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A Miocene Rhinocerotidae from El Bierzo Basin (León Province, northwestern Spain)

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ABSTRACT

We describe the partial rostrum and its associated mandible of a rhinoceros from the locality of Santalla del Bierzo (El Bierzo Basin, León Province, Spain). The craniomandibular morphology is characterized by robust nasal bones of roughly the same length of a slender and long premaxilla, a nasal notch at the level of the P4 and low and small orbits. The dentition shows continuous lingual cingula on premolars, large antecrochets and lingually-pierced hypocones on M1-3, and a continuous lingual cingulum on the M3. The studied remains are morphologically equivalent to the European early Miocene *Brachydiceratherium* from Bühler (Switzerland), Saulcet (France) and are therefore assigned to that genus. The present specimen represents not only the first macrovertebrate from El Bierzo Basin, but one of the most northwestern records of Miocene rhinocerotids in Iberia. This occurrence fills a geographic gap of the early forms of the genus, until know restricted to France, Germany and Switzerland and provides new information on the Teleoceratina migrations in Western Europe. The Santalla Formation of El Bierzo basin, previously interpreted as deposited during the late Oligocene or early Miocene, due to the lack of biostratigraphic or chronostratigraphic data, is assigned to the early Miocene, based on the fossil remains described in this study.

KEYWORDS **Teleoceratina. Perissodactyla. Early Miocene. El Bierzo Basin. Biostratigraphy.**

INTRODUCTION

The present-day El Bierzo basin, located in the Iberian Peninsula, is regarded as the western prolongation of the more extensive Duero foreland basin (Fig. 1A), which was divided during the Alpine uplift of the Galician-Leonesian Mountains through high to moderate-dipping reverse faults (de Vicente et al., 2011; Martín-González and Heredia, 2011a, b; Martín-González *et al.*, 2014; Rodríguez Fernández *et al.*, 2015). The El Bierzo basin is the largest of the North-Western continental Cenozoic basins complex, and was divided into several sedimentary sub-basins (Cunha et al., 2019, fig. 5.5). Its detrital sediments represent over 500 m of stratigraphic interval and are fed by a system of arid and semi-arid systems of alluvial fans (Manjón *et al.*, 1986; Martín-González and Heredia, 2011b), deposited mainly by catastrophic floods (flood-dominated systems, Heredia *et al.*, 2015). These strata were deposited unconformably over the partly weathered and heavily eroded Paleozoic basement. Since the 1980's, three stratigraphic formations have been described in the basin. These are, from base to top, the Toral, Santalla, and Las Médulas formations (Hérail, 1981, 1982). The Toral Formation (Fm.) was dated as Oligocene based on two late Rupelian assemblages of fossil rodents recorded in the northern part of the basin and assigned to the MP24 and MP25 biozones (Freudenthal *et al.*, 2010; Martín-González *et al.*, 2014). The Santalla and Las Médulas formations were regarded as Mio-Pliocene based on sedimentary correlations (Brell and Doval, 1974; Hérail, 1981, 1982; Martín-Serrano, 1982; Martín-Serrano *et al.*, 1996; Vergnolle, 1990). Both formations were interpreted as the mid-distal and proximal sides of an alluvial fan system established from the south (Heredia *et al.*, 2015; Martín-González and Heredia, 2011b). Conversely, an older Paleogene age for Las Médulas Fm. (older than the Toral Fm.) has also been proposed, and therefore the Santalla Fm. would be interpreted as the youngest pre-Quaternary unit of the basin (Gutiérrez-Marco, 2006; Hacar *et al.*, 1999; Pagés *et al.*, 2001). More recently, Las Médulas Fm. has been modified to integrate the Santalla Fm. as a lateral equivalent of the typical gold-bearing red conglomerates and sandstones (Heredia *et al.*, 2015), although Mínguez *et al.* (2016, fig. 4) interpreted the Santalla and Toral fms. of lateral gradations. In its type area of Santalla del Bierzo, the Santalla Fm. (early syn-orogenic strata) appear to rest unconformably over the early Oligocene Toral Fm. (pre-orogenic: late Rupelian to Chattian). According to some authors, the Santalla Fm. of El Bierzo Basin can be correlated with the Candanedo Fm. of the northern Duero Basin, which ranges in age from the Oligocene (Colmenero *et al.*, 1982; Corrochano, 1989) to the late Miocene (Herrero *et al.*, 2004). According to Manjón *et al.* (1986), the Santalla system comprises medial facies of alluvial fans forming a network of mudflows and braided conglomeratic channels intercalated within an approximately 150 m-thick sequence of finer debris and mud-flow sediments deposited in a floodplain environment. The main source of sediments originates from the Paleozoic reliefs situated to the south and south-southwest. A more detailed study by Heredia *et al.* (2015) in the type area northeast of Las Médulas revealed that the Santalla Fm. (= 'Santalla beds' or 'lower Las Médulas unit/Fm.' of these authors) is affected by Alpine faults and mainly comprises lobe elements showing a coarsening upward trend, with a maximum progradation of these mid-distal alluvial fans during the climax of Alpine deformation.

Fossil vertebrates are scarce in the Cenozoic basins of NW Spain outside the Duero basin. Previous records of large mammals come from the Eocene deposits of the Oviedo Basin (Truyols *et al.*, 1991) and the Oligocene coal basin of As Pontes (López-Martínez *et al.*, 1993). The occurrence of few rodent faunas is restricted to Oligocene samples from the El Bierzo and Sarria basins (Freudenthal *et al.*, 2010; Martín-González *et al.*, 2014). Correlation among the diverse Alpine Cenozoic basins of NW Iberia, which are remnants of the complex tectonic and tectonostratigraphic evolution and were enhanced by the western termination of the Pyrenean-Cantabrian Orogen (de Vicente *et al.*, 2011; Martín-González and Heredia, 2011a, b; Rodríguez Fernández *et al.*, 2015), is difficult due to the paucity of the palaeontological data.

GEOLOGICAL SETTING

The material studied in the present paper consists of a rostral skull fragment with associated mandible that was collected in 1970 in a temporary quarry extracting plastic mud lenses intercalated in sandstones, located just eastwards of the village of Santalla del Bierzo (El Bierzo region, west of the León province; Fig. 1B). These strata are immediately overlying those represented in the escarpment of the "Santalla Section" of Heredia *et al.*, 2015, fig. 7). The discovery was made by Mr. Ignacio Fidalgo Piensos (1934–2010), an historian and intellectual living in Ponferrada, who noticed the presence of fragments of large bones and some other postcranial remains belonging to a partially preserved, single skeleton. Unfortunately, only the skull and mandible were recovered, being embedded in a single argillaceous block. These were donated by his daughter to the Museo Geominero of Madrid and recently prepared for the present study. The abandoned quarry that provided the material studied is located south of the N-536 road, about 50 m to the east of "El Balcón del Bierzo" regional landscape viewpoint, at the northeastern end of Santalla del Bierzo (geographic coordinates: 42º30'23.5"N–6º41'10.9"W; Fig. 1B). The village of Santalla del Bierzo is in turn located 8.5 km southwest from Ponferrada city (Community of

Castilla and León, Spain). From a geological perspective, the fossiliferous bed lies in the upper part of the Santalla Fm. at its homonymous locality, where it comprises approximately 170 m of pale sandstones, gravels with polygenic pebbles (quartzite, sandstone, schist and shale) and reddish to yellowish mudstones. These overlie, on a progressive angular unconformity, a sequence approximately 200 m-thick, of clays, lacustrine limestones and arkosic sandstones belonging to the Toral Fm. (Fig. 1C).

