RESEARCH PAPER

New Pliocene Rhinocerotidae findings from the Iberian Peninsula and the revision of the Spanish Pliocene records

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Abstract
A fragmentary mandible from the early Pliocene of the Vera Basin is here investigated to clarify its taxonomic position. The studied specimen is here assigned to *Pliorhinus megarhinus*, documented in Europe from the latest Miocene to the mid-Pliocene. The morphometrical comparison reveals that this taxon is larger than *Stephanorhinus etruscus* and *S. jeanvireti* but overlaps with *Dihoplus schleiermacheri*. *P. megarhinus* and *D. schleiermacheri* differ in some characters of the lower molars, such as the length of the metalophid and the shape of the trigonid in occlusal view, thus allowing new considerations on the Pliocene Spanish rhinocerotine record. According to the results here obtained, three species are at least documented in Span during the Pliocene: *P. megarhinus*, *P. miguelcrusafonti*, and *S. etruscus*. The presence of *S. jeanvireti* has to be verified and confirmed by further evidence. The presence of *Dihoplus schleiermacheri* as a relict taxon in the Pliocene of Spain is here discarded.

Keywords Pliocene · Spain · Morphology · Morphometry · Biochronology

Introduction

Although the family Rhinocerotidae was widely distributed in Eurasia during the Neogene (Geraads et al. 2020), Pliocene rhinocerotine record is still poorly understood in respect to Miocene one, being usually documented by few localities and scanty remains (Pandolfi et al. 2020).

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During that time, only four taxa are recorded in Europe: *Pliorhinus megarhinus*, *P. miguelcrusafonti*, *Stephanorhinus etruscus* and *S. jeanvireti* (Guérin et al. 1969; Guérin 1972, 1980; Vekua 1972; Guérin and Santafé-Llopis 1978; Cerdeño 1992; Lacombat and Mörs 2008; Guérin and Tsoukala 2013; Pandolfi et al. 2017, 2019, 2020, 2021; Tsoukala 2018). The biochronological and geographic ranges of these taxa are far to be completely investigated and several records need to be deeply revised.

In the Iberian Peninsula, Spain in particular, the Pliocene rhinocerotine record is relatively scarce, and the material is usually represented by isolated remains. The systematic attribution of these specimens is controversial, and the occurrence of some species such as *S. jeanvireti* or *P. megarhinus* (Guérin 1980; Cerdeño 1992), as well as the persistence of the Miocene *Dihoplus schleiermacheri* (Montoya et al. 2006), still need to be confirmed or discarded.

The discovery of new rhinoceros remains from the early Pliocene of the Vera Basin (Southeast Spain), here described for the first time, raises the opportunity to revise the Pliocene Spanish rhinocerotine records. Accordingly, a first attempt to build up a new biochronological and paleobiogeographic framework of the Pliocene rhinocerotine species in Spain is reported.

Geological setting

The Vera Basin

The studied specimen was recovered in a Neogene intramountain basin located in the eastern part of the Betic Cordillera, the Vera Basin (Fig. 1). This basin was open to the east to the Mediterranean Sea. The Vera Basin was also connected with other intramountain basins such as the Sorbas Basin to the south and the Lorca Basin to the north, through narrow corridors (Fig. 1). Since the Pliocene, this basin has been subjected to low uplift rates around 11–21 m Ma^{-1} (Stokes 2008).

The Vera Basin is filled by marine and transitional deposits from the Burdigalian to Holocene. The studied remains
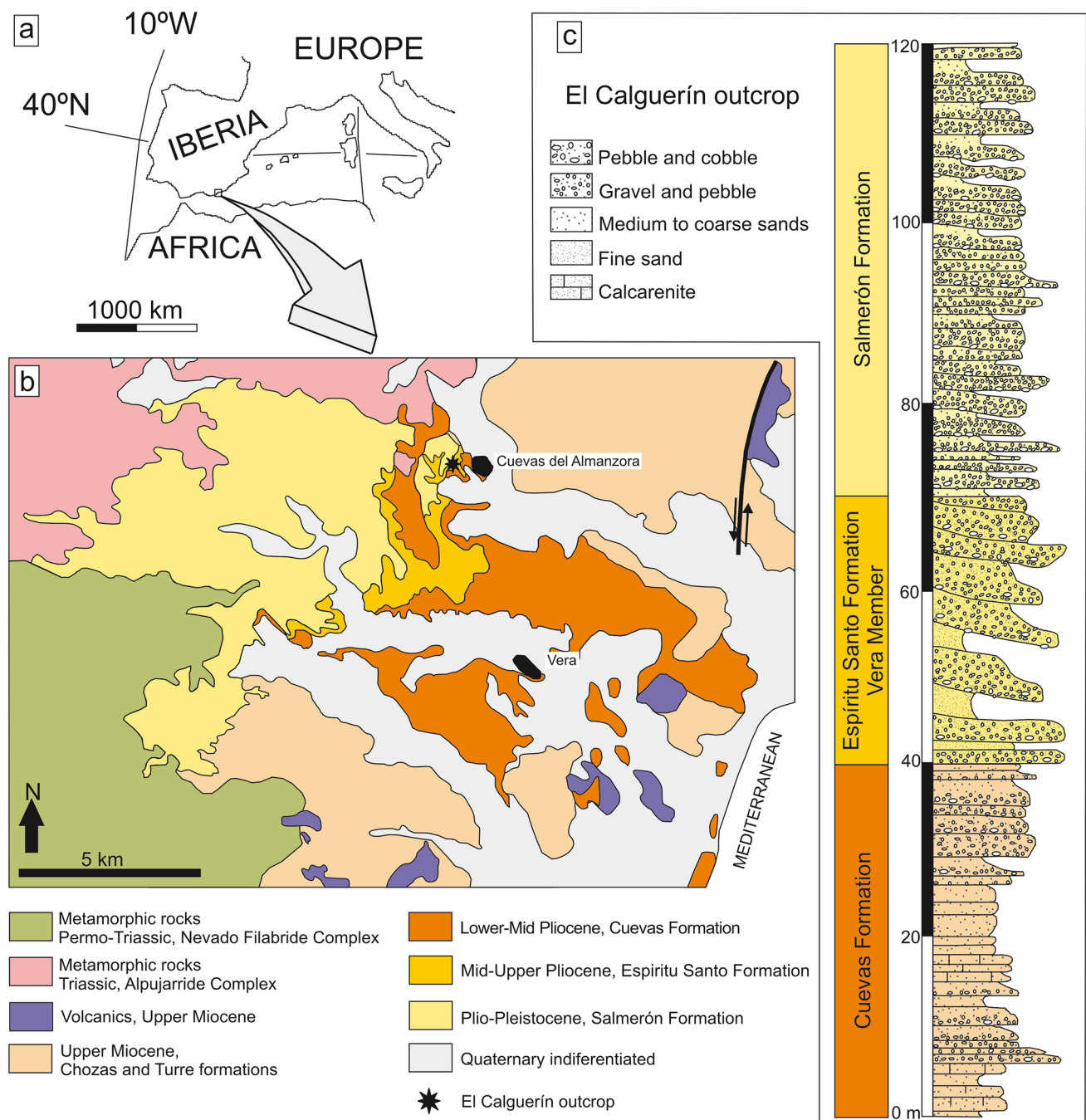

