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The Rhinocerotidae fossil record in the Iberian Peninsula

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ABSTRACT

The family Rhinocerotidae, also referred to as 'true rhinoceroses', is one of the multiple perissodactyl lineages that have independently evolved large body sizes, lophodonty (fully developed crests between dental cusps), a simplified anterior dentition, and the molarization of the premolars. During the last decades, descriptions of novel fossil collections, the update of previously published ones, and taxonomic reviews through cladistic analyses have brought to bear a new, comprehensive perspective on the group, significantly increasing its recorded deep-time diversity. This paper reviews the historical development of the study of Rhinocerotidae in the Iberian Peninsula, provides an up-to-date compendium of the regional rhinoceros fossil record by gathering the available references, and presents an updated taxonomic framework. As a result, 27 out of the more than 200 rhinoceros species described in the literature worldwide inhabited the Iberian Peninsula, regionally ranging from the Oligocene to the Late Pleistocene. Their systematics, stratigraphic, and geographical ranges are detailed in the present article and the occurrences and geographical ranges illustrated.

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Rhinocerotidae; Perissodactyla; Portugal; Spain; Oligocene; Miocene; Pliocene; Pleistocene

Introduction

The family Rhinocerotidae

From a morphological perspective, the family Rhinocerotidae has been typically, but not exclusively, defined based on the following dental traits (Prothero et al. 1989; Heissig 2012a): a 'π' – shaped occlusal surface of the first and second upper molars, lack of canines, reduction of the metacone on the M3, chisel-shaped I1 occluding with tusk-shaped i2, reduction of the remaining anterior dentition, or incisors separated from the cheek teeth by a diastema. Their most paradigmatic feature, the presence of a median nasal horn keratinous in nature, is not ubiquitous and has been developed independently by some lineages, being absent in others.

Rhinocerotids are amongst the most successful families of Perissodactyla and conspicuous components of the Iberian terrestrial communities of the Neogene, providing invaluable insights into the stratigraphic and ecological context of fossil assemblages (Cerdeño and Nieto 1995; Kahlke and Lacombat 2008). In addition, the Iberian Peninsula not only has acted as a key geographical crossroad between Europe and Africa (Antunes 1979; van der Made et al. 2006) but an intermittent climatic refugium for large herbivores adapted to arid and/or cold environments (Álvarez-Lao and García 2011).

Early findings

The Nineteenth century marked a period of intense interest in paleontological findings. Early studies on Iberian rhinoceros species echoed wide-reaching monographs on the topic, initiated by Kaup (1834), de Christol (1834), de Blainville (1844), Lartet (1851), or Duvernoy (1853) in Europe, Lydekkers (1884) study of Asian species, or Osborn's monographies (Osborn 1898, 1900, 1904) on North American and, to a minor extent, European species. The first Iberian rhinoceros remains were reported by P. Gervais from Alcoy in 1852. This finding was followed by additional mentions at the localities of Cerecinos (León) and Teruel (Ezquerra de Bayo 1850-1859), Briviesca (Burgos; Aranzazu 1860), Málaga (Ansted 1860), Brihuega (Guadalajara), Cueva de Mudá (Palencia), and the city of Madrid (Prado 1864), Quintana (León; Fernández Soba 1865), Gibraltar (Busk and Falconer 1865); Dehesa de Valdemimbre (de Uhagón 1873), the Udías area (Santander; Naranjo y Garza 1873, 1875; González Linares 1876), los Tejares (Málaga; Orueta 1874), Zamora (Vilanova in de Uhagón 1873) or Olías (Toledo; González Linares in Calderón and Arana 1876). Many of these pioneering discoveries were intimately linked with the first systematic mining prospections and geologic and cartographic surveys. In the 'Néogène continental dans la Basse Vallée du Tage', Roman and Torres (1907) described and figured the first rhinoceros remains from Portugal, including the initial report of *Protaceratherium minutum* and '*Ceratorhinus sansaniensis*' (currently known as *Lartetotherium sansaniense*) in the Iberian Peninsula. Shortly after, E. Hernández Pacheco, another major figure in the Spanish Paleontology, described some rhinoceros remains from the Miocene of Palencia, including a partial skull, used as holotype for a new species, '*Rhinoceros* (*Ceratorhinus*) *hispanicus*' (Figure 1d; Hernández-Pacheco and Dantín Cereceda 1915). Additionally, Royo Gómez and another Hernández Pacheco, Fernando (son of the latter), described the presence of *Alicornops simorrense* in Nombrevilla (Zaragoza), the Valladolid area, and Chiloeches (Guadalajara; Hernández-Pacheco 1926, 1930). These Neogene findings were complemented by scattered reports on Pleistocene deposits, most of them linked with cave fillings and included in archaeological studies (Harlé 1909, 1920; Carballo 1910; Royo y Gómez 1935). During the years after the Spanish Civil War and up to the beginning of the 1980's little systematic work was undertaken on the fossil rhinoceroses of the Iberian Peninsula. A bright exception to the aforementioned are the relevant contributions made by Crusafont and Villalta (Villalta and Crusafont 1934,

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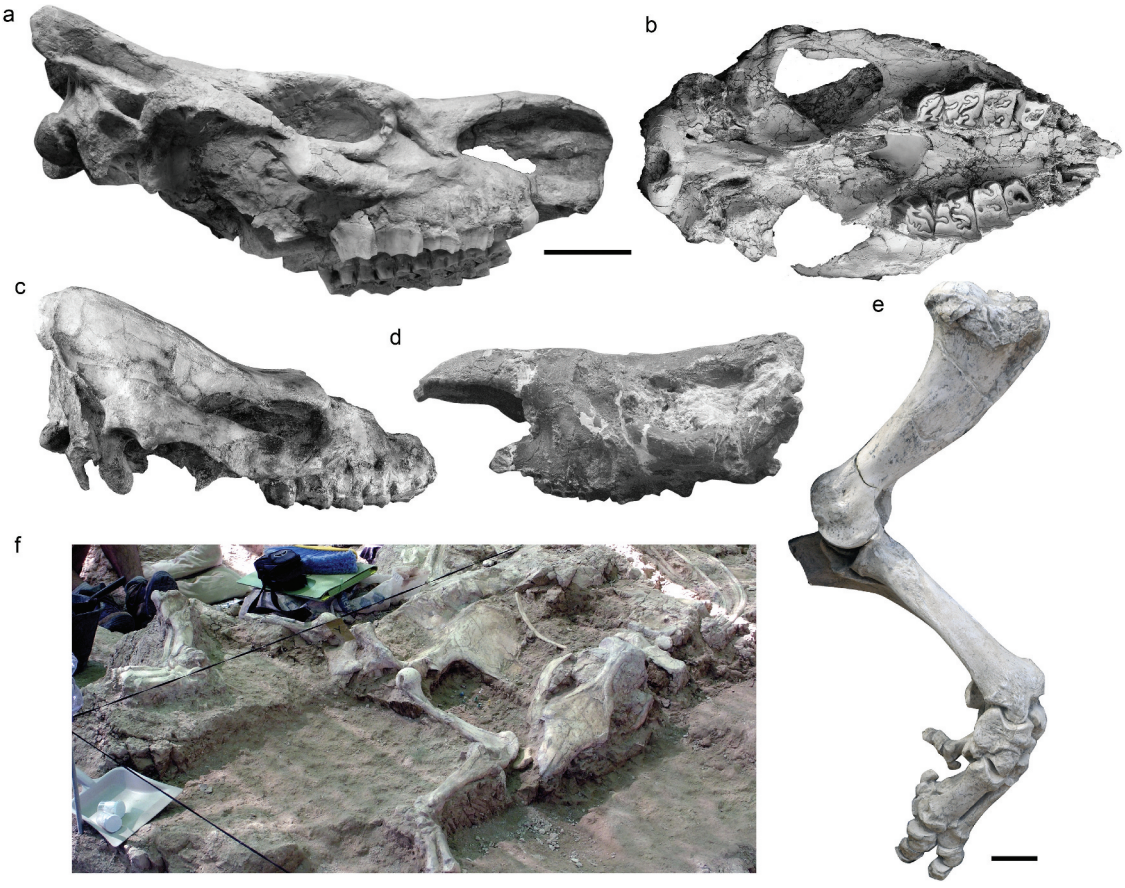

Figure 1 selected examples of rhinoceros remains from the Iberian Peninsula. a, skull of *Stephanorhinus etruscus* from Crespià, Girona; b, palatal view of the skull MNCN-05/101/2/7000 of *Hispanotherium matritense* from Príncipe Pío-2, Madrid; c, skull of *Alicornops simorrense* MNCN-47576 from Moraleja de Enmedio, Madrid; d, juvenile *Lartetotherium sansaniense* skull RE-927 from La Retama, Cuenca; e-f, left forelimb and general view of the skeleton of *Aceratherium incisivum* from Batallones-1, Madrid (BAT-1, multiple collection numbers), Madrid. Photograph of *S. etruscus* by the Museum Comarcal de Banyoles. *A. incisivum* in f by S. Fraile. Both scale bars equal 100 mm.

1945, 1955), which include the naming of the species '*Dromoceratherium mirallesi*' (Crusafont and Truyols 1955). Other exceptions are occasional papers, preliminary reports, and mentions in different faunal lists (e.g., Hernández-Pacheco and Crusafont 1960; Montenat and Crusafont 1970).

Modern studies on Iberian Rhinocerotidae

Two specialists, J. V. Santafé and E. Cerdeño, shaped the current knowledge of the Iberian Rhinocerotidae during the last decades of the 20th century. Both committed their PhD dissertations to the species systematics from the Miocene of eastern and central Iberia, respectively (Santafé 1978b; Cerdeño 1989). Around the same time, M. T. Antunes and L. Ginsburg published a series of papers focused on the coeval rhinoceros remains from the Lisbon area (Antunes 1960, 2000; Ginsburg and Antunes 1979; Antunes and Ginsburg 1983, 2000). Such immense body of knowledge was completed with the comprehensive review of European Cenozoic species assembled by C. Guérin (1980). Around this time, '*Dicerorhinus*' *montesi* and *Pliorhinus miguelcrusafonti*, two new Rhinocerotina species, were defined from the Iberian early Miocene and Pliocene respectively (Guérin and Santafé 1978; Santafé et al. 1987). These seminal works were followed by a series of studies on different aspects of rhinoceros paleontology from the Miocene, owing to both the finding of multiple new localities as a result of the urbanization and infrastructural work at the cities of Madrid, Lisbon, Sabadell/Terrassa, and their respective outskirts, and a renewed interest on classic sites (e.g., Santafé and Casanovas-Cladellas 1978, 1983-1984a, 1983-1984b; Santafé 1978a, 1982; Santafé et al. 1982, 1989-1990; Cerdeño and Alberdi 1983; Cerdeño 1986, 1992a, 1996a; Cerdeño and Alcalá 1989; Cerdeño and Iñigo 1997; Iñigo and Cerdeño 1997; Cerdeño and Sánchez 1998, 2000; Fernández and Cerdeño 1999; Antoine et al. 2002). They all benefited from the successive attempts to clarify the phylogenetic relationships of the group proposed by, among others Prothero et al. (1986), Fortelius and Heissig (1989), Cerdeño (1995), Antoine (2002), Antoine et al. (2003), and Becker et al. (2013), setting the modern foundations of the group's systematics. Much of this research on Miocene species was condensed in Cerdeño (1992b) and, posteriorly, Cerdeño and Alberdi (2006).

