This analysis included an exhaustive list of Elasmotheriina, among which *H. matritense* and '*H. matritense* from Córcoles' were treated as two distinct series. The results, developed in Section 3 and illustrated in Fig. 1 lead us to consider '*H. matritense* from Córcoles' as distinct from *H. matritense sensu stricto* and from other Elasmotheriina. Thus, we propose to name a new species for the former.

2. Systematics

Order Perissodactyla Owen, 1848

Family Rhinocerotidae Owen, 1845

Tribe Elasmotheriini Bonaparte, 1845

Subtribe Elasmotheriina Bonaparte, 1845

Hispanotherium Crusafont and Villalta, 1947

Type species. *H. matritense* (Lartet in Prado, 1864).

Other species. *H. grimmi* Heissig, 1974; *H. beonense* (Antoine, 1997); *H. corcolense* n. sp.

Diagnosis. Elasmotheriine rhinocerotid more evolved than *Kenyatherium*, *Bugtirhinus* and *Caementodon* in having an isolated hypocone on M1, a protocone constriction on P3-4, a straight medial border on the radius diaphysis, proximal radio-ulna facets generally isolated, a small trapezium-facet on the scaphoid, a straight posterior tuberosity on the magnum, a calcaneus-facet 1 generally wide and low on the astragalus and low intermediate relieves on central metapodials. *Procoelodonta*, *Huaqingtherium*, *Iranotherium*, *Sinootherium* and *Elasmotherium* are more evolved in possessing an always-simple crochet

on P2-4, a continuous posterior cingulum on M1-2, a lingual wall on D2 and a constricted entoconid on lower milk teeth.

Hispanotherium corcolense n. sp. (Fig. 2)

Holotype. Upper series of a single individual, with left and right P1-P4 and M2-M3 (Co-4934 to Co-4945). All the specimens are housed in the Laboratory of Palaeontology of the Universidad Complutense (LPUCM), Madrid, Spain.

Paratype. Right lower series, with p2-m1: Co-212, housed in the LPUCM, Spain.

Hypodigm. It mainly consists of 654 dental and postcranial specimens listed in Iñigo [19] and housed in the LPUCM. A few specimens are also stored in the Museo Geominero del Instituto Técnico Geominero de España (ITGE) and the Museo Nacional de Ciencias Naturales (MNCN), both in Madrid, Spain.

Locus typicus. Córcoles (Guadalajara, Spain).

Stratum typicum. Late Early Miocene, Early Aragonian, zone C and MN 4a mammal unit [21, 23].

Geographical and stratigraphical distributions. So far restricted to the type locality and type stratigraphical level.

Etymology. From the type locality (Córcoles).

Diagnosis. *Hispanotherium* with a labial cingulum generally present on the upper premolars (while generally absent in other species); antecrochet generally present on P4 (always absent in other species); posterior valley sometimes closed on d2 (always open in other species); glenoid fossa bearing a straight medial border on the scapula (oval otherwise); generally shallow medial indentation on the magnum (always shallow in *H. matritense* and always deep in both *H. grimmi* and '*A. beonense*'); expansion of the pyramidal-facet generally absent on the unciform (generally present in '*A. beonense*', always absent in both *H. grimmi* and *H. matritense*).

There is no need to further detail the dental and postcranial features of *H. corcolense* n. sp., which are precisely described in Iñigo [19] and Iñigo and Cerdeño [21].

3. Phylogenetic relationships

The phylogenetic relationships of *H. corcolense* n. sp. are assessed by a cladistic analysis, based on 282 anatomical characters [3] and checked in 26 terminal taxa. The outgroups are *Tapirus terrestris* (Linnaeus, 1758), *Hyrachyus eximius* Leidy, 1871, *Trigonias osborni* Lucas, 1900 and *Ronzotherium filholi* (Osborn, 1900). Other non-Elasmotheriina rhinocerotids included in the analysis are the Western European *Protaceratherium minutum* (Cuvier, 1822) and *Plesiaceratherium mirallesi* (Crusafont, Villalta and Truy-