Fig. 1 Geological setting of the Vera basin. **a** Location of the Vera Basin; **b** Geological map of the Vera Basin with the distribution of the Cueva and Espiritu Santo Formation; **c** sedimentary log of the El Calguerín area. Modified from Sendra et al. (2020)

are related to the sediments of a delta system that evolved to alluvial fan, developed during the Pliocene and Pleistocene (Stokes 2008; Sendra et al. 2020). Völk (1967) differentiated three formations: Cuevas Formation (lower Pliocene), Espiritu Santo Formation (middle to upper Pliocene), and Salmerón Formation (uppermost Pliocene and Quaternary).

The Cuevas Formation (lower Pliocene) is constituted by medium to coarse bioclastic sands (calcarenites) with conglomerate layers in the proximal areas that change into fine sands and silts in the center of the basin. The Espiritu Santo Formation (middle to upper Pliocene) consists of coarse sand and conglomerates in the margins of the basin that range to medium and fine sands and limestones in distal areas. The Salmerón Formation (uppermost Pliocene and Quaternary) is constituted by reddish conglomerates, sands, and red silts with calcretes. The Salmerón Formation represents the filling of the basin with continental alluvial-fan deposition.

The studied specimen was recovered in the northern margin of the Vera Basin and more exactly in the Cuevas Formation at the El Calguerín outcrop (coordinates 37° 18′ 04″ N, 1° 53′ 03″ W) close to the Cuevas del Almanzora locality, Almeria province.

The Cuevas Formation is characterized by yellow–beige bioclastic sandstones (calcarenites) and conglomerates (pebbles and cobbles) in the northern margin of the basin that grade to blue–gray mud–siltstones, silty marls and fine sandstones in the central basin areas. The thickness ranges from almost 200 m in the central part of the basin to less than 50 m in the northern margin. In northern and western regions, the Cuevas Formation unconformably onlaps metamorphic basement at the basin margins.

In the central area of the basin, the fine grain lithofacies (mudstones, siltstones, and fine sandstones) are commonly massive but locally with cm-scale planar cross-stratification. The trace fossils (*Ophiomorpha*, *Skolithos* and *Diplocraterion* and less common *Teichichnus*) are abundant and macroinvertebrates include thin-shelled bivalves (*Amusium cristatum*, *Aequipecten opercularis*, *Chlamys radians, Pecten benedictus*, and *Pecten jacobaeus*), oysters, brachiopods (*Terebratulla*), gastropods (*Turritella*, conids and olivids) and irregular echinoids (*Schizaster* and *Clypeaster*) (Sendra et al. 2020). Völk (1967) and Ott d'Estevou et al. (1991) proposed an early–mid-Pliocene age for this formation based on the microfossil assemblages.

In the northern and western margins of the Vera Basin, the lithofacies of the Cuevas Formation are relatively coarse (medium to very coarse sands and sandstones, pebbly sandstones, and conglomerates) with well-bedded units with planar and cross-stratification (cm-scale). The sands and conglomerates are mainly metamorphic grains and dolostones clasts, with small pieces of wood (< 10 cm) preserved as charcoal. Conglomerates show clast imbrication and graded-bedding (fining upwards) with erosive irregular base. Marine trace fossils are well preserved in sandstones. The bioclastic calcareous lens-shaped bodies pinch-out laterally (in less than 10 m long).

