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# The postcranial variability of Quaternary European rhinoceroses: the case study of *Stephanorhinus hundsheimensis* from the Middle Pleistocene site of Contrada Monticelli (Apulia, southern Italy)

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**ABSTRACT**

Five rhinoceros species, mainly distinguishable through cranial, mandibular and dental morphology, were recognized during the Quaternary across Europe. The postcranial morphology of these taxa is quite variable, with strong superposition among species, especially between *Stephanorhinus etruscus* and *Stephanorhinus hundsheimensis*. Here, the complete sample including 25 postcranial bones from the early Middle Pleistocene site of Contrada Monticelli (Apulia, southern Italy) is described and compared through morphological and biometric analyses. A few bones, in addition to cranial and mandibular remains from this site, have been previously referred to *Stephanorhinus hundsheimensis*. We explored the morphological variability of *Stephanorhinus hundsheimensis* from Contrada Monticelli against the diagnostic characters described in the literature. The size variation of the Contrada Monticelli sample is also investigated, through a comparison with other Quaternary European rhinoceros samples. Our results indicate a wide morphological variability with several distinct characters and a strong morphological affinity between *Stephanorhinus etruscus* and *S. hundsheimensis*. Our results suggest that *Stephanorhinus hundsheimensis* from Contrada Monticelli is a species with a high degree of intraspecific variability, possibly a hybrid population or a population including two morphotypes of the same species.

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## Introduction

During the Plio-Pleistocene, several mammal species are widespread throughout Eurasia acquiring a considerable importance for palaeoclimatic and palaeogeographic reconstructions, chronological correlation and evolutionary history of taxa (Gliozzi et al. 1997; Palombo 2009; Bellucci et al. 2014). Among these, rhinoceroses represent a common element of the Quaternary mammal palaeocommunities. Five species of rhinoceros from the Quaternary European record have been considered in this work (Figure 1): the Etruscan rhinoceros, *Stephanorhinus etruscus* (Falconer 1868) (Early Pleistocene); the Hundsheim rhinoceros (or Toula's rhinoceros), *Stephanorhinus hundsheimensis* (Toula 1902) (latest Early Pleistocene to Middle Pleistocene); the Merck's rhinoceros (or forest rhinoceros), *Stephanorhinus kirchbergensis* (Jäger 1835–39) (Middle to Late Pleistocene); the narrow-nosed rhinoceros (or steppe rhinoceros), *Stephanorhinus hemitoechus* (Falconer 1859) (Middle to Late Pleistocene); the woolly rhinoceros, *Coelodonta antiquitatis* (Blumenbach 1799) (late Middle Pleistocene to Late Pleistocene) (Guérin 1980; Gliozzi et al. 1997; Kahlke 1999; Stuart and Lister 2007, 2012; Kahlke and Lacombat 2008; Pandolfi et al. 2013, 2017, 2017; Pandolfi and Marra 2015; Uzunidis et al. 2022). The species *Stephanorhinus elatus* (= *Stephanorhinus jeanvireti*, see Ballatore and Breda 2016) has not been considered in this work as its last occurrence was reported in Les Étouaires site (3.18–2.35 Ma, Ballatore and Breda 2018). Elasmotherians were not included as their occurrence was limited to Asia and Eastern Europe, with their westernmost record in Moldova (Schvyreva 2015).

*Stephanorhinus etruscus* is recorded in the European Early Pleistocene, from the middle Villafranchian Faunal Unit of Saint Vallier (Guérin 1980; Mazza 1988; van der Made 2010, 2015), to the late Villafranchian Faunal Unit of Tasso (van der Made 2010, 2015) (see Figure 1). Pandolfi et al. (2017) and Pandolfi (2022) extend *S. etruscus* range back to the early Villafranchian, but the specimens considered do not show adequate morphologies for an unequivocal identification. Considering this, the European presence of *S. etruscus* in the Triversa Faunal Unit must be considered with caution.

Following Mazza et al. (1993), Fortelius et al. (1993) and Lacombat (2005), *S. hundsheimensis* dispersed into Europe at ca. 1.5 Ma, as attested by the records from the Italian localities of Pietrafitta (Umbria, central Italy; ca. 1.5 Ma; Martinetto et al. 2014) and Pirro Nord (Apulia, between 1.6–1.3 Ma; Arzarello et al. 2007, 2009; Bertok et al. 2013) and from the coeval French sites of Ceyssaguet and Sainzelles (both in Haute Loire Department, respectively 1.4 and 1.45 Ma; Argant and Bonifay 2011; Mourer-Chauviré and Bonifay 2018). Additional remains of *S. hundsheimensis* were found from: the German locality of Untermassfeld (ca 1.0 Ma; Kahlke 2001); the Greek localities of Platanochori-1 (ca. 1.2 Ma; Konidaris et al. 2015) and Apollonia (ca. 1.2 Ma; Konidaris et al. 2015); the Italian site of Collecurti (ca. 1.05 Ma; Mazza and Ventra 2011); the Spanish localities of Barranco Leon (1.4 Ma; Lacombat 2010), Fuente Nueva 3 (1.3 Ma; Lacombat 2010) and Vallparadís Composite section (Vallparadís Estació and Cal Guardiola) (ca. 1.2 to 0.78 Ma; Madurell-Malapeira et al. 2010, 2014).

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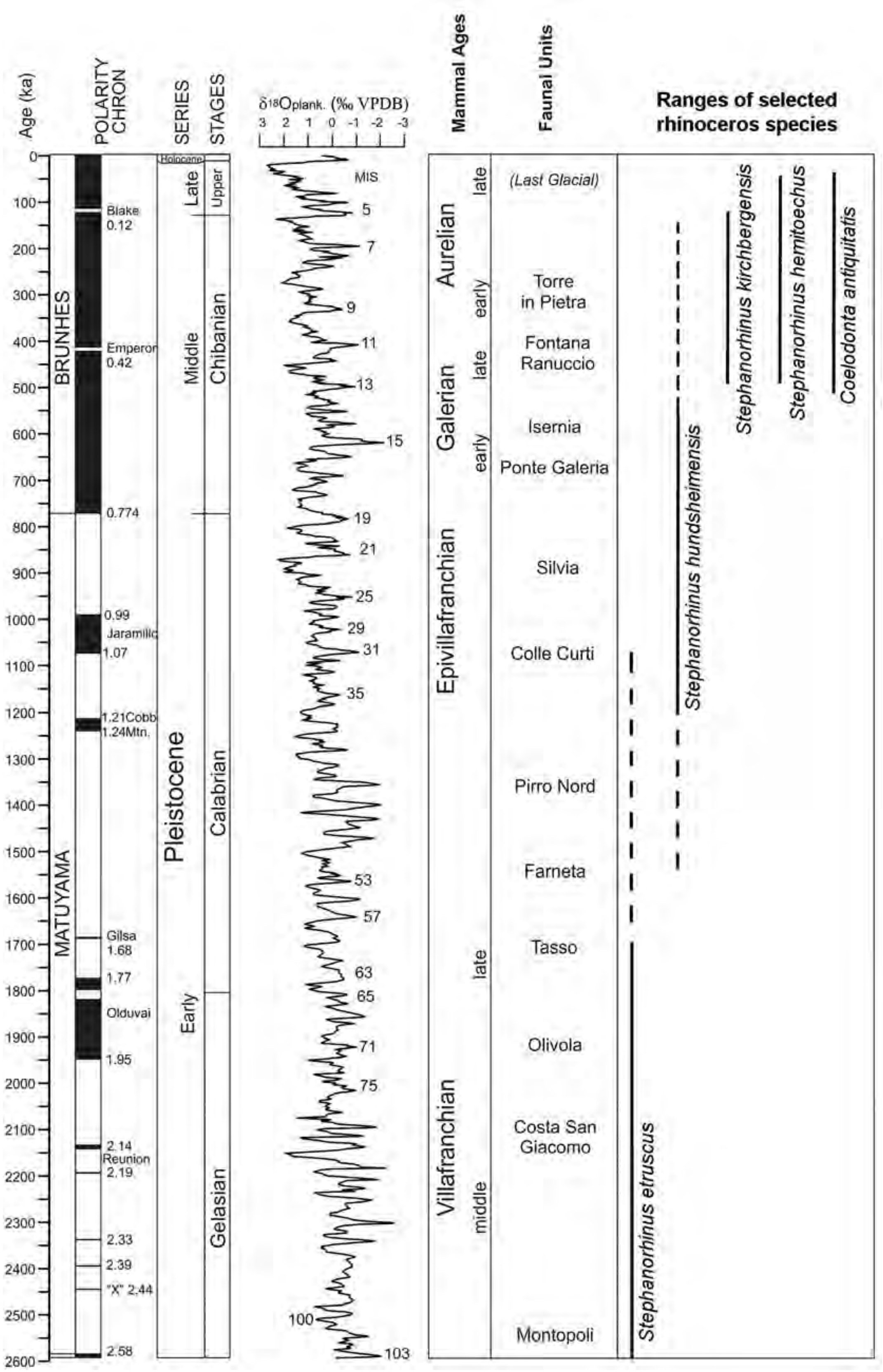

**Figure 1.** Biochronological scheme with ranges of selected rhinoceros species. Chronostratigraphy is from Cohen et al. (2013, updated), Marine isotope record is from Lourens (2004).

Other authors proposed that the majority of the records from the late Early Pleistocene sites of Europe should be attributed to *S. etruscus*: the Spanish localities of Atapuerca TD4, TD6 and TD8 (Brunhes-Matuyama transition; van der Made 1998, 1999, 2010), Cueva Victoria (ca. 1 Ma; Cerdeño 1993; Pandolfi and Erten 2017), El Chaparral (ca. 1 Ma; Pacheco et al. 2011) and Huescar (ca. 0.9 Ma; Cerdeño 1993; van der Made 2010; Pandolfi and Erten 2017); the Italian sites of Imola Basin (latest Villafranchian), Madonna della Strada (ca. 1.2 Ma), Pietrafitta (1.6 Ma; van der Made 2010; Pandolfi and Petronio 2011b; Pandolfi et al. 2015) and Pirro Nord (ca. 1.6–1.3 Ma; Pandolfi and Petronio 2011b); the French site of Bois-de-Riquet (1.3–1.1 Ma; Bourguignon et al. 2015).

This lack of agreement on the earliest occurrence of *S. hundsheimensis* is in line with the peculiarity found in several large mammal taxa of the second half of the late Villafranchian (Farneta and Pirro Nord FUs), with the appearance of representatives of typically Epivillafranchian/Galerian taxa with primitive morphology, whose identification is often not easy. Among them, the appearance of the earliest praemegacerine, *Praemegaceros obscurus* (Abbazzi 2004) and the earliest bisontine, *Bison* (*Eobison*) *degiulii* at 1.5 Ma (Sorbelli et al. 2023), suggests that precursors of the long-lived *S. hundsheimensis* might have been already present at 1.5 Ma as asserted by Mazza et al. (1993). However, the taxonomic attribution of the *Stephanorhinus* remains from the second half of the late Villafranchian is far beyond the scope of this paper; therefore, the specimens from Pietrafitta and Pirro Nord localities will be attributed here to *Stephanorhinus* sp.

Leaving aside the doubtful taxonomic position of the late Villafranchian record, *S. hundsheimensis* is then well attested in the Italian Peninsula and Western Europe through the Epivillafranchian and Galerian. This species occurred through a long-time span in the western Palearctic, as documented by the impressive record of Isernia La Pineta (Molise, southern Italy; Ballatore and Breda 2013) or the sample recovered from the type locality of Hundsheim (Niederösterreich, Austria; Toula 1902). In the palaeontological literature, the extinction of *S. hundsheimensis* was placed at ca. 600 ka, but a recent work by García-Fernández et al. (2023) suggests that it survived in western Europe until the early Late Pleistocene, based on the impressive record from Cova del Rinoceront (Spain) including two nearly complete skeletons and other isolated fossils. Pierucini et al. (2022) redefined the chronostratigraphic setting of Grotta Romanelli (Lecce, southern Italy), attributing the lower levels (ISU1 and ISU2, levels I and K *sensu* Blanc 1920, 1928) to the late Middle Pleistocene (ca. 350–200 ka). Remains of rhinoceroses from these levels were referred to *S. hundsheimensis* by Pandolfi et al. (2018). If the specific attribution will be confirmed, the new age assignment of the lower complex of Grotta Romanelli will reinforce the idea that this species survived in south-estern Europe up to the end of the Middle Pleistocene or the beginning of the Late Pleistocene.

The arrival of *Stephanorhinus kirchbergensis* in Europe occurred in the early Middle Pleistocene site of Mosbach-2 (Fortelius et al. 1993) and Ponte Molle (Di Stefano et al. 1998; Capasso Barbato et al. 1998; Billia and Petronio 2009; Mecozzi et al. 2021), which may confidently be ascribed to the mid-Middle Pleistocene (Isernia and Fontana Ranuccio FUs). This species remained in Europe up to the Eemian Interglacial (substage 5e, ca. 123 ka; Billia 2011) (Figure 1).

The species *Stephanorhinus hemitoechus* has been recorded in several European fossiliferous localities since ca. 0.5 Ma until the end of the last glaciation (e.g. Guérin 1980; Cerdeño 1990; Fortelius et al. 1993) (Figure 1).

The genus *Coelodonta* probably arrived in Europe only around 460–400 ka (MIS 13/12) in the form of *Coelodonta tologoijensis* in Bad Frankenhausen (Germany, Kahlke and Lacombat (2008) – but see also Guérin (2010) and Uzunidis et al. (2022) for the specific identification of early European *Coelodonta*). The species became extinct during the latest Pleistocene (Orlova et al. 2004; Stuart and Lister 2007; Kuzmin 2010; Uzunidis et al. 2022) (Figure 1).

According to Guérin (1980), both *S. hundsheimensis* (= *Dicerorhinus etruscus brachycephalus*) and *S. hemitoechus* evolved from *S. etruscus*, but other authors (Fortelius et al. 1993; Lacombat 2007) assume a derivation of *S. hundsheimensis* from the species *Stephanorhinus elatus* from the Late Pliocene and early Early Pleistocene of Europe (Lacombat 2007; Ros-Montoya et al. 2017).