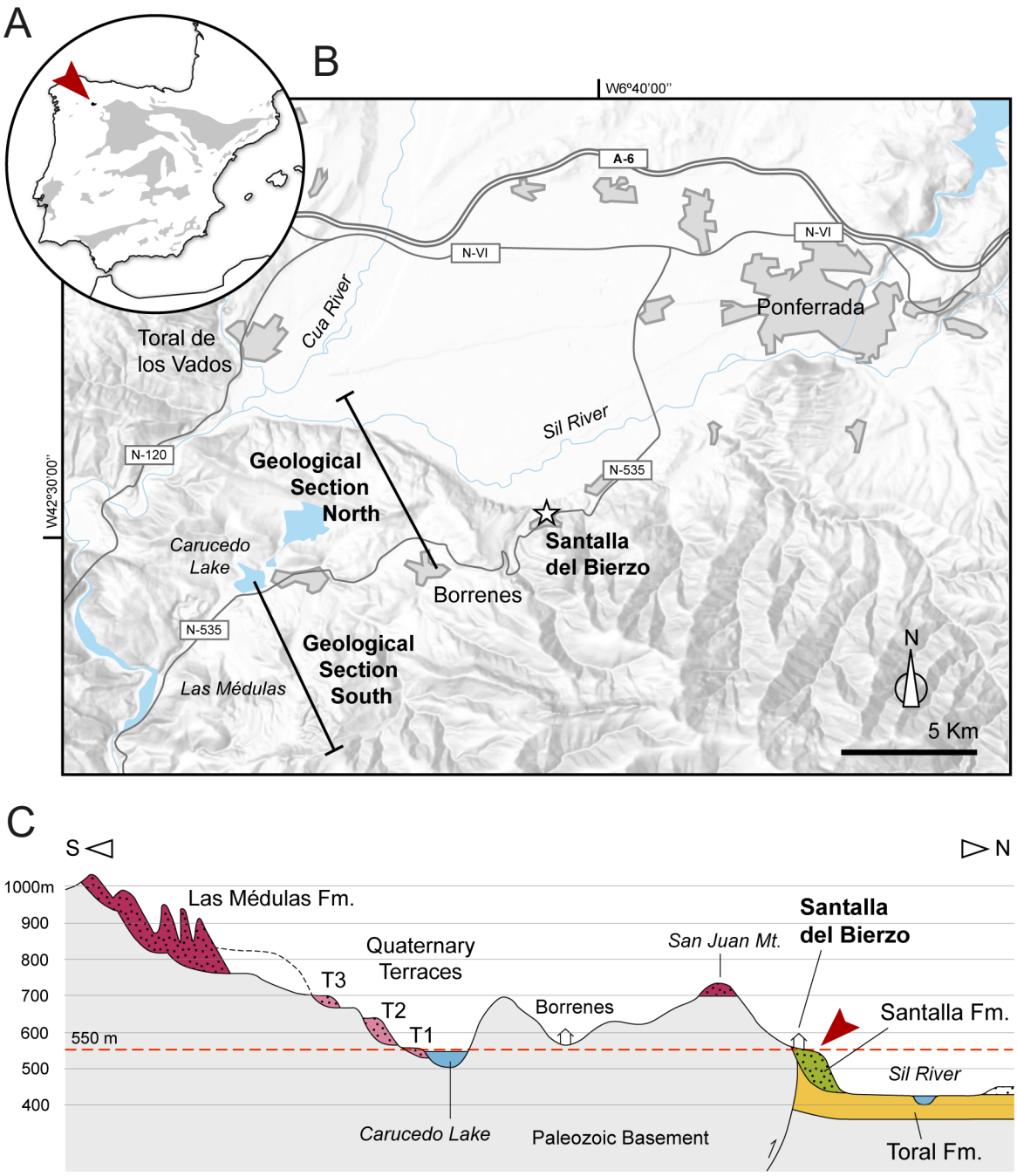

FIGURE 1. A) Simplified map of the Iberian Peninsula with the main Cenozoic basins represented in gray and the Bierzo basin in black. B) Simplified map showing the fossil locality of Santalla del Bierzo (represented with a star), about 8.5 km southwest of the city of Ponferrada. C) Simplified cross section of the SW margin of the El Bierzo Basin (see position of cross section transects on the map on B) showing the depositional relationships of the Cenozoic Las Médulas (alluvial fans, resting on old erosive surfaces), Santalla and Toral formations and the Quaternary terraces (T1-T3) above Lake Carucedo. Rhinocerotid remains (represented with an arrow) were found at an altitude of 545 m, within the upper part of the Santalla Fm. at the Santalla del Bierzo section. Variscan and other Alpine fractures affecting the Palaeozoic basement have been omitted. Sketch after M. Hacar, partly based on Hacar *et al.* (1999, fig. 3).

The described specimen represents the first Cenozoic macrovertebrate remain from the entire area and, consequently, the younger pre-Quaternary paleontological data for the region. Moreover, it involves interesting implications for the regional geology of the Cenozoic basins. Until now, vertebrate remains were unknown in the Santalla Fm. The systematic arrangement of the studied fossil suggests an early Miocene age. The closest rhinoceros-bearing localities known to date come from the middle Miocene sediments in the vicinity of the city of Palencia (Palencia Province), included in the large Duero Basin. The most relevant material includes two skulls, originally mentioned by Dantín Cereceda (1914) and Hernández-Pacheco and Dantín Cereceda (1915), and subsequently reviewed as *Alicornops simorrense* and *Lartetotherium sansaniense* by Cerdeño (1989). Other localities in the area have provided additional fragmentary remains of the two species. In the present work we describe the skull and associated mandible (including both upper and lower dental series) found in Santalla del Bierzo area and compare them with several Miocene species to refine their taxonomic affinities.

MATERIAL & METHODS

Institutional and locality abbreviations. In addition to the studied specimen, prefixed MGM, Museo Geominero-CSIC, Madrid, the abbreviations of additional localities used for comparative purposes are detailed as follows: BSPG, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich; MNCN, Museo Nacional de Ciencias Naturales, Madrid; MfN, Museum für Naturkunde, Berlin; MNHN, Museum national d'Histoire naturelle de Paris; MHNT, Museum d'Histoire naturelle de Toulouse. The specimen list used for comparison can be found in the Appendix (Table I).

Measurements and biostratigraphic framework. All measurements are given in millimeters. Approximate measurements are given in brackets. Measurements were made with a digital caliper and a measuring tape for elements larger than 150 mm. Cranial measurements follow those defined by Guérin (1980). The stratigraphic framework is based on geological time scales and European Land Mammal Ages (ELMA) for the Neogene and successions of Mammal Neogene units (MN; Hilgen *et al.*, 2012).

Anatomical nomenclature and characters. Capital letters are used for upper teeth (P, M) and lower-case letters for lower teeth (p, m); m, muscle. The dental terminology follows Antoine (2002), Heissig (1969) and Uhlig (1999). APD, Antero-Posterior Diameter; H, Height; L, Length: TD, Transverse Diameter, and W, Width. The cranio-dental and osteological features described correspond basically to cladistic characters used and listed by Antoine (2002) and Antoine *et al.* (2010) and then refined by Becker *et al.* (2013).

Suprageneric classification. The generic and suprageneric classification of the Rhinocerotidae employed herein follows Antoine *et al.* (2025) and Sizov *et al.* (2024). We are nonetheless aware that recent phylogenetic and systematic studies have proposed substantially different higher-level arrangements, placing teleoceratine genera (including *Brachydiceratherium* and *Diaceratherium*) within the subfamily Aceratheriinae as members of the tribe Teleoceratini (Lu et al., 2021, 2023).

Studied material. The rostrum MGM-920M-a was preserved in two fragments. The first includes the nasal and premaxillary bones (Fig. 2; Table 1), the second is a palate with the two upper dental series (left P1-M3 and right M1-3; Figs. 2; 4A, Tables 1; 2), and an incomplete mandible (MGM-920M-b) with part of the lower series with the right p3-m3 (being the left m3 incomplete) and roots of the right p2 and left p3-m2 series (both p3 and m2 incomplete; Figs. 3; 4B, Table 2). Both skull and mandible pertain to the same individual. The referred specimen is stored in the collections of the Museo Geominero belonging to the Spanish Geological Survey (IGME-CSIC), Madrid.

SYSTEMATIC PALEONTOLOGY

Family: Rhinocerothidae Gray, 1821
Subfamily: Rhinocerothinae Gray, 1821
Tribe: Rhinocerothini Gray, 1821
Subtribe: Teleoceratina Hay, 1902

Genus: *Brachydiceratherium* Lavocat, 1951
Syn. *Diaceratherium* Dietrich, 1931 (partim)

Type species. originally described as *Acerotherium lemanense* Pomel, 1853, and recently reassigned to *Brachydiceratherium lemanense* (Pomel, 1853) by Sizov *et al.* (2024).

Included species. *Brachydiceratherium aginense* (Répelin, 1917); *B. askazansorense* (Kordikova, 2001); *B. asphaltense* (Depéret and Douxami, 1902); *B. aurelianense* (Nouel, 1866); *B. lemanense* (Pomel, 1853), *B. intermedium* (Lydekker, 1884), *B. fatehjangense* (Pilgrim, 1910), *B. aginense* (Répelin, 1917), *B. lamilloquense* (Michel, in Brunet *et al.*, 1987), *B. shanwangense* (Wang, 1965).