Some remains of fossil marine mammals have been previously recorded from the Cuevas Formation (see Sendra et al. 2020) such as sirenians (Family Dugongidae, genus *Metaxytherium*), and cetaceans such as Odontoceti (Family Delphinidae, genus *Astadelphis*) and Mysticeti (Family Balaenidae). In addition, some continental mammals have been recorded in the more proximal areas (Sendra et al. 2020), such as a hemimandible of *Lynx issiodorensis*, a molar of a deer, and a hemimandible of a rhinoceros which is the subject of this work. These continental remains were found in shallow coarse marine facies.

Materials and methods

The studied material is stored at MGUV. The dental nomenclature used in this paper is reported in Fig. 2. The morphometric methodology follows Guérin (1980: p. 66, p. 71) and Lacombat (2006: Fig. 43). The measurements of the considered specimens are reported in Supplementary data and Table 1. The studied specimen was acquired using the structured blue led light 3D Scanner Artec Space Spider. A downloadable 3D model is available as Supplementary Resource File.

Anatomical abbreviations

i—lower incisor; m—lower molar.

Morphometric abbreviations

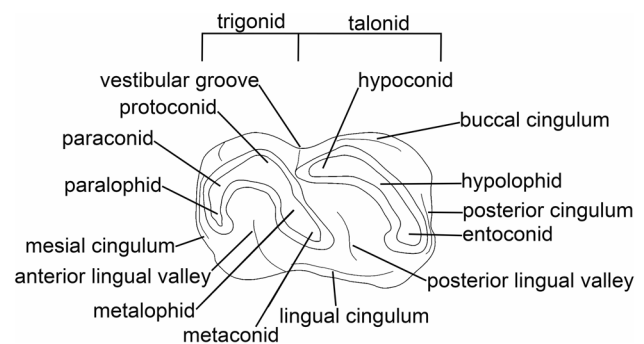Lbm—length of the molar row, buccal side (= maximal length of the molar row in Guérin 1980; Lacombat 2006, Fig. 43).

Fig. 2 Dental nomenclature of a rhinocerotine lower molar

Table 1 Comparative measurements for the length of the molar row (Lbm) among the Pliocene–earliest Pleistocene European rhinoceroses

Name	Lbm	Locality	ID	References
Vera Basin	156.47	Vera Basin	MGUV 39018	
P. megarhinus	142	Fratesti		Guérin et al. (1969)
P. megarhinus	149.5	Gödöllö	HNHM	
P. megarhinus	158	Kávás	HNHM v.79.117	
P. megarhinus	165	Millas		Guérin et al. (1969)
P. megarhinus	130–133	Monte Giogo		Pandolfi (2013)
P. megarhinus	151.8	Montpellier	NMB MP1031	
P. megarhinus	131–163	Montpellier		Guérin et al. (1969)
P. megarhinus	158.09	Montpellier	NHMUK 40805	
P. megarhinus	144.97	Palaia	IGF13091	
P. megarhinus	140–152	Saint Laurent		Guérin et al. (1969)
P. megarhinus	139	Val di Pugna	MSNAF4747	
D. schleiermacheri	151.31	Eppelsheim	NHMUK M2781	
D. schleiermacheri	148.82	Eppelsheim	NHMUK M2781	
D. schleiermacheri	145.71	Eppelsheim	NHMUK M2782	
D. schleiermacheri	136.52	Eppelsheim	NHMUK M3150	
D. schleiermacheri	142.71	Eppelsheim	NHMUK 21022	
D. schleiermacheri	150	Eppelsheim	NHMUK 21021	
D. schleiermacheri	139	Venta del Moro	MNCN 10977	Estimated from Morales (1984)
S. etruscus	123.6	Aivaliki		Pandolfi and Erten (2017)
S. etruscus	130	Capitone		Pandolfi et al. (2015)
S. etruscus	122.5	Castellana		Pandolfi and Erten (2017)
S. etruscus	135	Monte delle Piche		Pandolfi et al. (2015)
S. etruscus	125–134	Montevarchi		Mazza (1988)
S. etruscus	127.1–132	Pietrafitta		Pandolfi et al. (2017)
S. etruscus	122.09–122.7	Senèze		Lacombat (2006)
S. etruscus	118–131	Upper Valdarno	IGF755	Mazza (1988)
S. jeanvireti	133.15	Capannoli	IGF1449v	
S. jeanvireti	133–140	Milia		Guérin and Tsoukala (2013)
S. jeanvireti	128	Monte Pulgnasco	MGC9352	
S. jeanvireti	138.9	Monte San Pietro	MGC9354	
S. jeanvireti	131–138	Vialette		Guérin (1972)

Institutional abbreviations

HNHM—Magyar Természettudományi Múzeum, Budapest, Hungary; IGF—Museo di Storia Naturale, sezione di Geologia e Paleontologia, Università degli Studi di Firenze, Florence, Italy;¸ MFS, Museo Civico di Scienze Naturali, Faenza, Italy; MGC—Museo di Geologia G. Capellini, Università di Bologna, Italy; MGUV—Museu de Geologia de la Universitat de València, Valencia, Spain; ML—Musée Guimet d'Histoire Naturelle de Lyon, Lyon, France; MNCN—Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN—Muséum National d'Histoire Naturelle, Paris, France; MSNAF—Museo di Storia Naturale, Accademia dei Fisiocritici, Siena, Italy; NHMUK—Natural History Museum, London, UK; NMB—Naturhistorisches Museum, Basel, Switzerland.