Due to the significant intraspecific variability, there is an important morphological overlap among different species, and it is sometimes difficult to discriminate between different species of the genus *Stephanorhinus* (Radović et al. 2020). Several authors have proposed diagnostic characters for the specific identification of the Pleistocene rhinoceroses (Guérin 1980; Fortelius et al. 1993; Lacombat 2005, 2006; Ballatore and Breda 2018), which however show a strong morphological affinity to each other. This similarity often makes a specific attribution virtually impossible, also because of the recurrent scarcity of remains collected in the different sites (Ballatore and Breda 2013).

In recent years, several works investigated the specific variability of the postcranial elements of this group, as for example those from Neumark-Nord (Vogtland, Germany; van der Made 2010), from several Apulian localities (southern Italy; Petronio and Pandolfi 2008; Pandolfi and Petronio 2011a, 2011b; Pandolfi et al. 2018) and from Valle Radice (Latium, central Italy; Pandolfi and Tagliacozzo 2015).

Most of the literature on rhinoceroses is mainly focused on the description of craniodental remains and their taxonomic value for the specific identification. The knowledge on Pleistocene inter- and intraspecific variability is still limited, and more efforts are needed to investigate postcranial bone morphology and its possible taxonomic value although several authors already dealt with it (e.g. Guérin 1980; Fortelius et al. 1993; Lacombat 2005; van der Made (2010), Chitoglou et al. 2023).

The aim of this work is to study the rhinoceros postcranial remains from the Middle Pleistocene site of Contrada Monticelli (abbreviated CM, Apulia, southern Italy). Luperto Sinni and Colucci (1985) described the site and its infilling deposit for the first time, also reporting the presence of few cranial and postcranial remains attributed to *Rhinoceros merckii* (=*Stephanorhinus kirchbergensis*). Later, this sample was revised by Mazza and Varola (1999) that ascribed these specimens to *S. hundsheimensis* mainly based on cranial and madibular morphologies (Figure 2).

Here, the morphological and the biometric analyses of the complete postcranial sample of CM, consisting of 25 postcranial bones, are performed, including the material presented by Luperto Sinni and Colucci (1985) and Mazza and Varola (1999) and additional new material.

## Geological and palaeontological framework

The fossiliferous deposit of Contrada Monticelli is located about 5 km south-east of Putignano (Bari, southern Italy), near the crossroad between the 'Strada Statale 172 Putignano-Alberobello' and the 'Strada Comunale Monticelli' (Figure 3).

The CM deposit belongs to an area extensively studied from a geological point of view, within the Altamura Limestone Formation (Azzaroli 1968; Azzaroli et al. 1968), regionally Upper Turonian-Maastrichtian in age (Ciaranfi et al. 1988). The Altamura Limestone Formation together with the underlying Bari Limestone

Figure 2. Cranial and mandibular remains of *Stephanorhinus hundsheimensis* on display at the Museum of Earth Sciences of the University of Bari.

Formation (Valduga 1965), Early-early Late Cretaceous (dating back to the Valanginian – lower Turonian; Ciaranfi et al. 1988) form the group of Murge's limestones (Azzaroli and Cita 1963) and constitute a carbonate succession as part of the Apulian Carbonate Platform (*sensu* D'Argenio 1974) cropping out in the region extensively (Gargano, Murge and Salento areas; Ricchetti et al. 1988).

The CM site was discovered during the excavation work for the construction of a rural house during the 1970s. Thanks to the involvement of the Superintendency of Antiquities of Bari and the Institute of Geology and Paleontology of the Bari University, the deposit was excavated starting by the spring 1978, under the direction of Elena Luperto Sinni. The CM deposit was a karst cavity with an opening of about 4.5 × 5 m, locally known as 'grave' (sinkhole), formed into the Cretaceous formation filled by Quaternary sediments. The deposit included 11-m-thick reddish sands and some interbedded cinerite levels (Luperto Sinni and Colucci 1985). The fossil remains were found from about 3 m to 11 m below the ground surface but a precise stratigraphic scheme of the infilling deposits during the fossil rescue is missing. Nowadays, the site is buried below anthropogenic deposits, which hamper a precise dating or detailed stratigraphic and taphonomic analyses.

Contrada Monticelli yielded remains of bovids, equids, *Dama* cf. *roberti*, *Palaeoloxodon antiquus, Canis mosbachensis*, lagomorphs as well as rhinoceros material referred to *S. hundsheimensis* (Luperto Sinni and Colucci 1985; Mazza and Varola 1999; Mecozzi et al. 2017; Stefanelli et al. 2019, 2021). This Galerian faunal assemblage has been attributed to the Isernia Faunal Unit (early Middle Pleistocene) (Mazza and Varola 1999; Mecozzi et al. 2017; Stefanelli et al. 2021). The age-assignment of CM makes the site particularly relevant within the early Middle Pleistocene European framework and the debate on the 'Faunal revolution' which took place during the Early-Middle Pleistocene Transition (EMPT) a fundamental transition in the Earth's climate during the ~1.4–0.4 Ma interval (Ruddiman et al. 1986).

## Materials and methods

The postcranial sample of *Stephanorhinus hundsheimensis* from CM is represented by 25 specimens (Table 1). The material is currently stored at the Museum of Earth Sciences of the University of Bari. The specimens are labelled with progressive numbers preceded by the acronym MSTB – CM - (Museo di Scienze della Terra Bari – Contrada Monticelli).

The fossil sample is in a poor state of preservation, with specimens often incomplete and bones generally fractured and encrusted by a reddish patina. As documented by Luperto Sinni and Colucci

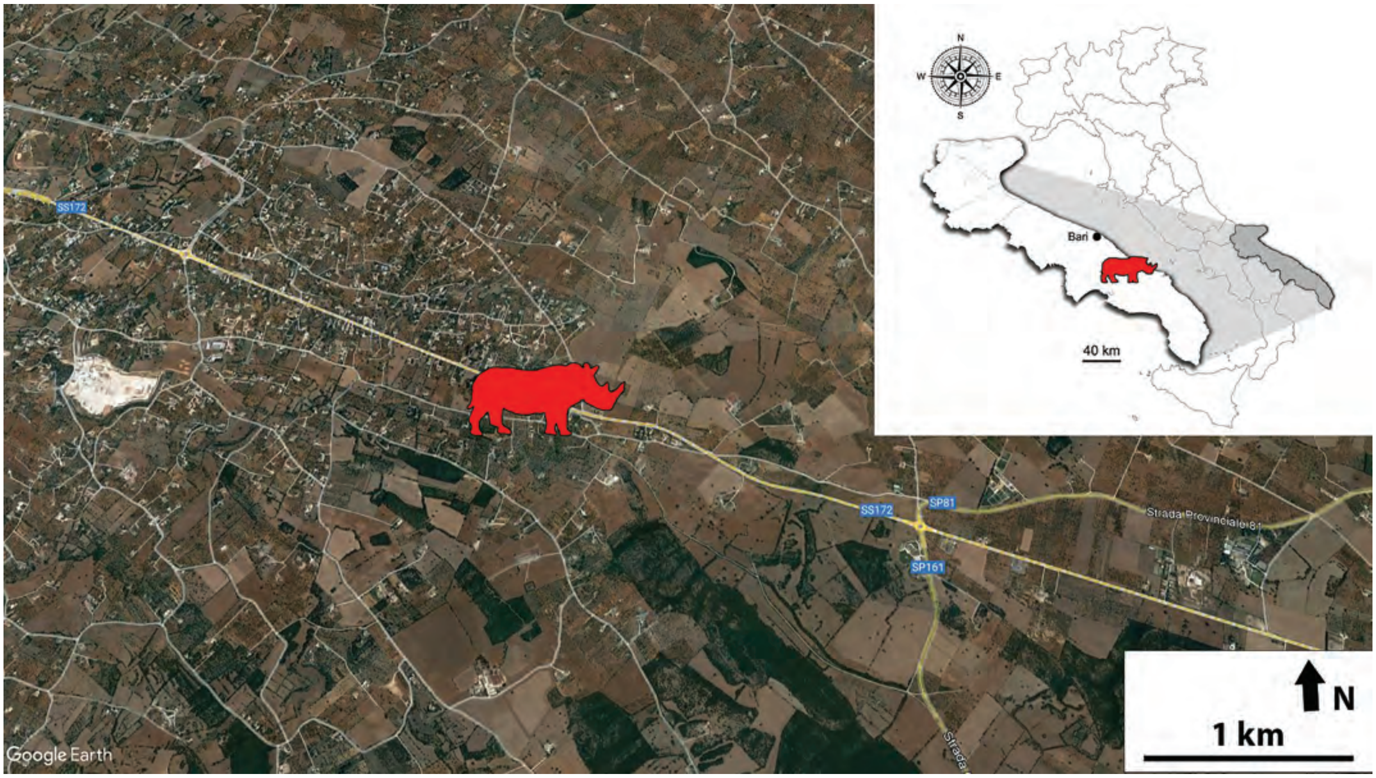

Figure 3. Geographic location of the Contrada Monticelli fossiliferous site (Apulia, southern Italy).

**Table 1.** List of postcranial remains of *Stephanorhinus hundsheimensis* from Contrada Monticelli considered in this work and in previous studies.

| Postcranial elements | Luperto Sinni and Colucci (1985) | Mazza and Varola (1999) | This work |
|---|---|---|---|
| Atlas | | 1 | 1 |
| Vertebrae | 2 | | 2 |
| Scapula | | | 4 |
| Humerus | 2 | 3 | 3 |
| Ulna | 1 | 1 | 1 |
| Second metacarpal | | | 1 |
| Third metacarpal | | | 1 |
| Fourth metacarpal | | | 1 |
| Coxal bone | 2 | 2 | 2 |
| Femur | 1 | 2 | 5 |
| Tibia | 1 | 1 | 3 |
| Third metatarsal | | | 1 |
| Total | 9 | 10 | 25 |

(1985), various fossils show abraded surfaces, suggesting a quite prolonged transport before their final deposition. Therefore, due to the incompleteness and poor preservation, a few measurements were possible in some cases and the observation of some morphological features was hindered.

The nomenclatural terms used in the morphological descriptions are taken from Barone (1980), Guérin (1980) and Lacombat (2005) and are illustrated in the anatomical tables in Supplementary Data (SD 1-SD Figures 1-16). The in-depth morphological descriptions of the studied sample are reported in Supplementary Data (SD 2) and additional figures have been added in SD 3.

The biometric measurements of the CM sample have been taken to the nearest 0.1 mm with a digital calliper following Mazza (1988), Lacombat (2005) and van der Made (2010). They are provided in Supplementary Data (SD 4-SD Tables 1-9), with the legend of abbreviations for each measurement used in the text.

The studied material has been morphologically compared with data from the literature on different rhinoceros specimens from European localities covering a time span from the late Early to the Late Pleistocene (Guérin 1980; Fortelius et al. 1993; Lacombat 2005; Pandolfi and Tagliacozzo 2015; Pandolfi et al. 2018; Uzunidis and Brugal 2018). This comparison has been attempted using the morphological descriptions by previous authors using the terms introduced by them.

Some rhinoceros postcranial bones from other localities were also directly analysed in this work: *Coelodonta antiquitatis* from Cardamone, kept at the State Institute of Higher Education 'Galilei-Costa-Scarambone' (Lecce, southern Italy), and Ingarano, preserved at PaleoFactory Laboratory, Department of Earth Science, Sapienza University of Rome; *Stephanorhinus hemitoechus* from Melpignano, preserved at PaleoFactory Laboratory, Department of Earth Science, Sapienza University of Rome and at Museum of Paleontology, University of Naples Federico II, Ingarano and Cretone, kept at PaleoFactory Laboratory, Department of Earth Science, Sapienza University of Rome; *Stephanorhinus* cf. *hundsheimensis* from Casal Selce, stored at PaleoFactory Laboratory, Department of Earth Science, Sapienza University of Rome; *Stephanorhinus hundsheimensis* from Vitinia, stored at University Museum of Earth Science, Sapienza University of Rome.

The most important measurements have been plotted in scatter diagrams (see SD 5) made with PAST v. 4.13 (Hammer et al. 2001).

As a comparison, metric data of adult or sub-adult individuals of *Stephanorhinus* and *Coelodonta* from the literature have been also included (see SD 6 and SD 7). Due to the scarcity of comparative information in the literature, morphological and biometric comparisons of the vertebrae and coxal bones have not been carried out.

## Systematic palaeontology

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Gray, 1821
Subfamily RHINOCEROTINAE Gray, 1821
Tribe RHINOCEROTINI Gray, 1821
Genus STEPHANORHINUS Kretzoi, 1942a
Species *Stephanorhinus hundsheimensis* (Toula 1902)

### *Morphological and morphometric comparison*

The diagnostic characters of the Pleistocene rhinoceroses, and their comparison with the CM specimens, are listed in Tables 2–10.

*Scapula* - MSTB – CM 30616, MSTB – CM 30617, MSTB – CM 30618, MSTB – CM 30809 (Figure 4A–F)

Two scapulae from CM (MSTB – CM 30616 and MSTB – CM 30618) show a well-developed supraglenoid tubercle and a little-developed coracoid process. The surface that separates the supraglenoid tubercle from the glenoid cavity is present, except for MSTB – CM 30809. These characters are generally observed in *S. etruscus* and *S. hundsheimensis* (chs. 1, 2 and 3, Table 2). Overall, *S. etruscus* and *S. hundsheimensis* share all the features considered for this bone (chs. 1, 2 and 3, Table 2) except for possible slight differences in the development of the coracoid process.