Brachydiceratherium sp.
Figures. 2; 4, Tables 1; 2, Figures II; III

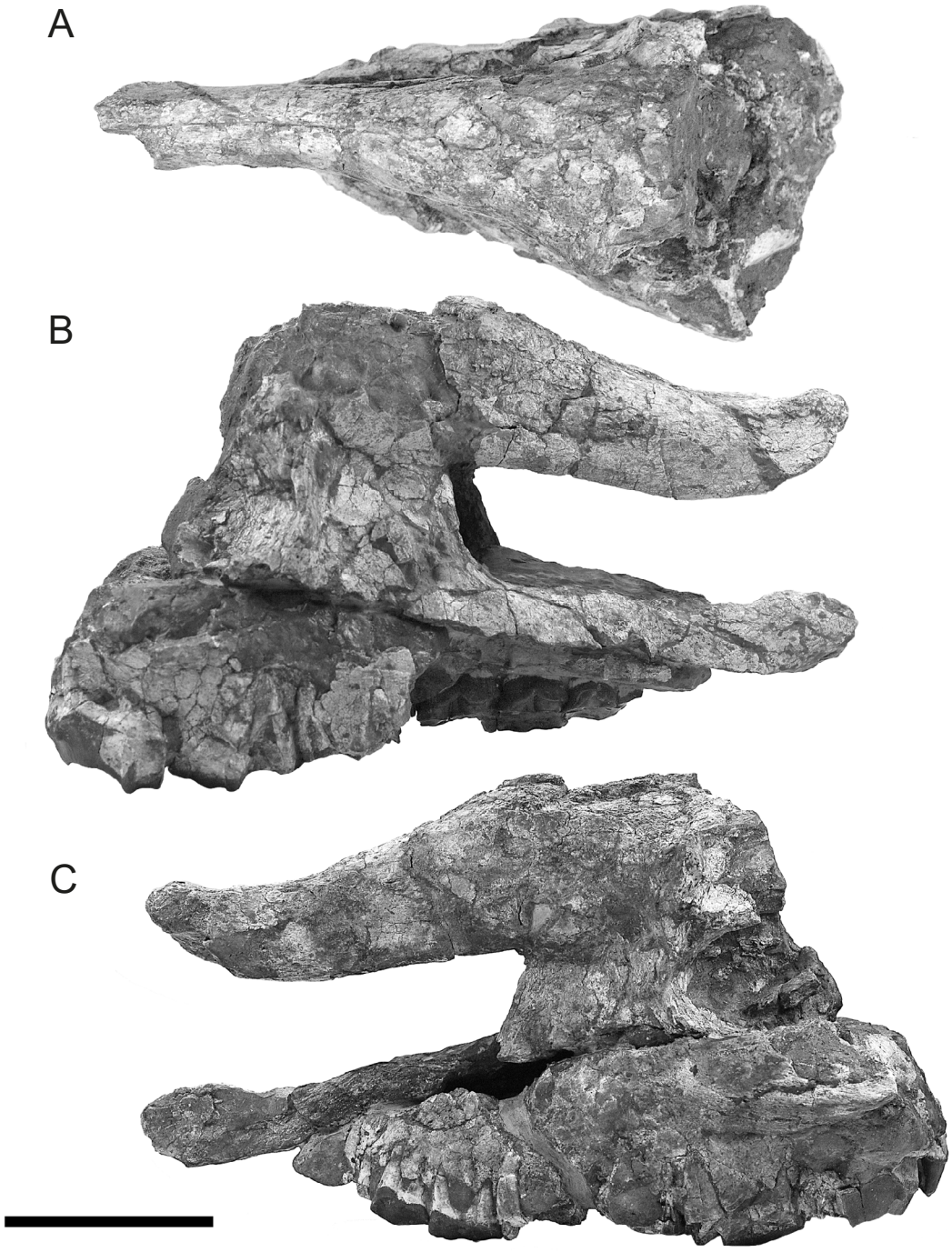

FIGURE 2. *Brachydiceratherium* sp. Partial rostrum MGM-920M-a from Santalla del Bierzo (León province, Spain) in A) proximal; B) right and C) left views. Scale bar equals 50 mm.

Description

Skull (Fig. 2, Table 1)**.** The preserved rostrum is laterally compressed and has a missing left premaxilla. The preserved right premaxilla is long, almost reaching the length of the nasal bones, distally expanded, and laterally flattened. Its rostral end is broken, and the total length of the bone, if complete, would reach the level of the nasal bones, if not exceeding them. The latter are separated and moderate in length (≈149 mm long from the point at the level of the caudalmost point of the nasal notch), have a straight ventral profile and a slightly concave dorsal one. The section of the nasal bones at their base is C-shaped, due to the partial lateral collapse of their lateral borders.

TABLE 1. Measurements (mm) of the fragmentary skull MGM-920M-a of *Brachydiceratherium* sp. from Santalla del Bierzo (León Province, Spain) according to the numbering proposed by Guérin (1980) and illustrated in Appendix, Figure I

Cranial Measurements	MGM-920-M (l/r)
4. Distance between the nasal tip and notch	153.8
9. Distance between nasal notch and orbit	74.5 / 74.9
14. Distance between the nasal tip and the orbit	215.0 / 240.0
19. Width between supraorbital tuberosities	105.0
20. Width between lachrimal tubercles	110.0
22. Width of nasal base	55.1
25. Cranial height in front of P2	132.0
26. Cranial height in front of M1	17.0

The nasal tip is best preserved on the right side. It shows a rough, pitted surface restricted to the rostral end, pointing to the presence of a very small, conspicuous, nasal horn towards the tip of the nasals. The nasal notch is deep and has parallel dorso-ventral borders. The caudo-ventral border of the notch is nearly straight and forms an acute angle with the dorsal one. The nasal suture reaches the level of the caudalmost side of the nasal notch, being lost along the sagittal plane due to the cracked surface of the skull. The insertion of the nasal bone is robust, high, and slightly widened above the orbits. The rostral border of the orbit has no trace of lachrymal tubercle and is placed at the level of the M1-2 boundary. The lachrymal foramen is oval, ≈95 mm high, and placed over the level of the infraorbital foramen. Such foramen, more evident on the right side, is separated ≈18 mm from the nasal notch wall, aligned with the dorsal border of the premaxilla, and placed at the level of P4. The orbit is small and rounded. Both the rostral border of the orbit and the implantation of the zygomatic arch are located at the level of M2. The zygomatic arch is raised 20 mm over the molar row and slender. Due to the overall lateral compression of the skull, the original dimensions of the processus zygomaticus maxillary is difficult to establish, but the observed transition with the rest of the maxilla is smooth.

Mandible (Fig. 3)**.** The mandible lacks the symphiseal region and the posterior half, including the ascending ramus. Furthermore, the cranial part of the left side is fractured and displaced. Only the anterior part of the mandible is preserved. Its lower border curves upwards. Both horizontal rami seem to be laterally compressed.

Upper series (Fig. 4, Table 2)**.** The crowns are low, partially due to the advanced wear, pointing to an adult specimen. The advanced wear points to an adult and the worn M3 together with the open median valleys of the M1-2 (the first nearly closed) places it within a late IDAS 3 stage according to Anders (2011). A very thin layer of patchy cement is visible at the base of some ectolophs. The shape of the enamel is slightly wrinkled and presents evident horizontal Hunter-Schreger bands.

P1 is heavily worn. Its fragmentary condition impedes a more detailed description. P2 has a wide ectoloph (≈16 mm width), with an evenly convex labial border. The parastyle is constricted by a paracone fold on the labial side and a small notch in the anterior valley on the lingual one. The latter is triangular. The protocone is smaller than the hypocone. Both are tear-shaped, present loose connections with the ectoloph and contact through a lingual bridge (sensu Antoine, 2002), leaving a small, subtriangular closed median valley. The advanced wear stage has favored the contact of the hypocone with the posterior cingulum in the form of a hooked posterior expansion of the first, almost enclosing a small and oval postfossette. There is a low and continuous labial cingulum following the shape of the gingival border. The lingual cingulum is only evident on the entrance of the (closed) median valley in form of a blunt tubercle.

P3 has a rectangular outline. The ectoloph is very wide (18.4 mm) and has smoothly undulated border. Both paracone style and parastyle are faint and barely protrude from the labial border. The paracone fold left in between is very shallow. Protocone and hypocone are about the same size. Both contact by means of a wide area. The protocone presents a big antecrochet delimited by a poorly marked posterior protocone fold. The tooth lacks an anterior protocone fold. The anterior cingulum continues lingually. The lingual cingulum reaches the lingual midpoint of the hypocone (could be continuous and more elevated on its postero-lingual side, but the advanced wear fades out its morphology). The labial cingulum is continuous and low.

P4 has lost part of the ectoloph. As in P3, the antecrochet is large and rounded. The median valley of P4 is not closed but very narrow (with the enamel of both antecrochet and

hypocone almost in contact), sinuous and forked at its inner side. The hypocone has a narrow connection with the ectoloph through a sigmoid bridge. The closed posterior valley left posteriorly is tear-shaped. As in P3, the advanced wear stage might have fused the crochet with the ectoloph. The lingual cingulum is continuous, reaching the level of the hypocone and contacts the anterior and the posterior cingula.

M1 and M2 are morphologically similar. Both M1 lack the whole ectoloph (as in the left P4) and both M2 lack the anterior side of the paracone style and parastyle. Nevertheless, the ectoloph of M2 and the maximum width of M1 point to a rectangular outline in M1. M2, on the other hand, presents a more squared outline. The antecrochet is smaller than in P4 and defined by a marked posterior protocone fold. The anterior protocone fold is also present and well-marked. In M1, the anterior side of the protoloph is swollen, nearly straight in M2. The protocone is rounded (with a slightly more flattened lingual side in M2). The median valley is curved in M1 and closed by the contact of the enamel between antecrochet and metaloph (while remaining unfused). In M2, the median valley is sigmoid and wider. Antecrochet and metaloph do not contact in these teeth. There is a blunt crochet attached to the contact between metaloph and ectoloph of M2. In M1 the crochet is restricted to a small and pointed salient on the right side, with no trace of it on the left one. The hypocone presents a well-marked anterior folding, leaving an anterior convex area. The posterior is not as evident. The advanced wear favors the contact between hypocone and the posterior cingulum, producing a squared area of dentine with an angulous postero-lingual side. There is a continuous cingulum from the anterior through the entrance of the median valley on the labial one, where a big, blunt enamel bump is present (in both M1 and M2). The lingual-most extent of the hypocone is devoid of lingual cingulum. The labial side of the M2 ectoloph (the only preserved) is straight and presents a short labial cingulum attached to its posterior side.