Systematic paleontology

Order **Perissodactyla** Owen, 1848
    Family **Rhinocerotidae** Gray, 1821
    Subfamily **Rhinocerotinae** Gray, 1821
    Tribe **Rhinocerotini** Gray, 1821
    Subtribe **Rhinocerotina** Gray, 1821
    Genus *Pliorhinus* Pandolfi et al., 2021

Type species: *Pliorhinus megarhinus* (de Christol 1834) from the Pliocene of Montpellier, France.

Other species: *Pliorhinus miguelcrusafonti* (Guérin and Santafé-Llopis 1978).

Fig. 3 Rhinocerotidae specimen from Vera basin, MGUV 39018. **a** Occlusal view of the mandible with m1–m2, **b** lingual view of the mandible with m1–m2, **c** occlusal, lingual and buccal views of m1

*Pliorhinus megarhinus* (de Christol 1834).
Figure 3.

Material: A fragmentary right hemimandible with the molar row (39018) housed at MGUV.

Description: The specimen MGUV 39018 is a fragment of the right mandibular corpus with the molar row (Fig. 3). The specimen belongs to an adult individual with m3 fully erupted and slightly worn. Vestibular cingula are absent on m1 and m3 whilst m2 has a reduced mesial–vestibular cingulum. The vestibular groove is opened and shallow and reaches the neck on all the molars. A small distal cingulum is present on all the teeth. In occlusal view, the paralophid reaches the lingual rim. In the same view, the trigonid forms an obtuse dihedron. The anterior and posterior lingual valleys are U-shaped on m3 and broad V-shaped on m2. The posterior lingual valley is broad V-shaped on m1 whilst the anterior one is not observable. Lingual cingula are absent (Fig. 3).

Comparisons: Lower teeth morphology is quite conservative in Pliocene Rhinocerotini and only a combination of characters can be useful to distinguish among the different species. Vestibular and lingual cingula are absent on *Pliorhinus miguelcrusafonti* (Guérin and Santafé-Llopis 1978). The lingual valleys on the lower molars of *P. miguelcrusafonti* are V-shaped and the vestibular groove is narrower and deeper than in the studied specimen. In *Stephanorhinus etruscus* a lingual cingulum occurs sometimes on the lower teeth, whilst the vestibular cingulum is normally present (Guérin 1980, 2004). According to Lacombat (2003), distal and mesial cingula are absent on the lower molars of *S. etruscus*. In *S. etruscus* the vestibular groove is normally opened and shallow, and the metalophid is short, as observed in different specimens from Upper Valdarno (Italy, Early Pleistocene: IGF, NMB) and Senèze (France, Early Pleistocene; MNHN, NMB). Concerning *Stephanorhinus jeanvireti*, Guérin (1980) did not list useful characters to distinguish this taxon from the other Pliocene species, he only reported a description of the lingual valleys (Guérin 1980: p. 467). On the mandible from Vialette (ML V377), the vestibular grove and the lingual valleys on the molars are narrower in respect to those on the studied specimen; further the trigonid forms an acute dihedron in occlusal view. On *S. jeanvireti* from Monte San Pietro (MGGC) and Capannoli (IGF) the occlusal surface of molars displays a deeper vestibular groove and a shorter metalophid compared to that on the studied specimen, as well as a trigonid forming an acute dihedron. On the lower teeth of *S. jeanvireti* from Montopoli (IGF) the vestibular groove is narrower than in the studied specimen and it does not reach the neck. The morphology of the studied molars closely resembles the m3 from Baccinello V3 (Pandolfi and Rook 2017) and several molars from Montpellier (MN14, France; NMB, NHMUK) assigned to *Pliorhinus megarhinus*. In particular, the absence of developed vestibular cingulum, the shape of the vestibular groove (opened and shallow), the broad posterior lingual valleys, the long hypolophid and the obtuse trigonid are shared between the studied specimen and the studied sample of *P. megarhinus*. The length of the molar row, as well as the measurements of the single molars, falls within the range size of *P. megarhinus* (Fig. 4; Table 1; Supplementary table) being larger than the other Pliocene European species (Table 1). Furthermore,

Fig. 4 Box-plots of the Lbm (length of the molar row in mm) for the species considered in this work and the specimen from Vera Basin (MGUV 39018). The dataset is reported in Table 1
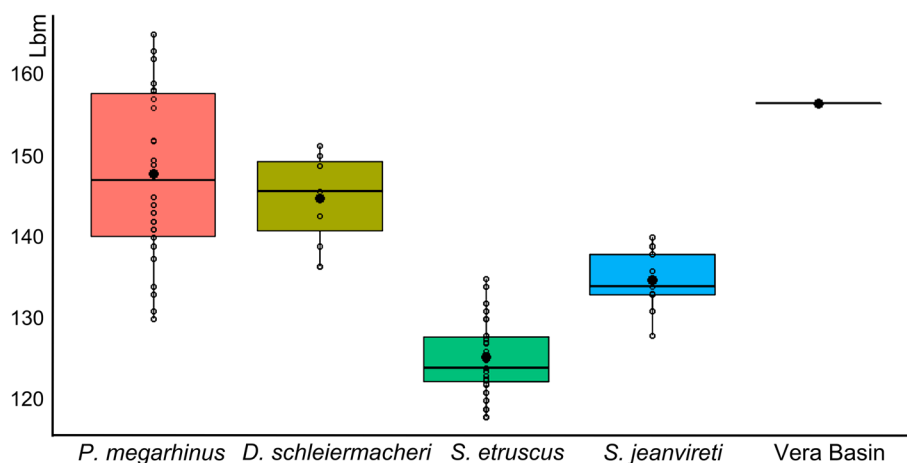
the Miocene *Dihoplus schleiermacheri* differs from the studied specimen by having a shorter trigonid, and V-shaped lingual valleys. The hypolophid on the molars of *D. schleiermacheri* is shorter than that on the specimens from Vera Basin and *P. megarhinus*. Contrary to the studied material, the entoconid on m2s and m3s of *D. schleiermacheri* from Eppelsheim is usually constricted.