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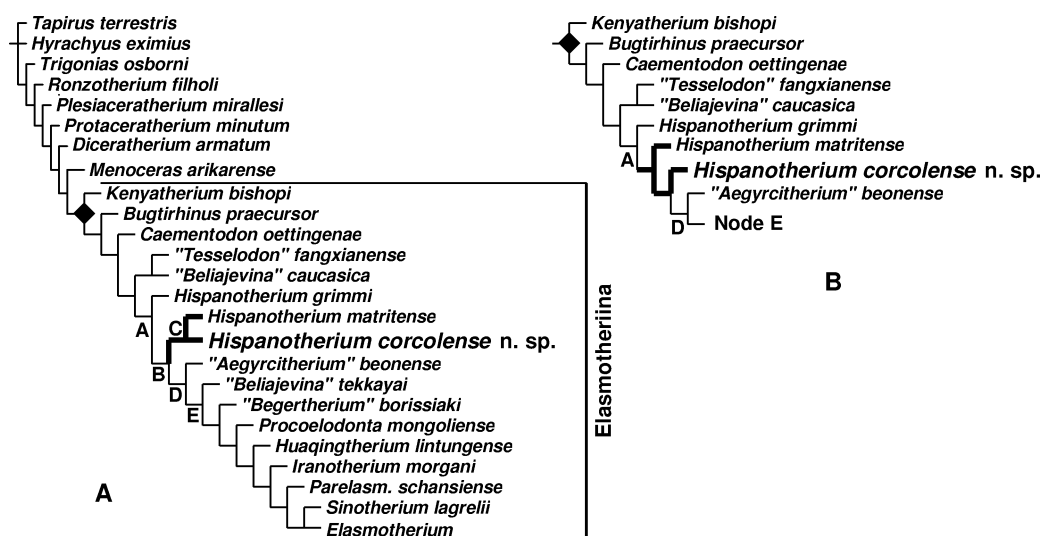


Figure 1. Phylogenetic relationships of *Hispanotherium corcolense* n. sp. within Elasmotheriina (Rhinocerotidae). Cladistic analysis based on 282 anatomical characters [3] checked in 26 terminal taxa listed in Section 3. Two parsimonious trees (746 steps; CI = 0.47; RI = 0.64) are obtained by means of Hennig86, v. 1.5 [11]. **A.** Tree 1, selected by successive weighting. *H. corcolense* n. sp. and *H. matritense* are sister groups. The capital letters A to E correspond to the nodes for which the distribution of characters is discussed in the text. **B.** Tree 2, alternative topology (detail focusing on the Elasmotheriina). The nodes A, D and E of Tree 1 are supported. *H. matritense* is the sister group of (*H. corcolense* n. sp.; node D). The lozenge indicates the hypothetical ancestor of the Elasmotheriina in both trees. The ambiguous branches are thickened.

Figure 1. Relations phylogénétiques d'*Hispanotherium corcolense* n. sp. au sein des Elasmotheriina (Rhinocerotidae). Analyse cladistique fondée sur 282 caractères anatomiques [3] contrôlés chez 26 taxons terminaux (listés au Section 3). Deux arbres également parcimonieux (746 pas; IC = 0,47; IR = 0,64) sont obtenus grâce à Hennig86, v. 1.5 [11]. **A.** Arbre 1, sélectionné par pondération successive. *H. corcolense* n. sp. et *H. matritense* sont des groupes frères. Les lettres capitales A à E correspondent aux nœuds pour lesquels la distribution des caractères est discutée dans le texte. **B.** Arbre 2, topologie alternative (détail des Elasmotheriina). Les nœuds A, D et E de l'arbre 1 sont soutenus. *H. matritense* est le groupe frère de (*H. corcolense* n. sp.; nœud D). Le losange indique l'ancêtre hypothétique des Elasmotheriina dans les deux arbres. Les branches ambiguës sont marquées par des traits épais.

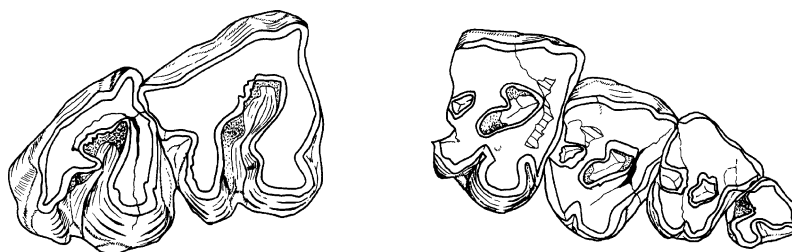


Figure 2. *Hispanotherium corcolense* n. sp.: holotype. Right upper series with P1-P4 (Co-4943, 4942, 4937, 4940) and M2-3 (Co-4935, 4939) from the same individual. Córcoles (Spain, Guadalajara). Occlusal views. Scale bar: 5 cm.