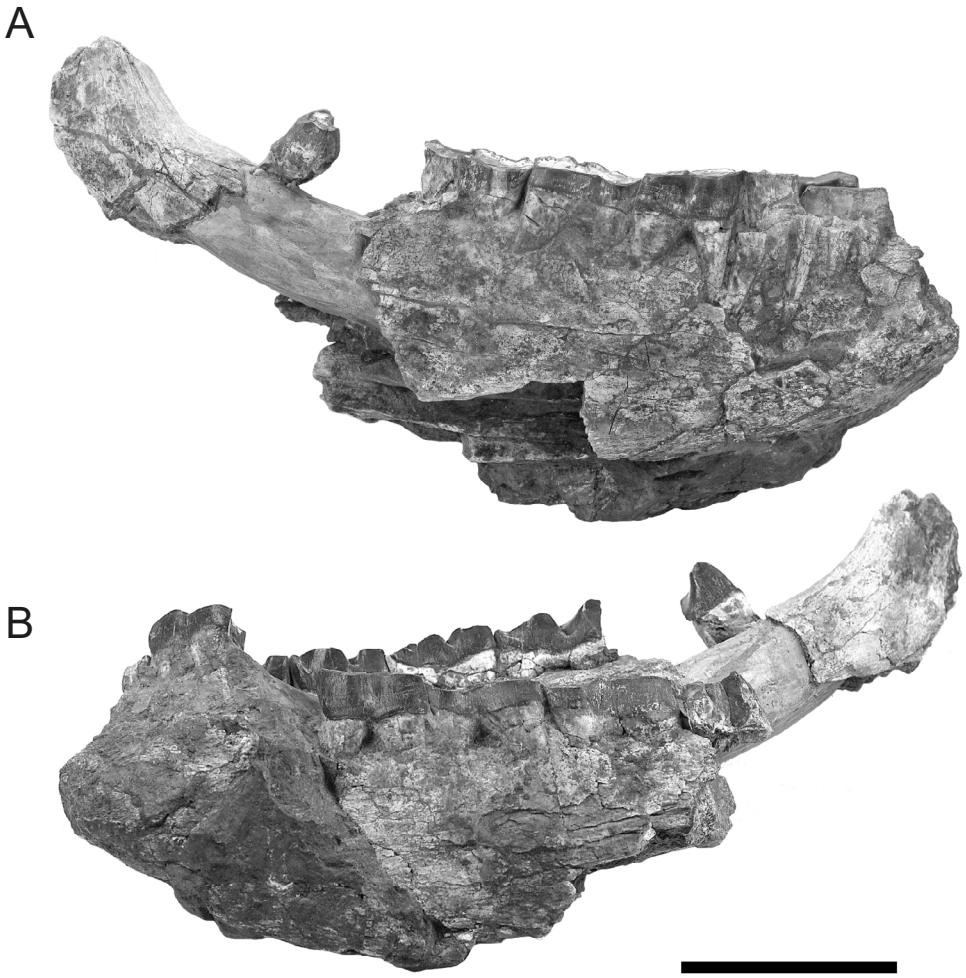

FIGURE 3. *Brachydiceratherium* sp. Incomplete mandible MGM-920M-b from Santalla del Bierzo (León province, Spain) in A) right and B) left views. Scale bar equals 50 mm.

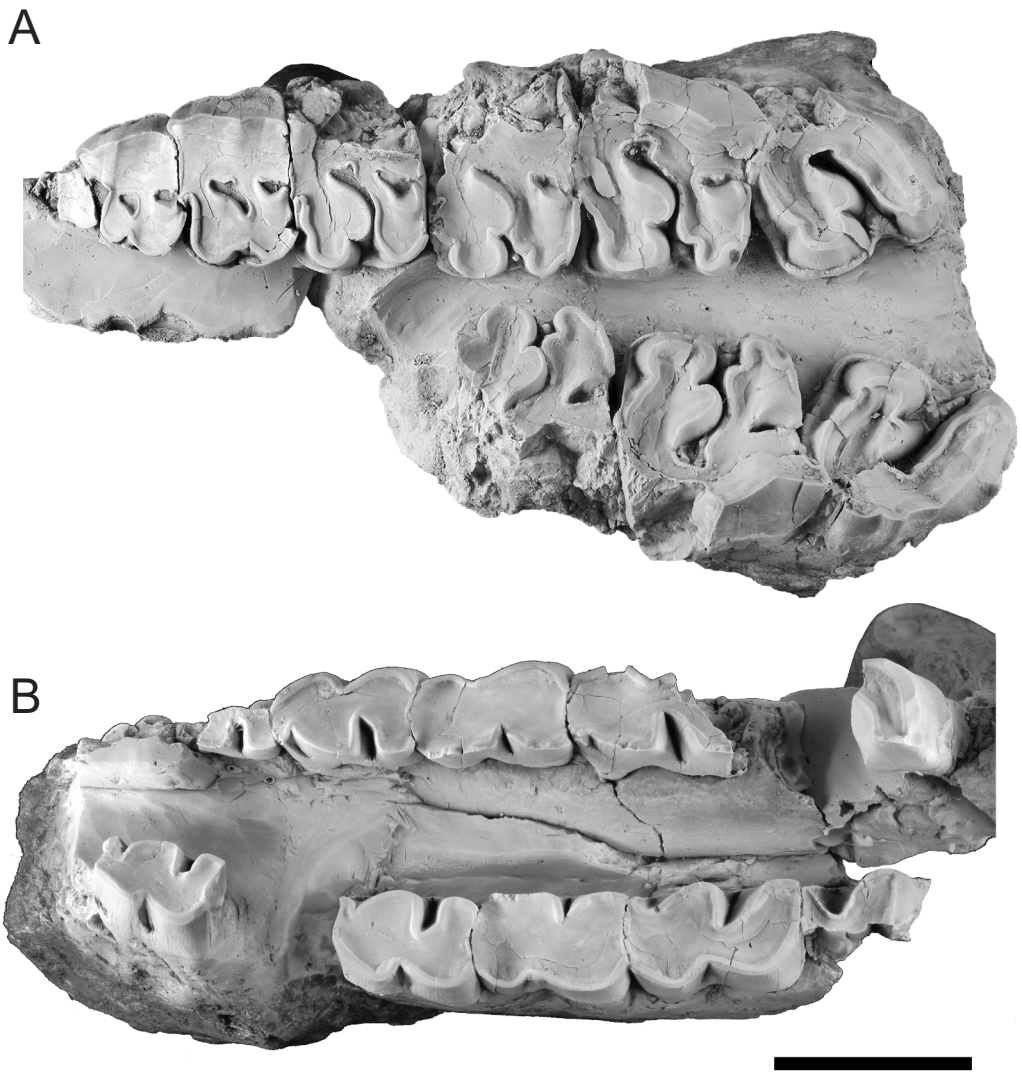

FIGURE 4. *Brachydiceratherium* sp. from Santalla del Bierzo (León province, Spain). Specimens whitened with MgO. A) Upper teeth MGM-920M-a with P1 (fragmentary)-P4 and M1-3 in occlusal view; B) partial mandible MGM-920M-b with both p3-m3 in B1, occlusal and B2, right labial views. Scale bar represents 50 mm.

M3 has a characteristic quadrangular outline, giving the protoloph and ectometaloph a 'horseshoe' appearance. The ectometaloph presents a constant width and a protruding lingual border at the level of the hypocone. Its labial surface is covered with a thin layer of tartar (sensu Heissig, 2012). Both paracone style and parastyle are about the same size, short, blunt and separated by a wide and smooth paracone fold. The median valley is wide. A small enamel fold is present attached to the anterior side of the metaloph, the remains of a worn-out crochet. Likewise, in the remaining molar teeth the antecrochet is well-developed and individualized from the protocone by a marked posterior protocone fold. The anterior protocone fold is also present but weaker. The protocone has a flattened lingual side. The anterior cingulum continues along the lingual side connecting with the lingual one. The cingulum in that area is bumpy, low and encircles the total lingual perimeter of the tooth up to its posterior side (getting somewhat weaker in the posterior half and almost imperceptible on the postero-lingual side of the hypocone). The lingual cingulum is strengthened by 3-4 bumps at the entrance of the median valley. It continues as a faint ridge on the posterior side and a small tubercle at the level of the interior-most border of the median valley. There is a conspicuous posterior cingulum that ends almost at the postero-lingual side of the protocone (2 mm apart from the beginning of the lingual one).

Lower series (Fig. 4, Table 2)**.** Lower teeth are represented by a left p3-m3 and roots of the missing right p2 (m3 is fragmentary) series and a right p3-m2 (both p3 and m2 are incomplete).

The left p3 is anteriorly displaced from its original position in the lower series. As in the remaining teeth, the posterior valley is V-shaped, deep and shows a small ridge on its anterior side. The lingual side of the metalophid is concave.

p4 shows a narrower anterior side. The anterior labial groove is narrow and triangular. The posterior valley is similar to that of p3 but deeper. The labial groove is present but smoothed (forming an obtuse angle). It does not reach the gingival border, vanishing before the neck (which presents some bumps). The lingual side of the metalophid is concave. Its lingual border on the occlusal surface is convex. The anterior valley is V-shaped too (but wider) and flanked by a faint cingulid on its anterior border. Such cingulid is present in m1-2 too (and seems stronger as the tooth is placed more posteriorly).

The m1 are heavily worn. As a result, the ectolophid have a straight lingual border in occlusal view and the anterior valleys have almost disappeared. The posterior ones are V-shaped. As in p4, the lingual surface of the ectolophid is concave. An important feature distinguishes premolar and molar teeth: the labial grooves are slightly oblique and displaced over the trigonid (clearly noticeable in m1, not as much in m2).

m2 resembles m1 but less worn. It presents a strong antero-lingual cingulid. The hypolophid is rounded, the protoconid angulous. The lingual side of the entoconid is flat. In occlusal view, the posterior valley is triangular and anteriorly curved, the anterior is rounded and shallower. m3 is only represented by a partial posterior side. The lingual border of the entoconid is flat and there is a short posterior cingulum that gets stronger towards the lingual side of the tooth.

Discussion

Rhinoceroses are common representatives of the European faunas from the Oligocene to the Late Pleistocene, although the group blooms in terms of taxonomic and morphological diversity during the Miocene. All the main clades that diversified during the Neogene in Eurasia (*i.e.* Elasmotheriina, Teleoceratina, 'aceratheres' sensu lato, Aceratheriina and Rhinocerotini) have been recorded in the Iberian Peninsula. Due to the controversial stratigraphic setting of the locality of Santalla del Bierzo, all of them have been taken into consideration to establish a reliable taxonomic determination.