Discussion

Morphology and morphometry of the lower teeth in Pliocene Rhinocerotidae

The mandibular fragment from the Vera Basin differs from the Pliocene European rhinoceroses belonging to *Stephanorhinus* (*S. etruscus* and *S. jeanvireti*) and to *P. miguelcrusafonti*, and it is morphologically and morphometrically closer to *P. megarhinus*. A few characters only can be considered as morphologically useful to distinguish among the Pliocene species due to the conservative traits displayed by this group of Rhinocerotidae.

The comparison with *S. etruscus* is here mainly based on the material collected from the Upper Valdarno type area and coeval sites. The lower teeth of this species can display a lingual cingulum and the vestibular groove is normally open and shallow. The molar toothrows of the Etruscan rhino considered in this work are shorter than that of the studied specimen, yet than the other Pliocene considered species. This morphometric value represents therefore a useful distinguishing character among the Pliocene rhinoceroses and in particular to discard the occurrence of the Etruscan rhinoceros in the Vera Basin and in other early and mid-Pliocene localities.

Stephanorhinus jeanvireti is larger than the Etruscan rhinoceros but its dimensions are sometimes close or slightly smaller than *P. megarhinus*. The molar lengths of

S. jeanvireti, here calculated on the material from Vialette, Milia and several Italian localities, is intermediate between *S. etruscus* and *P. megarhinus* and smaller than the specimen from Vera Basin (Fig. 4). A few morphological characters of the lower teeth can be taken into account to distinguish this species from the studied material: the shape of the lingual valleys, the depth of the external groove and the shape of the trigonid.

Pliorhinus miguelcrusafonti is poorly known, being documented by a few specimens. The diagnostic features detectable on the lower teeth of this taxon are the absence of cingula on the vestibular and lingual side, the narrow V-shaped lingual valleys and the narrow and deep vestibular groove. Morphometric features of the lower teeth are included within those of other Pliocene taxa such as *S. jeanvireti* and cannot be considered for a certain taxonomic attribution.

Pliorhinus megarhinus is well-distinguishable from the other Pliocene species, notably by its larger dimensions. Anyway, small representatives of this taxon are close in size to *S. jeanvireti*. *Pliorhinus megarhinus* has wider lingual valleys in respect to the other considered taxa and, in addition, it is characterized by a long hypolophid, a shallow vestibular groove and a less angular trigonid. The presence of these characters combined with the size of the specimens are useful for a certain attribution of some remains as it is the case of the Vera Basin specimen. A resuming table of the main diagnostic features here considered for each taxon is reported in the Table 2.

The Spanish Pliocene records revised: biochronology and paleobiogeography

Stephanorhinus etruscus is a relatively well-known Early Pleistocene species, documented also from some latest Pliocene localities (Pandolfi et al. 2017). This taxon is generally smaller in size than the other Plio-Pleistocene species. However, its morphological distinguishing

Table 2 Main morphological distinguish characters for the lower teeth of Pliocene Western European Rhinocerotidae considered in this paper

Lower molars	Buccal cingulum	Lingual cingulum	Lingual valleys	Trigonid	Metalophid	Entoconid	External groove
P. megarhinus	Absent	Absent	Mainly U-shaped	Obtuse	Long	Not constricted	Shallow
P. miguelcrusa-fonti	Absent	Absent	V-shaped	Acute dihedron	Long	Not constricted	Deep
D. schleiermacheri	Rarely present	Absent	Normally V-shaped	Obtuse	Short	Constricted	Deep
S. etruscus	Usually present	Sometimes present	Mainly V-shaped	Obtuse	Short	Not constricted	Shallow
S. jeanvireti	Usually absent	Absent	V-shaped	Acute dihedron	Short	Not constricted	Deep
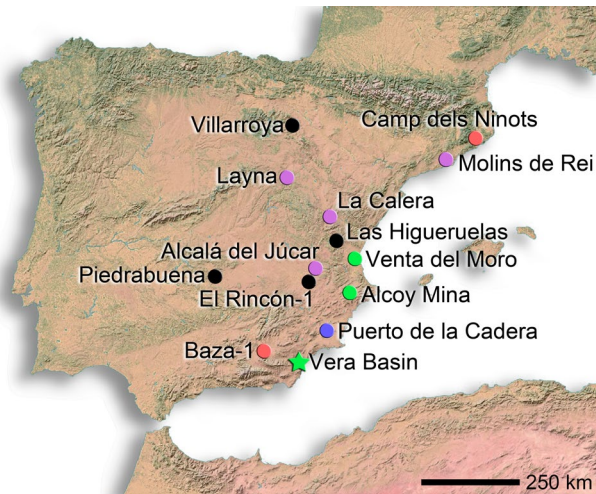
Fig. 5 Geographical map showing the Spanish Pliocene localities discussed in the text and listed in Table 2. Black circle = *S. etruscus*; Purple circle = *P. miguelcrusafonti*; Green circle = *P. megarhinus*; other colors correspond to indeterminate attribution. Interactive map is available as Supplementary File