The ratio between the transverse articular diameter and the antero-posterior articular diameter is plotted in SD 5-SD Figure 21. MSTB – CM 30616 is very close to the variation range of the Middle Pleistocene *S. hundsheimensis*, whereas MSTB – CM 30809 is more isolated, with a large antero-posterior diameter. *Stephanorhinus etruscus* is the species with the lowest values, except for the *Stephanorhinus* sp. from Pirro Nord, which is even smaller. *Stephanorhinus hemitoechus* partially superposes to the Middle Pleistocene *S. hundsheimensis* but reaches slightly higher values concerning the transverse articular diameter. *Stephanorhinus kirchbergensis* and *Coelodonta antiquitatis* show a larger size.

*Humerus* - MSTB – CM 30602, MSTB – CM 30603, MSTB – CM 30604. (Figure 5A–I)

In the three humeri from CM, the articular head has a rounded outline (ch. 1 – Table 3). The distal trochlea is wide and oblique (MSTB – CM 30602 and MSTB – CM 30604; Figure 5A–I) or wide and slightly oblique (MSTB – CM 30603; Figure 5E) (ch. 4 – Table 3). The trochlear groove is very large and little deep or very large and moderately deep (ch. 3 – Table 3). The coronoid fossa is generally little deep (ch. 5 – Table 3) and the shape of the olecranon fossa is elliptical (ch. 7 – Table 3). The epicondylar ridge is generally well developed (ch. 6 – Table 3).

The CM specimens resemble *S. hundsheimensis* in many characters (Table 3). However, MSTB – CM 30603 shows some slight differences in the distal epiphysis when compared to the other two studied specimens (MSTB – CM 30602 and MSTB – CM 30604): its lateral epicondyle is more laterally developed and its medial epicondyle is more posteriorly pointed. However, these features are not described in literature for the other considered species. MSTB – CM 30604 has a less pronounced obliquity of the distal trochlea (ch. 4 – Table 3).

The comparison between the maximum length of the bone and the minimum transverse diameter of the diaphysis (SD 5-SD Figure 22) reveals that the CM fossils are larger than plotted *S. etruscus* and *S. hundsheimensis*. The five species have distinct ranges of variability:

*S. etruscus* shows a reduced range of maximum length values, but some variability in thickness; the Middle Pleistocene *S. hundsheimensis* appears very similar in size to *S. etruscus*, while the Early Pleistocene *Stephanorhinus* sp. is shorter; *S. hemitoechus* occupies an intermediate position between these small specimens and the large fossils of CM and *C. antiquitatis*.

In the comparison between the maximum transverse diameter of the distal epiphysis and maximum antero-posterior diameter of the distal epiphysis (SD 5-SD Figure 23), the CM sample has an antero-posterior diameter consistent with *S. hemitoechus* and *C. antiquitatis*. *Stephanorhinus etruscus* and *S. hundsheimensis* are consistent with each other in the antero-posterior diameter with the Middle Pleistocene *S. hundsheimensis* on higher transverse diameters. The specimens of *C. antiquitatis* are generally larger. Again, *S. hemitoechus* shows intermediate values among the five species.

*Ulna* - MSTB – CM 30614 (SD 2-SD Figure 19a-b)

The ulna from CM (MSTB – CM 30614) shows a strong morphological affinity to *S. hundsheimensis* and *S. hemitoechus*, with the exception of the development of the anconeus process (ch. 2 – Table 4), which is prominent as in *S. etruscus*. It differs from *S. etruscus* in the greater breadth of the olecranon and width of the articular surface to the humerus (chs. 1 and 3 - Table 4).

The ratio between maximum length of the bone and transverse diameter of the diaphysis is plotted in SD 5-SD Figure 24. MSTB – CM 30614 has one of the largest transverse diameters. Its maximum length, however, is within the value range of the *S. hundsheimensis* population from Untermassfeld (not shown in graph, see SD. 7). The minimum length values belong to *S. etruscus*. The *S. hemitoechus* specimen has a higher thickness value than the two previous species.

*Second metacarpal* - MSTB – CM 30702 (Figure 6A–C)

In the second metacarpal from CM, the posterior tuberosity (ch. 1 – Table 5) is well developed and the articular surface to the trapezium (ch. 21 – Table 5) is trapezoidal in shape. The articular surfaces to the magnum and third metacarpal (ch. 3 – Table 5) appear fused together. The concavity of the distal edge of the lateral articulation (ch. 4 – Table 5) is moderately developed and the section of the diaphysis is trapezoidal in shape (ch. 5 – Table 5). The CM specimen shares all these characters with *S. hundsheimensis* and the latter two also with *S. etruscus* (Table 5).

The ratio between maximum length and minimum transverse diameter of the diaphysis is considered in SD 5-SD Figure 25. The size of MSTB – CM 30702 falls within the variation range of *C. antiquitatis*, the Middle Pleistocene *S. hundsheimensis* and *S. etruscus*. *Stephanorhinus hemitoechus* shows a reduced length for this bone, although its range of variation is quite large. The remains of *S. kirchbergensis* are among the longest specimens. The records of *C. antiquitatis* display both the smallest and the largest transverse diameter of the diaphysis, but in general, it is the species that shows the greatest thickness.

*Third metacarpal* - MSTB – CM 30698 (Figure 6D–F)

The third metacarpal possesses a trapezoidal articular surface to the magnum and a sub-trapezoidal articular surface to the uncinated (ch. 1 – Table 6). The anterior margin of the proximal epiphysis is straight and the anterior articular surface to the fourth metacarpal is elliptical in shape (chs. 2 and 3 – Table 6). The salience that separates the articular surface to the magnum from that to the uncinated is marked (ch. 5 - Table 6). Some of these features are shared with *S. hundsheimensis* as the shape of the articular surface to the magnum, the anterior articular surface to the mc IV and how marked is the salience separating the articular surfaces to magnum and to uncinate (chs. 1, 3 and 5 – Table 6).

The ratio between maximum length and minimum transverse diameter of the diaphysis is plotted in SD 5-SD Figure 26. MSTB – CM 30698 has a high value of the minimum transversal diameter of the diaphysis. For this bone, the ranges of variation between species overlap significantly, with Early Pleistocene *Stepahanorhinus* sp. and Middle Pleistocene *S. hundsheimensis* overlapping among each other and with *S. etruscus*. *Stephanorhinus hemitoechus* equals them in length but has a larger diaphysis. *Coelodonta antiquitatis* has rather compact measures, but high thickness. *Stephanorhinus kirchbergensis* is the species with the largest values.

*Fourth metacarpal* - MSTB – CM 30703 (Figure 6G–I)

The fourth metacarpal shows a concave anterior border of the proximal epiphysis. This feature resembles the condition of *S. hundsheimensis* (ch. 1 – Table 7). The morphology of this bone differs from each other at the level of the anterior border of the proximal epiphysis, the posterior articular surface to the third metacarpal and the shape of the section of the diaphysis (chs. 1, 3, and 4 – Table 7).

*Femur* - MSTB – CM 30605, MSTB – CM 30606 (Figure 7A–D), MSTB – CM 30607, MSTB – CM 30615, MSTB – CM 30802

The femora from CM display a spherical head of the femur with a distinct ligamentous dimple impressed and a third trochanter trapezoidal in shape in cranial views (chs. 1 and 2 – Table 8). In the distal epiphysis, the trochlea is strongly asymmetrical with a trochlear groove wide and deep (chs. 3 and 4 – Table 8). Furthermore, the medial lip is clearly larger than the lateral one (ch. 6 - Table 8). The intercondylar fossa is deep and slightly wide while the supracondylar fossa is marked (chs. 7 and 8 – Table 8).

These characters are shared partly with *S. etruscus* (chs. 3, 4, 5, and 7 – Table 8) and partly with *S. hundsheimensis* (chs. 2, 6, and 8 - Table 8). The head morphology (ch. 1 – Table 8) and the width of the medial condyle are shared with both.

The comparison between the maximum length of the bone and the minimum transverse diameter of the diaphysis (SD 5-SD Figure 27) reveals that MSTB – CM 30606 has the smallest dimensions, comparable only to the smallest specimen of the plotted *S. etruscus*. In general, the latter species shows the smallest dimension, even if two specimens reach the variation range of *Stephanorhinus* sp. from Pietrafitta and *S. hemitoechus*. The size of plotted Middle Pleistocene *S. hundsheimensis* is slightly distinct from that of *S. etruscus* and partially overlap with *S. hemitoechus*. The single *C. antiquitatis* plotted specimen has a transverse diameter of the diaphysis significantly larger than all the other species.

The comparison between the maximum antero-posterior and transverse diameters of the distal epiphysis (SD 5-SD Figure 28) shows for MSTB – CM 30606 values close to *S. etruscus*, the species with the lowest values. The only plotted specimen of Early Pleistocene *S. hundsheimensis* falls within the range of *S. etruscus*, whereas the Middle Pleistocene *S. hundsheimensis*. is larger but not far from *S. etruscus*. The *S. hemitoechus* range stands at significantly higher values than the two previous species. The single *S. kirchbergensis* plotted specimen shows the highest antero-posterior length value and one of the highest transverse diameter values, the latter surpassed only by *C. antiquitatis*.

*Tibia* - MSTB – CM 30608, MSTB CM 30609, MSTB CM 30610 (Figure 8A–F)

The tibia displays a thick tuberosity and a strong mid-lateral development of the distal epiphysis (chs. 1 and 4 – Table 9). The lateral intercondylar tubercle is displaced posteriorly and it is higher than the medial one (chs. 2 and 3 – Table 9). In the distal epiphysis, the medial articular surface is elliptical in shape and the lateral one is sub-trapezoidal (chs. 5 and 6 – Table 9). The fibular notch is shallow (ch. 7 – Table 9).

The studied remains show some distinctive traits when compared to the five considered species (Table 9) in the shape of the medial and lateral articular surfaces (chs. 5 and 6 – Table 9).

The ratio between the maximum length of the bone and the transverse diameter of the diaphysis is plotted (SD 5-SD Figure 29). CM tibias are within or very close to the variability of *C. antiquitatis*, the species that possesses the highest thickness values. *Stephanorhinus etruscus* and almost all *S. hundsheimensis* specimens show a slender tibia but comparable length. The only Early Pleistocene *S. hundsheimensis* is rather short in length. *Stephanorhinus hemitoechus* value falls in the bottom-left side of the graphs.

*Third metatarsal* - MSTB – CM 30699 (Figure 9A–C)

The specimen possesses a convex anterior border of the proximal epiphysis, the anterior articular surfaces to the fourth metatarsal is triangular and the posterior one is elliptical (chs. 1, 2, and 3 – Table 10). The third metatarsal of *S. hundsheimensis* exhibits important morphological variability. This applies to the profile of the cranial border and the shape of the articular surfaces to the second and fourth metatarsal (chs. 1, 2, 3, 4, 5, and 6 - Table 10). The CM specimen (MSTB – CM 30699) shows affinity with both *S. etruscus* and *S. hundsheimensis* in all the characters that was possible to score (chs. 1, 2, and 3 – Table 10).

## Discussion

### *Morphological variability of quaternary European rhinoceroses*

The taxonomic attribution of the Quaternary European rhinoceroses is mainly based on cranial and mandibular remains, which mostly allow the identification of five taxa: *S. etruscus, S. hundsheimensis, S. hemitoechus, S. kirchbergensis* and *C. antiquitatis*. At CM, Mazza and Varola (1999) recorded *S. hundsheimensis* mainly based on the presence of one fragmentary cranium, two fragmented mandibles and two fragmented hemimandibles (Figure 2). The morphological characters of postcranial bones from CM and their comparison with those described in the literature allow the following considerations.

Some diagnostic morphological characters in the rhinoceros's scapula are observable on the articular surface for the humerus (Table 2), which can have a sub-elliptical (MSTB – CM 30616) or elliptical (MSTB – CM 30618) outline. The scapula of *S. hemitoechus* is well distinguished by the lack of the surface separating the supraglenoid tubercle from the glenoid cavity (Lacombat 2005). Only MSTB – CM 30809 although is very badly preserved, seems to have the latter character (Figure 4c).

The CM sample includes three humeri, which have characteristics very similar to those of *S. hundsheimensis* (Table 3). However, especially at the level of the distal epiphysis, the three specimens show some significant differences between them (see SD 2).

For the ulna, the only variable character is the development of the anconeus process, which appears different in *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus* (Table 4).

In the metapodials, almost all the diagnostic characters are in the proximal epiphysis, in particular the shape of the articular surfaces to the carpal/tarsal bones and to adjacent metapodials.

In the second metacarpal, a few characters have been adequately described in the literature, as the lateral articular surfaces (to the magnum and the third metacarpal) (Table 5). *Stephanorhinus etruscus* and *S. hundsheimensis* are similar but distinguished by the development of the posterior tuberosity and the shape of the articular surface to the trapezium (Table 5).