The exploration of additional underground karstic features, particularly in the Cantabrian Range, led to the discovery of a considerable collection of fossil remains and provided important insights on the distribution, biostratigraphy, and paleoecology of Pliocene-Pleistocene rhinoceros species, including their connection with the shifting climate of that time. Numerous reports of narrow-nosed (*Stephanorhinus hemitoechus*) and woolly rhinos (*Coelodonta antiquitatis*) among others have been published in the last decades, either in form of monographs (Cerdeño 1990, 1993; Mazo 1995; García-Fernández et al. 2003; Ros et al. 2003; Del Río and Cuenca-Bescós 2005; van der Made and Montoya 2007; Álvarez-Lao and García 2011)

or incorporated in faunal reports. Finally, recent reviews on Pliocene species have brought back to light these poorly represented faunas, many of them still to be re-studied in detail (Malapeira et al. 2014; Pandolfi et al. 2022). The list of contributions, too long to be described here exhaustively, is included in Supplementary Data S1. As a result of all these efforts, the known Iberian record of Rhinocerotidae has increased considerably since its pioneering reports, placing the Iberian Peninsula as one of the poles of fossil research from Europe.

Aim of this work

The present paper represents a summarized review of what has been the outcome of a long thread of studies on Iberian rhinoceroses starting at the middle of the 19th Century. It addresses three main objectives: 1) Generate the first updated and comprehensive list of all Rhinocerotidae remains recorded in the Iberian Peninsula in the light of new discoveries, spanning from the Oligocene up to Pleistocene times. 2) Discuss the Iberian rhinoceros record with particular emphasis on its relationship to paleogeographic and climatic changes through time. 3) Assess whether the diversity patterns, as recovered from the fossil record, have a true biological signal, falling beyond the effect of the collecting effort.

Material and methods

Occurrences have been compiled from bibliographic sources and direct observations. A list of the localities with presence of Rhinocerotidae in the Iberian Peninsula is summarized in Supplementary Table S1 and Figures 2–4. In the systematic paleontology section, species taxonomy and relevant diagnostic insights are detailed when appropriate in each description. Suprageneric taxonomy follows the criteria of arrangement proposed by Antoine (2002) and Becker et al. (2013; Figure 2b). The chronostratigraphical framework is based on geological time scales for the Paleogene (Luterbacher et al. 2004) and the Neogene (Steininger 1999; Lourens et al. 2004). Durations of Oligocene European mammal reference levels follow those proposed by Schmidt-Kittler et al. (1987) and posteriorly modified by Luterbacher et al. (2004), whereas mammal biozones for the Early Miocene are based on the Neogene land mammal zonation (Mein 1999; Steininger 1999; Agustí et al. 2001).

Anatomical abbreviations: Mc, metacarpal; Mt, metatarsal. In describing the dental elements, we follow the terminology proposed by Jepsen (1996). 'I/i', 'M/m' and 'P/p' designate incisors, molar, and premolar, respectively. Lowercase letters designate teeth from lower series and upper-case letters teeth from upper ones. A preceding 'D' or 'd' indicate decidual teeth (e.g., DP4 or dp2).

Diversity signals are modulated by the completeness of data. Therefore, controlling for sampling is critical for a critical analysis of life history dynamics. An inspection on the available occurrence sampling per time bin has been performed by means of standardizing species diversity using a shareholder quorum subsampling (SQS), implemented algorithmically by Alroy (2009) and described in Jost (2010). The delivered sampling-standardized trajectories ensure fair comparisons of richness under limited sampling (Close et al. 2018).

Systematic paleontology

Order Perissodactyla Owen, 1848

Family Rhinocerotidae Gray, 1821

Unnamed clade

Ronzotherium Aymard, 1854

Ronzotherium entered Europe after the Grand Coupure event, at the earliest Oligocene, becoming extinct by the latest Oligocene. The simplified dentition (lack of secondary enamel folding) contrasts with subsequent Miocene genera. The cranial morphology of the genus displays a considerable variability. In general, the neurocranium is elongated, the nasal notch high, and the premaxilla long, straight, and robust. The postcranial skeleton is generally slender and preserves some basal traits such as the presence of a gracile but functional fifth anterior digit (Tissier et al. 2021). Cladistic hypotheses placed the genus *Ronzotherium* basal to the two main rhinoceros subfamilies, Elasmotheriinae and Rhinocerotinae, stressing its key evolutionary position (Tissier et al. 2021).

Ronzotherium filholi (Osborn, 1900)

Stratigraphic range

Iberian Peninsula: early Oligocene, MP 21–MP 23. Total range: possibly restricted to the early Oligocene, MP 20–MP 23.

Geographic distribution

France, Germany, Romania, Spain, Switzerland.

Iberian localities

Montalbán and Palomera B (Sierra Palomera).

Remarks

Ronzotherium filholi is a common species of the European Oligocene. The diagnosis, updated by Tissier et al. (2021), includes a weak coronoid process of the mandible, large and simple premolars provided with labial cingula, molariform P2′s, fused procone and hypocone, or the retention of the dp1 among other characters. The only Iberian records of the species come from localities of Montalbán (MP 23) and Palomera B (early Oligocene).

Subfamily Elasmotheriinae Bonaparte, 1845

Subtribe Elasmotheriina Bonaparte, 1845

Hispanotherium Crusafont and Villalta, 1947

Hispanotherium is the only elasmotheriine genus formally described in western Europe. It spans the late early-early middle Miocene interval. The presence of multiple elasmothere forms related with *Hispanotherium* along Western Europe underlines its important role as a regional diversification hotspot for the group

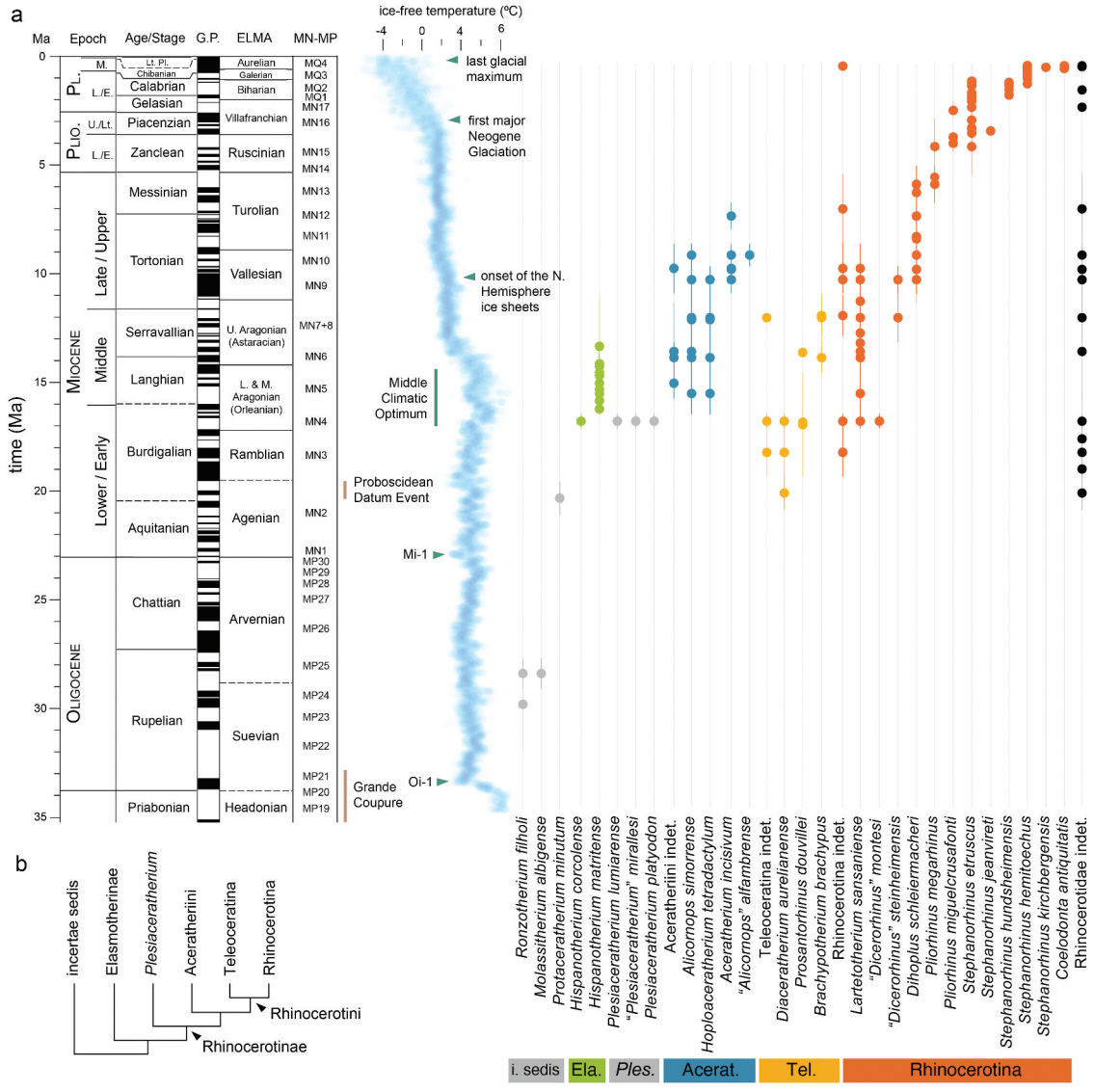

Figure 2 a, standard stratigraphy and biostratigraphic ranges of Iberian Rhinocerotidae. Circles represent the average age of each locality and lines their time span. Stratigraphic framework follows Gradstein et al. (2020); MN/MP biozones according to Steininger (1999). The global oxygen isotope record, together with the development of ice sheets and major climatic/physiographic events, are also included. Age boundaries for epochs, stages, European Land Mammal Ages (ELMA) and Paleogene Mammal Zones (MP) after Luterbacher et al. (2004). Climatic data follows Zachos et al. (2001). b, supragenetic arrangement followed in the present work according to Antoine and Becker (2013). E: early; Ela: Elasmotherina; ELMA: European Land Mammal Ages; G.P.: Geomagnetic Polarity; L: lower; Lt: late; N: North, M: middle; Plio: Pliocene; Pl: Pleistocene; Tel.: Teleoceratina; U: upper; MN / MP / MQ: Mammalian Neogene / Paleogene / Quaternary ages respectively.

during the Middle Miocene outside Asia. The genus *Hispanotherium* is defined as follows (Antoine et al. 2002): M1 with constricted hypocone, protocone constricted on the P3–4, straight medial border on the radius, isolated proximal radio-ulnar facets, small trapezium facet on the scaphoid, straight posterior tuberosity on the magnum, low and long facet-1 for the calcaneum, and low intermediate distal protrusions in the central metapodials.

Hispanotherium matritense (Lartet in Prado, 1854)

Stratigraphic range

Iberian Peninsula: MN 5. Total range: MN 5–MN 6.

Geographic distribution

Bosnia-Herzegovina, France?, Portugal, Spain.

Iberian localities

Hispanotherium matritense has been recorded in the following Iberian localities: Ebro basin: Tarazona de Aragón; Tagus basin: Amor; Tagus basin (Lisbon area, included in Chelas and Charneca do Lumiar): Areeiro do José da Graça, Casal das Chitas, Courelas do Covão, Quinta da Musgueira, Quinta Grande, Quinta da Raposa, Quinta da Silvéria, Quinta do Conceição, Sabliére de Quinta das Mantegais, Olival da Suzana, Quinta da Farinheira, Quinta das Flamengas, Quintanelas, and a series of unnamed localities around the Musgueira airport; Tagus basin (Madrid area): Barajas-17; Casa de Campo/Marqués de Monistrol M-30, Cerro de San Isidro, Embajadores-R, Estación Imperial, Fábrica Mahou, Fresno de Torote, La Peineta, Los Nogales, Paseo de la Esperanza, La Hidroeléctrica, Paso de las Acacias, PAR-Peñuelas, Príncipe Pío-2, Puente de Toledo (type locality), Torrijos-1, and Yunquera de Henares; Calatayud-Daroca: Munébrega-1, Munébrega-3, Valdemoros 1A, Valdemoros 2, Valdemoros 3C, and Valdemoros 4A.