features, in particular on teeth and postcranials, are still partially discussed, raising doubts concerning the attribution of some latest Early Pleistocene remains (Pandolfi et al. 2017). *S. etruscus* occurred in the Iberian Peninsula during the latest Pliocene (MN16) as recently revised in Pandolfi et al. (2017). Remains attributable to this taxon are from Las Higueruelas (Ciudad Real Province, ca. 3.3 Ma; Mazo 1995), Piedrabuena (Ciudad Real Province, MN15–MN16 transition; Mazo 1999) and El Rincón-1 (Albacete Province, MN16; Alberdi et al. 1997) (Fig. 5; Table 3). The first occurrence of the Etruscan rhinoceros is biochronologically coeval with that from sites in Italy and in the Dacian Basin, between 3.5 and 3.0 Ma (Pandolfi et al. 2017). The origin of this taxon is still unknown, and the hypothesis proposed by Heissig (1996) on a phyletic relationship with *D. pikermiensis* cannot be ruled out albeit still in the need to be confirmed by further evidence. The occurrence of the Etruscan rhinoceros would represent the faunal renewal that occurs in Europe at the Ruscinian–Villafranchian transition.

Stephanorhinus jeanvireti was named by Guérin (1972) on some cranial and postcranial material from Vialette (around 3 Ma, MN16a; France); the author also recorded this taxon in several other European localities biochronologically placed in MN16a and b (Guérin 1972, 1980; Pandolfi et al. 2019). Despite the name of this species was recently disputed (Pandolfi et al. 2019), several authors agreed to accept the Guérin's name for nomenclatural stability (see Geraads et al. 2020). In Spain *S. jeanvireti* has been dubitatively recorded in the Guadiz-Baza depression, at Baza-1 (*Stephanorhinus* cf. *S. jeanvireti*; around 4.0–4.5 Ma: Ros-Montoya et al. 2017). The rhinoceros material from Baza-1 is scarce and not highly diagnostic, being represented by two isolated lower molars and a metapodial fragment. Accordingly, a generic attribution of this material could be at present reasonable, pending the discovery of additional specimens, even if the morphology of the m2 (Ros-Montoya et al. 2017: Fig. 7A) closely resembles *P. megarhinus* in having a U-shaped lingual valley, a long metalophid and an obtuse trigonid. *Stephanorhinus* cf. *jeanvireti* has also been reported at Camp dels Ninots (Girona; MN16a; Gómez de Soler et al. 2012). The taxon is there represented by partially complete skeletons but they have been never described in detail, so it is difficult to verify the correct attribution of these specimens. Pending the systematic description of the material from Camp dels Ninots, the presence of *S. jeanvireti* in Spain is not confirmed here, even if its occurrence during the MN16a would be in agreement with its record in several other European areas (France, Italy, Romania: Pandolfi et al. 2019).

The rhinoceros from Layna was described by Guérin and Santafé-Llopis (1978) as a new species: *Dicerorhinus miguelcrusafonti*. The taxon was dubitatively retained within *Stephanorhinus* following the proposal of Cerdeño (1992) but it has been recently referred to the genus *Pliorhinus* (Pandolfi et al. 2021). The species was recorded at La Calera (Teruel) and Alcalá del Júcar (Albacete) (Cerdeño 1992; Mazo 1997), based on a few isolated postcranial remains (Table 3). The postcranial material described and

Table 3 Spanish Pliocene rhinocerotine records discussed in the text with the revised identification here proposed (List of localities updated and modified from Geraads et al. 2020)

Lat	Lon	Locality	Age	Ma	Main references	Previous identification	Revised identification
39.19	− 1.43	Alcalá del Júcar	MN15	3.5 Ma	Mazo (1997)	*Stephanorhinus miguelcrusafonti*	*Pliorhinus miguelcrusafonti*
38.7	− 0.53	Alcoy Mina	MN14		Montoya et al. (2006)	"*Dihoplus*" sp.	*Pliorhinus megarhinus*
37.48	− 2.81	Baza-1	MN14	4–4.5 Ma	Ros-Montoya et al. (2017)	*Stephanorhinus* sp. cf. *S. jeanvireti*	*Stephanorhinus?*
41.83	2.82	Camp del Ninots	MN16a	3.2 Ma	Gómez de Soler et al. (2012)	*Stephanorhinus* cf. *jeanvireti*	*Stephanorhinus?*
38.917	− 1.633	El Rincón-1	MN16b		Alberdi et al. (1997)	*Stephanorhinus etruscus*	*Stephanorhinus etruscus*
40.26	− 1.06	La Calera	MN15	4 Ma	Cerdeño (1992)	"*Stephanorhinus*" *miguelcrusafonti*	*Pliorhinus miguelcrusafonti*
39.78	− 0.87	Las Higueruelas	MN16a	3.3–3.1 Ma	Mazo (1995)	*Stephanorhinus etruscus*	*Stephanorhinus etruscus*
41.05	− 2.19	Layna	MN15	3.5–3.4 Ma	Guérin and Santafé (1978)	"*Stephanorhinus*" *miguelcrusafonti*	*Pliorhinus miguelcrusafonti*
41.41	2.03	Molins de Rei	Late Pliocene		García-Fernández (2000)	*Stephanorhinus megarhinus*	*Pliorhinus miguelcrusafonti*
39.02	− 4.1	Piedrabuena	MN16a		Mazo and Torres (1990)	*Stephanorhinus etruscus*	*Stephanorhinus etruscus*
37.91	− 1.15	Puerto de la Cadena	MN14	4.997–4.896 Ma	Piñero et al. (2017)	*Dihoplus schleiermacheri/megarhinus*	*Dihoplus?*
39.4	− 0.4	Venta del Moro	MN13-14		Cerdeño (1992)	*Dihoplus schleiermacheri*	*Pliorhinus megarhinus*
37.29	− 1.88	Vera Basin	Early Pliocene		This work	Rhinocerotidae indet	*Pliorhinus megarhinus*
42.08	− 2.04	Villarroya	MN16a		Cerdeño (1993)	*Stephanorhinus etruscus*	*Stephanorhinus etruscus*