The third metacarpal (Table 6) shows an interspecific variability in the shape of the posterior articular surface to the fourth metacarpal and in the anterior margin of the proximal epiphysis (Table 6). Our comparative analysis for third metacarpal confirms

**Table 2.** Comparison among the main diagnostic characters of the scapula between Contrada Monticelli and Pleistocene European rhinoceros species. N.A. = not available. The descriptive-diagnostic characters are shown in SD Figure 1.

| | Scapula | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| N° | Descriptive-diagnostic character | *S. etruscus* | *S. hundsheimensis* | *S. hemitoechus* | *S. kirchbergensis* | *C. antiquitatis* | Contrada Monticelli *(MSTB – CM 30616 and MSTB – CM 30,618)* | Contrada Monticelli *(MSTB – CM 30809)* |
| 1 | Surface that separates the supraglenoid tubercle from the glenoid cavity | *Present* (Lacombat 2005) | *Present* (Lacombat 2005) | *Absent* (Lacombat 2005) | *Present* (Pandolfi and Tagliacozzo 2015) | *Present* (Guérin 1980) | Present | Absent |
| 2 | Development of the coracoid process | *Little developed* (Lacombat 2005) | *Little developed* (Pandolfi et al. 2018)<br>*Very little developed* (Lacombat 2005) | *N.a.* (Lacombat 2005; Pandolfi and Tagliacozzo 2015) | *Well developed* (Lacombat 2005) | *Little developed* (Pandolfi and Tagliacozzo 2015)<br>*Very little developed* (Guérin 1980) | Little developed | N.a. |
| 3 | Shape of the glenoid cavity | *Elliptical* (Lacombat 2005) | *Elliptical* (Pandolfi et al. 2018) | *Elliptical* (Pandolfi and Tagliacozzo 2015) | *Sub-rectangular* (Guérin 1980; Lacombat 2005; Pandolfi and Tagliacozzo 2015) | *Sub-rectangular* (Guérin 1980; Pandolfi and Tagliacozzo 2015)<br>*Elliptical* (Guérin 1980) | Elliptical | Elliptical |

**Table 3.** Comparison between the main diagnostic characters of the humerus between Contrada Monticelli and Pleistocene European rhinoceros species. The descriptive-diagnostic characters are shown in SD Figures 2 and 3.

| | | Humerus | | | | | | |
|---|---|---|---|---|---|---|---|---|
| N° | Descriptive-diagnostic character | *S. etruscus* | *S. hundsheimensis* | *S. hemitoechus* | *S. kirchbergensis* | *C. antiquitatis* | Contrada Monticelli *(MSTB – CM 30602 and MSTB – CM 30604)* | Contrada Monticelli *(MSTB – CM 30603)* |
| 1 | Articular head shape | *Sub-rectangular outline* (Guérin 1980) | *Sub-rectangular* (Guérin 1980) *Rounded outline* (Lacombat 2005) | *Rounded outline* (Guérin 1980; Pandolfi and Tagliacozzo 2015) | *Rounded outline* (Guérin 1980) | Very rounded outline (Guérin 1980) | Rounded outline | Rounded outline |
| 2 | Development of the greater tubercle | *Moderately developed* (Guérin 1980) | *Moderately developed* (Guérin 1980) | *Little developed* (Guérin 1980) | *Well developed* (Guérin 1980) | *Well developed* (Guérin 1980) | _ | _ |
| 3 | Trochlea width | *Wide* (Guérin 1980) | *Wide* (Guérin 1980) *Narrow* (Lacombat 2005) | *Wide* (Guérin 1980) | *Very wide* (Guérin 1980) | *Very wide* (Guérin 1980) | Wide | Wide |
| 4 | Trochlea tilt | *Slightly oblique* (Guérin 1980) | *Oblique* (Lacombat 2005) *Slightly oblique* (Guérin 1980) | *Straight* (Lacombat 2005) *Oblique* (Guérin 1980; Lacombat 2005) | *Slightly oblique* (Guérin 1980) | *Oblique* (Guérin 1980) | Oblique | Slightly oblique |
| 5 | Coronoid fossa | *Deep* (Lacombat 2005) | *Little deep* (Lacombat 2005) | *Little deep* (Lacombat 2005) | _ | _ | Little deep | Little deep |
| 6 | Development of the epicondylar ridge | *Developed* (Guérin 1980) | *Well developed* (Guérin 1980) *Developed* (Lacombat 2005) | *Little developed* (Lacombat 2005) | *Well developed* (Guérin 1980) | *Very well developed* (Guérin 1980) | Well developed | Well developed |
| 7 | Shape of the olecranon fossa | *Triangular* (Lacombat 2005) | *Elliptical* (Lacombat 2005) | *Elliptical* (Lacombat 2005) | _ | _ | Elliptical | Elliptical |

**Table 4.** Comparison between the main diagnostic characters of the ulna between Contrada Monticelli and Pleistocene European rhinoceros species. The descriptive-diagnostic characters are shown in SD Figure 4.

| | | Ulna | | | | | |
|---|---|---|---|---|---|---|---|
| N° | Descriptive-diagnostic character | *S. etruscus* | *S. hundsheimensis* | *S. hemitoechus* | *S. kirchbergensis* | *C. antiquitatis* | Contrada Monticelli *(MSTB – CM 30614)* |
| 1 | Breadth of the olecranon | *Regular* (Fortelius et al. 1993) | *Wide* (Lacombat 2005) | *Wide* (Lacombat 2005) | *Wide* (Guérin 1980) | _ | Wide |
| 2 | Anconeus process | *Prominent* (Lacombat 2005) | *Moderately prominent* (Lacombat 2005) | *Very prominent* (Lacombat 2005) | _ | _ | Prominent |
| 3 | Articular surface to the humerus | *Wide* (Lacombat 2005) | *Very wide* (Lacombat 2005) | *Very wide* (Lacombat 2005) | *Wide* (Guérin 1980) | *Very wide* (Guérin 1980) | Very wide |

**Table 5.** Comparison between the main diagnostic characters of the second metacarpal between Contrada Monticelli and Pleistocene European rhinoceros species. The descriptive-diagnostic characters are shown in SD Figures 5 and 7.

| | | Second Metacarpal | | | | | |
|---|---|---|---|---|---|---|---|
| N° | Descriptive-diagnostic character | *S. etruscus* | *S. hundsheimensis* | *S. hemitoechus* | *S. kirchbergensis* | *C. antiquitatis* | Contrada Monicelli *(MSTB – CM 30702)* |
| 1 | Posterior tuberosity | *Developed* (Lacombat 2005) | *Well developed* (Guérin 1980; Lacombat 2005; Pandolfi and Tagliacozzo 2015) | *Little developed* (Guérin 1980; Lacombat 2005; Pandolfi and Tagliacozzo 2015) | *Well developed* (Guérin 1980; Pandolfi and Tagliacozzo 2015; Pandolfi et al. 2018; Uzunidis and Brugal 2018) | *Little developed* (Guérin 1980; Uzunidis and Brugal 2018) | _ |
| 2 | Shape of the articular surface to the trapezius | *Triangular* (Lacombat 2005) | *Trapezoidal* (Pandolfi et al. 2018) | *Trapezoidal* (Lacombat 2005) | *Absent* (Uzunidis and Brugal 2018) | *Sub-trapezoidal* (Guérin 1980) | Trapezoidal |
| 3 | Shape of the proximal border to the articular surface with the magnum | *Convex* (Pandolfi et al. 2018) | _ | *Convex* (Pandolfi and Tagliacozzo 2015) | *Straight* (Pandolfi and Tagliacozzo 2015; Pandolfi et al. 2018) | _ | Little convex |
| 4 | Concavity of the distal edge of the lateral articulation | *Moderately developed* (Lacombat 2005) | *Moderately developed* (Lacombat 2005) | *Slightly developed* (Lacombat 2005) | *Strongly or moderately developed* (Guérin 1980) | *Strongly develpoed* (Guérin 1980) | Moderately developed |
| 5 | Section of the diaphysis | *Trapezoidal* (Guérin 1980) | *Trapezoidal* (Guérin 1980; Lacombat 2005) | *Trapezoidal* (Guérin 1980) | *Triangular or elliptical* (Guérin 1980) | *Elliptical* (Guérin 1980) | Trapezoidal |

**Table 6.** Comparison between the main diagnostic characters of the third metacarpal between Contrada Monticelli and Pleistocene European rhinoceros species. The descriptive-diagnostic characters are shown in SD Figures 8 and 9.

| | | Third metacarpal | | | | | |
|---|---|---|---|---|---|---|---|
| N° | Descriptive-diagnostic character | *S. etruscus* | *S. hundsheimensis* | *S. hemitoechus* | *S. kirchbergensis* | *C. antiquitatis* | Contrada Monticelli (*MSTB – CM 30698*) |
| 1 | Articular surface to the magnum | *Sub-triangular* (Lacombat 2005) | *Sub-trapezoidal or trapezoidal* (Lacombat 2005; Pandolfi et al. 2018) | *Sub-triangular* (Pandolfi and Tagliacozzo 2015) | *Sub-trapezoidal* (Guérin 1980) | _ | Trapezoidal |
| 2 | Anterior margin proximal epiphysis | *Convex* (Lacombat 2005) | *Convex* (Lacombat 2005) *Slighty convex* (Guérin 1980) | *Slightly concave* (Guérin 1980; Lacombat 2005; Pandolfi and Tagliacozzo 2015; Pandolfi et al. 2018) | *Slightly concave* (Guérin 1980) | *Convex* (Guérin 1980) | Straight |
| 3 | Anterior articular surface to the Mc IV | *Sub-elliptical* (Lacombat 2005) | *Trapezoidal* (Lacombat 2005) *Elliptical* (Pandolfi et al. 2018) | *Sub-elliptical* (Pandolfi and Tagliacozzo 2015) | *Sub-elliptical* (Guérin 1980; Pandolfi and Tagliacozzo 2015) | *Pentagonal* (Guérin 1980) | Elliptical |
| 4 | Posterior articular surface to the Mc IV | *Sub-elliptical* (Lacombat 2005) | *Sub-circular* (Lacombat 2005; Pandolfi et al. 2018) *Triangular* (Pandolfi et al. 2018) | *Elliptical* (Guérin 1980; Lacombat 2005; Pandolfi and Tagliacozzo 2015) *Triangular* (Guérin 1980) | *Trapezoidal* (Guérin 1980) *Elliptical* (Guérin 1980) *Sub-triangular* (Pandolfi and Tagliacozzo 2015) | *Elliptical* (Guérin 1980) | _ |
| 5 | Salience separating the articular surfaces to magnum and to uncinate | _ | *Slightly marked or marked* (Pandolfi and Tagliacozzo 2015; Pandolfi et al. 2018) | *Marked* (Pandolfi and Tagliacozzo 2015) | *Slightly marked* (Pandolfi et al. 2018) | _ | Marked |
| 6 | Section of the diaphysis | *Elliptical* (Guérin 1980) | *Elliptical* (Guérin 1980; Lacombat 2005) | *Sub-elliptical* (Guérin 1980) | *Sub-elliptical* (Guérin 1980) | *Elliptical* (Guérin 1980) | _ |

**Table 7.** Comparison between the main diagnostic characters of the fourth metacarpal between Contrada Monticelli and Pleistocene European rhinoceros species. The descriptive-diagnostic characters are shown in SD Figures 10 and 12.

| | | Fourth metacarpal | | | | | |
|---|---|---|---|---|---|---|---|
| N° | Descriptive-diagnostic character | *S. etruscus* | *S. hundsheimensis* | *S. hemitoechus* | *S. kirchbergensis* | *C. antiquitatis* | Contrada Monticelli (*MSTB – CM 30703*) |
| 1 | Anterior border of the proximal epiphysis | *Highly concave* (Lacombat 2005) | *Concave* (Lacombat 2005) | *Slighty concave* (Lacombat 2005) | _ | _ | Concave |
| 2 | Anterior articular surface to the Mc III | *Sub-elliptical* (Lacombat 2005) | *Sub-elliptical* (Lacombat 2005) | _ | *Elliptical* (Lacombat 2005; Pandolfi et al. 2018) | *Elliptical* (Lacombat 2005; Pandolfi et al. 2018) | _ |
| 3 | Posterior articular surface to the Mc III | *Sub-elliptical* (Lacombat 2005) | *Elliptical* (Guérin 1980) *Sub-elliptical* (Lacombat 2005) *Circular* (Pandolfi et al. 2018) | *Rectangular* (Lacombat 2005) *Elliptical* (Lacombat 2005; Pandolfi et al. 2018) | _ | *Sub-circular* (Lacombat 2005; Pandolfi et al. 2018) | _ |
| 4 | Section of the diaphysis | *Trapezoidal* (Lacombat 2005) | *Trapezoidal* (Lacombat 2005) | *Triangular or trapezoidal* (Guérin 1980) | *Trapezoidal* (Guérin 1980) | *Elliptical or triangular* (Guérin 1980) | _ |

that this bone plays an important role in the diagnosis of Pleistocene rhinoceroses even if the presence of a certain degree of intraspecific variability must be considered.

The fourth metacarpal displays a minor number of characters diagnostic for the different species with respect to the other metacarpals (Table 7).

The femur has some diagnostic morphological characters, which are found mainly in the distal epiphysis (Table 8). The femora of *S. etruscus* and *S. hundsheimensis* show differences in the third trochanter and the distal end of the bone.