Remarks

The report of a small collection of dental remains from the Madrid Province made by É. Lartet and published in del Prado (1864) led to the establishment of a new species with affinities with Asian elasmotheres. The species, originally named as '*Rhinoceros matritensis*', was posteriorly transferred to its own genus, *Hispanotherium*, by Crusafont and Villalta (1947). From the late 1970′s on, *H. matritense* has been regularly found in the middle Aragonian central and western basins of the Iberian Peninsula, making it the most abundant species in places like the Madrid area (Antunes 1979; Antunes and Ginsburg 1983; Cerdeño and Alberdi 1983; Cerdeño 1987, 1992a). The only occurrences outside Iberia come from the locality of Gračanica (Bosnia-Herzegovina) and, almost certainly, Hommes (France; Ginsburg et al. 1987; Antoine 2002; Becker and Tissier 2020). The series of dental remains from China ascribed to the species (Deng 2003), although undoubtedly of elasmothere origin, show more derived dental features than those found in *H. matritense*, being therefore excluded from the species hypodigm. The public works in Madrid city during the last two decades revealed additional material, including cranial remains (Figure 1b; Sanisidro et al. 2012). *Hispanotherium matritense* is a small to medium-sized elasmothere with long, hornless nasal bones and relatively long rostrum (the anterior orbital margin is located above the M3). Its dentition is subhypsodont and presents very thick cement cover, deeply constricted protocone and slightly constricted metaconid, and secondary folds of the enamel developed. The i2 are like small tusks, with sexual dimorphism in shape and size. The cursorial adaptations of the species are represented by a gracile postcranial skeleton and a reduced non-functional Mc V (Sanisidro et al. 2012). All the derived dental and postcranial features of crown-Elasmotheriina (e.g., *Elasmotherium*) to cope with wear and open habitats were already present in *H. matritense*.

Hispanotherium corcolense Antoine et al. 2002

Stratigraphic range

Local zone C, MN4, lower Aragonian.

Geographic distribution

The species distribution is restricted to central Spain.

Iberian localities

Hispanotherium corcolense has been only recorded in Córcoles (type locality).

Hispanotherium corcolense is a small member of the genus *Hispanotherium*, so far restricted to the type locality of Córcoles. In general, the species exhibit a slightly more plesiomorphic and brachydont dental configuration than the nominal species: the P4 occasionally lacks antecrochet, premolars bear labial cingula, and the posterior valley of the dp2 is not always closed, Additional differences with other *Hispanotherium* species are the straight medial border of the scapular glenoid fossa, a shallow medial side of the magnum, and the occasional presence of a posterior unciform pyramidal facet (Antoine et al. 2002).

Subfamily Rhinocerotinae Gray, 1821

Molassitherium Becker et al. 2013

Molassitherium is a genus of small-sized Rhinocerotinae with a backward-slanted occipital plate, short nasal bones, shallow and high nasal incision, a forked occipital crest, lacking any crochet on upper molars, and M2 with mesostyle (Becker et al. 2013).

Molassitherium albigense (Roman, 1912)

Stratigraphic range

Iberian Peninsula: MP 23?. Total range: MP 23?–MP 28.

Geographic distribution

Austria, Belgium, France, Hungary, Portugal, Spain, Turkey.

Iberian localities

Montalbán?.

Remarks

Originally placed within *Acerotherium* and, posteriorly, *Protaceratherium*, the species was lately recombined as *Molassitherium* (Becker et al. 2013). *Molassitherium albigense* has shortened nasals, a partially closed external auditory pseudomeatus, a backward-oriented occipital plate provided with a weakly developed nuchal tubercle, a deeply forked occipital crest, a subtriangular foramen magnum, or the strong cingulid on lower cheek teeth (Lihoreau et al. 2009). The only potential record from the Iberian Peninsula comes from the locality of Montalbán (Ménouret and Guérin 2009).

Protaceratherium Abel, 1910

Protaceratherium is a very small and slender hornless rhinoceros. The nasal bones are very long, slender, and are slightly domed insertion area. The remaining cranial dorsal profile is straight, the dentition brachydont and void of secondary folding, and the postcranial proportions are amongst the slenderest recorded for rhinoceroses.*Protaceratherium minutum* (Cuvier, 1822).

Stratigraphic range

Iberian Peninsula: MN 2. Total range: MN1–MN4.

Geographic distribution

Czech Republic, Germany, France, Portugal, Spain, Switzerland.

Iberian localities

Loranca del Campo, La Encinilla, and Valquemado.

Remarks

Protaceratherium minutum has been reported from the localities of Loranca, Valquemado, La Encinilla, and La Retama (Cerdeño 1989). The fossils of *P. minutum* from the Lisbon area include two upper dental series from Horta das Tripas (Lisbon area), identified as '*Protaceratherium tagicum*' by Roman and Torres (1907). Even though their small size is compatible with

Protaceratherium remains like the *P. minutum* skeleton from Budenheim, other morphological features like the development of an incipient lingual wall or the considerable inner enamel folding on premolars discards their ascription to the genus. Many small-sized European rhinocerotid remains from the early Miocene have been classically assigned to *P. minutum*, resulting into a hotchpotch that could likely contain more than one species. The confirmation of the presence of the poorly known *Menoceras* in Europe, a small-sized elasmotheriine species reported from France and Germany with clear North American affinities, expands the list of candidates for these small remains and stresses the need of a comprehensive review of these Iberian collections. Additional *Protaceratherium* remains from Lisbon (Lisbon div. I; Antunes and Ginsburg 2000), Can Canals (Papiol), Molí Calopa, or Rubielos de Mora 1 are problematic and have been provisionally considered as undetermined species.

Plesiaceratherium Young, 1937

Plesiaceratherium is a small to medium-sized hornless genus diagnosed on the basis of the following: skull and dentition primitive with poorly developed upper incisors, hornless skull with a deep nasal notch and a narrow braincase, horizontally implanted and flattened i2, upper teeth with weak protocone and hypocone constriction, upper premolars with high labial cingulum, long and narrow lower premolars with shallow labial groove and flattened protoconid, presence of rugosities on the ectoloph and slender limbs with tetradactyl manus (Yan and Heissig 1986; Geraads 2010). Recent phylogenetic analyses place some *Plesiaceratherium* basal to both Rhinocerotini and Aceratherini, at the root of Rhinocerotinae (Becker et al. 2013), phylogenetically close to the evolutionary split between horned and hornless rhinoceroses.

Plesiaceratherium platyodon (Mermier, 1896)

Stratigraphic range
MN 3–MN 4.

Geographic distribution
France, Portugal, Spain.

Iberian localities
Lisboa-1, Córcoles, Can Mas, and Buñol.

Remarks
Plesiaceratherium platyodon is diagnosed by its long braincase with separated parietal ridges, weakly moralized upper premolars, flattened lower incisors, upwards-curved and long symphysis, rather long diastema and rugous outer surface of the lower premolars (Yan and Heissig 1986). *Plesiaceratherium platyodon* remains of Can Mas (El Papiol) comprise a left hemimandible, three isolated teeth, and several postcranial bones (Santafé, 1978). The lower teeth show closer proportions to the French Pont de Manne and Bézian, with comparable lengths and lower widths (reaching their minimum values (Iñigo 1994). Additional remains of *P. platyodon* were found at Córcoles (Iñigo 1994), Buñol (Belinchón and Robles 1984; Santafé et al. 1985, 1988), and the Lisbon area (Antunes and Ginsburg 1983).

'Plesiaceratherium' mirallesi Crusafont, Villalta & Truyols, 1955

Stratigraphic range
Iberian Peninsula: MN 4. Stratigraphic range: MN 4–MN 5.

Geographic distribution
France, Germany, Spain,

Iberian localities
Can Julià, Els Casots, and Les Cases de la Valenciana.

Remarks
The species '*P*'. *mirallesi* is based on lower teeth and postcranial elements from Can Julià (MN 4), where it was originally defined as *Dromoceratherium mirallesi* (Crusafont and Truyols 1955). The large and robust postcranial proportions clearly differ from other *Plesiaceratherium* species. Additionally, it shows longer and thicker lower i2, less flattened protoconid edge, deeper labial groove, and a typical vertically wrinkled outer wall (Yan and Heissig 1986). The large fossil collection reported at the French locality of Béon-2 (Montréal-du-Gers; Antoine 2002) expanded the current knowledge of the species, confirming its uniqueness in terms of morphology and proportions.

Plesiaceratherium lumiarense (Antunes and Ginsburg 1983)

Stratigraphic range
Iberian Peninsula: MN 4. Total range: MN 4–MN 5.

Geographic distribution
France, Portugal.

Iberian localities
Charneca do Lumiar (type locality).

Remarks
Plesiaceratherium species with connected protoloph and ectoloph, on P2-4, protocone and hypocone is mostly separated and the medifossette sometimes present. On P3-4, the lingual cingulum is incised. The crochet of the cheek teeth is strong and the crista absent. The shape of the M3 is quadrangular (Becker and Tissier 2020). The only locality with presence of the species is Charneca do Lumiar (Lisbon Area, Tagus Basin).

Tribe Aceratheriini Dollo, 1885

Group of hornless rhinoceroses with laterally projected maxillary process of the zygomatic arch anteriorly, developed posttympanic process, diverging and developed i2, a constricted metaloph on the P2–4, or a strong posterior cingulum on the M3 (Antoine et al. 2003).

Alicornops (Lartet in Laurillard, 1848)

Alicornops is a small aceratheriine genus characterized by its strong postglenoid apophyses, nasals with a small horn insertion, developed anterior dentition (in contrast to *Hoploaceratherium*), convex mandibular corpus, wide mandibular symphysis, upwards-curved i2, strong paracone folding, some cement on the cheek teeth, protocone slightly smaller than the hypocone on the P2, antecrochet often present in the M2, angulous trigonid and talonid forming

an acute dihedron in the lower cheek teeth and well-developed crochet and crista, lower molars devoid of lingual cingulids, or the insertion of the m. biceps brachii forming a profound depression in the radius (Ginsburg and Guérin 1979; Cerdeño and Sánchez 2000; Antoine et al. 2003).

Alicornops simorrense (Lartet in Laurillard, 1848)

Stratigraphic range: MN 5–MN 10.

Geographic distribution

France, Germany, Moldova, Poland, Spain, Turkey.

Iberian localities

Tagus Basin: Chiloeches, Cendejas, Moraleja de Enmedio, Paracuellos III; Calatayud-Teruel Basin: Nombrevilla, Carrilanga-1, Andurriales, Daroca área, Toril-3, Montejo de la Vega, Armantes-1; Duero Basin: El Lugarejo, Los Valles de Fuentidueña, Relea, La Cistérniga, Coca, Cerro del Otero, Fuensaldaña; Vallès-Penedès Basin: Can Jofresa, Can Gabarró, Can Llobateres, Can Ponsic, Can Almirall, Poble Nou, Trinchera del Ferrocarril, Can Feliu, Can Barberà, Hostalets de Pierola, and San Pere de Ribes.

Remarks

Alicornops simorrense is one of the most widely distributed and most abundant taxa from the Iberian late middle Miocene (Guérin 1980; Cerdeño and Sánchez 2000). The Iberian record not only includes dental and postcranial remains but several complete skulls (i.e., Moraleja de Enmedio, Figure 1c, M-407 Rotonda, El Lugarejo, Cerro del Otero, or Toril 3A, the latter ones unpublished). The skull has a raised occiput; the dental incision has a 'V'-shaped incision, the nasal bones are straight, slightly upraised, and bear very faint rugosities at their tip. Limb proportions are typically aceratheriine-like, robust (but not as much as teleocerateres), mediportal, and small-sized. The metapodials from the late Aragonian levels of Hostalets de Pierola and those from the localities of Can Llobateres and Can Jofresa show an augment in size towards the Vallesian, but independent from robustness variations (Cerdeño and Sánchez 2000).