Figure 2. *Hispanotherium corcolense* n. sp. : holotype. Série supérieure droite avec P1-P4 (Co-4943, 4942, 4937, 4940) et M2-3 (Co-4935, 4939) appartenant au même individu. Córcoles (Espagne, Guadalajara). Vues occlusales. Échelle : 5 cm.

ols, 1955) and the North-American *Diceratherium armatum* Marsh, 1875 and *Menoceras arikarense* (Barbour, 1906). *H. matritense* and *H. corcolense* n. sp. are separately checked as distinct series.

The elasmotheriines included in the analysis are *Elasmotherium sibiricum* Fischer, 1809, *Hispanotherium matritense* (Lartet in Prado, 1864), *Iranotherium morgani* (Mecquenem, 1908), *Elasmotherium causicum* Borissiak, 1914, *Sinootherium lagrelii* Ringström, 1923, *Parelasmotherium schansiense* Killgus, 1923 (= *Ninxiatherium longirhinus* Chen, 1977), *Procoelodonta mongoliense* (Osborn, 1924), *Beliajevina caucasica* (Borissiak, 1935), *Begertherium borissiaki* Beliajeva, 1971, *Caementodon oettingenae* Heissig, 1972, *Beliajevina tekkayai* Heissig, 1974, *Hispanotherium grimmii* Heissig, 1974, *Kenyatherium bishopi* Aguirre and Guérin, 1974, *Huaqingtherium lintungense* (Zhai, 1978) (= *Hispanotherium tungurensis* Cerdeño, 1996, = *Caementodon tongxinenensis* Guan, 1993), *Tesselodon fangxianense* Yan, 1979, 'Aegyrcitherium' *beonense* Antoine, 1997, *Bugtirhinus praecursor* Antoine and Welcomme, 2000 and *Hispanotherium corcolense* n. sp.

Beliajevina caucasica (Borissiak, 1935), *Begertherium borissiaki* Beliajeva, 1971, *Caementodon oettingenae* Heissig, 1972, *Beliajevina tekkayai* Heissig, 1974, *Hispanotherium grimmii* Heissig, 1974, *Kenyatherium bishopi* Aguirre and Guérin, 1974, *Huaqingtherium lintungense* (Zhai, 1978) (= *Hispanotherium tungurensis* Cerdeño, 1996, = *Caementodon tongxinenensis* Guan, 1993), *Tesselodon fangxianense* Yan, 1979, 'Aegyrcitherium' *beonense* Antoine, 1997, *Bugtirhinus praecursor* Antoine and Welcomme, 2000 and *Hispanotherium corcolense* n. sp.

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Two equally parsimonious trees are obtained by means of Hennig86, version 1.5 [11]. The trees are 746 steps long, with an average consistency index (0.47) and a rather good retention index (0.64). In both trees, the Elasmotheriina are monophyletic, with *Menoceras arikareense* as a sister-group (Fig. 1). The only uncertainty concerns the relative positions of *Hispanotherium matritense* and *H. corcolense*: in the first tree (Fig. 1A), *H. matritense* and *H. corcolense* form a monophyletic group, whereas *H. matritense* is the sister-group of the (*H. corcolense* ('A.' *beonense* – more evolved Elasmotheriina –) clade in the second tree (Fig. 1B). The former topology, with a (*H. matritense*, *H. corcolense*) clade, is selected by successive weighting.

The detailed branching sequence of the Elasmotheriina is (*K. bishopi* (*B. praecursor* (*C. oettingenae* ((*B. caucasica*, *T. fangxianense*) (*H. grimmi* ((*H. matritense*, *H. corcolense*) ('A.' *beonense* (*B. tekayai* (*B. borissiaki* (*P. mongoliense* (*H. lintungense* (*I. morgani* (*P. schansiense* (*S. lagrelii* (*Elasmotherium*)))))))))))). The exhaustive distribution of characters is detailed in Antoine (in press), but discussing the distribution of characters from the nodes A to E (Fig. 1A) is sufficient in order to express the phylogenetic relationships of *H. corcolense* n. sp.

The node A excludes the most primitive Elasmotheriina (i.e. *K. bishopi*, *B. praecursor*, *C. oettingenae*, *B. caucasica* and *T. fangxianense*). It defines the (*H. grimmi* (Node B)) clade. This node is strongly supported by three non-homoplastic synapomorphies (CI = RI = 1), thus justifying a generic distinction: an isolated hypocone on M1, a straight medial border on the radius diaphysis and low intermediate relieves on central metapodials. The protocone constriction on P3-4 (RI = 0.83) is further supporting the node A, together with four postcranial characters: proximal radio-ulna facets generally isolated, small trapezium-facet on the scaphoid, posterior tuberosity straight on the magnum, calcaneus-facet 1 generally wide and low on the astragalus.