Some diagnostic features make the tibia relevant for rhinoceros taxonomic purpose (Table 9). Also in this case, *S. hundsheimensis* and *S. etruscus* share several morphological features (5 out of 7 characters considered). The three specimens from CM (MSTB – CM 30608, MSTB – CM 30609, MSTB – CM 30610) are morphologically similar to each other and slightly differ from the described tibiae of both *S. etruscus* and *S. hundsheimensis*. For example, the displacement of the intercondylar tubercles differs from the typical condition observed in both *S. hundsheimensis* and *S. etruscus*. In addition, the

**Table 8.** Comparison between the main diagnostic characters of the femur between Contrada Monticelli and Pleistocene European rhinoceros species. The descriptive-diagnostic characters are shown in SD Figures 13 and 14.

| | | Femur | | | | | |
|---|---|---|---|---|---|---|---|
| N° | Descriptive-diagnostic character | *S. etruscus* | *S. hundsheimensis* | *S. hemitoechus* | *S. kirchbergensis* | *C. antiquitatis* | Contrada Monticelli *(MSTB – CM 30606)* |
| 1 | Head of the femur | *With a distinct ligamentous dimple* (Guérin 1980; Lacombat 2005) | *With a distinct ligamentous dimple* (Guérin 1980; Lacombat 2005) | *With a slight ligamentous dimple* (Lacombat 2005) | *With a marked ligamentous dimple* (Lacombat 2005) | *With a distinct ligamentous dimple* (Guérin 1980) | With a distinct ligamentous dimple |
| 2 | Third trochanter | *Rectangular* (Lacombat 2005) | *Trapezoidal* (Lacombat 2005) | *Rectangular* (Lacombat 2005) | _ | _ | Trapezoidal |
| 3 | Troclea | *Strongly asymmetrical* (Guérin 1980; Lacombat 2005) | *Asymmetrical* (Guérin 1980; Lacombat 2005) | *Asymmetrical* (Lacombat 2005) | *Asymmetrical* (Guérin 1980) | _ | Strongly asymmetrical |
| 4 | Trochlear throat width | *Wide* (Lacombat 2005) | *Very wide* (Lacombat 2005) | *Wide* (Lacombat 2005; Pandolfi and Tagliacozzo 2015) | _ | _ | Wide and deep |
| 5 | Trochlear throat depth | *Deep* (Lacombat 2005) | *Shallow* (Lacombat 2005) | *Shallow* (Lacombat 2005) | _ | _ | Deep |
| 6 | Medial lip | *Larger than the other lip* (Guérin 1980; Lacombat 2005) | *Clearly larger than the other lip* (Guérin 1980) | *Clearly larger than the other lip* (Lacombat 2005) | *Clearly larger than the other lip* (Guérin 1980) | *Slightly larger than the other lip* (Guérin 1980) | Clearly larger than the other lip |
| 7 | Intercondylar fossa width | *Slightly wide* (Lacombat 2005) | *Wide* (Lacombat 2005) | *Wide* (Lacombat 2005; Pandolfi and Tagliacozzo 2015) | _ | _ | Slightly wide |
| 8 | Supracondylar fossa | *Little marked* (Lacombat 2005) | *Marked* (Lacombat 2005) | *Little marked* (Lacombat 2005) | _ | _ | Marked |

**Table 9.** Comparison between the main diagnostic characters of the tibia between Contrada Monticelli and Pleistocene European rhinoceros species. The descriptive-diagnostic characters are shown in SD Figure 15.

| | | Tibia | | | | | |
|---|---|---|---|---|---|---|---|
| N° | Descriptive-diagnostic character | *S. etruscus* | *S. hundsheimensis* | *S. hemitoechus* | *S. kirchbergensis* | *C. antiquitatis* | Contrada Monticelli *(MSTB – CM 30608, MSTB – CM 30609, MSTB – CM 30610)* |
| 1 | Tibial tuberosity | *Thick* (Lacombat 2005) | *Thick* (Lacombat 2005) | *Very thick* (Guérin 1980; Pandolfi and Tagliacozzo 2015) | *Very thick* (Guérin 1980) | *Very thick* (Guérin 1980) | Thick |
| 2 | Displace of intercondylar tubercles | *The medial tubercle is displaced posteriorly* (Lacombat 2005) | *The medial tubercle is displaced posteriorly* (Lacombat 2005) | *The lateral tubercle is displaced posteriorly* (Guérin 1980; Lacombat 2005) | *The lateral tubercle is displaced posteriorly* (Guérin 1980) | *The lateral tubercle is displaced posteriorly* (Guérin 1980) | The lateral tubercle is displaced posteriorly |
| 3 | High of intercondylar tubercles | *The medial tubercle is higher than the lateral tubercle* (Lacombat 2005) | *The medial tubercle is lower than the lateral tubercle* (Lacombat 2005) | *The medial tubercle is lower than the lateral tubercle* (Guérin 1980) | *The medial tubercle is lower than the lateral tubercle* (Guérin 1980) | *The medial tubercle is lower than the lateral tubercle* (Guérin 1980) | The medial tubercle is lower than the lateral tubercle |
| 4 | Mid-lateral development of the distal epiphysis | *Weak* (Lacombat 2005) | *Moderate* (Lacombat 2005) | *Strong* (Lacombat 2005) | *Very strong* (Guérin 1980) | *Very strong* (Guérin 1980) | Strong |
| 5 | Medial throat | *Trapezoidal or rectangular* (Lacombat 2005) | *Trapezoidal* (Lacombat 2005) | *Trapezoidal or sub-trapezoidal* (Lacombat 2005; Pandolfi and Tagliacozzo 2015) | *Sub-rectangular* (Pandolfi and Tagliacozzo 2015) | _ | Elliptical |
| 6 | Lateral throat | *Elliptical* (Lacombat 2005) | *Elliptical* (Lacombat 2005) | *Elliptical or sub-elliptical* (Lacombat 2005; Pandolfi and Tagliacozzo 2015) | _ | _ | Sub-trapezoidal |
| 7 | Fibular notch | *Shallow* (Guérin 1980; Lacombat 2005) | *Shallow* (Guérin 1980; Lacombat 2005) | *Marked* (Guérin 1980) | *Marked* (Guérin 1980) | *Shallow* (Guérin 1980) | Shallow |

**Table 10.** Comparison between the main diagnostic characters of the third metatarsal between Contrada Monticelli and Pleistocene European rhinoceros species. The descriptive-diagnostic characters are shown in SD Figure 16.

| Third metatarsal | | | | | | | |
|---|---|---|---|---|---|---|---|
| N° | Descriptive-diagnostic character | *S. etruscus* | *S. hundsheimensis* | *S. hemitoechus* | *S. kirchbergensis* | *C. antiquitatis* | Contrada Monticelli *(MSTB – CM 30699)* |
| 1 | Anterior border | *Convex* (Guérin 1980) *Slightly concave* (Lacombat 2005) | *Straight* (Lacombat 2005) *Slightly convex* (Lacombat 2005) *Convex* (Guérin 1980; Pandolfi et al. 2018) | *Concave-convex* (Guérin 1980; Pandolfi and Tagliacozzo 2015) *Straight* (Lacombat 2005) | *Concave-convex* (Guérin 1980; Pandolfi and Tagliacozzo 2015; Pandolfi et al. 2018) | *Slightly convex* (Guérin 1980) | Convex |
| 2 | Anterior articular surface to Mt IV | *Triangular* (Guérin 1980) *Sub-circular* (Lacombat 2005) | *Triangular* (Guérin 1980) *Trapezoidal* (Pandolfi et al. 2018) *Elliptical* (Lacombat 2005) | *Triangular* (Guérin 1980) *Trapezoidal* (Guérin 1980; Lacombat 2005) *Sub-rectangular* (Pandolfi and Tagliacozzo 2015) | *Trapezoidal* (Guérin 1980) | *Trapezoidal* (Guérin 1980) | Triangular |
| 3 | Posterior articular surface to Mt IV | *Sub-circular* (Guérin 1980) *Elliptical* (Lacombat 2005) | *Circular* (Guérin 1980; Pandolfi et al. 2018) *Elliptical* (Guérin 1980) *Triangular* (Lacombat 2005) | *Sub-circular* (Lacombat 2005) *Circular* (Pandolfi and Tagliacozzo 2015) *Elliptical* (Guérin 1980) | *Sub-elliptical* (Pandolfi and Tagliacozzo 2015) *Elliptical* (Guérin 1980) | *Circular* (Guérin 1980) | Elliptical |
| 4 | Anterior articular surface to Mt II | *Triangular or sub-circular* (Guérin 1980; Lacombat 2005) | *Triangular or sub-circular* (Guérin 1980) *Elliptical* (Pandolfi et al. 2018) | *Sub-triangular* (Pandolfi and Tagliacozzo 2015) *Triangular* (Lacombat 2005; Pandolfi et al. 2018) | _ | _ | _ |
| 5 | Posterior articular surface to Mt II | *Triangular or sub-circular* (Guérin 1980; Lacombat 2005) | *Triangular, sub-circular* (Guérin 1980) *Elliptical* (Pandolfi et al. 2018) | *Sub-triangular* (Pandolfi and Tagliacozzo 2015) *Triangular* (Lacombat 2005; Pandolfi et al. 2018) | _ | _ | _ |
| 6 | Section of the diaphysis | *Elliptical* (Guérin 1980; Lacombat 2005) | *Elliptical* (Guérin 1980) | *Elliptical* (Guérin 1980; Lacombat 2005) | *Elliptical* (Guérin 1980) | *Rectangular or elliptical* (Guérin 1980) | _ |

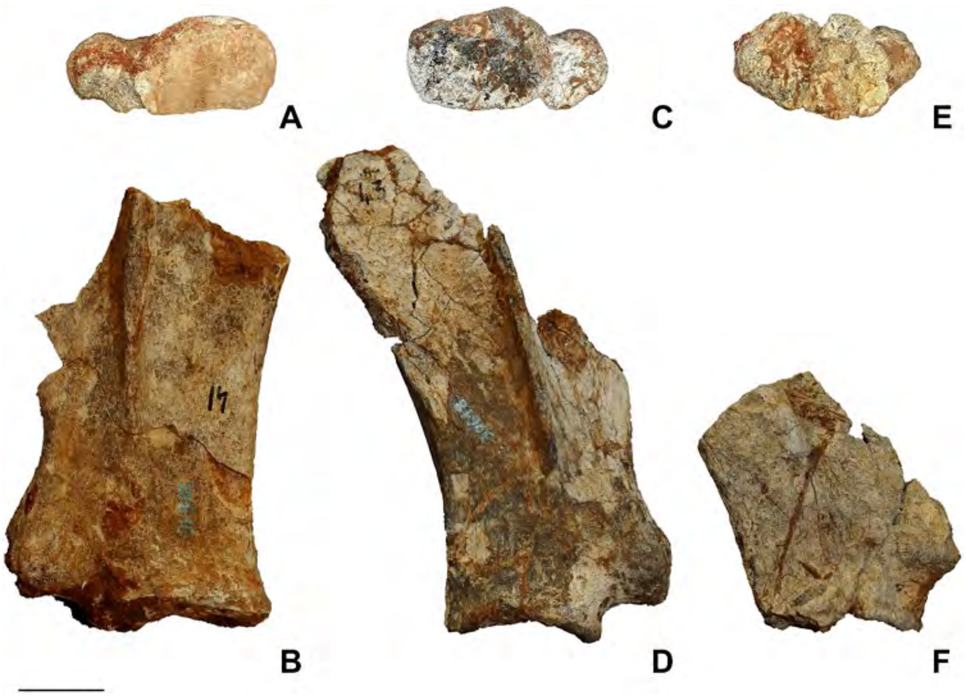

**Figure 4.** Postcranial remains of *Stephanorhinus hundsheimensis* from Contrada Monticelli: MSTB – CM 30616, left scapula (a-b); MSTB – CM 30618, right scapula (c-d); MSTB – CM 30809, right scapula (e-f), in articular (a, c, e) and lateral (b, d, f) views. Scale bar 5 cm.

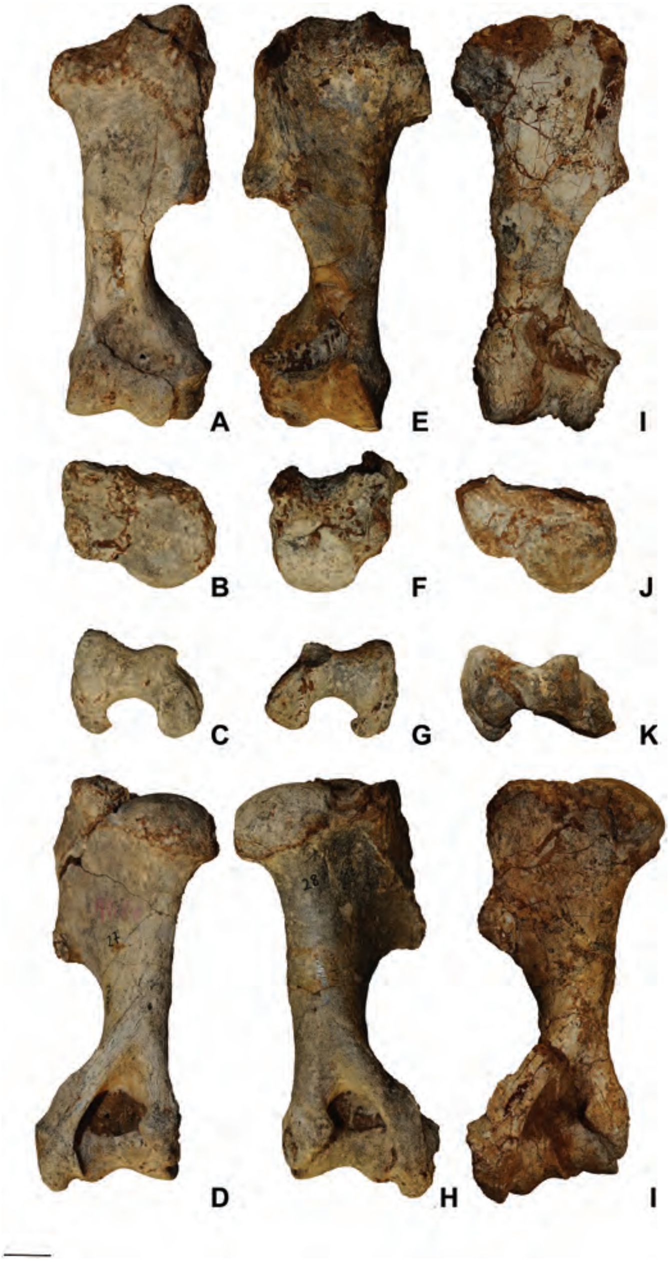

**Figure 5.** Postcranial remains of *Stephanorhinus hundsheimensis* from Contrada Monticelli: MSTB – CM 30602, left humerus (a-d); MSTB – CM 30603 - right humerus (e-h); MSTB – CM 30604 - left humerus (i-l), in cranial (a, e, i), proximal (b, f, j), distal (c, g, k) and caudal (d, h, l) views. Scale bar 5 cm.

morphologies of the medial and lateral articular surface of the distal epiphysis are different from those observed in all the other taxa.

Similarly to the third metacarpal, the third metatarsal has an important role for taxonomic determination (Table 10), despite some intraspecific variability exists, especially in *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus*. Only by combining the observations of more morphological features, this bone can be identified at specific level.