'Alicornops' alfambrense Cerdeño and Alcalá, 1989

Stratigraphic range: MN 10.

Geographic distribution

France, Spain.

Iberian localities

La Roma-2.

Remarks

'*Alicornops*' *alfambrense* was defined from a small collection of postcranial bones (Cerdeño and Alcalá 1989). This acerathere has been reported at the late Vallesian locality of La Roma 2 (Alfambra, Teruel). Its generic ascription is questionable: while definitively an acerathere, it is larger and more robust than any other Iberian acerathere remain, and clearly distinct from *Alicornops*. Alternative candidates with equivalent proportions from Western and Southeastern Europe include the robust acerathere postcranial remains from Eppelsheim, *Chilotherium*, a robust acerathere commonly found in the Eastern Mediterranean faunas from the late Miocene, or *Acerorhinus*, another acerathere reported from Monte delle Piche (Italy; Pandolfi et al. 2013) and a typical from Greek and Anatolian late Miocene assemblages (Antoine et al. 2003). Unfortunately, little studies on the postcranial skeleton of these Asian genera have been published so far, preventing further comparisons.

Hoploaceratherium Ginsburg and Heissig, 1989

Ginsburg and Heissig (1989) erected the genus *Hoploaceratherium*, differencing it from all European Aceratheriini based on the retention of a rough horn boss on the tip of the nasals and the loss of upper incisors, a high skull with a narrow neurocranium, a long, thin, an edentulous premaxilla, i2 long and curved, and i1 sometimes present (and displaced labially; Heissig 2012b). Cerdeño (1996c) consider *Hoploaceratherium* as synonym of *Acerorhinus*. However, posterior morphological studies revalidated the former (Antoine et al. 2003; Heissig 2012b).

Hoploaceratherium tetradactylum (Lartet, 1836)

Stratigraphic range

Iberian Peninsula: MN 6–MN 9. Total range: MN 5–MN 8.

Geographic distribution

Austria, France, Germany, Spain.

Iberian localities

Abocador de Can Mata, Can Casablanques, Arroyo del Val-4, Chiloeches, Hostalets de Pierola (upper Miocene levels), Manchones, Nombrevilla, Polinyà, Saldaña, Subsuelo de Sabadell, Trinchera del Ferrocarril, Paracuellos-1, Paracuellos-2, Paracuellos-5, Henares-1, Cerro de la Plata, Benavente, Alhambra-túneles, and Puente de Vallecas.

Remarks

Hoploaceratherium tetradactylum is diagnosed with the following characters (Heissig 2012b): 'Aceratherine rhinoceros with unfused long nasals topped with a faint horn boss at its tip, skull with a long edentulous premaxilla narrowing posteriorly, narrow symphyseal region with large and little-curved tusk-like i2, navicular with a lunate outline and slender limbs with tetradactyl forefoot'. The remains of this species in the Vallès-Penedès originally identified as '*Aceratherium bi-tetradactylum*' belong to this species (Emery et al. 2016). If compared with the remains of Nombrevilla (MN9; Calatayud-Montalbán Basin), the *H. tetradactylum* sample from el Vallès-Penedès show a smaller size and presents smaller crochet and antecrochet (Santafé et al. 1982). However, most of these reports need a thorough review after the comprehensive report on the holotype material from Sansan (Heissig 2012b). Another skull from Ca n'Albinyana (Montcada i Reixac; García-Fernández and Abad, 1997), originally assigned to '*Acerorhinus*' *tetradactylum*, was confirmed by posterior works (García, 2015). The skull is undoubtedly from an aceratheriine, but the generic status is questionable. Its neurocranium is short, the occiput slightly raised, and the insertion of the zygomatic arch very robust, all characters shared with *Alicornops*. Similarly, the dental dimensions are smaller than those of *Aceratherium*, or *Hoploaceratherium*, but closer to the *A. simorrense* holotype (OR-33525) from Villefranche d'Astarac (middle Miocene SW France).

Aceratherium Kaup, 1832

Aceratherium is a small to medium-sized aceratheriine genus with hornless nasal bones (modified from (Deng et al. 2013; p. 982); 'elongated skull, non-projecting orbits; moderate

supraorbital tuberosities, nearly vertical zygomatic arches, rounded braincase, narrow nuchal crest, wide intercondylar notch, compressed and straight postglenoid processes, thin and weakly expanded posttympanic processes, a wide U-shaped choana reaching the M2/M3 boundary, subhypsodont teeth, tusk-like i2, strong crochets, shallowly undulated labial walls, weak paracone ribs, narrow parastyles, constricted molar protocones, short and posteriorly pointed molar antecrochets, absent lingual cingulum on molars, a well-developed labial cingulum on the lower premolars, a weak or absent crista on the upper molars, a molar protocone with a rounded lingual margin, a strong molar parastyle fold, and a slightly constricted protocone on the molars'. Most of the genus' cranial anatomy is known in the type species *Aceratherium incisivum*, while the postcranial information mostly comes from the German locality of Höwenegg. It has a short skull, hornless and pointed nasal bones, a single sagittal crest, brachyodont teeth, I1 missing or poorly developed, slightly broadened symphysis, and mediportal postcranial proportions (Hünnerman 1989). Undetermined *Aceratherium* remains have been cited in Can Perellada, Can Jofresa complex (Trinchera Norte Autopista and Trinchera Sur Autopista), and Torrent de les Febulines.

Aceratherium incisivum Kaup, 1832-1834

Stratigraphic range
MN 9–MN 12.

Geographic distribution
Austria, France, Germany, Hungary, Moldova, Romania, Spain, and Switzerland. Reported Turkish remains could belong to another Aceratheriina species, a group extremely diverse along the late Miocene Anatolian basins.

Iberian localities
Can Llobateres, Can Ponsic, Polinyà, Can Feu, Can Perellada, La Tarumba, Autovía Orbital B-40, Piera (Torrentet des Traginers), Los Valles de Fuentidueña, La Roma 2, Concud, and Los Batallones fossil complex.

Remarks
Aceratherium incisivum was defined by Kaup (1832) from the lower Vallesian of Eppelsheim (Germany). It is a mediportal rhinoceros with hornless, upraised nasal bones, small upper incisors, strongly curved lower ones and reduced ectocuneiforms. Initially, all 'acerathere'-like remains were shoehorned into '*Rhinoceros incisivus*', the nominal species. These should be taken with caution, in line with the early intricate nomenclatural history of the species (detailed in Giaourtsakis and Heissig 2004). The first report of the species in the Iberian Peninsula comes from the Teruel area (Ezquerra de Bayo 1837) and Zamora (Vilanova in de Uhagón 1873) but have not been reviewed by posterior studies. Its presence in the Iberian Peninsula is mainly restricted to the Vallès-Penedès Basin, being scarce elsewhere. Among the abundant Vallès-Penedès sample, the juvenile skull IPS, CLL 15356 stands out for its fine preservation, giving valuable information about the morphology of the early developmental stages of the species. Additional skulls from Autovía Orbital de Barcelona B40 (Tomàs et al. 2010) and the Batallones fossil complex represent mature individuals. It is in the latter locality where an exceptionally preserved complete articulated skeleton was found (Figures 1 e-1 f), partially described in Cerdeño and Sánchez (1998).

Tribe Rhinocerotini Gray 1823

Subtribe Rhinocerotina Gray 1823

The subtribe Rhinocerotina (sensu Antoine 2002) includes all five extant rhinoceros species. Their first representatives come from the earliest Miocene of Southeast Asia (Antoine et al 2003), from where they spread to Africa by the late early Miocene. They are currently considered as monophyletic and have been defined based on the elongation of the nasal region, a trend to the ossification of the nasal septum, or the presence of a median frontal horn (Antoine 2002, 2003). However, many of these characters are strongly plesiomorphic and appear repeatedly during the evolution of the group.

Subtribe Teleoceratina Hay 1902

Teleoceratines are rarely documented in the Iberian basins. Their body proportions are variable: from the slender or mediportal late Oligocene – early Miocene species to the short-legged and barrel-like later taxa from the middle to late Miocene. The lower i2 are dimorphic and can reach large dimensions in males. The nasal bones are relatively short and usually bear a rough pinched surface (unique or double) at its tip as horn insertion.

Diaceratherium Dietrich, 1931

Diaceratherium is an early genus of small to medium-sized teleoceratine rhinocerotid. It is first recorded in the European Late Oligocene (MP 29). Thereinafter, the genus experiences a high diversity phase in the earliest Miocene (MN 1–2) followed by a diversity impoverishment and a geographic expansion of *D. aurelianense*, its last European representative, during the MN 3–4 biozones (Becker et al. 2009). The genus *Diaceratherium* genus shows a wide variability in terms of size, cranial morphology, and postcranial proportions. The latter is particularly striking considering the differences between the mediportal *Diaceratherium* aff. *lemanense* from Thézels (MP 30) and the graviportal *Diaceratherium aurelianense* plus the multiple intermediate forms (Becker et al. 2009). These differences led some authors to include *D. aurelianense* within the more robust genus *Prosantorhinus* (Heissig 2017).

Diaceratherium aurelianense (Nouel, 1866)

Stratigraphic range
Iberian Peninsula: MN 2b (cf.)–MN 4a. Total range: MN 2b–earliest MN 4b (both considered as cf.).

Geographic distribution
France, Germany, Portugal, Spain, Switzerland.

Iberian localities
Horta das Tripas, Loranca del Campo (cf.), Molí Calopa, Buñol, and Rubielos de Mora 3.

Remarks
Diaceratherium aurelianense attains graviportal limb proportions and a medium to large body size. Additionally, is characterized by several particularities on its upper (molariform premolars with very strong paracone and crochet, crista and antecrochet on molars) and lower dentition (i.e., profound labial groove between the lophids of the molars, weak hypolophid and low lingual wall of the premolar series and the m1; Becker et al. 2009). The species is widely represented in

the Burdigalian of Central Europe, being scarce in the Iberian basins. In the Vallès-Penedès, *D. aurelianense* has been solely recorded in Molí Calopa (MN 3b; Santafé 1978a). Additional Iberian records of the species come from Horta das Tripas, Loranca del Campo (cf.), and Rubielos de Mora 3 (Cerdeño 1989; Becker et al. 2009).

Prosantorhinus Heissig, 1974

Prosantorhinus is a small to medium-sized, European teleoceratine genus with a concave dorsal skull profile, upraised nasals, shortened upper premolars compared with the molars, and triangular occlusal outline of the M3 (Heissig 2017). In addition, the genus can be discriminated based on nasal bones bearing a small median area for the horn insertion together with latero-ventral expansions, zygomatic arch with a low cranial insertion and a high dorso-caudal border, smooth processus postorbitalis, well-developed processus paraoccipitalis, fused proximal radius-ulna facets, and robust postcranial proportions. It is best known from the type species, *P. germanicus*, well represented in the locality of Sandelzhausen, and *P. douvillei*, common in Béon 1 (Antoine 2002; Antoine et al. 2018). The robust but small remains from the locality of Buñol could belong to an undetermined *Prosantorhinus* species. The robust teleoceratine remains from the area of Lisboa either assigned to *Diaceratherium* or *Gaindatherium rexmanueli* might belong to this genus as well, being in need of an exhaustive revision (Ginsburg et al. 1987; Cerdeño 1992b, 1996b; Heissig 2017).