The Western European record of elasmotheriine rhinoceroses is restricted to the Aragonian (Middle Miocene) and the genus *Hispanotherium*. *Hispanotherium matritense* is by far the commonest Aragonian rhinoceros in the central Iberian basins. It shows very distinctive dental characters related to a highly hypsodont dentition. These include abundant cementum covering the ectoloph wall and filling the inner valleys, absence of lingual cingula, deeper enamel folding, and bigger overall dimensions. All these traits are typical of post-early to middle Miocene elasmotheriine species and absent in Santalla del Bierzo's specimen MGM-920M). Additionally, the rostrum of *H. matritense* differs from the described specimen on its slenderer nasal bone void of rugosities at their tips (Sanisidro *et al.*, 2012). Other Western European elasmotheriines like *Hispanotherium beonense* or *Hispanotherium corcolense* show more plesiomorphic

TABLE 2. Measurements (mm) of the upper and lower dentition of Brachydiceratherium sp. (MGM-920M) from Santalla del Bierzo (León Province, Spain). L, length; W, width; H, height; l, left; r, right

Tooth	Measurement	l	r
Upper teeth			
P2	L	24.4	—
	W	—	—
	H	18.3	—
P3	L	30.7	—
	W	42.1	—
	H	14.3	—
P4	L	~33	—
	W	~48	—
	H	—	—
M1	L	~41	—
	W	~57	—
	H	—	—
M2	L	~54	~55
	W	~52	~50
	H	—	—
M3	L	—	51.6
	W	54.3	47.2
	H	—	—
Lower teeth			
p3	L	31.9	—
	W	—	—
	H	—	—
p4	L	36.8	37.0
	W	26.0	26.8
	H	16.4	12.3
m1	L	39.4	39.0
	W	26.6	27.7
	H	9.3	9.1
m2	L	44.3	—
	W	25.3	25.4
	H	8.9	10.2

characters and smaller dimensions but still lack the lingual cingula, the strong hypocone folding, or the antecrochet on the M3 of the studied specimen.

Rhinoceroses from the Subtribe Rhinocerotina are firstly recorded in the Iberian early Aragonian, persisting until the last glacial maximum (Álvarez-Lao and García, 2011; Cerdeño, 1992; Sanisidro and Cantalapiedra, 2022). The strong constriction of the lingual cusps in P4-M2 of the specimen from Santalla del Bierzo discards the ascription of several Rhinocerotina genera (*e.g.*, *Lartetotherium*, *Dihoplus*, or *Stephanorhinus*), as they display simpler teeth morphology, parallel orientation of protoloph and metaloph, and a completely distinct rostral morphology dominated by its most prominent feature: a dome-like dorsal surface of the nasal bones topped with a insertion for the nasal horn together with a more elongated rostrum. Therefore, the shortened rostrum, absence of a large nasal horn insertion, presence of constricted lingual cusps and the protocone/hypocone proportions in the P2-3 rule out assignment to Elasmotheriina or to the subtribe Rhinocerotina sensu stricto, supporting instead its classification within the subtribe Teleoceratina.

Small rhinoceros forms were cited in the early Miocene sites of Loranca and Valquemado (Cerdeño, 1989). These remains, identified as *Protaceratherium minutum*, share a similar cingular pattern with the specimen from Santalla del Bierzo: continuous lingual cingula on the premolars, incomplete on the molars, and faint labial ones restricted to the anterior and posterior borders in some individuals. However, they are smaller and show simpler enamel folding (*e.g.* they lack the lingual expansion of the hypocone or the deep anterior and posterior protocone fold). The same comparisons could be established between MGM-920M and the European remains of *P. minutum* (like those from the German locality of Budenheim).

'Aceratheres' sensu lato (as defined in Becker *et al.*, 2013) are a paraphyletic group with hornless and slender nasal bones and brachydont dentitions. The genus *Plesiaceratherium* is characterized by the presence of upper cheek teeth with clumsy paracone and faint constrictions on their inner cusps. Lower premolars are long and narrow, with shallow outer groove and flattened outer edge of the protoconid (together with common rugosities on the outer wall; Yan and Heissig, 1986). Premolar series of some *Plesiaceratherium* species (*i.e. P. gracile* or *P. fahlbuschi*) always present independent protocone and hypocone (Yan and Heissig, 1986; Fig. 3), in contrast with MGM-920M. Most *Plesiaceratherium* species share a continuous cingulum on premolars. However, the presence of a cingulum among molar teeth is variable within the genus. *Plesiaceratherium gracile* presents a developed anterior cingulum (which continues to the anterior side of the protocone) and a strong posterior cingulum (Yan and Heissig, 1986, p. 88). On the other hand, *P. fahlbuschi* share the anterior cingulum but lacks the tubercle on the entrance of the median valley (*e.g.* BSPG specimens from Sandelzhausen). In this sense, the dental remains from Santalla del Bierzo are closer to those of *P. gracile*. The type series of *P. mirallesi* consists of the lower dentition and some limb-bones (mainly carpal bones) of a single individual (Crusafont *et al.*, 1955). While the size is compatible to the lower dental series of MGM-920M, the absence of cingula prevents the ascription to the species. Additional larger *Plesiaceratherium* remains with uncertain systematic affinities have been cited in the French localities of Pellecahus and Montréal-du-Gers (Béon 1; Antoine *et al.*, 2000a, 2000b, 2018). The specimen from Santalla del Bierzo shares a similar cingular pattern (at both lingual and labial sides) and presence of lingual bridges on premolar teeth with MHNT Béon 1040. Alternatively, it lacks the deeply-constricted hypocone on M1-2 (probably as a result of the different wear degree), the large antecrochets, the inflated ectometaloph and the continuous lingual cingulum on M3, or the presence of an anterior hypocone fold on P4 (together with a large antecrochet). MGM-920M differs from *Plesiaceratherium aquitanicum* and *Plesiaceratherium balkanicum* on its smaller dimensions and separated protoloph and ectoloph on P2 (Antoine and Becker, 2013; Becker and Tissier, 2019; Répelin, 1917). MGM-920M shares with the former the connection between protocone and hypocone, but other characters like the shape of the lingual cingulum on premolars, or the triangular outline of M3 separate both. Premolar teeth from Santalla del Bierzo are shorter than *P. fahlbuschi* from Sandelzhausen and the *Plesiaceratherium* from Georgensmünd, and the molars longer, reflecting some similarities with *Plesiaceratherium lumiarense* (Fig. II). When compared with *P. lumiarense*, MGM-920M shares a quadrangular M3, absence of crista on the M2-3, protocone and hypocone of P2-4 mostly separated, and the occasional presence of medifossette on premolars. Regarding the skull, the nasal bone morphology (shorter with an upraised tip with rugosities at their lateral sides) is distinct from most *Plesiaceratherium* forms with preserved cranial remains (*i.e. Plesiaceratherium fahlbuschi*, *P. gracile* and the large *Plesiaceratherium* from Montréal-du-Gers), which share straight and longer nasal bones (Fig. 5). The only skull vaguely resembling the specimen from Santalla del Bierzo comes from Gannat (MP30-MN1, France). The specimen (FSL-213944), previously used as a reference material for *Diaceratherium lemanense* (Becker *et al.*, 2009, 2018) and illustrated by Roman (1911, pl. 8, fig. 1 and 1a), likely belongs to the genus *Plesiaceratherium* (Jame *et al.*, 2019). Both share a robust frontal area, slightly ventrally oriented nasal bones, and small orbits accompanied by a relatively narrow zygomatic arch, and a long premaxilla. Differences between them are restricted to the outline of the