documented by Cerdeño (1992) and Mazo (1997) is morphometrically and morphologically close to the type material of *P. miguelcrusafonti* from Layna, thus confirming the occurrence of this taxon in the two above mentioned localities. According to Cerdeño (1992), there are a few morphological differences between this species and *P. megarhinus*, and the Spanish species could possibly be a subspecies of the latter. In our opinion, the morphological and morphometric differences between *P. megarhinus* and *P. miguelcrusafonti* are consistent with a specific differentiation, but the two species are phylogenetically related (Pandolfi et al. 2021). Considering its restricted geographic and biochronological distribution, *P. miguelcrusafonti* represents a useful marked for correlation among Pliocene Spanish faunas.

A typical Miocene taxon, *Dihoplus schleiermacheri* has been also reported in Spain during the early Pliocene. A few isolated teeth from Alcoy Mina have been referred to this species by Guérin (1980) and recently by Montoya et al. (2006) who assigned this locality to MN14. *D. schleiermacheri* has been also reported at Venta del Moro (Turolian–Ruscinian transition) (Guérin 1980; Cerdeño 1992). In agreement with Montoya et al. (2006; Fig. 13), the lower

teeth from Alcoy Mina resemble those from Venta del Moro and belong to the same taxon (Table 3). The teeth from both localities resemble those from Vera Basin and *P. megarhinus* rather than *D. schleiermacheri* in having a wide lingual valley and a long metalophid in particular on the m3 (Montoya et al. 2006; Fig. 13G). In addition, the almost complete mandible from Venta del Moro (MNCN10977) displays a short symphyseal area, and clearly lacks the large i2 alveoli that characterize the mandibles of *D. schleiermacheri*. The molars on the mandible from Venta del Moro are much worn, but they display an open and shallow vestibular groove and lack of the entoconid constriction. *Dihoplus schleiermacheri/megarhinus* has been recently listed within the faunal remains collected at Puerto de la Cadena (Murcia region; MN14) (Piñero et al. 2017). The rhinoceros material is here represented by a fragment of a relatively worn lower molar (Piñero et al. 2017; Fig. 7E) and a fragment of symphysis (Piñero et al. 2017; Fig. 7A). The material from Puerto de la Cadena can be cautiously assigned to *Dihoplus*? pending the discovery of additional well-preserved specimens. Accordingly, the presence of *D. schleiermacheri* in Spain during the Pliocene is at present discarded.
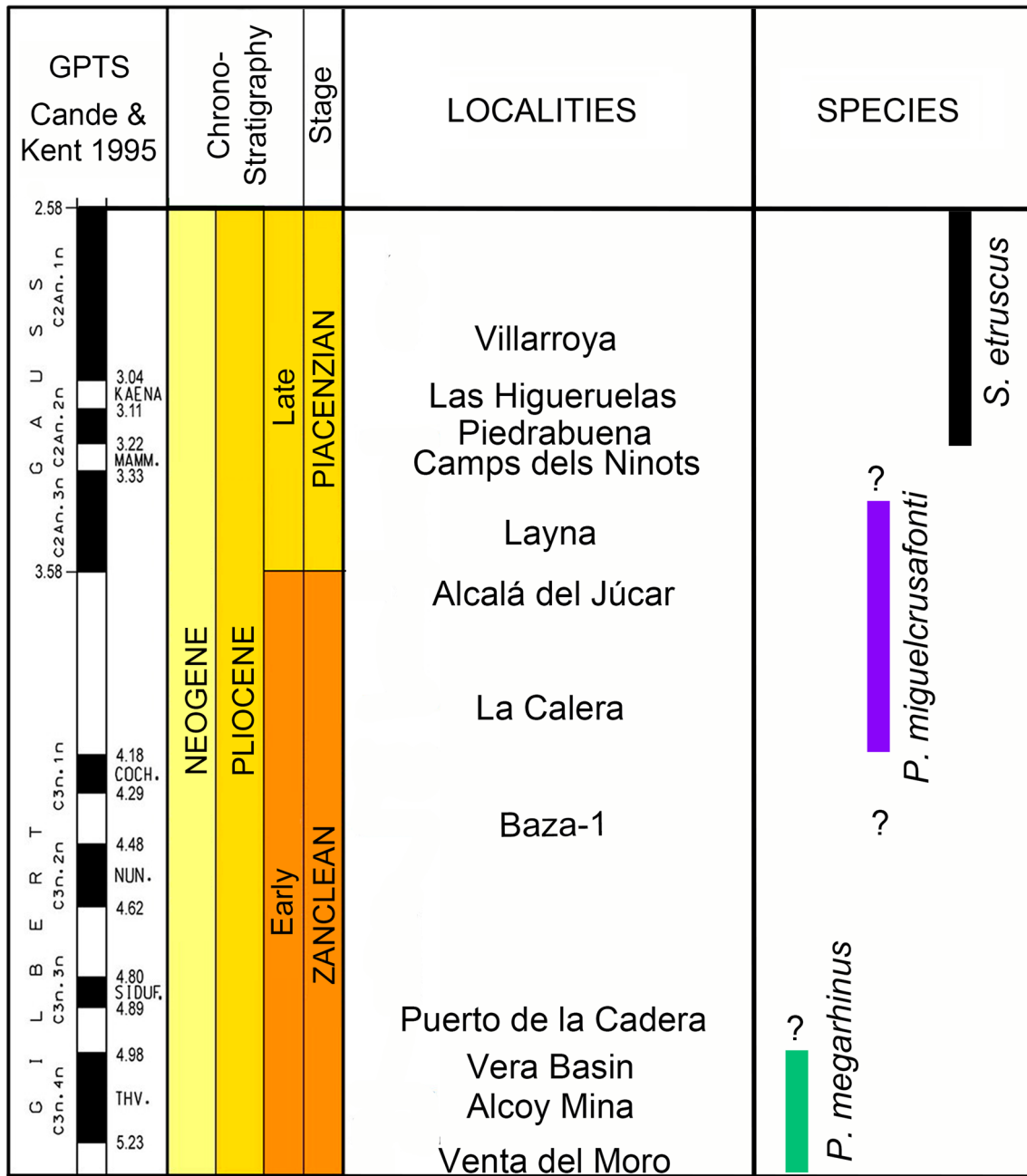
Fig. 6 New biochronological scheme for the Spanish Pliocene rhinocerotines (Table 1 for references)