Analysing the five extant rhinoceros species, Guérin (1980) concludes that each taxon morphologically differs from the others, in both the cranial and postcranial remains. The existence of important differences in postcranial bones of extant taxa was recently confirmed by Mallet et al. (2019). The authors identified three main morphotypes using 3D geometric morphometrics: the African morphotype grouping *Ceratotherium simum* and *Diceros bicornis*, the *Rhinoceros* morphotype including *Rhinoceros sondaicus* and *Rhinoceros unicornis*, and the *Dicerorhinus sumatrensis* morphotype. When compared to extant species, the postcranial anatomy of the Pleistocene European rhinoceroses (Guérin 1980; Fortelius et al. 1993; Lacombat 2005 and this work) shows quite limited morphological differences. This was expected since, apart from the wholly rhino, all the other extinct species belong to the same genus, in contrast to the extant species, which are not as closely related to each other. Two of the five species here considered, *S. etruscus* and *S. hundsheimensis*, show a strong morphological affinity, so much so that the Hundsheim rhinoceros was considered a subspecies of the Etruscan rhinoceros by Guérin (1980) who classified it as *Dicerorhinus etruscus brachycephalus*. Mazza (1988) suggested a possible derivation of *S. hundsheimensis* from *S. etruscus*, while Fortelius et al. (1993) acknowledged the close relationship between the two taxa. However, the authors

**Figure 6.** Postcranial remains of *Stephanorhinus hundsheimensis* from Contrada Monticelli: MSTB – CM 30702, left second metacarpal (A-C); MSTB – CM 30698, left third (D-F); MSTB – CM 30703, left fourth metacarpal (G-I), in cranial (A, D, G), lateral (B, E, H) and proximal (C, F, I) views. Scale bar 5 cm.

grouped the two species together with the Late Pliocene *S. elatus* as a group probably strictly related to the late Middle Pleistocene *S. hemitoechus*. Although Fortelius et al. (1993) reported that some dental and cranial characters could suggest a possible derivation of *S. hundsheimensis* from *S. elatus* and of *S. hemitoechus* from *S. etruscus*, they prudently left the nodes of the cladogram unresolved. In their opinion, the small-sized rhinoceroses from several Early Pleistocene localities (e.g. Pietrafitta, Pirro Nord, Westerhoven, Brabant) might either be a transitional form between *S. etruscus* and *S. hundsheimensis* or a small-sized population unrelated to a speciation event. Pandolfi (2022) agrees in some way with Fortelius et al. (1993) suggesting a strong relationship between *S. elatus* and *S. hundsheimensis*, and also Deng et al. (2011), who claimed *S. etruscus* and *S. hundsheimensis* are sister taxa within

**Figure 7.** Postcranial remains of *S.* cf. *hundsheimensis* from Contrada Monticelli: MSTB – CM 30606, right femur, in cranial (a), caudal (b), proximal (c) and distal (d) views. Scale bar 5 cm.

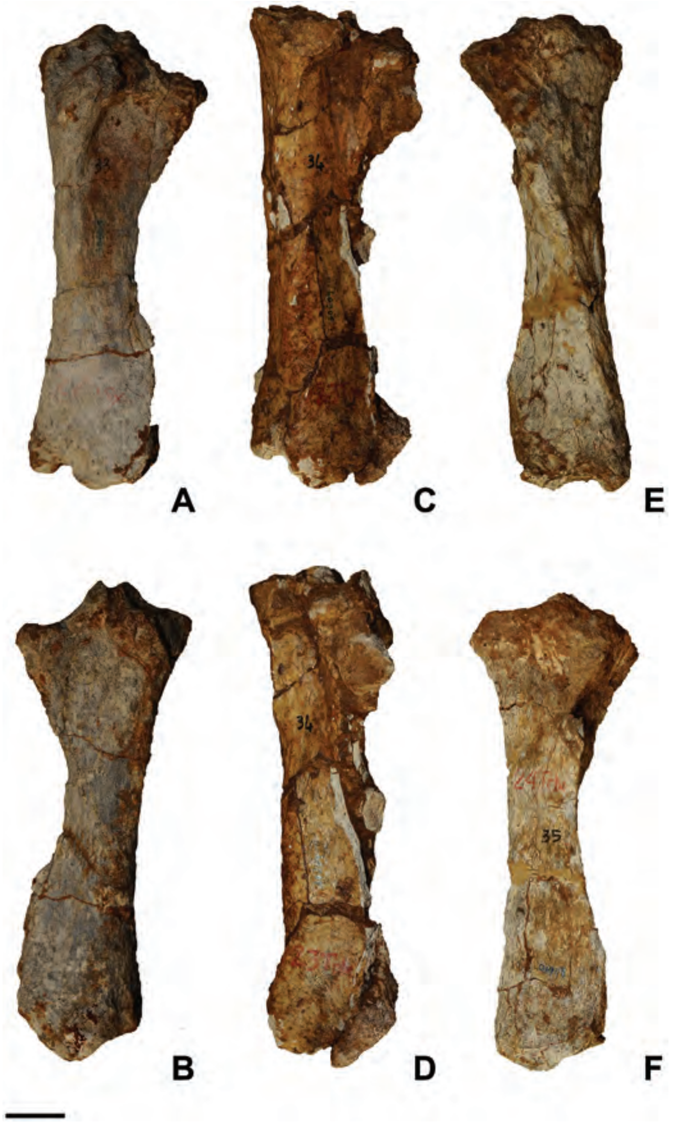

**Figure 8.** Postcranial remains of *Stephanorhinus hundsheimensis* from Contrada Monticelli: MSTB – CM 30608, left tibia (a-b); MSTB – CM 30609, left tibia (c-d); MSTB – CM 30610, right tibia (e-f), in cranial (a, c, e) and proximal (b, d, f) views. Scale bar 5 cm.

a clade that also includes *S. hemitoechus* and all species of the genus *Coelodonta*.

Morphological differences in the postcranial elements between *S. etruscus* and *S. hundsheimensis* were tentatively described by Guérin (1980), Fortelius et al. (1993) and Lacombat (2005). However, the study of the much more abundant dental material suggested that there is a wide morphological superposition among different species, with all the species showing a large intraspecific variability (Fortelius et al. 1993; Lacombat 2006; Ballatore and Breda 2013). This means that the identification beyond the genus level is not possible if based only on few isolated specimens (Ballatore and Breda 2013). This concept can be applied, as a general baseline, to all the *Stephanorhinus* species but is particularly true for the couple *S. etruscus* - *S. hundsheimensis* because of their morphological closeness. As aforementioned, these species share a considerable number of morphological traits, and, as a matter of fact, the same remains have been attributed to *S. etruscus* by some authors and to *Stephanorhinus* cf. *S. hundsheimensis* by others (e.g. Pandolfi and Petronio 2011b, *versus*; Mazza et al. 1993 for specimens from Pietrafitta and Pirro Nord) or even have been identified as *Stephanorhinus* ex gr. *etruscus* to stress how the distinction among the two species might not be possible (e.g. Breda and Marchetti 2007 for the specimens from Leffe, northern Italy).

Our analysis of the CM postcranial sample reveals a wide morphological variability with several intraspecific variable characters. This variability is even greater than previously described for any Pleistocene species of the genus *Stephanorhinus* with most characters matching the morphology described for *S. hundsheimensis*, but many characters fit *S. etruscus* and some actually match the morphology recorded in *S. hemitoechus* (see Tables 2-10). These somehow unexpected results could allow different interpretations for the CM sample:

- it could include more species from different stratigraphic layers;
- it could include more species from a single stratigraphic layer;
- it could include a single species but with high intraspecific variability from a single stratigraphic layer.

The first hypothesis must be discussed in the framework of the CM deposition history. As described above, the CM faunal sample was

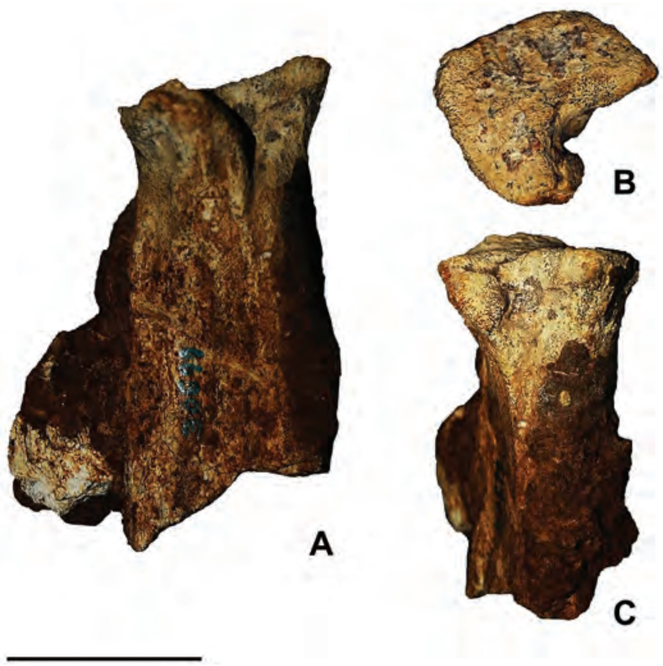

**Figure 9.** Postcranial remains of *Stephanorhinus hundsheimensis* from Contrada Monticelli: MSTB – CM 30699, right third metatarsal, in cranial (a), proximal (b) and lateral (c) views. Scale bar 5 cm.

collected from a karst infilling deposit, developed into a Cretaceous formation. This type of deposit is well known in Apulia with limestone rocks outcropping almost everywhere in the region. Renowned examples are Pirro Nord (e.g. Arzarello et al. 2007, 2009; Pavia et al. 2012) and Maglie area (e.g. Mecozzi et al. 2021). The mammal remains recovered from each single karst infilling have been considered contemporaneous in geological terms (Arzarello et al. 2007, 2009; Mecozzi et al. 2021). The identified mammal taxa from each of these karst fissures are consistent with a single faunal assemblage and, in the majority of cases, they are the only indication of the age of the deposits. Over the years, other taxa have been identified in CM such as *Palaeoloxodon antiquus* (Luperto Sinni and Colucci 1985), *Canis mosbachensis* (Mecozzi et al. 2017) and *Dama* cf. *roberti* (Stefanelli et al. 2021), that overall indicate a Middle Pleistocene age, in terms of biochronology. Thus, even if the stratigraphic provenance of most fossils studied in this work is missing, they can be considered coeval.

The second hypothesis cannot be completely ruled out since more than one rhinoceros' species can live in different niches within the same geographic area at the same time. This applies, for example, to present-day white and black rhinoceros from African savannahs, to the late Middle Pleistocene *S. hemitoechus* and *S. kirchbergensis* from Mosbach (Baden-Württemberg; Fortelius et al. 1993), and to the early Villafranchian *S. jeanvireti* and *S. etruscus* from Perrier-Les Etouaires (Auvergne; Guérin 1972; Ballatore and Breda 2018). Nevertheless, it is worth noting that cranial and mandibular material of CM suggests the presence of a single species, *S. hundsheimensis* (Mazza and Varola 1999).

The third hypothesis, of a single species at CM but with a high degree of intraspecific variability, cannot be ruled out either, because the morphological variability of the different species could be greater than originally thought. This has been demonstrated for *S. hundsheimensis* by Ballatore and Breda (2013), who assessed a wider morphological variability for the dental remains from Isernia La Pineta (southern Italy) than previously described by Lacombat (2005) on samples of the same species from other western European localities. A case study, explanatory of intraspecific variability in Quaternary rhinoceroses, is that published by Pandolfi et al. (2021) based on the record from Dmanisi (1.85–1.77 Ma, Georgia). The two *Stephanorhinus* crania recovered in the site show morphological differences not related to intraspecific variability or sexual dimorphism (Pandolfi et al. 2021). Following the hypothesis of the authors, these findings suggest the presence of two different feeding strategies or the presence of two ecomorphotypes. The scenario where the European continent was alternately occupied by *S. etruscus* (a browser) and *S. hundsheimensis* (highly flexible feeder) during the Early Pleistocene is currently not documented, but this is compatible with the patchy environments recognised at Dmanisi (Pandolfi et al. 2021).

Given the quite marginal geographic position of CM, in the heel of Italy, a fourth hypothesis could be taken into consideration: the large amount of mixed *S. etruscus* and *S. hundsheimensis* morphological characters, together with their large size range (see the Morphological and morphometric comparison section), could suggest that the CM sample may represent a hybrid population. In other words, a relict *S. etruscus* population could have interbred with *S. hundsheimensis* invaders from the North, absorbing part of their morphology to develop a mix of characters of the two species. Mosaic evolution and interbreeding has been postulated in several occasions to explain mixed features in some Quaternary large mammal populations, iconically in the *Mammuthus* lineage, which represents one of the better-resolved examples of species-level evolution among vertebrates (Lister et al. 2005; Lister and Sher 2015). In the mammoth lineage, this interbreeding has been recently confirmed through genomic data (Valkvander et al. 2021). As a matter of fact, in both the *M. meridionalis*-*M. trogontherii* and the *M. trogontherii*-*M. primigenius* transitions, the advanced form originated in a peripheral area (respectively, China and NE Siberia) and subsequently spread into their full areal following a multi-population, gene-flow model (Lister et al. 2005). Incursions of individuals of the newly evolved species into Europe occurred progressively, supplanting indigenous representatives of the parental species; this process was not linear and homogeneous, and produced several populations with different mosaics of primitive and derived features, often described as subspecies (among others *M. meridionalis vestinus*, *M. meridionalis voigtstedtensis*, *M. trogontherii chosaricus*, and so on) (Lister et al. 2005).

Mosaic evolution has been suggested also for other Quaternary large mammal taxa (e.g. the moose tribe, *Cervalces* and *Alces*; Breda and Marchetti 2005), but none of them reached the sampling richness and accuracy possible with the mammoths. A similar scenario could be postulated for the genus *Stephanorhinus* and would give reason of the numerous and often conflicting views on its taxonomy and even of the specific identification of single populations. The mixture of *S. hundsheimensis* and *S. etruscus* characters on the rhinoceros postcranial bones from CM could account for such explanation even though we are well aware that it is far from being demonstrated.

## Was *Stephanorhinus hundsheimensis* a small- to medium-sized rhinoceros?

During the last decades, several authors proposed a size-related evolutionary pattern for *S. hundsheimensis*, recognising two distinct groups: an early small-sized form, from the late Early Pleistocene, and a large-sized form, from the early Middle Pleistocene (Fortelius et al. 1993; Lacombat 2005; Breda and Marchetti 2007). Large specimens of *S. hundsheimensis* from the early Middle Pleistocene, for example, were reported in the Italian site of Cesi (Mazza 1996; Ficcarelli et al. 1997) and in the French site of Soleilhac (Lacombat 2005).