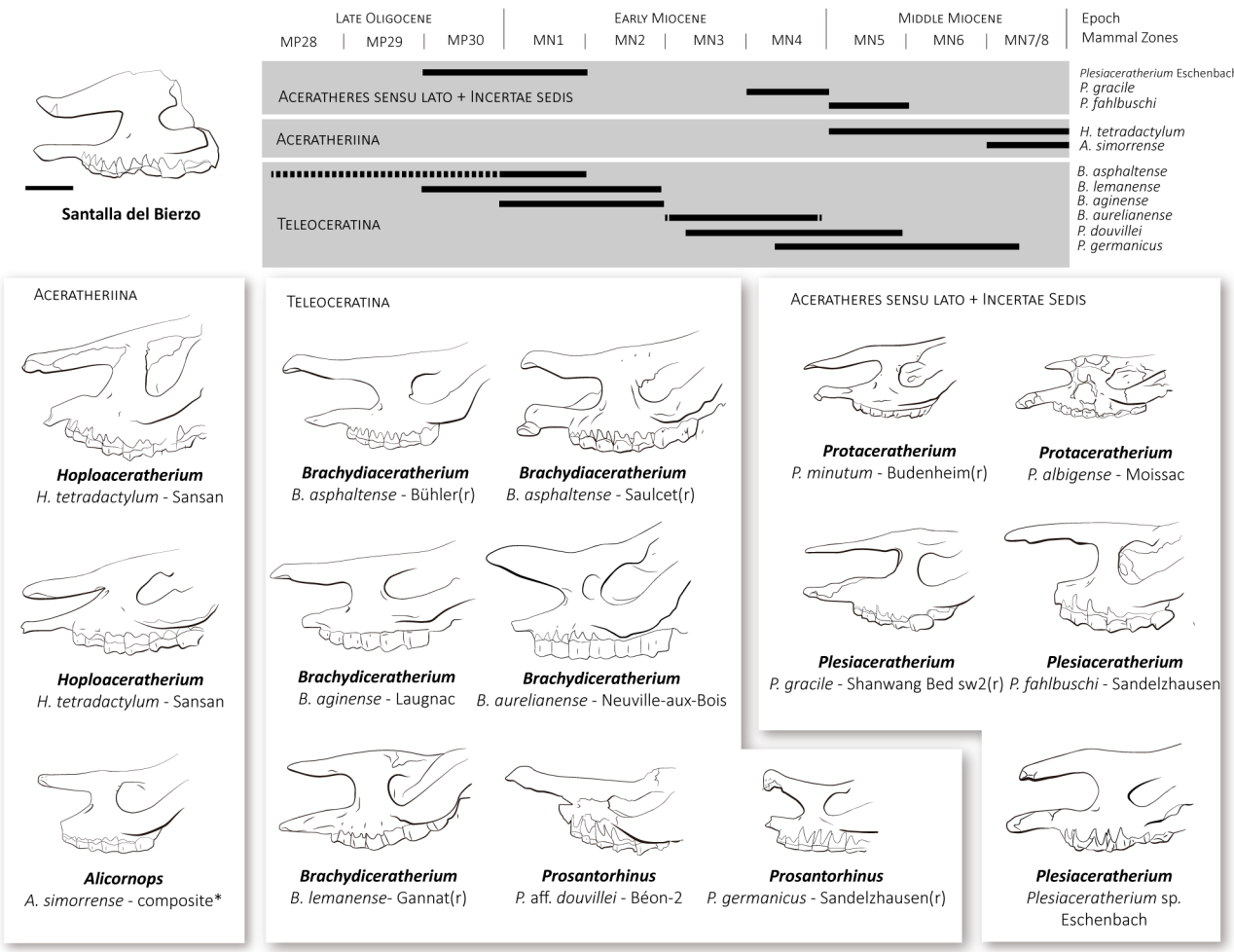

FIGURE 5. Stratigraphic distribution and rostral comparison of several rhinoceros species discussed in the text from the lower and middle Miocene from Western Europe (except for *Plesiaceratherium gracile*; China). Biostratigraphic data obtained from Becker and Tissier (2018) and Becker et al. (2009). *Plesiaceratherium gracile* redrawn from Yan and Heissig (1983); *Hoploaceratherium tetradactylum* redrawn from Heissig (2012b); *Brachydiceratherium aurelianense* redrawn from Nouel (1866); *Brachydiceratherium aginense* from Répelin (1917); *Brachydiceratherium asphaltense* and *Brachydiceratherium lemanense* skulls, redrawn from Becker *et al.* (2018); *Alicornops simorrense* skull figured according to different unpublished MNCN specimens; *Prosantorhinus* aff. *douvillei* traced according to Antoine et al. (2018) figure 2. The remaining specimens have been traced from photographs of the specimens made by the authors. Reversed skulls from the original publication are represented with a (r).

nasal incision, more acute in Santalla del Bierzo, a convex proximal profile of the premaxilla, and the upraised tip of the nasal bone (which appears to be somewhat displaced in MGM-920M). All this leads to discard its inclusion in *Plesiaceratherium*.

Among Aceratheriina, the genus *Hoploaceratherium* was created by Ginsburg and Heissig (1989) to distinguish the species *Hoploaceratherium tetradactylum* and *Hoploaceratherium bavaricum* from other European aceratheres. Yan and Heissig (1986) listed the evolutionary changes between *Plesiaceratherium* towards later 'true' aceratheriines like *Hoploaceratherium*, based mainly on dental characters. The paracone is narrow (and sometimes flattened) in *Plesiaceratherium*, becoming large and obtuse in *Hoploaceratherium*. On the other hand, the parastyle fold is sharp in *Plesiaceratherium* and turns faint in the latter (Yan and Heissig, 1986). Finally, the lingual cingula of the upper premolars are continuous and reduced respectively. Other dental characters like the presence of the upper I1 (present in *Plesiaceratherium*, absent or vestigial in *Hoploaceratherium*) are missing in the studied specimen. With respect to the skull, the nasal tips of the nasals are pointed and void of rugosities in *Plesiaceratherium*, more robust and with some rugosities in *Hoploaceratherium*.

Out of the diagnostic characters originally proposed for *H. tetradactylum*, only one, the presence of a "faint horn boss at the tip of the unfused nasals" can be observed in MGM-920M from Santalla del Bierzo. However, and as mentioned by the authors, this character is also shared by

Teleoceratine species. *Hoploaceratherium tetradactylum* has been reported from the Central Iberian localities of Andurriales, Coca, and, possibly, Cerro de la Plata and Henares-1 (Cerdeño, 1992). On the other hand, the species is more abundant in France and Germany. The comprehensive review of the remains of *H. tetradactylum* from Sansan (Heissig, 2012b) and our direct observations of the skulls at the MNHN and the MfN collections serve as a reference for our comparative purposes. The upper dental series of *H. tetradactylum* resembles those from Santalla del Bierzo: both have roughly similar lingual cingular configuration (with both premolar and molar series and in the lingual and labial sides), shape and disposition of the lingual cones in P3, folded protocone in P4-M3 and U-shaped M3. There are still some differences: for a similar wear stage, the rhinoceros from Santalla del Bierzo has deeper protocone and hypocone folding, together with the mentioned small, rounded, lingual expansion of the hypocone (MNHN Sa 10170-1, fig. 9 in Heissig, 2012b) and continuous lingual cingula on M3; interrupted at the level of the cusps in *Hoploaceratherium* (Heissig, 2012b, p. 336). On the other hand, the dimensions of the premolar teeth are somewhat smaller (shorter and narrower P2; shorter P3, and narrower P4; Appendix, Fig. II). The same can be observed on the lower series (Appendix, Fig. III). The skull of *H. tetradactylum* has a relatively longer and straighter nasal bone, higher orbit, and shorter distance between the nasal notch and the orbit. Coincides with MGM-920M in the swollen frontals, the nasal notch outline and the configuration of the premaxilla. The dentition of the second European *Hoploaceratherium* species, *Hoploaceratherium belvederense*, is poorly known and the only known skull (BSPG 1950 I 31) has a missing rostral area. In summary, while vaguely similar, its distinct dimensions and mentioned craniodental particularities exclude the specimen from Santalla del Bierzo from *Hoploaceratherium*. The other two acerathere species recorded in the Iberian Peninsula, *Aceratherium incisivum* and *Alicornops simorrense*, show shorter rostra, shorter nasal notches, and stouter nasal bones.

The Teleoceratine rhinoceroses in the Iberian Peninsula are restricted to the Ramblian and lower and middle Aragonian (Antunes and Ginsburg, 2000; Cerdeño, 1992). Four different taxa have been cited so far: *Brachypotherium brachypus*, *Prosantorhinus douvillei*, *Prosantorhinus germanicus*, and *Brachydiceratherium aurelianense*. The specimen from Santalla del Bierzo, despite similar to *Brachypotherium* in the short and broad premolar teeth and the shallow labial groove on the lower molars, differs on its deeper folding of the protocone in M3, smaller size (in both skull and dentition) and distinct rostrum (particularly on the longer nasal bones, development of the zygomatic arches, and distance between the nasal incision and the orbit (Cerdeño, 1993, pl. 4, fig. 11). The species *P. douvillei* has been recorded in the Iberian locality of Somosaguas Norte (Hernández Fernández *et al.*, 2006). While the dental dimensions resemble those of MGM-920M (Figs. II; III), it has an upraised nasal bone, extremely developed zygomatic arches, and poorly developed labial cingula, clearly different from the specimen from Santalla del Bierzo (Antoine et al., 2018, figs. 2A; 3A). *Prosantorhinus germanicus* has been reported from the Burdigalian (lower Miocene) of Lisbon (Antunes and Ginsburg, 2000).

The comparison with the BSPG collection of *P. germanicus* from Sandelzhausen, MGM-920M shows a similar P4-M2 morphology. However, both differ on the clearly distinct morphology of the P2 and M3 (the latter lacks the deep protocone fold), the shorter and raised nasal bone, and the shallower nasal notch (Fig. 5).

The genus *Brachydiceratherium* has been recently resurrected by Sizov *et al.* (2024) to host a series of Teleoceratina species previously grouped within *Diaceratherium*, leaving only the type species *D. tomerdingense* in the latter genus. The type material of *D. tomerdingense* (Tomerdingen, Germany; SMNS collection) includes a partial nasal bone with dental remains, and postcranial elements (Dietrich, 1931; Jame *et al.*, 2019). It is readily distinguished from MGM-920M by the absence of a lingual cingulum beneath the protocone and at the opening of the median valley on M1-2 (Jame *et al.*, 2019), a character conspicuously present in the Santalla del Bierzo specimen, thus excluding its assignment to *Diaceratherium* sensu stricto. The nasal bone also presents a rugous area on the anterior end. *Brachydiceratherium* is a diverse clade of early teleoceratine rhinocerotids ranging from the latest Oligocene up to the middle Miocene in Eurasia. Its postcranial anatomy is highly variable, ranging from slender early forms to graviportal later ones. From the list of synapomorphic characters diagnosing *Brachydiceratherium* detailed in Sizov *et al.* (2024), only three are preserved in the specimen from Santalla del Bierzo. These are: cheek teeth usually coated with some cement in *Brachydiceratherium*, protocone always constricted on P3-4, and labial cingulum usually absent on lower premolars and always present on lower molars. All three features are found in the individual from Santalla del Bierzo. However, it differs from the continuous lingual cingulum on the upper premolars and M3, the well-developed antecrochet and the pierced hypocone on M1-3.

In the Iberian Peninsula, the genus is represented by *B. aurelianense*, which has been reported from the localities of Rubielos de Mora, La Artesilla and Molí Calopa (Cerdeño, 1992; Hernández Fernández *et al.*, 2006; Sanisidro and Cantalapiedra, 2022). It can be distinguished from other Western European teleoceratine rhinoceroses by its moderate size, upper premolars void of crista, short M3, lower cheek teeth with not-so straight labial wall and labial cingulid rarely present (Cerdeño, 1993). The left upper row of *B. aurelianense* from Artenay specimen MNHN Ar-2160 is very similar to the upper row from Santalla del Bierzo: from the distribution and development of the labial and lingual

cingula to the horseshoe-like M3 (including the marked posterior protocone fold). Additionally, the hypocones of the M1-2 from MNHN Ar-2160 seem to be entangled at their bases, thus they are expected to produce the lingual rounded expansion of the hypocone at more advanced wear stages (like those observed in Santalla del Bierzo). As in MNHN Ar-2160, the crista on the premolar teeth is faint. Apart from some minor differences in their dentition (*i.e.* the stronger lingual cingulum on molar teeth and the weaker antero-posterior constriction of the hypocone, a characteristic partially explained by the smaller wear degree in MNHN Ar-2160), their rostral morphology clearly diverges.