The node B sets *H. grimmi* as the sister-group of the ((*H. matritense*, *H. corcolense*) ('A.' *beonense* (Node E)) clade. It is feebly supported by five homoplastic apomorphies: a sagittal lingual groove is present on the mandible, the *foramen mandibulare* is located above the neck line, the paracone fold is strong on M1-2, the metaconid constriction is absent on lower milk teeth and the proximal radio-ulna facets are always fused.

The node C isolates the (*H. matritense*, *H. corcolense*) clade, owing to two characters: the crista is generally absent on the upper molars and the anterior indentation on the medial side of the magnum is generally shallow.

The node D sets 'A.' *beonense* together with more evolved Elasmotheriina (i.e. node E). Three characters appear: the protocone and the hypocone are equally developed on P2, the calcaneus-facet 1 is always high and narrow on the astragalus and the calcaneus always bears a fibula-facet. This node is not very well supported.

At last, the node E is robustly setting apart *B. tekayai* and more evolved Elasmotheriina (from Middle Miocene and later) from *Hispanotherium*. These taxa (i.e. *B. tekayai*, *B. borissiaki*, *P. mongoliense*, *H. lintungense*, *I. morgani*, *P. schansiense*, *S. lagrelii* and *Elasmotherium*) share at least four dental synapomorphies: the crochet is always simple on P2-4, the posterior cingulum is continuous on M1-2, a lingual wall is present on D2, as a constricted entoconid on lower milk teeth (non-homoplastic synapomorphy: CI = RI = 1).

4. Comparison

Apart from the cladistic analysis, which sets the phylogenetic relationships of *H. corcolense* as shown in Fig. 1, we have made a character-by-character comparison between *H. corcolense* and the closest Elasmotheriina, which are *H. grimmi*, *H. matritense* and 'A.' *beonense*. This comparison, restricted to the characters checked in the four taxa, is synthesized in Table (split into seven subtables).

Eight features, shared by *H. corcolense*, *H. matritense* and 'A.' *beonense*, differ in *H. grimmi* (subtable a): the lingual groove present on the *corpus mandibulae*, the strong paracone fold on M1-2, the metaconid constriction on lower milk teeth and the proximal radio-ulna facets always fused are four synapomorphies located at node B (Fig. 1A). The presence of i2, the lacking of a medifossette on P3-4, the reduction of the posterior cingulum on M1-2 and the trigonid determining an acute dihedral on the lower cheek teeth further distinguish these three taxa from *H. grimmi*.

Eight characters rally *H. corcolense*, *H. grimmi* and 'A.' *beonense*, but exclude *H. matritense* (subtable b): the crochet generally simple on P2-4, the lingual wall absent on D2, the double paralophid on d3, the acute distal border of the semi-lunate, the straight posterior tuberosity of the magnum, and three characters on the MtIII (sigmoid proximal border, distally widened diaphysis and cuboid-facet present). Alternative character states define the autapomorphies of *H. matritense* (column 3).

Eight characters put *H. corcolense*, *H. grimmi* and *H. matritense* together in contrast with 'A.' *beonense* (subtable c): the protocone weaker than the

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Table. Morphological comparison between *Hispanotherium corcolense* n. sp. and the closest Elasmotheriina, *H. matritense*, *H. grimmi* and *H. beonense*. Subtables a-c, features respectively isolating *H. grimmi*, *H. matritense* and *H. beonense*. Subtables d, f, characters jointly present in *H. corcolense* n. sp. and (successively) *H. grimmi*, *H. matritense* and *H. beonense*. Subtable g, diagnostic features of *H. corcolense* n. sp. (autapomorphies).