Prosantorhinus douvillei (Osborn, 1900)

Stratigraphic range
Iberian Peninsula: MN4–MN5. Total range: Early to Middle Miocene, MN 3b–MN 5.

Geographic distribution
France, Germany, Portugal, Spain.

Iberian localities
Charneca do Lumiar, Quinta das Pedreiras, Quinta do Narigão, and Somosaguas Norte.

Remarks
Prosantorhinus douvillei is a large *Prosantorhinus* species. The nasal bones are much longer, swollen at it base, and partly fused, the premolar series longer with respect to the molar series, the P2-4 always present an antecrochet, and manus tri- or tetradactyl. The remains from Portugal named as *Gaindatherium* (*Iberotherium*) *rexmanueli* (Antunes and Ginsburg 1983) are morphologically close to *P. douvillei*, but the proportions fit *D. aurelianense*. We here refer these remains to the former, following Cerdeño (1996b) and Heissig (2017).

Brachypotherium Roger 1904

Brachypotherium is a genus of large rhinoceros species with short, massive limbs (being particularly evident in the autopodium), dorsoventrally compressed carpal and tarsal bones, short hornless nasals, cranially placed orbits, robust anterior dentition, brachydont but broad molar teeth, and large and curved i2 (Geraads 2010; Heissig 2012b). Its presence in the Iberian Peninsula is questionable (see remarks).

Brachypotherium brachypus (Lartet, 1837)

Stratigraphic range
MN 4–MN 7 + 8.

Geographic distribution
Bulgaria, France, Germany, Greece, Spain?, Switzerland, Turkey.

Iberian localities
Arroyo del Val-4, Manchones-1, and Manchones-2.

Remarks
Although large for rhinoceros standards, *B. brachypus* is in fact the second smallest species of the genus after the African *Brachypotherium minor*. The species shows large upper teeth and developed buccal cingula, lacks crochet and antecrochet, and both protocone and hypocone are slightly pinched (Geraads and Spassov 2009; Heissig 2012b). Its presence at the localities of Artesilla, Masquefa, Can Marcet, Monteagudo (Yesos de Monteagudo; Santafé 1978b; Azanza et al. 1993) needs further support. Additional undetermined *Brachypotherium* remains were reported at Can Canals (Papiol, Vallès-Penedès; Santafé and Belinchón 1988) and Alto del Ballester-1 (Montoya et al. 1996), or Trinchera del Ferrocarril (Santafé 1978a) are too diverse and/or fragmentary to confirm this ascription, being therefore discarded following the arguments provided by Heissig (2012b).

Subtribe Rhinocerotina

Lartetotherium (Ginsburg, 1974)

'Medium-sized one-horned rhinoceros with a skull of medium length with a strongly concave dorsal profile. Anterior dentition with two pairs of lower incisors in each hemimandible, the anterior ones being sometimes lost in older individuals. Jugal teeth unirradicular, with a deep groove along the root. Strong metacone fold on the premolar teeth, weaker but present in the molars. Limbs with primitive characters of the tribe'. (Heissig 2012b). The genus *Lartetotherium* is defined from the complete collection of Rhinocerotina remains from Sansan (Ginsburg 1974). The diagnosis of *Lartetotherium* corresponds to that of the species, by monotypy. It is a middle-sized and primitive Rhinocerotina with an uncertain phylogenetic position: Deng et al. (2011) consider it basal to extant African species while other authors place it as a basal rhinocerotine (Cerdeño 1995; Antoine 2003; Pandolfi et al 2021b; Antoine et al. 2022).

Lartetotherium sansaniense (Lartet in Laurillard, 1848)

Stratigraphic range
MN4 – MN9.

Geographic distribution
Austria, France, Germany, Spain, Switzerland.

Iberian localities
Arroyo del Val-4, Aveiras de Baixo, Benavente, Bolaños de Campos, Brihuega, Buñol, Ca n'Almirall, Can Gabarró, Can Llobateres, Can Mas (El Papiol), Can Missert, Can Ponsic, Cendejas de la Torre (=Los Canalizos/Matillas), Cerro del Otero, Charneca do Lumiar, Coca, Fuensaldaña, Hostalets de Pierola (Can Mata I), La

Cistérniga, La Retama, Las Planas (=Villafeliche), M-407 Rotonda, Manchones, Mas d'Antolino-3, Monteagudo (= Yesos de Monteagudo), Nombrevilla, Paracuellos 3, Pero Filho, Póvoa de Santarém, Quinta da Farinheira, Quinta das Flamengas, Relea, Sant Pere de Ribes, Toril 3A, Toril 3B, and Trinchera (=Trinchera del Ferrocarril).

Remarks

Lartetotherium sansaniense is a medium-sized one-horned rhinocerotine with long rostrum, nasal septum not ossified, absence of supraorbital processes, posteriorly projected margins of the pterygoids, simple brachyodont dentition with tusk-like i2 and vestigial i1 and slender limbs. The study of the postcranial bones of the species in the Iberian Peninsula revealed two groups according to their size (Cerdeño 1986). However, no size differences have been detected among their dentitions. Postcranial remains from El Papiol (Can Mas) pertain to the larger group, showing comparable proportions to those of the type locality of Sansan or Buñol (Cerdeño 1986). Cranial remains of the species have been recovered from the sites of La Retama (Figure 1d) and M-407 Rotonda.

'Dicerorhinus' Gloger, 1841

The genus *Dicerorhinus* has been used as a wildcard for Miocene–Pleistocene Rhinocerotina. Although most of them have been relocated in genera such as *Lartetotherium, Stephanorhinus*, or *Dihoplus*, the ascription of some poorly known species, are still under debate. *Dicerorhinus* is nowadays restricted to few Pliocene-Pleistocene Asian species related to the extant Sumatran rhino *Dicerorhinus sumatrensis* (Groves 1983). Therefore, the review of these undetermined *Dicerorhinus* remains (El Canyet or Can Mas) is necessary, particularly at the light of the updated description of the cranial and postcranial material of *L. sansaniense* (Heissig 2012b) and the presence of early Miocene Rhinocerotina of the genus *Gaindatherium* from the Levantine corridor (Pandolfi et al. 2021c).

'Dicerorhinus' montesi Santafé et al. 1987

Stratigraphic range

MN 4.

Geographic distribution

the species is restricted to eastern Iberia.

Iberian localities

Buñol.

Remarks

The small size of the isolated postcranial elements from Buñol (MN4) justified naming a species separated from *Lartetotherium sansaniense* (used under the binomen '*Dicerorhinus sansaniensis*'; Santafé et al. 1987). The species has been solely found at the type locality of Buñol, making it one the scarcest Rhinocerotina species of the European fossil record. A thorough analysis of the remains from Buñol would clarify its phylogenetic position, as no systematic studies on the remains of '*D*'. *montesi* have been made since its original description.

'Dicerorhinus' steinheimensis Jäger 1835

Stratigraphic range in the Iberian Peninsula

MN 7 + 8–MN 9. Total range: middle to late Miocene.

Geographic distribution

France, Germany, Spain.

Iberian localities

Can Casablanques, Can Feliu, Can Ponsic, and Castell de Barberà.

Remarks

The species '*D*'. *steinheimensis* is another elusive European rhinocerotine from the Miocene. Its size is smaller than that of *L. sansaniense*. The dentition is simple, with remarkably trapezoidal outline in the M1, smooth ectolophs and a marked lingually inclined posterior half of the ectoloph in P4-M2. The Iberian record of this species is restricted to the Vallès-Penedès Basin, although part of the remains originally ascribed to the species was updated as belonging to *L. sansaniense*. We provisionally maintained part of these records inside '*D*'. *steinheimensis*.

Dihoplus Brandt, 1878

Dihoplus is a two-horned rhinoceros genus with quite caudal tooth row, expanded and high occipital crest; nasal bones wide and thick; rounded and short nasal notch located above the anterior premolars; short cranial base; close postglenoid and paroccipital processes; post-glenoid apophysis close to the post-tympanic one; absence of P1; primitive submolariform upper premolars; molars with vestigial antecrochet and weak crista (missing on DP3–4), and presence of i2 (Geraads and Spassov 2009).

Dihoplus schleiermacheri (Kaup 1832–34)

Stratigraphic range

MN 9–earliest MN 14

Geographic distribution

Spain, France, Germany, Bulgaria, Hungary, and Turkey.

Iberian localities

Masía del Barbo 2A, Masía del Barbo 2B, La Roma 2, Puente Minero, Concud Barranco, Concud Cerro de la Garita, El Arquillo (Arquillo de la Fontana/Rambla de Valdecebro), Las Casiones, La Alberca, Cenes de la Vega, El Fargue-Fábrica de Pólvora (cf.), El Fargue-Río Beiro (cf.), Los Hornillos, Can Llobateres, Can Jofresa, Subsuelo de Sabadell, Can Trullàs, Piera, Can Perellada, Cellórigo, Crevillente-2, and Crevillente-15.

Remarks

The type species of *Dihoplus, D. schleiermacheri* is the largest rhinoceros from the Iberian late Miocene. It retains several plesiomorphic characters for a Rhinocerotina such as a functional anterior dentition, the presence of a single sagittal crest, or the retracted orbit (Geraads 1988; Giaourtsakis et al. 2006). The nasal notch reaches only the anterior border of the P2, its temporal crests closely approach, bears a robust zygomatic arch and long paroccipital process, large upper I1, functional I2 and a strong symphysis with large i2 and small i1 (Geraads and Spassov 2009). Its presence in the lower Vallesian of the Vallès-Penedès Basin is scarcer than *A. incisivum*. In contrast, the species is dominant in the Calatayud-Montalbán and Teruel basins.

An augment in the robustness of the carpus and in the trochlear asymmetry of the astragalus through time has been observed among the Iberian sample (Guérin 1980; Santafé and Casanovas-Cladellas 1983-1984a). Guérin (1980) defines '*Dicerorhinus*' *schleiermacheri* according to the following diagnosis: long skull with bulky nasal bones finishing in a downwards curved tip; a frontal convexity that corresponds to the insertion of the second horn; high occipital crest and occipital plate little backwards and upwards inclined; sagittal crest preset; open auditory meatus; posttympanic apophysis longer than postglenoid; long mandibular symphysis with a constant width forming a strong angle with the horizontal ramus; high ascending ramus with a concave-convex ventral border; strong angular process; developed anterior dentition (I1, small I2, and i2). Upper cheek teeth with undulated ectoloph, crista and crochet generally present and variable development, sometimes multiple.

Pliorhinus Pandolfi et al., 2021

Cerdeño (1992b) considered *Pliorhinus miguelcrusafonti* as a smaller subspecies of *Pliorhinus megarhinus*. This relation has been posteriorly confirmed by the comprehensive study of the Georgian remains from Kvabebi, which allowed linking the post-cranial remains from Layna to craniodental data and justified the creation of a new genus, *Pliorhinus*, together with *P. megarhinus* (Pandolfi et al. 2021a). *Pliorhinus* is a recently coined two-horned rhinoceros genus characterized by the flat dorsal profile of the skull, the convex cross section of the processus postglenoidalis, usually absent labial cingulum on upper and lower teeth, the presence of crochet on upper premolars, or the presence of a lingual bridge in P3–4 among other characters (Pandolfi et al. 2021a).

Pliorhinus miguelcrusafonti (Guérin and Santafé, 1978)

Stratigraphic range in the Iberian Peninsula
MN 15. Total range: MN 15–MN 16.

Geographic distribution
Spain and Georgia.

Iberian localities
Layna, La Calera, Alcalá del Júcar, and Molins de Rei.