Brachydiceratherium lemanense is one of the best known European teleoceratines. The earliest remains of the species come from the latest Oligocene of France and Germany, between MP 29-30 (Antoine and Becker, 2013), becoming very abundant through the earliest Miocene (MN 1-2). The rostral morphology of *B. lemanense* resembles that of MGM-920M due to their similar cranial proportions and resembling overall morphology. However, some dental characters differ. The molars of *B. lemanense* have smooth hypocones and the labial cingula are poorly developed to non-existent. A dental series from Cindré (France), associated with *B. lemanense* and illustrated in Roman (1911, pl. 8, fig. 2a) has more developed cingular patterns on the molars, subquadratic M3, or deeply pinched hypocones, all traits shared with the specimen from Santalla del Bierzo. Premolar dimensions fit within the size of *B. lemanense*, while molars from Santalla del Bierzo are slightly smaller. *Brachydiceratherium asphaltense* is another early Miocene teleoceratine species well-known from cranial and postcranial material. The species has been found in France and Switzerland and its stratigraphic range spans from the latest Oligocene (MP 28-30) to the earliest Miocene (MN 1). It shares similar dental dimensions to Santalla del Bierzo and specimen NMB-SAU1662 of *Brachydiceratherium asphaltense* from Saulcet figured in Becker *et al.* (2009, fig. 4d) matches the observed morphology: from the cingular pattern to the constriction of the hypocone in M1. In this case, the reported cranial remains of *B. asphaltense* show a characteristic dorsally-curved nasal bone (like those from Bühler or Saulcet; Jame *et al.*, 2019), are somewhat different from MGM-920M. In conclusion, according to the cited unique combination of characters the studied rhinoceros remains are kept in open nomenclature to an undetermined *Brachydiceratherium* species with certain affinities to *B. asphaltense* or *B. lemanense*.

CONCLUSIONS

The new rhinoceros specimen from Santalla del Bierzo represents the first macromammal remains from the El Bierzo Basin, extending the geographical distribution of fossil rhinoceros to the North-Western basins of the Iberian Peninsula. Both skull and mandible pertain to a single, adult individual. The upper dentition is morphologically and sizewise comparable with medium-sized early Miocene teleoceratines like *B. asphaltense*, *B. lamilloquense*, or *B. aginense*. In contrast, the skull displays a unique combination of characters (*i.e.* angulous nasal notch together with an inflated frontal bone, a long premaxilla, and, possibly, an upwards-oriented nasal tip) unique among Teleoceratina. Consequently, these remains have been determined as belonging to an undetermined form similar to the earliest forms of *Brachydiceratherium* described in the lowest Miocene of Bühler (MP30-MN1) or Saulcet (MN 1). These early *Brachydiceratherium* species are part of the phase 2 regional radiation through Germany, Switzerland, up to Western France during the earliest Miocene (MN 1-2; Becker *et al.*, 2009). Our data widens the geographic boundaries of the cited diversification event of the lowest Miocene to the Northern Iberian Peninsula. However, the absence of further stratigraphic context or more detailed systematic placement prevents clarify whether the presence of the genus in the northwestern part of the Iberian Peninsula is part of the second diversification or a possible persistence of the primitive forms of *Brachydiceratherium* posterior to the MN 1-2 in El Bierzo Basin.

The record of a large rhinocerotid from the El Bierzo Basin follows the relatively recent finding of Oligocene micromammals in the Toral Fm., in two localities of the same basin (Freudenthal *et al.*, 2010; Martín-González *et al.*, 2014). Although the Santalla Fm. of El Bierzo Basin is being traditionally assigned to the Miocene epoch, this is the first paleontological confirmation of such dating.

From a geologic perspective, we agree with Rodríguez-Fernández *et al.* (2015) in maintaining the Santalla Fm. as a separate unit with a typical syn-tectonic character and whose stratigraphic precedence below Las Médulas Fm. still requires to be unambiguously demonstrated. The most updated geological map of the region (Rodríguez-Fernández *et al.*, 2021) also uses the three formations of Hérail (1981) with some conditions. The conflicting data presented by Hacar *et al.* (1999) and Pagés *et al.* (1998, 2001), with regards to the traditional geology of the area, have only partially been solved by Heredia et al. (2015), where some interpretations are not in total agreement with field evidence. This is a discussion that falls outside the aims of this paper. We hope that the present remains of a rhinoceros collected in a small quarry abandoned more than 50 years ago will contribute to filling a critical gap in the Neogene large mammal record of the Iberian Peninsula, both temporally and geographically, while highlighting the paleontological potential of the largely unexplored continental basins of northwestern Spain.

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APPENDIX I

TABLE I. Sources for the cranial and dental material used in the morphological comparisons. Institutional Abbreviations: AMNH, American Museum of Natural History, New York; BSPG, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich; FSL, Faculté des Sciences et Technologies, Université Claude Bernard, Lyon 1, Lyon; HLMD, Hessisches Landesmuseum Darmstadt; ICP, Institut Català de Paleontologia; MfN, Museum für Naturkunde, Berlin; MGUV, Museu de Geología i Paleontología de la Universitat de València, Valencia; MHNT, Museum d'Histoire naturelle de Toulouse; MNCN, Museo Nacional de Ciencias Naturales, Madrid; MNHN, Museum national d'Histoire Naturelle, Paris

Species	Direct Observation	References
Alicornops simorrense	MNHN, MNCN, MNHN	Heissig (2012)
Protaceratherium minutum	FSL (cast), MNCN	Cerdeño (1993)
Brachypotherium brachypus	MNHN	
Protaceratherium albigense	MfN, MNHN	
Hoploaceratherium tetradactylum	MNHN	Becker *et al.* (2009)
Prosantorhinus douvillei		Antoine *et al.* (2018)
Plesiaceratherium mirallesi	ICP, MHNT	
Brachydiceratherium aurelianense	MNHN, FSL	Becker *et al.* (2009)
Brachydiceratherium asphaltense	FSL	Jame *et al.* (2019)
Brachydiceratherium lemanense	AMNH	
Dihoplus pikermiensis	MNHN, FSL	
Pliorhinus megarhinus	HLMD, FSL, MGUV	
Dihoplus schleiermacheri	MNHN, MNHN	
Lartetotherium sansaniense	MNCN, MNHN	

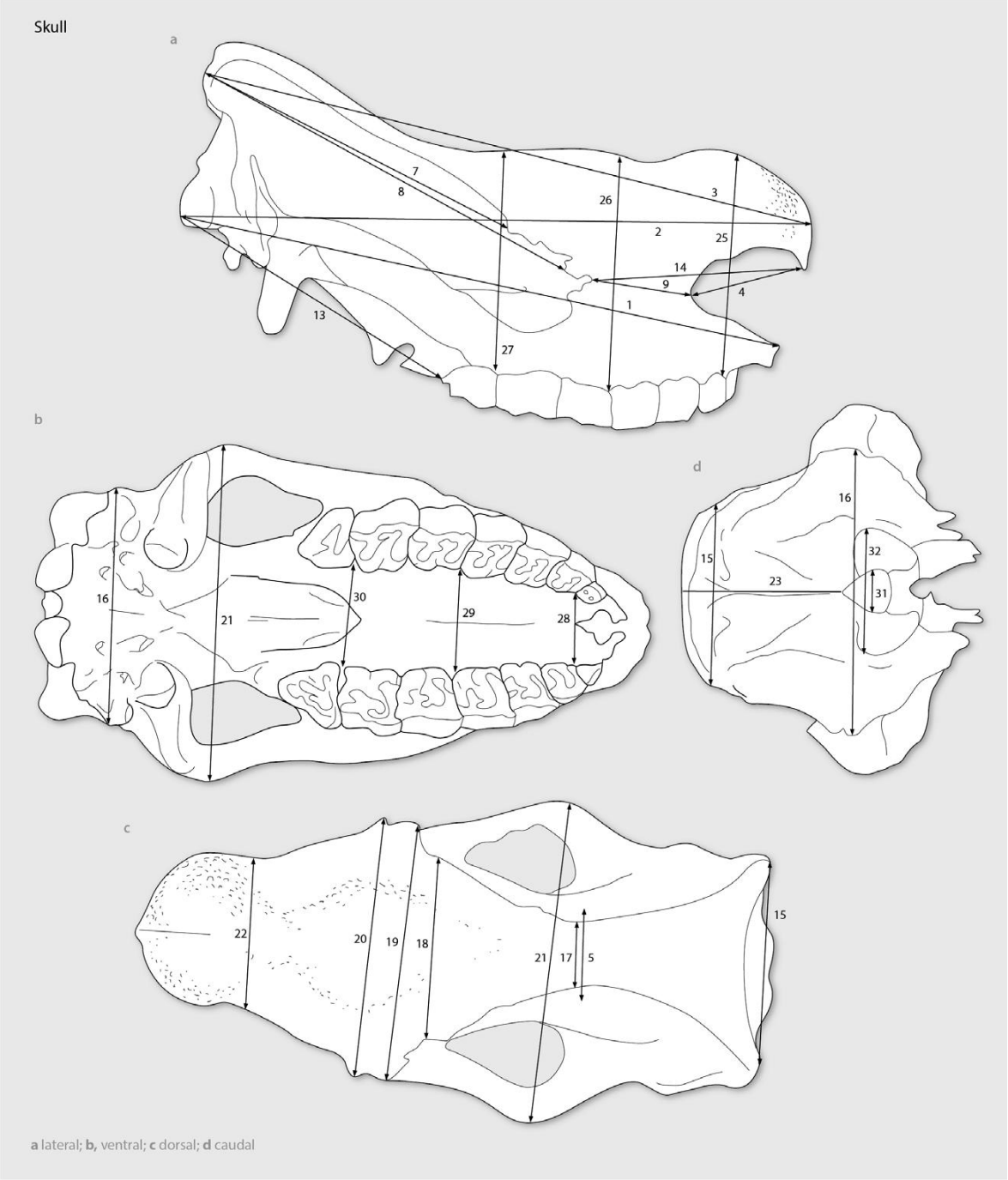

FIGURE I. Craniomandibular and dental measurements used in the present work from the skull from Santalla del Bierzo, following Guérin (1980) (image modified). 4: Distance between nasal tip and notch; 9: Distance between nasal notch and orbit; 14: Distance between nasal tip and orbit; 19: Width between supraorbital tubercles; 20: Width between lachrymal tubercles; 22: Width of nasal base; 25: Cranial height in front of P2; 26: Cranial height in front of M1.