Tableau. Comparaison morphologique entre *Hispanotherium corcolense* n. sp. et les Elasmotheriina les plus proches, *H. matritense*, *H. grimmi* et *H. beonense*. Sous-tableaux a-c, caractères isolant respectivement *H. grimmi*, *H. matritense* et *H. beonense*. Sous-tableaux d, f, caractères conjointement présents chez *H. corcolense* n. sp. et (successivement) *H. grimmi*, *H. matritense* et *H. beonense*. Sous-tableau g, caractères diagnostiques de *H. corcolense* n. sp. (autapomorphies).

a	<i>H. corcolense</i> n. sp.	<i>H. matritense</i>	<i>A. beonense</i>	<i>H. grimmi</i>
Corpus mandibulae (lingual groove)	present			absent
i2	present			absent
P3-4 (medifossette)	always absent			gen. absent
M1-2 (paracone fold)	strong			weak
M1-2 (posterior cingulum)	reduced			continuous
Lower cheek teeth (shape of trigonid)	acute dihedron			obtuse
Lower milk teeth (metaconid constriction)	present			absent
Radius (proximal ulna-facets)	always fused			gen. separated
b	<i>H. corcolense</i> n. sp.	<i>H. grimmi</i>	<i>A. beonense</i>	<i>H. matritense</i>
P2-4 (crochet)	generally simple			generally multiple
D2 (lingual wall)	absent			present
d3 (paralophid)	double			simple
Semi-lunate (distal border of anterior side)	acute			rounded
Magnum (posterior tuberosity)	straight			concave
MtIII (proximal border, anterior view)	sigmoid			concave
MtIII (distal widening of the diaphysis)	present			absent
MtIII (cuboid-facet)	present			absent
c	<i>H. corcolense</i> n. sp.	<i>H. grimmi</i>	<i>H. matritense</i>	<i>A. beonense</i>
P2 (protocone/hypocone)	protocone weaker			equal
P2 (protoloph)	present			absent
P3 (protoloph/ectoloph)	joined			isolated
Unciform (pyramidal- and McV-facets)	always independent			gen. independent
McII (posterior McIII-facet)	always absent			generally absent
Astragalus (DT/H)	$1 \leq TD/H < 1.2$			$1.2 \leq TD/H$
Astragalus (calcaneus-facet 1, expansion)	generally wide and low			high and narrow
Ectocuneiform (postero-lateral process)	weak			developed
d	<i>H. corcolense</i> n. sp.	<i>H. grimmi</i>	<i>H. matritense</i>	<i>A. beonense</i>
M2 (protocone, lingual groove)	always absent		generally absent	always present
e	<i>H. corcolense</i> n. sp.	<i>H. matritense</i>	<i>H. grimmi</i>	<i>A. beonense</i>
Upper molars (crista)	generally absent		always absent	
M1-2 (posterior part of the ectoloph)	straight		concave	
Calcaneus (fibula-facet)	generally absent		always absent	always present
f	<i>H. corcolense</i> n. sp.	<i>A. beonense</i>	<i>H. grimmi</i>	<i>H. matritense</i>
P2-4 (lingual cingulum)	generally present		generally absent	
P3 (crista)	always absent		always present	generally absent
Astragalus (fibula-facet)	concave		flat	
g	<i>H. corcolense</i> n. sp.	<i>H. grimmi</i>	<i>H. matritense</i>	<i>A. beonense</i>
Upper premolars (labial cingulum)	generally present		generally absent	
P4 (antecrochet)	generally present		always absent	
d2 (posterior valley)	generally open		always open	
Scapula (glenoid fossa, medial border)	straight		convex (glenoid fossa oval)	
Magnum (medial side, indentation)	generally shallow		always deep	always shallow
Unciform (pyramidal-facet, posterior digit)	generally absent		always absent	
				generally present

hypocone and the continuous protoloph on P2, the protoloph-ectoloph connection on P3, the independence of the pyramidal- and McV-facets on the unciform, the posterior McII-facet always absent on the McIII, the TD/H ratio lower than 1.2 and the expansion

of the calcaneus-facet 1, generally wide and low on the astragalus, and the weak development of the postero-lateral process on the ectocuneiform. Alternative character states correspond to the autapomorphies of *A. beonense* (column 3).

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Three features separate *H. corcolense* and 'A.' *beonense* from *H. grimmi* and *H. matritense* (subtable d): the lingual cingulum generally present on P2-4, the crista always absent on P3 (always present in *H. grimmi* and generally absent in *H. matritense*) and the fibula-facet concave on the astragalus.

Three characters bring together *H. corcolense* and *H. matritense*, with respect to *H. grimmi* and 'A.' *beonense* (subtable e): the crista generally absent on the upper molars, which is a synapomorphy of the node C (Fig. 1A), the posterior part of the ectoloph straight on M1-2 and the fibula-facet generally absent on the calcaneus (always absent in *H. grimmi* and always present in 'A.' *beonense*).

The absence of a lingual groove on the protocone of M2 is jointly characterizing *H. corcolense* and *H. grimmi* (subtable f), contrary to *H. matritense* (generally absent) and 'A.' *beonense* (always present).