Remarks
This rare species can be defined from its low anterior insertion of the zygomatic process, concave dorsal surface of the skull, a foramen mandibulare above the teeth necks level, wrinkled enamel, premolars bearing multiple crochets and continuous but reduced lingual cingula, and constriction of the protocone always found on upper cheek teeth, or an open posterior valley on p2 (Pandolfi et al. 2021a). The species was first recognized from post-cranial remains from Layna (Soria, Castilla La Mancha; Guérin and Santafé 1978; Guérin 1980). It has been additionally identified at the La Calera and Alcalá del Júcar (Cerdeño 1989; Mazo 1997). *P. miquelcrusafonti* is medium to large and more robust than the coeval Villafranchian species *S. etruscus*, but smaller than *P. megarhinus*. Additional remains potentially related to *P. miguelcrusafonti* from United Kingdom (Pandolfi et al. 2021b) suggest a broader expansion of related forms through Western Europe and the Caucasus.

Pliorhinus megarhinus (de Christol 1834)

Stratigraphic range in the Iberian Peninsula
MN13-16. Total range: MN 12–MN 16.

Geographic distribution
The species is ubiquitous, being reported in Spain, France, Germany, Italy, Romania, Poland, Turkey, Ukraine, Belgium, Russia, Hungary, and China (considering *Dihoplus ringstroemi* as a junior synonym).

Iberian localities
Venta del Moro, Alcoy-Mina, Cornellà del Terri, and the Vera Basin.

Remarks
The species is best known from French and Italian localities, being diagnosed as a large, tandem-horned rhinoceros with long and thick nasal and frontal bones, it lacks an ossified nasal septum, the dental row is rather caudal, the nasal notch located above premolars, and close paraoccipital processes and post-glenoid apophysis. The upper premolars are primitive while the molars are simple, with vestigial antecrochets and weak or absent crista. The i2 is still present (Pandolfi et al. 2015). Its presence in the Iberian Peninsula is best represented by the latest Miocene locality of Venta del Moro (although previously determined to as *D. schleiermacheri*; Cerdeño 1989). The upper molar from Sords (described in Sanz et al. 1987 and reported lost; Galobart et al. 1996), as well as the first report of the species in Iberia from Los Tejares (Málaga; Orueta 1874) did not include a description of the remains nor have been mentioned in the literature posteriorly. The presence of the species at Villaroya (La Rioja; Guérin 1980) has been posteriorly discarded in favor of *S. etruscus* (Malapeira et al. 2014) and the Mt IV cited in Fernandez (2000) has been reassigned to *P. miguelcrusafonti* (Pandolfi et al. 2021a).

Stephanorhinus Kretzoï, 1942

Stephanorhinus is a genus of Palearctic rhinos typically distributed during the Neogene through the latest Pleistocene. In general, species of the genus *Stephanorhinus* share a not functional anterior dentition, ossification of the nasal septum often incomplete, long nasal incision, very long rostrum, and a strong anterior insertion of the zygomatic arches, dolichocephalic skull bearing two tandem-placed horns, and strongly molarized premolars. However, most of these characters all also shared by *Coelodonta*. In fact, the paraphyletic status of *Stephanorhinus* has been suggested based on the intrusion of the latter genus within the clade (Geraads 1988; Pandolfi et al. 2021b; Antoine et al. 2022). *Stephanorhinus* is the rhinoceros genus with the most occurrences in the Iberian Peninsula, being a common component of the regional Pliocene-Pleistocene megafauna. Undetermined *Stephanorhinus* species are listed from the localities of Cova Gran, Baza-1, Cueva de A Valiña, Cueva de los Peines, El Molinar (=Carretera del Molinar), Llantrales quarry, Mazarredonda (= Cueva del Cubo), Mestas de Con, Pontón de la Oliva, Cueva de los Huesos, and Toledo.

Stephanorhinus etruscus (Falconer, 1859)

Stratigraphic range
Early Villafranchian to Early Galerian (3.3–0.9. Ma).

Geographic distribution
Spain, France, Italy, Romania, Netherlands, Germany, Greece, Israel, and Hungary.

Iberian localities
Atapuerca TD4, Atapuerca TD6, Atapuerca TD8, Avenc Marcel, Barranco del Paso, Bòbila Ordis, Cornellà del Terri, Crespià, Cueva Victoria, El Chaparral (Villaluenga del Rosario), El Rincón-1, Fonelas P-1, Fuente Nueva 2, Huélago, Huescar-1, Incarcal, La Puebla de Valverde (= Puebla), Láchar, Las Higueruelas, Pozo de Piedrabuena, and Villaroya.,

Remarks
The Etruscan rhino is one of the best-known, Eurasian species of rhinoceros. It can be distinguished from other Pliocene taxa from its shortened mandibular symphysis, the relatively low vertical rami of the mandible, weaker crochets on the upper teeth, and slenderer metapodials. The fossil record of the species in the Iberian Peninsula is abundant and includes a complete skeleton from Crespià (including a complete skull; Figure 1a) and a partial one from Villaroya, plus multiple cranial remains (e.g., Las Higueruelas). It replaces other pre-Ruscinian Rhinocerotina such as *P. miguelcrusafonti* or *S. jeanvireti*. Las Higueruelas (ca. 3.3 Ma; (Mazo 1995) and El Pozo de Piedrabuena (ca. 3 Ma) are amongst the first ocurrences for the species. Different specialists interpreted the smaller *S. etruscus*-like remains recorded at around 1.7–1.3 Ma as a different subspecies *Stephanorhinus etruscus brachycephalus* equivalent to *Stephanorhinus hundsheimensis* (Guérin 1980; Kahlke 2001), transitional *S.* aff. *hundsheimensis* remains (Fortelius et al. 1993; Mazza et al. 1993), the first records of *Stephanorhinus hundsheimensis* (Lacombat 2006), or a distinct but small *Stephanorhinus* coexisting with *S. hundsheimensis* (van der Made 2010). This later, reduced *S. etruscus* have been recorded in the Iberian sites of Atapuerca Gran Dolina (TD4, TD6, and TD8) or El Chaparral. The last global record of these small *S. etruscus* occurs at Atapuerca TD8, at around 0.78 Ma. However, such a size reduction remains controversial (Pandolfi et al. 2017).

Stephanorhinus jeanvireti (Guérin, 1972)

Stratigraphic range in the Iberian Peninsula
MN 15/16 transition. Stratigraphic range: end of MN 15–MN 17/18.

Geographic distribution
Spain, France.

Iberian localities
Camp dels Ninots.

Remarks
A Pliocene *Stephanorhinus* species larger and more robust than *S. etruscus*. The cranial morphology is clearly distinct from other *Stephanorhinus* species: the nasal bones are slenderer, the postorbital region shorter. The synonymy of the species with *Stephanorhinus elatus* (Ballatore and Breda 2019) has been questioned (Pandolfi et al. 2019). In the Iberian Peninsula, the species has been only reported from Camp dels Ninots. The reported remains include a nearly complete skeleton with a partial cranium still to be studied in detail. Its presence at Baza-1 (MN 14), reported as *Stephanorhinus* sp. cf. *S. jeanvireti* (Maldonado-Garrido et al. 2017; Ros-Montoya et al. 2017) predates in ~1 Ma the first record for the species, and should be taken with caution until additional remains are found, being therefore excluded from the hypodigm of the species.

Stephanorhinus hemitoechus (Falconer, 1868)

Stratigraphic range in the Iberian Peninsula
Middle Pleistocene–Aurignacian. Total range: middle Galerian and Aurelian (500 ka BP–45 ka BP).

Geographic distribution
Stephanorhinus hemitoechus is widely distributed through Europe, near East and North Africa.

Iberian localities
Galeria Pesada, Gruta da Aroeira, Gruta da Figueira Brava (Setúbal), Gruta da Furninha, Gruta do Correio-Mor, Gruta do Escoural, Gruta Nova da Columbeira (Level 8), Lorga de Dine, Pedreira das Salemas, Serra dos Moinhos Cave (= Serra dos Molianos), Abric Romaní, Abrigo de Eudoviges, Aitzbitarte, Arenero de, Arriaga Iia, Arrillor, Atxagakoa, Axlor, Bolomor (= Bolomor Cave), Caus del Duc, Coscobilo, Cova de Molí Mató, Cova del Gegant, Cova del Toll, Cova Negra, Cueva Antón, Cueva de Arnero, Cueva de Cobalejos, Cueva de la Ventana (= La Ventana), Cueva de la Zarzamora (= Cueva del Búho), Cueva de los Moros de Gabasa, Cueva de los Torrejones, Cueva de Mollet (= Reclau, Serinyà), Cueva de Valdegoba (Nivel V, Valdegoba), Cueva del Castillo, Cueva del Conde, Cueva del Congosto, Cueva del Hueso, Cueva del Otero, Cueva del Pendo, Cueva del Rinoceronte (= El Pozu la Peruyal), Cueva Horá, Cueva Millán (Nivel 1A), Cueva Morín, Cueva de los Huesos de Obón (= Obón), Cueva Oscura de Ania (= Cueva Oscura), El Baradello, Ermitons, Galería-Cueva de los Zarpazos, Gran Dolina TD4, La Alfaguara, La Carihuela, Las Majólicas, Los Casares, Peña Miel, Pinilla del Valle (= Cueva del Camino, Camino Cave), Plaça de la República, Portalón de Tejadilla, Punta Lucero, Sierra de la Yedra (= Alfaguara), Solana de Zamborino, Torralba y Ambrona, Turruncún, Udías (= Cueva Bonita/Cueva de las Buenitas/Mina de Buenita), Vaciamadrid, and Villavieja.

Remarks
The 'narrow-nosed rhino' is the most abundant rhinoceros from the Iberian fossil record in terms of number of occurrences and includes remains as interesting as the heavily mineralized complete skeleton from El Pozo la Peruyal (Pinto Llona et al. 2006). The species is first recorded in the Iberian Peninsula in the middle Pleistocene, expanding its presence up to, probably, the Aurignacian. It has been frequently misidentified as either '*Stephanorhinus mercki*' or *Stephanorhinus kirchbergensis* (Cerdeño 1990). It is a medium-sized graviportal *Stephanorhinus* with tooth crowns higher than in *S. etruscus*, rugous enamel and patches of cement, upper premolars with an undulated ectoloph, acute and clearly 'V'-shaped dental valleys, and conspicuous paracone and metacone folds, crochet and crista well-developed, and elongated cheek teeth void of lingual cingulum. The postcranial skeleton varies in size across the Iberian localities, contrasting with the rather homogeneous dentition (Cerdeño 1990). The narrow-nosed rhino has been proposed as a grazer/mixed feeder based on meso and microwear analyses (Rivals and Lister 2016; Rivals and Ziegler 2018).

Stephanorhinus hundsheimensis (Toula, 1902)

Stratigraphic range in the Iberian Peninsula
Early Pleistocene, Epivillafranchian. Total range: late Villafranchian to Galerian (~1.4 Ma–~0.5 Ma).

Geographic distribution
Portugal, Spain, France, Germany,

Iberian localities
Arenero de los Rosales (=Arenero de las Mercedes), Barranco León 5, Cal Guardiola Lower Unit (layers D1, D2 and D3), Cal Guardiola Upper Unit (Layers D4, D5, D6, D7), Cova del Rinoceront (= Cova de la Pedrera de Ca n'Aimerich), Fuente Nueva 3, Incarcal I, Vallparadís Estació Lower Unit (Layers EVT10, EVT11 and EVT12), Vallparadís Estació Middle Unit (Layers EVT6, EVT7 and EVT8), Venta Micena, Venta Micena-1, Venta Micena-2.