Pliorhinus megarhinus is commonly documented in several early Pliocene localities of Europe, and it has been also reported in uppermost Miocene deposits (Pandolfi and Rook 2017). In Spain this taxon was previously documented at Molins de Rei (Table 3), based on a proximal epiphysis of metatarsal IV (Fernández 2000). Anyway, the bone there collected is morphologically close to *P. miguelcrusafonti* from Layna than to the typical *P. megarhinus* from Montpellier, being the proximal articular surface less developed than the proximal epiphysis (observations at MNCN, NMB). Thus,

we provisionally re-assigned this specimen to the Layna species. Accordingly, in Spain *P. megarhinus* is only recorded in Vera Basin, Alcoy Mina and Venta del Moro (Fig. 5). The two first localities are referred to MN14, whilst Venta del Moro is biochronologically placed between the latest Turolian and the early Ruscinian (Table 3). The occurrence of *P. megarhinus* during that time agrees with the records of this species in France, Italy and Hungary (Pandolfi et al. 2015, 2016; Pandolfi and Rook 2017). A dispersal of this taxon from East to West Europe during the latest Miocene has been

indeed proposed by Pandolfi et al. (2015, 2016) and Pandolfi and Rook (2017) who recorded *P. megarhinus* in several MN13 localities. The species probably reached the Iberian Peninsula at the Turolian–Ruscinian transition and occurred there till the mid-Pliocene (MN14–15 transition) (Fig. 6).

Conclusions

The systematic study of the rhinoceros specimen collected from the early Pliocene deposits of the Vera Basin is here assigned to *Pliorhinus megarhinus*. The morphometrical comparison reveals that this taxon is larger than *S. etruscus* and *S. jeanvireti* but overlaps with *Dihoplus schleiermacheri*.

Pliorhinus megarhinus and *D. schleiermacheri* differ in some characters of the lower molars, such as the length of the metalophid and the shape of the trigonid in occlusal view, thus allowing new considerations on the Pliocene Spanish rhinocerotine record. According to the results here obtained, three species are at least documented in Span during the Pliocene: *P. megarhinus*, recorded in the Vera Basin, Alcoy Mina and Venta del Moro, from the latest Turolian and the early Pliocene; *P. miguelcrusafonti*, recorded at Layna, La Calera, Molins de Rei and Alcalá del Júcar, mid-Pliocene in age; and *S. etruscus*, recorded at Las Higueruelas, Piedrabuena and El Rincón-1, all referred to the latest Pliocene. The presence of *S. jeanvireti* has to be verified and confirmed by a detailed study of the remains from Camp dels Ninots whilst the specimen from Baza-1 cannot be attributed to a species. The presence of *Dihoplus schleiermacheri* as a relict taxon in Spain is not confirmed here, being the specimens from Alcoy Mina re-assigned to *P. megarhinus*.

The present contribution represents a new insight into the biochronology and systematics on Pliocene rhinocerotines from Spain and represents the first attempt to clarify the occurrences and dispersal of this group in the Iberian Peninsula during the Pliocene.

Data availability Data and material are available within the cited collections and institutions.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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