The results of our biometric analysis confirm the chronological trend proposed, because the Middle Pleistocene specimens of *S. hundsheimensis* often exceed in size the Early Pleistocene samples here provisionally kept as *Stephanorhinus* sp. Their large size is particularly evident in the humerus (SD 5-SD Figure 22), the second metacarpal (SD 5-SD Figure 25), the femur (SD 5-SD Figure 27), and the tibia (SD 5-SD Figure 29). However, the largest specimens of Early Pleistocene *S. hundsheimensis* were all collected from Untermassfeld (Thuringia, Germany).

In addition, a closer look reveals that the measures in which the rhino from Untermassfeld exceeds coeval remains from other localities, is the length of the long bones. Thus, rather than being described as large-sized, it should more precisely be described as long-legged. This finding is extremely interesting and should be further investigated since it matches the same trend recorded in other taxa from this locality as, for example, the *Bison* (Sorbelli et al. 2023) and the eucladocerine (Breda et al. 2020).

Our analysis also reveals a huge size variation in the Hundsheim rhinoceros, the widest among Pleistocene taxa (see SD 5 - Biometric comparison and SD 7 - Comparative dataset of Pleistocene Rhinoceros). The size variation observed at CM exceeds the dimensional range of this species, recording large humeri and third metacarpal and, conversely, a femur smaller than any plotted *S. hundsheimensis* specimen. This result in a way matches the wide morphological plasticity of the CM sample above discussed, supporting the hypothesis of either a hybrid population or the co-presence of two morphotypes of the same species.

Regarding the differences between *S. hundsheimensis* and *S. etruscus*, the biometric analysis confirms that the former species is generally larger than the latter. The specimens from CM are generally larger than those attributed to the Etruscan rhinoceros and also support this trend. As aforementioned, the size of femur MSTB – CM 30606 contrasts this trend, being much smaller than other specimens included in our comparative dataset (SD. 7). The *etruscus*-like characteristics, combined with the particularly small size, led Mazza and Varola (1999) to identify the femur as *S.* cf. *etruscus* and consider it as a probably reworked element. However, we believe this last hypothesis is unlikely, as all the other fossils of the site are consistent with each other both in terms of preservation and biochronological range. The size of this femur is indeed close to that of *S. etruscus* from the early Early Pleistocene of Upper Valdarno (Fortelius et al. 1993) and to *Stephanorhinus* sp. from the late Early Pleistocene of Pietrafitta (Mazza et al. 1993). In addition, Guérin (1980) analysed 29 *S. hundsheimensis* femura, reporting a large size variability, encompassing MSTB – CM 30,606 size. The wide morphometrical variation of *S. hundsheimensis*, confirmed in our work, allows the interpretation of MSTB – CM 30606 as a representative of this species rather than as a single evidence of *S. etruscus*. However, the wide morphometrical range of the CM sample matches its huge morphological variability and fits also the hypothesis of a hybrid population or of the co-presence of two morphotypes. The living white rhinos (*Ceratotherium simum*) were found in two discontinuous populations, one from South Africa to Zambia, the Southern white rhino (*Ceratotherium simum simum*) and the other, the Northern white rhino (*Ceratotherium simum cottoni*) in South Sudan, the Democratic Republic of the Congo, Uganda, Chad, and the Central African Republic (Emslie and Brooks 1999; Ryder et al. 2020). The taxonomy of the white rhinos is contested, the focus of disagreement being whether the observed differences warrant species-level differentiation (Groves et al. 2010) or continued differentiation at the subspecies level (Tunstall et al. 2018). However, George et al. (1993) identified clear and significant genetic differences between the two populations. Considering when it happened in Africa with these two populations of the same species that differentiated in an open continent, one can also assume an even clearer differentiation occurred within populations of a rhinoceros species that occupied the territory of the Italian peninsula. In fact, with its narrow and long shape and its important physiographic barriers (e.g. Alps and Apennines), Italy and in particular the Apulian peninsula, may have constituted an area of isolation for some rhinoceros populations which over time have gradually more and more differentiated.

Since the sample collected at CM includes mainly postcranial elements, we attempted an investigation of its locomotor adaptations. Reconstructing unquestionable locomotion strategies for extinct mammals is impossible, but some hints can be drawn from the adaptations living relatives. Mallet et al. (2019, 2022). recognised three main morphotypes in extant rhinoceroses: the African morphotype grouping *Ceratotherium simum* and *Diceros bicornis*, the *Rhinoceros* morphotype including *Rhinoceros sondaicus* and *Rhinoceros unicornis*, and the *Dicerorhinus sumatrensis* morphotype. This highlights a strong link between the increase in body mass and the increase in general robustness, more pronounced attachments for muscles and development of the medial parts of the bones (Mallet et al. 2019, 2022). In addition, the five modern species show more or less important morphological differences depending on the bones considered. For example, humerus and femur yield evident interspecific differences between African and Asian rhinoceroses, associated with significant differences in body mass (Mallet et al. 2019).

The CM humerus and femur present a much lower overlap in their fields of variability compared to other bones, such as the scapula and metapodials (Figures 21–24 and 27–29 in SD 5). Forelimb bones play a crucial role in supporting body weight and in braking during locomotion in quadrupeds (Hildebrand 1974; Dutto et al. 2006; Henderson 2006). The shape of the humerus changes allometrically and exhibits a strong phylogenetic signal, while the shapes of radius and ulna display a stronger link with body mass repartition than with the absolute mass itself (Mallet et al. 2021). The CM humeri and ulna stand out due to their truly remarkable size (SD 5–SD Figures 22 and 23). In particular, the humeri show a significantly longer length than both *S. etrucus* and *S. hundsheimensis*. They are as long as *C. antiquitatis* but much slenderer. The strength of the distal epiphysis also presents a similar situation, with a particularly accentuated elongation in the antero-posterior diameter.

The single complete CM femur (MSTB – CM 30606) is exceptionally small compared to all the other plotted species, even if in the case of the antero-posterior elongation of the distal epiphysis, it is not the lowest value (SD 5-SD Figures 27 and 28). However, it would be a mistake to think that CM rhinoceroses had such a clear imbalance in proportion between the anterior and posterior stylopodium. In fact, it is possible to note how the incomplete femur specimens present an articular head with significantly larger diameters (SD 4-SD Table 8), which therefore suggests that MSTB – CM 30606 only testifies the presence of an exceptionally small individual within a sample of much larger dimensions. The tibiae of CM rhinos tend to have among the highest maximum length values compared to *S. etruscus* and *S. hundsheimensis* (SD 5-SD Figure 29). However, the robustness is significantly greater than in these two species so much so that it is comparable to *C. antiquitatis*.

All in all, the limbs of CM rhinoceroses are in average longer and more robust than those of *S. etruscus* and *S. hundsheimensis*. This would suggest a possible tendency towards greater graviportality for the species recognised by Mazza and Varola (1999) during the early Middle Pleistocene, but simultaneously, more cursorial than the highly graviportal woolly rhinoceroses (e.g. Borsuk-Białynicka 1973; Kahlke and Lacombat 2008).

## Conclusion

The combined study of unpublished material, together with the revision of the published postcranial sample of the *Stephanorhinus* remains from Contrada Monticelli, reveals a large morphological and biometric variability.

Since cranial and dental remains from CM have clear *S. hundsheimensis* morphology (Mazza and Varola 1999), the most parsimonious interpretation is that the postcranial remains belong to this species as well. However, the presence, in the postcranials, of several morphological characters shared by *S. etruscus* and *S. hundsheimensis*, together with the wide size-range, confirms the strong morphological affinity between these two taxa, in agreement with Guérin (1980) and Lacombat (2005), and could indicate a possible presence of both species at CM.

This result could suggest three possible explanations:

- either *S. hundsheimensis* morphological and biometric variability is even wider than previously thought and the specimens from CM all belong to this species.
- or, the CM fossil sample could represent a hybrid population between *S. etruscus* and *S. hundsheimensis*. In consideration of the isolated position of the site with respect to the European continent, of which CM is one of the southernmost records, we could imagine that a relict *S. etruscus* population could have interbred with *S. hundsheimensis* invaders from the North, absorbing part of their morphology to develop a mix of characters of the two species. In this view, the CM huge specimens could be the result of heterosis (outbreeding enhancement).
- or even, the rhinoceros CM sample could testify the presence of two morphotypes of the same species as suggested for the early late Villafranchian of Dmanisi (Pandolfi et al. 2021).

The answer to this question remains unsolved, but this study offered the opportunity to evaluate how large the morphological and biometric variability within a rhinoceros population can be. Our results open new discussions and encourage to further investigate the postcranial skeleton of extinct rhinoceroses.

## Author contributions

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## References

Abbazzi L. 2004. Alcuni commenti sulla validità del nome generico Praemegaceros Portis 1920 e una sintesi della distribuzione delle specie di Praemegaceros in Italia. Rend Lincei Sci Fis Nat. 15(2):115–132. doi: 10.1007/BF02904712.

Argant J, Bonifay M-F. 2011. Hyaena coprolites (*Pachycrocuta brevirostris*) from the Ceyssaguet villafranchian site (Lavoute-sur-Loire, Haute-Loire, France) : pollen analyses and palaeoenvironmental indications. Quaternaire. 22(1):3–11. doi: 10.4000/quaternaire.5808.

Arzarello M, Marcolini F, Pavia G, Pavia M, Petronio C, Petrucci M, Rook L, Sardella R. 2007. Evidence of earliest human occurrence in Europe: the site of Pirro Nord (Southern Italy). Naturwissenschaften. 94(2):107–112. doi: 10.1007/s00114-006-0173-3.

Arzarello M, Marcolini F, Pavia G, Pavia M, Petronio C, Petrucci M, Rook L, Sardella R. 2009. L'industrie lithique du site Pléistocène inferieur de Pirro Nord (Apricena, Italie du sud): une occupation humaine entre 1,3 et 1,7 Ma. L'anthropologie. 113:47–58. doi: 10.1016/j.anthro.2009.01.004.

Azzaroli A. 1968. Calcare di Altamura. Servizio Geologico Italiano. Formazioni geologiche. 1:151–156.

Azzaroli A, Cita MB. 1963. Geologia stratigrafica. Vol. II, Milano: La Goliardica.

Azzaroli A, Radina B, Ricchetti G, Valduga A. 1968. Note Illustrative della Carta Geologica d'Italia, Foglio 189, Altamura. Roma: Servizio Geologico Italiano.

Ballatore M, Breda M. 2013. *Stephanorhinus hundsheimensis* (Rhinocerontidae, Mammalia) teeth from the early Middle Pleistocene of Isernia La Pineta (Molise, Italy) and comparison with coeval British material. Quat Internat. 302:169–183. doi: 10.1016/j.quaint.2013.02.002.

Ballatore M, Breda M. 2016. *Stephanorhinus elatus* (Rhinocerotidae, Mammalia): proposal for the conservation of the earlier specific name and designation of a lectotype. Geodiversitas. 38(4):579–594. doi: 10.5252/g2016n4a7.

Ballatore M, Breda M. 2018. Revision of the rhinoceros remains (Rhinocerotidae, Mammalia) from the late Pliocene of Etouaires (Auvergne, France) and the morphological distinction between the postcranial bones of *Stephanorhinus elatus* and *S. etruscus*. C R Palevol. 18 (2):191–208. doi: 10.1016/j.crpv.2018.06.003.

Barone R. 1980. Anatomia Comparata dei Mammiferi Domestici – Vol. 1° Osteologia. Terza edizione italiana a cura di Ruggero Bortolami ed Emilio Callegari (2017). Milano: Edizioni Agricole New Business Media.

Bellucci L, Sardella R, Rook L. 2014. Large mammal biochronology framework in Europe at Jaramillo: The Epivillafranchian as a formal biochron. Quat Internat. 389:84–89. doi: 10.1016/j.quaint.2014.11.012.

Bertok C, Masini F, Donato VD, Martire L, Pavia M, Zunino M, Pavia G. 2013. Stratigraphic framework of the type-locality of Pirro Nord mammal Faunal Unit (Late Villafranchian, Apricena, south- eastern Italy). Palaeontographica Abteilung a -Stuttgart. 298(6):5–17. doi: 10.1127/pala/298/2013/5.

Billia EME. 2011. Occurrences of *Stephanorhinus kirchbergensis* (Jager, 1839) (Mammalia, Rhinocerotidae) in Eurasia. An account. Acta Palaeontol Rom. 7:17–40.

Billia EME, Petronio C. 2009. Selected records of *Stephanorhinus kirchbergensis* (Jäger, 1839) (Mammalia, Rhinocerotidae) in Italy. Bollettino della Società Paleontologica Italiana. 481:21–32.

Blanc GA. 1920. Grotta Romanelli. Archivio per l'Antropologia e la Etnologia. 50:1–39.

Blanc GA. 1928. Grotta Romanelli. Archivio per l'Antropologia e la Etnologia. 58:1–49.

Blumenbach JF. 1799. Handbuch der Naturgeschichte. Göttingen.

Borsuk-Białynicka M. 1973. Studies on the Pleistocene rhinoceros *Coelodonta antiquitatis* (Blumenbach). Palaeontol Pol. 29:1–94.

Bourguignon L, Crochet J-Y, Capdevila R, Ivorra J, Antoine P-O, Agustí J, Barsky D, Blain HA, Boulbes N, Bruxelles L, et al. 2015. Bois-de-Riquet (Lézignan-la-Cèbe, Hérault): A late Early Pleistocene archeological occurrence in southern France. Quat Internat. 393:24–40. doi: 10.1016/j.quaint.2015.06.037.

Breda M, Kahlke R-D, Lister AM. 2020. New results on cervids from the Early Pleistocene site of Untermassfeld. In: Kahlke RD, editor. The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany). Part 4. Weimar: Senckenberg. p. 1197–1249.