Remarks
A brachydont *Stephanorhinus* species typical from Pleistocene interglacial of the Middle and Late Pleistocene. Many of the Iberian occurrences listed as '*Dicerorhinus*' or '*Stephanorhinus etruscus brachycephalus*' would belong to this species (van der Made and Montoya 2007). It shows cursorial proportions and long limbs, a vertical occipital plate, pointing to a mixed-feeder diet with a broad range of dietary regimes and habitats. Its premolars are always provided of a crochet, either simple or multiple, or 'U'-shaped median valleys. The first Iberian record of the species comes from Incarcal I (1.5–1.4 Ma). Additional occurrences include a finely preserved skull from the Vallès-Penedès Basin, described in Madurell-Malapeira et al. (2010). On the other hand, the small remains from Venta Micena (ca. 1.6 Ma; Malapeira et al. 2014), Barranco León 5, and Fuente Nueva 2 (Guadix-Baza Basin, ca. 1.4–1.3 Ma), originally identified as a small *S. hundsheimensis* (Lacombat 2010), have been posteriorly listed as *S. etruscus* (Pandolfi and Erten 2017). The remains from Los Rosales (Arenero de los Rosales/Las Mercedes), briefly reported but not described in 1935 (Royo y Gómez 1935), are apparently lost and have not been reviewed since their original description (Soto and Sesé 1987). Finally, the *S. hundsheimensis* from Cova del Rinoceront (level III; MIS 5; Daura et al. 2015), if confirmed, would represent the latest for the species, ~ 400 ka BP after the previous occurrence.

Stephanorhinus kirchbergensis (Jäger, 1839)

Stratigraphic range in the Iberian Peninsula
MIS 5. Total range: middle Galerian (MIS 15)–Aurelian (Eemian Interglacial), Middle Pleistocene in Western Europe.

Geographic distribution
Eurasian Palearctic.

Iberian localities
Cova Negra and Lezetxiki.

Remarks
Stephanorhinus kirchbergensis is a rare *Stephanorhinus* species. It is considered a senior synonym of the Merck's rhino, *Stephanorhinus mercki*. It is a large species, with long nasal bones and a partially ossified nasal septum. The anterior insertion of the zygomatic arch is very robust, the neurocranium not as elongated as in *S. hemitoechus*, and the occipital plate nearly vertical, closer to *S. hundsheimensis*. As in *S. hundsheimensis*, the median valleys are 'U'-shaped. Its presence in the Iberian Peninsula is questionable. Many of original occurrences of the species (e.g: Cueva del Castillo or Cueva de Arnero) were posteriorly reassigned to *S. hundsheimensis* (see description of the latter for further details). The only remains included here, from Cova Negra and Lezetxiki, were cited but not reviewed by Cerdeño (1990).

Coelodonta Bronn, 1831

The earliest member of this cold-adapted genus evolved at the early Pliocene of Tibetan plateau (Deng et al. 2011). Molecular analyses place *Coelodonta* as the sister group of *Stephanorhinus*, and the modern Sumatran rhino (*Dicerorhinus sumatrensis*) as their closest living relative (Cappellini et al. 2019; Liu et al. 2021). A single species, *C. antiquitatis*, has been recorded in the Iberian Middle to Late Pleistocene interval. The genus was first documented in high-altitude environments of the Tibetan Plateau, from where it eventually dispersed across Eurasia during Pleistocene times (Deng et al. 2011).

Coelodonta antiquitatis (Blumenbach, 1799)

Stratigraphic range in the Iberian Peninsula
188 ka BP–20 ka BP. Total range: 460 ka BP–11 ka BP.

Geographic distribution
Coelodonta antiquitatis was a ubiquitous species at the Pleistocene glacial maxima, ranging from Spain to China.

Iberian localities
Abauntz (level f), Abrigo del Cuco (= El Cuco), Aldehuela (= Arenero de la Fábrica de Ladrillos), Arenys de Mar, Arrikrutz, Arroyo Culebro, Baio, Cantera de Castrejana (= Cantera de Castresana), Cantera de La Vía, Canyars (= Riera dels Canyars), Covacho, de Arenillas (level II; = Covacho Arenillas), Cueva de Nando, Cueva de San Pedro, Cueva del Sidrón, El Cuco (level XIII), El Toll, Jou Puerta, La Gándara, La Liñera (= San Vicente de la Barquera), La Mina, La Parte, La Rexidora (= Rexidora), La Xana (= Cueva de la Xana), Labeko Koba (level IX sup.), Las Caldas (= Cueva de las Caldas), Las Cáscaras, Las Cáscaras (= Cáscaras de Pelurgo), Leguintxiki, Lezetxiki (level IIIa), Lezika, Los Rosales, Mainea, Mataró, Minas de Udías, Olopte B, Peña de Mudá, Portalón de Tejadilla, Teixoneres Cave (unit III),Unquera (= Trinchera de Unquera), and Urtiagako Leizea.

Remarks
Coelodonta antiquitatis, or woolly rhino, was firstly reported by Fernández Soba (1865) in León. The distribution of this species, relatively common in numerous Eurasian sites, is mainly restricted to the Northern half of the Iberian Peninsula. It shows a long, dolichocephalic skull with long nasal bones and a completely ossified nasal septum in adult individuals. Their cheek teeth are relatively high crowned (for Rhinocerotina standards), covered with abundant cement, bear closed mediofossettes, undulated ectoloph, and coarse enamel crenulations. As in other Plio-Pleistocene species, the anterior dentition is reduced. The species presence in the Iberian Peninsula can be linked to three main events: during the Mousterian occupation, between Heinrich 4 (H4) and H3 events, and the recent most localities of Abauntz and Leguintxiki around 20 ka BP (Rodríguez-Almagro et al. 2021), becoming extinct at ca. 10.7 ka BP worldwide (Orlova et al. 2008).

Undetermined remains

Fossil remains of rhinoceros are frequent amongst the Iberian Neogene basins. However, their preservation and abundance are not always optimal for a direct identification. The isolated small i2 from the early Miocene of Cabezo de La Junta (MN2b-MN3; Las Bárdenas Reales, Navarra) shows a short, triangular crown and rather straight root (Murelaga et al. 2004), discarding teleoceratine affinities. Unfortunately, no further remains have been reported from this locality. Santafé (1978a) reports undetermined remains

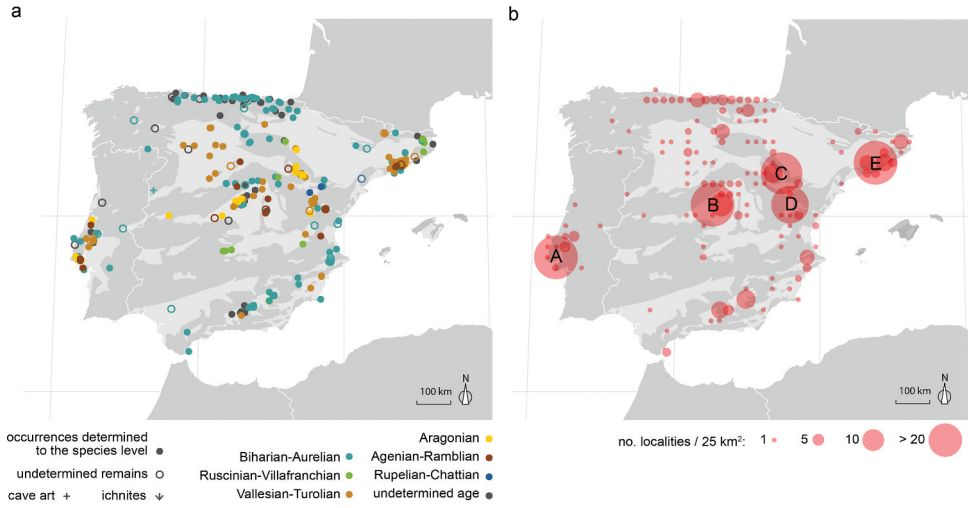

Figure 3 a, sampling map of Rhinocerotidae in the Iberian Peninsula. a, localities colored by temporal setting; b, sampling map of the localities with remains on Rhinocerotidae. Lighter colors represent Neogene basins. Main fossiliferous areas are detailed as follows: A, Lisbon area (Tagus Basin); B, Madrid Area (Tagus Basin); C, Calatayud-Montalbán Basin; D, Teruel Basin; E, Vallès-Penedès Basin. Each geographic bin in b equals 40 km^2.

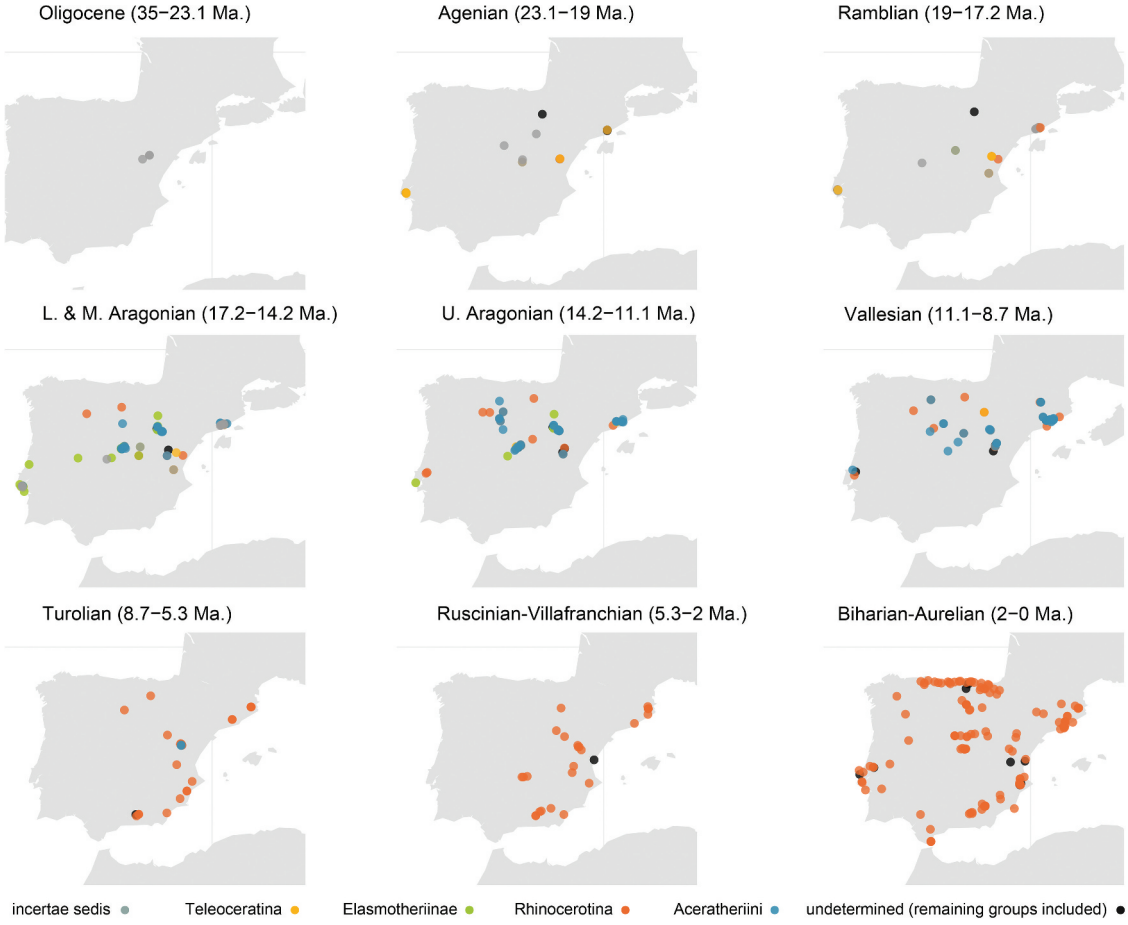

Figure 4 Distribution of the rhinocerotid faunas from the Iberian Peninsula from the late Oligocene to the latest Pleistocene divided according to the ELMA. Geographical reconstruction according to the 'Paleomap' reconstruction model (https://www.gplates.org). Some outlying distributions are the result of the loose stratigraphic constrain of some localities (e.g., the presence of Elasmotheriinae in the upper Aragonian).

from Poble Nou de Sant Quirze (MN 7 + 8), the lower tooth from El Fallol (Rubí), or the badly preserved distal humeral epiphysis from Subirats (Crusafont and Truyols 1955), all from the Vallès-Penedès Basin, are too fragmentary to assess a specific determination. Finally, the very particular morphology of the fragmentary and scarce remains from Cetina de Aragón have been related with *Pleuroceros* (Cerdeño 1992b) but are too fragmentary to pinpoint their systematic affinities. Additional localities with citations of undetermined rhinoceros remains are detailed in Supplementary Table S1.