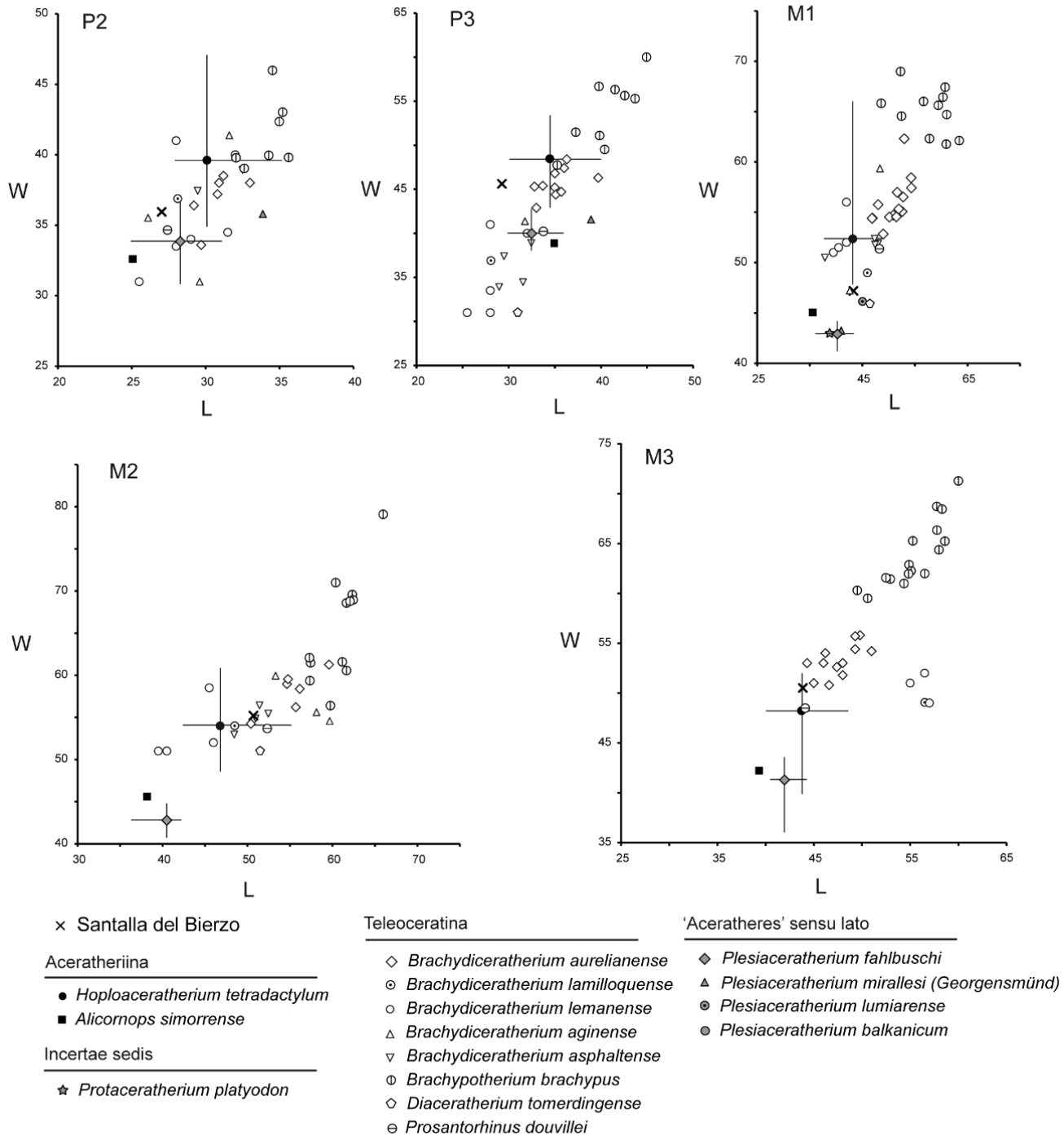

FIGURE II. Scatter plots of the upper teeth of several rhinoceros species discussed in the text together with the sample from Santalla del Bierzo (León Province, Spain), marked as a cross. Measurements obtained from the following sources: Becker and Tissier (2019); Becker *et al.* (2009); Cerdeño (1993); Defa and Heissig (1986); Heissig (2012); Peter (2002). Measurements are given in mm.

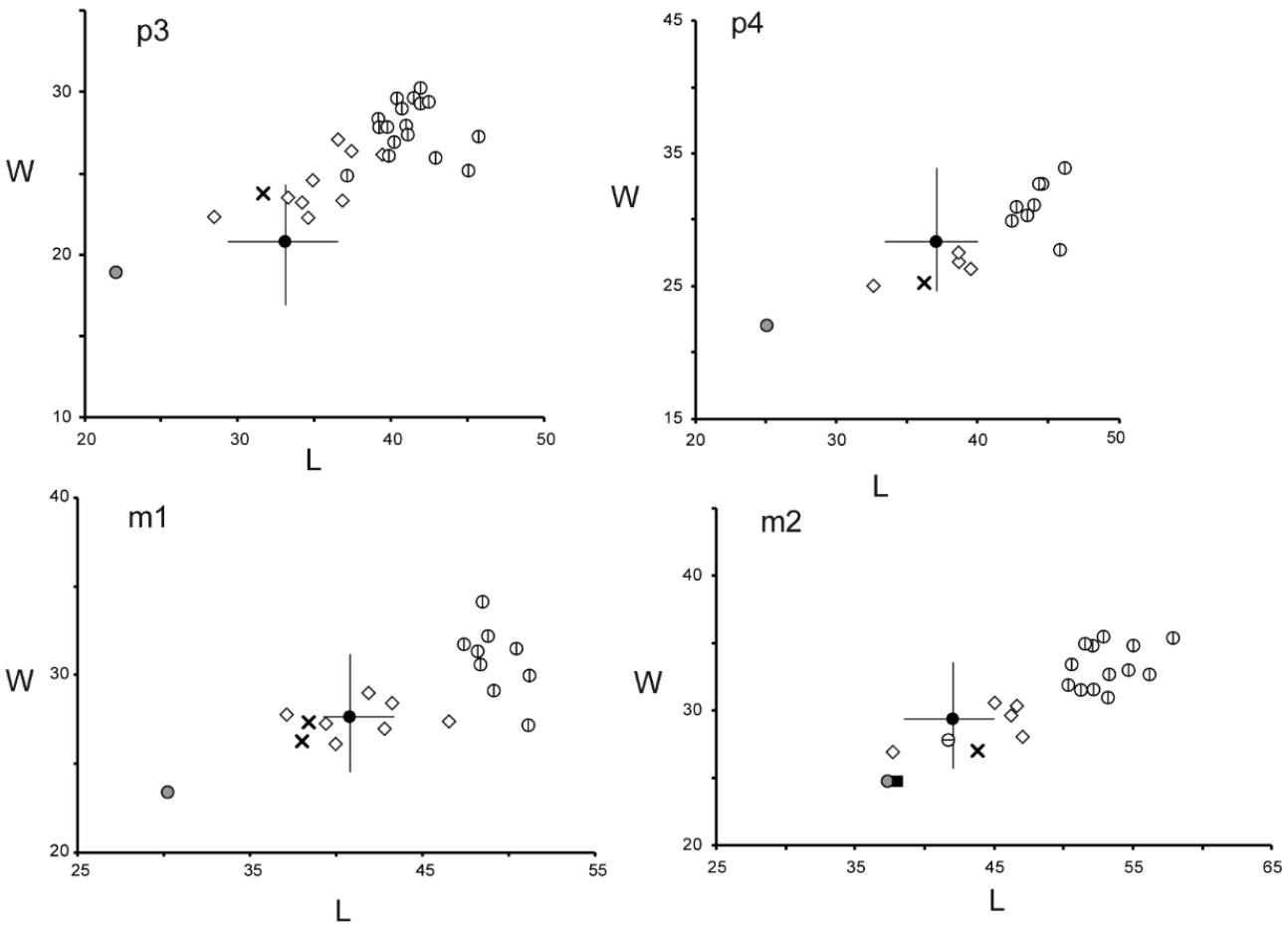

FIGURE III. Scatter plots of the lower teeth of several rhinoceros species discussed in the text. Measurements obtained from Becker and Tissier (2019); Cerdeño (1993); Heissig (2012); Peter (2002); Yan and Heissig (1986). Symbols equivalence follows that detailed in Figure I. Measurements are given in mm.

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