At last, six characters define only *H. corcolense*, as autapomorphies (subtable g): the labial cingulum generally present on the upper premolars (while generally absent in other species); the antecrochet generally present on P4 (always absent in other species); the posterior valley sometimes closed on d2 (always open in other species); the glenoid fossa bearing a straight medial border on the scapula (oval otherwise); the generally shallow medial indentation on the magnum (the parsimony of which is interpreted as a synapomorphy acquired at the node C; Fig. 1A). This indentation is always shallow in *H. matritense* and always deep in both *H. agrimmi* and 'A.' *beonense*; the expansion of the pyramidal-facet generally absent on the unciform (generally present in 'A.' *beonense*, always absent in both *H. grimmi* and *H. matritense*).

5. Discussion and conclusions

Various authors [6-10, 21, 24] do consider that Early and Middle Miocene Elasmotheriina from Eurasia (i.e. *Caementodon oettingenae* Heissig, 1972, *Beliajevina caucasica* (Borissiak, 1935), *Tesselodon fangxianense* (Yan, 1979), *Hispanotherium grimmi* Heissig, 1974, *Beliajevina tekkayai* Heissig, 1974) must be included within the genus *Hispanotherium*. Meanwhile, other authors [2-5, 12, 13, 15-18] assume that these taxa correspond to different species and/or genera.

The present work confirms the second opinion (Fig. 1): not only *C. oettingenae*, *Beliajevina caucasica* and *Tesselodon fangxianense* must be excluded from *Hispanotherium* (Fig. 1A; node A), but *Kenyatherium bishopi* Aguirre and Guérin, 1974

and *Bugtirhinus praecursor* Antoine and Welcomme, 2000 are also much more primitive than *Hispanotherium matritense*, type species of the genus, and its closest relatives. Still, the phylogenetic relationships within Elasmotheriina in the surroundings of *H. corcolense* are not robustly solved (Fig. 1A; nodes B-D, weakly supported), but *H. corcolense* does represent a distinct species. At last, other Elasmotheriina from the Middle Miocene and later (i.e. *B. tekkayai*, *B. borissiakii*, *P. mongoliense*, *H. lintungense*, *I. morgani*, *P. schansiense*, *S. lagrelii* and *Elasmotherium*) are definitely more evolved than *H. matritense* and its closest relatives, as shown in Fig. 1A (node E).

All this leads us to put *H. matritense*, *H. grimmi*, *A. beonense* Antoine, 1997 and *H. corcolense* n. sp. together within the genus *Hispanotherium*, in agreement with Antoine [3], but not with Antoine [2] and Antoine and Welcomme [4]. As noticed in Section 3, the nodes B to D (Fig. 1A) are not supported enough to justify any generic distinction between the involved species. Thus, the genus *Hispanotherium* is paraphyletic, representing a grade within Elasmotheriina. Still the monophyly of (*H. corcolense*, *H. matritense*) cannot be excluded.

The earliest elasmotheriine, *Bugtirhinus praecursor*, is reported in the basal Miocene of Balochistan [3, 4]. The following branches in the parsimonious trees successively lead to elasmotheriines restricted to Asia, Caucasus and Minor Asia (Anatolia). Thus, the group may have differentiated in Asia and dispersed westward throughout the Early Miocene. *Hispanotherium* or a close relative has probably joined Western Europe through Anatolian plate, as a consequence of the Eurasian and Arabo-African plates collision, also responsible for the major dispersal event named 'Proboscidean Datum Event' [22].

H. corcolense is so far restricted to the locality of Córcoles, which represents the oldest occurrence of an elasmotheriine in Iberia (MN 4a, zone C). So far, *H. matritense* only occurs in younger deposits (MN 4b and MN 5, zones D-E) [3, 21]. On the other hand, *H. beonense* occurs also during the MN 4a zone, in the French locality of Pellecahus, almost contemporaneous of Córcoles [5]. Its time range is extending up to the MN 4b and the MN 5 zones in the Aquitaine and Loire basins [2, 3]. *H. grimmi* is so far restricted to the Middle Miocene of Anatolia [16-18].

Thus, three distinct elasmotheriines have been recorded in Western Europe during the MN 4-5 zones: *H. corcolense* and *H. beonense* during the MN 4a zone; *H. beonense* and *H. matritense* during the MN 4b-MN 5 zones). *H. beonense* and *H. matritense* have been sympatric in the Loire Basin [3, 14].

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