Results

The gathered data comprise a total of 463 occurrences containing 27 rhinoceros species corresponding to 17 genera spanning more than 30 million years. This information is summarized in Figures 2–3, which show the spatiotemporal ranges of Iberian rhinocerotid taxa during the Oligocene-Plesitocene. The distribution of fossil occurrences is concentrated along the Miocene, and, particularly, Pleistocene (Biharian-Aurelian) intervals (Figure 4–5). The initial testing of its completeness reveals that the highly disparate number of species recorded across highly sampled temporal intervals contain a robust underlying signal beyond coverage subsampling effects (Figure 5). The resulting diversity curve shows a total maximum by the late early Miocene, a plateau through the Aragonian, and a second, more moderate diversity pulse at the Vallesian. From there on, rhinoceros diversity declines, although a potential minor recovery during Pliocene-Pleistocene times is recovered only in the most complete resampled datasets (Figure 5). From a geographic perspective, we have recognized five rich major areas of fossil occurrences in the Iberian Peninsula (figure 3b). These are the Lisbon Area (lower Tagus basin), the Madrid area (higher Tagus basin), Calatayud-Daroca, Teruel (both within the Calatayud-Montalbán basin), and the Vallès-Penedès basin, the latter storing the higher density of rhinoceros-bearing localities from the studied region. Other, secondary areas are the Cantabrian range, mostly composed by Pleistocene karstic deposits and the Guadix-Baza basin (Granada).

With the onset of the Oligocene, rhinoceroses achieved a broad distribution, extending their range east to west across Eurasia. Such migration is part of the 'Grande Coupure', a pronounced mammalian faunal replacement of endemic European faunas by Asian immigrants. Early Oligocene European faunas were populated by a diverse assemblage of basal species of the genera *Ronzotherium* and *Epiaceratherium* (Tissier et al. 2021). In contrast, only *R. filholi* and, possibly, *M. albigense*, have been recorded from Iberia at that time, probably due to the scarce regional record of Oligocene macromammals (Figures 4–5). The early Miocene saw a progressive warming increase after the end of the final Oligocene Antarctic Glaciation at 23.5 Ma. (Zachos et al. 2001). The beginning Miocene was also marked by intensive faunal dispersals. Despite those, Iberian rhinoceroses remained low in diversity for some time, with only two taxa, *Protaceratherium* and *Diaceratherium*, recorded up to the MN 2 and recognized for the first time at Loranca del Campo. By the late early Miocene (MN 4), rhinocerotid faunas from the Iberian Peninsula were enriched with the additional *Protaceratherium*? and teleoceratine of the genus *Diaceratherium* and, posteriorly, *Prosantorhinus*, basal genera such as *Plesiaceratherium* and two species related to *Lartetotherium* (comprising, with La Romieu, the first appearance of Rhinocerotina in Europe). This moment witnessed a progressive global temperature rise which led to the development of open habitats in the central basins of the Iberian Peninsula (Casas-Gallego et al 2021). Elasmotheres, restricted to central Asia, Caucasus, and Anatolia up to that time, dispersed westward during the late Burdigalian. This expansion is embodied by the ephemeral occurrence of *H. corcolense*, the first documented Iberian *Hispanotherium* species. As a result, rhinoceros diversity hit an all-time maximum. This peaking high signal in Iberia was already described in Cerdeño (1992b) and stays strong after controlling for sampling (Figure 5).

The warming trend that began in the early Miocene abruptly accelerated at the beginning of the middle Miocene. The Miocene Climatic Optimum (~16.9–14.7 Ma), one of the warmest phases since the Eocene, resulted in the consolidation of the arid climate already present through Anatolia, the southern peri-Tethyan region, and central Iberia (Antunes and Pais 1984; Meulen and Daams 1992). Another *Hispanotherium* species, *H. matritense*, becomes widespread by the middle Aragonian. *Hispanotherium matritense* was so abundant in the central Iberian basins that coins its coeval faunal assemblages characterized by high hypsodonty and cursoriality (i.e., '*Hispanotherium* faunas'), and serves as a regional biostratigraphic indicator, equivalent to the MN 5 (Antunes 1979; Antunes and Ginsburg 1983; Cerdeño and Alberdi 1983; Cerdeño 1987, 1992a). The presence of *H. corcolense* and *H. matritense*, exemplifies the importance of

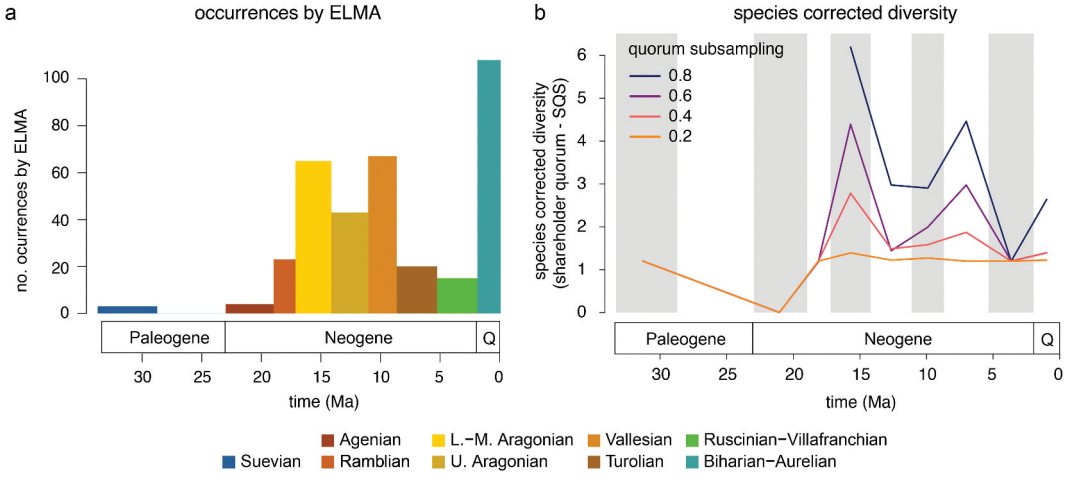

Figure 5 a, ocurrences of Rhinocerotidae from the Iberian Peninsula divided by their corresponding ELMA; b, species diversity after correcting sampling through shareholder quorum (SQS) at four different sampling steps.*Hispanotherium matritense* in the upper Aragonian). *Hispanotherium matritense* in the upper Aragonian).

these forms in the Iberian Peninsula along the middle Aragonian, whereas additional European elasmothere fossils from France and Bosnia-Herzegovina confirm the geographic scale of this event (Ginsburg et al. 1987; Antoine et al. 1997; Becker and Tissier 2020). When temperatures dropped by the end of the Miocene Climatic Optimum, elasmotheriine rhinos rapidly declined. On the contrary, the first aceratheres (*A. simorrense* and *H. tetradactylum*) entered the Peninsula and the rhinocerotine *L. sansaniense* persisted. *Alicornops simorrense* was the dominant species at that time, being repeatedly recorded in association with *L. sansaniense* or, more rarely, *B. brachypus*.

Middle to upper Miocene continental formations of the Vallès-Penedès Basin have furnished one of the most abundant mammalian faunas from Western Europe. Regional climatic conditions in the area favored the settlement of rhinocerotid assemblages more similar in composition to those from Central Europe, yielding species scarcely recorded elsewhere in Iberia (Santafé 1978b; Gómez Cano et al. 2011). Examples of these idiosyncratic faunas are the abundant of *H. tetradactylum* and teleoceratine remains, the latter virtually absent in central Iberia. During the Vallesian, these faunal assemblages were progressively replaced by two dominant species: the aceratheriine *Aceratherium incisivum* and the large rhinocerotine *Dihoplus schleiermacheri*. The small acerathere *A. simorrense* still survives into Vallesian times, based on a single occurrence from Can Jofresa. These were joined by a second acerathere form, the larger and robust '*A*'. *alfambrense*, only documented at La Roma 2. Both *A. incisivum* and *D. schleiermacheri* are the dominant species at the Iberian Turolian (late late Miocene). The extinction of the former at the late Turolian of the Teruel area marked the end of the last Aceratheriina from western Europe, leaving the rhinocerotines *D. schleiermacheri* and, later, *P. megarhinus* as the only surviving species of the latest Miocene. Eustatic changes associated with the cooling climate at the latest Miocene final stage of the Messinian Salinity Crisis favored the establishment of new land bridges in the Mediterranean area and the subsequent faunal interchange of Eurasian and African faunas through Iberia (Booth-Rea et al. 2018). During this transition, Iberian rhinoceros diversity remained stable and low at this time due to the heavily depleted species number.

After the latest Miocene ice pulse, temperature from most oceans recovered, pointing to a warmer episode (Zachos et al. 2001). The post Messinian-event faunas witnessed the extinction of the last *P. megarhinus* and its replacement by the smaller *P. miguelcrusafonti* by the late Ruscinian (MN 15). Although the first *Stephanorhinus* forms were probably present at this time in the Peninsula, it is not until the late Villafranchian (MN 16a) when the first confirmed remains of *S. etruscus* are recorded, following the aridity maximum at 3.95 Ma. From the late Early to the Middle Pleistocene, the generalist and common species *S. hundsheimensis* became widespread through Eurasia. By the Middle Pleistocene, other two species, the grazer *S. hemitoechus* and the browser *S. kirchbergensis*, are occasionally recorded. These *Stephanorhinus* species were intermittently replaced by the woolly rhinoceros (*C. antiquitatis*) along the interspersed glacial maxima of the late Middle to Late Pleistocene. The first woolly rhinos reached the Iberian Peninsula during the first glacial pulses of the Middle to Late Pleistocene circa 150 ka BP (~ 188–141 ka BP), at the end of the Middle Pleistocene. It constitutes, together with the woolly mammoth (*Mammuthus primigenius*) and the reindeer (*Rangifer tarandus*), the most iconic representatives of the so-called 'cold-adapted faunas'. These successive dispersals of specialists like *C. antiquitatis* into the Iberian Peninsula Europe must be understood within the framework of the significant faunal turnovers that took place in Europe by this time linked to the expansion of the 'Mammoth steppe' environment (Álvarez-Lao and García 2011; Álvarez-Lao et al. 2017). With the termination of the Last Glacial Maximum, (LGM; 26–19.5 ka), tundra-steppe habitats fragmented, leading to the retreat of cold-adapted species into northern refuge areas and the loss of the last populations of southern woolly rhinos, ending the rhinoceros fossil record in Iberia.

Conclusions

A summary of Iberian rhinocerotid taxa and localities from the Cenozoic is provided here. We discuss rhinocerotid diversity dynamics in the Iberian Peninsula through time, further emphasizing its interplay with global and regional paleogeographic and climatic events. Conflicting identifications from multiple systematic studies and those based on highly fragmentary and/or damaged fossils indicate the number of unresolved species assignations is probably underestimated. Additional taxonomic work still ahead will shed light on these unresolved questions.

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