Breda M, Marchetti M. 2005. Systematical and biochronological review of Plio-Pleistocene Alceini (Cervidae; Mammalia) from Eurasia. Quat Sci Review. 24(5–6):775–805. doi: 10.1016/j.quascirev.2004.05.005.

Breda M, Marchetti M. 2007. Pleistocene mammal faunas from the Leffe Basin (Bergamo, Northern Italy): revision and new data. Courier Forschungsinstitut Senckenberg. 259:61–77.

Capasso Barbato L, Di Stefano G, Petronio C, Sardella R. 1998. Pleistocene mammal faunas from Ponte Molle (Rome). Quater Internat. 47-48:73–75. doi: 10.1016/S1040-6182(97)00072-4.

Cerdeño E. 1990. *Stephanorhinus hemitoechus* (Falc.) (Rhinocerolidae, Mammalia) del Pleistoceno medio y superior de Espana. Estud geol. 46(5–6):465–479. doi: 10.3989/egeol.90465-6475.

Cerdeño E. 1993. Remarks on the spanish Plio-Pleistocene *Stephanorhinus etruscus* (Rhinocerotidae). Comptes Rendus de l'Académie des sciences. Paris. 317:1363–1367.

Chitoglou K, Pandolfi L, Kostopoulos SD. 2023. First occurrence of Pliorhinus cf. megarhinus (*Perrissodactyla, Rhinocerotidae*) in Greece. Bulletin Geological Society of Greece. 60:1–13.

Ciaranfi N, Pieri P, Ricchetti G. 1988. Note alla carta geologica delle Murge e del Salento (Puglia centromeridionale). Memorie Società Geologica Italiana. 41:499–460.

Cohen KM, Finney SC, Gibbard PL, Fan JX. 2013. The ICS International Chronostratigraphic Chart. Episod. 36:199–204. doi: 10.18814/epiiugs/2013/v36i3/002.

D'Argenio B. 1974. Le piattaforme carbonatiche periadriatiche. Una rassegna di problemi nel quadro geodinamico mesozoico dell'area mediterranea. Memorie Società Geologica Italiana. 13(2):137–159.

Deng T, Wang X, Fortelius M, Li Q, Wang Y, Tseng ZJ, Takeuchi GT, Saylor JE, Saila LK, Xie G, et al. 2011. Out of Tibet: Pliocene woolly rhino suggests high plateau origin of Ice Age megaherbivores. Science 333(6047):1285–1288. doi:10.1126/science.1206594.

Di Stefano G, Petronio C, Sardella R. 1998. Biochronology of the Pleistocene mammal faunas from Rome urban area. Il Quaternario. 11(2):191–199.

Dutto DJ, Hoyt DF, Clayton HM, Cogger EA, Wickler SJ. 2006. Joint work and power for both the forelimb and hindlimb during trotting in the horse. J Exp Biol. 209(20):3990–3999. doi: 10.1242/jeb.02471.

Emslie R, Brooks M. 1999. African rhino: status survey and conservation action plan. Gland, Switzerland and Cambridge, UK: IUCN/SSC African Rhino Specialist Group, IUCN.

Falconer H. 1868. On the European Pliocene and Postpliocene species of the genus *Rhinoceros*. Paleontological and Notes. 2:309–403.

Ficcarelli G, Masini F, Torre D, Mazza P. 1997. The mammals of the latest Villafranchian in Italy (in Turner Ch, ed:the Early Middle Pleistocene in Europe). Rotterdam: Balkema Publishing House; p. 263–272.

Fortelius M, Mazza P, Sala B. 1993. *Stephanorhinus* (Mammalia, Rhinocerotidae) of the Western European Pleistocene, with a special revision of *Stephanorhinus etruscus (Falconer 1868)*. Palaeontogr ital. 80:63–155.

García-Fernández D, Cerdeño E, Sanz M, Daura J. 2023. The Latest Occurrence of Stephanorhinus hundsheimensis (Rhinocerotidae) in Europe: The Skeletons from the Cova del Rinoceront Site (Castelldefels, Barcelona). Quaternary. 6(4):60. doi: 10.3390/quat6040060.

George M, Chemnick LG, Cisova D, Gabrisova E, Stratil A, Ryder OA 1993. Genetic differentiation of white rhinoceros subspecies: Diagnostic differences in mitochondrial DNA and serum proteins. Paper presented at the International Conference Rhinoceros Biology and Conservation; San Diego, CA, USA. p. 9–11.

Gliozzi E, Abbazi L, Ambrosetti P, Argenti P, Azzaroli A, Caloi L, Capasso Barbato L, Di Stefano G, Esu D, Ficcarelli G, et al. 1997. Biochronology of selected mammals, molluscs, ostracods from the Middle Pliocene to the Late Pleistocene in Italy. state Art Rivista Italiana di Paleontologia e Stratigrafia. 103:369–388.

Groves CP, Fernando P, Robovský J, DeSalle R. 2010. The sixth rhino: A taxonomic re-assessment of the critically endangered northern white rhinoceros. PloS One. 5(4):e9703. doi: 10.1371/journal.pone.0009703.

Guérin C. 1972. Une nouvelle espèce de rhinocéros (Mammalia, Perissodactyla) à Vialette (Haute-Loire, France) et dans d'autres gisements du Villafranchien inférieur européen: *Dicerorhinus jeanvireti* n. sp. Documents du Laboratoire de Géologie de Lyon (Faculté des Sciences). 49:53–150.

Guérin C. 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les espèces actuelles. Documents du Laboratoire de Géologie de Lyon. 79(1–3):1–1185.

Guérin C. 2010. *Coelodonta antiquitatis* praecursor (Rhinocerotidae) du Pleistocene moyen final de l'aven de Romain-la-Roche (Doubs, France). Rev Paleobiol. 29:697–746.

Hammer Ø, Harper DA, Ryan PD. 2001. PAST: paleontological statistics software package for education and data analysis. Paleontologia Electronica. 4:1–9.

Henderson DM. 2006. Burly gaits: centers of mass, stability, and the trackways of sauropod dinosaurs. J Vertebr Paleontol. 26(4):907–921. doi: 10.1671/0272-4634(2006)26[907:BGCOMS]2.0.CO;2.

Hildebrand M. 1974. Analysis of vertebrate structure. New York: John Wiley & Sons.

Jäger GF. 1835–39. Über die fossilen Säugetiere welche in Württemberg in verschiedenen Formationen aufgefunden worden sind, nebst geognotischen Bemerkungen über diese Formationen. C. Erhard Verlag, Stuttgart. pp. 139.

Kahlke R-D. 1999. The History of the Origin, Evolution and Dispersal of the Late Pleistocene Mammuthus-Coelodonta Faunal Complex in Eurasia (Large Mammals). Rapid City: Fenske Companies.

Kahlke R-D. 2001. Die Unterpleistozäne Komplexfundstelle Untermaßfeld - Zusammenfassung Des kenntnisstandes Sowie Synthetische Betrachtungen Zu Genesemodell, Paläoökologie und Stratigraphie. In: Kahlke RD, editor. Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen). Monographien des Römisch-Germanischen Zentralmuseums, Band. Vol. 40. Bonn: Rudolf Habelt; p. 931–1030.

Kahlke R-D, Lacombat F. 2008. The earliest immigration of woolly rhinoceros (*Coelodonta tologoijensis*, Rhinocerotidae, Mammalia) into Europe and its adaptive evolution in Palaearctic cold stage mammal faunas. Quat Sci Rev. 27 (21–22):1951–1961. doi: 10.1016/j.quascirev.2008.07.013.

Konidaris GE, Tourloukis V, Kostopoulos DS, Thompson N, Giusti D, Michailidis D, Koufos GD, Harvati K. 2015. Two new vertebrate localities from the Early Pleistocene of Mygdonia Basin (Macedonia, Greece): Preliminary results. C R Palevol. 14(5):353–362. doi: 10.1016/j.crpv.2015.05.004.

Kuzmin Y. 2010. Extinction of the woolly mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*) in Eurasia: review of chronological and environmental issues. Boreas. 39(2):247–261. doi: 10.1111/j.1502-3885.2009.00122.x.

Lacombat F 2005. Les rhinocéros fossiles des sites préhistoriques de l'Europe méditerranéenne et du Massif central. Paléontologie et implications biochronologiques [dissertation]. Oxford: BAR Archaeopress. 1419:1–175.

Lacombat F. 2006. Morphological and biometrical differentiation of the teeth from Pleistocene species of *Stephanorhinus* (Mammalia, Perissodactyla, Rhinocerotidae) in Mediterranean Europe and the Massif Central, France. Palaeontographica Abteilung A Paläozoologie Stratigraphie. 274(3–6):71–111. doi: 10.1127/pala/274/2006/71.

Lacombat F. 2007. Phylogeny of the genus *Stephanorhinus* in the Plio-Pleistocene of Europe [Phylogenie der Gattung Stephanorhinus im Plio-Pleistozän Europas]. Hallesches Jahrbuch Geowissenschaften. 23:63–64.

Lacombat F. 2010. Estudio paleontológico de *Stephanorhinus hundsheimensis* de Fuente Nueva-3 y Barranco León. In: Toro I, Martínez-Navarro B, and Agustí J, editors. Ocupaciones humanas en el Pleistoceno inferior y medio de la cuenca de Guadix-Baza. Sevilla: Junta de Andalucía. p. 237–246.

Lister AM, Sher AV. 2015. Evolution and dispersal of mammoths across the Northern Hemisphere. Sci. 350(6262):805–809. doi: 10.1126/science.aac5660.

Lister AM, Sher AV, van Essen H, Wei G. 2005. The pattern and process of mammoth evolution in Eurasia. Quat Internat. 126-128:49–64. doi: 10.1016/j.quaint.2004.04.014.

Lourens L. 2004. Revised tuning of Ocean Drilling Program Site 964 and KC01B (Mediterranean) and implications for the δ18O, tephra, calcareous nannofossil, and geomagnetic reversal chronologies of the past 1.1 Myr. Paleoceanography. 19(3):A3010. doi: 10.1029/2003PA000997.

Luperto Sinni E, Colucci M. 1985. Il giacimento fossilifero di Contrada Monticelli. Atti del I Convegno Regionale di Speleologia Castellana-Grotte. 1:207–219.

Madurell-Malapeira J, Minwer-Barakat R, Alba DM, Garcés M, Gómez M, Aurell-Garrido J, Ros-Montoya S, Moyà-Solà S, Berástegu X. 2010. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. Quat Sci Rev. 29(27–28):3972–3982. doi: 10.1016/j.quascirev.2010.09.020.

Madurell-Malapeira J, Ros-Montoya S, Espigares MP, Alba DM, Aurell-Garrido J. 2014. Villafranchian large mammals from the Iberian Peninsula: paleobiogeography, paleoecology and dispersal events. J Iber Geol. 40(1):167–178. doi: 10.5209/rev_JIGE.2014.v40.n1.44093.

Mallet C, Billet G, Cornette R, Houssaye A. 2022. Adaptation to graviportality in Rhinocerotoidea? An investigation through the long bone shape variation in their hindlimb. Zool J Linn Soc. 196(3):1235–1271. doi: 10.1093/zoolinnean/zlac007.

Mallet C, Cornette R, Billet G, Houssaye A. 2019. Interspecific variation in the limb long bones among modern rhinoceroses-extent and drivers. PeerJ. 7: e7647. doi: 10.7717/peerj.7647.

Mallet C, Houssaye A, Cornette R, Billet G. 2021. Long bone shape variation in the forelimb of Rhinocerotoidea: relation with size, body mass and body proportions. Zool J Linn Soc. 196(3):1201–1234. doi: 10.1093/zoolinnean/zlab095.

Martinetto E, Bertini A, Basilici G, Baldanza A, Bizzarri R, Cherin M, Gentili S, Pontini MR. 2014. The plant record of the Dunarobba and Pietrafitta sites in the Plio-Pleistocene palaeoenvironmental context of Central Italy. Alp Mediterr Quat. 27:29–72.

Mazza P. 1988. The Tuscan Early Pleistocene rhinoceros *Dicerorhinus etruscus*. Palaeontographia Ltalica. 75:1–87.

Mazza P. 1996. The Middle Pleistocene rhinoceros remains from Cesi (Colfiorito Basin, Umbro-Marchean Apennines, Central Italy). Bollettino della Società Paleontologica Italiana. 35(3):349–355.

Mazza P, Sala B, Fortelius M. 1993. A small latest Villafranchian (late Early Pleistocene) rhinoceros from Pietrafitta (Perugia, Umbria, Central Italy), with notes on the Pirro and Westerhoven rhinoceroses. Palaeontogr ital. 80:25–50.

Mazza P, Varola A. 1999. Revision of the Middle Pleistocene Rhinoceros remains from Contrada Monticelli (Castellana, Bari, Southern Italy). Il Quaternario. 12:99–104.

Mazza P, Ventra D. 2011. Pleistocene debris-flow deposition of the hippopotamus-bearing Collecurti bonebed (Macerata, Central Italy): Taphonomic and paleoenvironmental analysis. Palaeogeogr Palaeoclimatol Palaeoecol. 310(3–4):296–314. doi: 10.1016/j.palaeo.2011.07.022.

Mecozzi B, Bellucci L, Giustini F, Iannucci A, Iurino DA, Mazzini I, Strani F, Sardella R. 2021. A reappraisal of the Pleistocene mammals from the karst infilling deposits of the Maglie Area (Lecce, Apulia, Southern Italy). Riv Ital Paleontol S. 127(2):355–382.

Mecozzi B, Iannucci A, Mancini M, Sardella R. 2021. Redefining Ponte Molle (Rome, central Italy): an important locality for Middle Pleistocene mammal assemblages of Europe. Alp Mediterr Quat. 34 (1):131–154.

Mecozzi B, Iurino D, Bertè D, Sardella R. 2017. *Canis mosbachensis* (Canidae, Mammalia), from the Middle Pleistocene of Contrada Monticelli (Putignano, Apulia, southern Italy). Bollettino della Società Paleontologica Italiana. 56 (1):71–78.

Mourer-Chauviré C, Bonifay M-F-. 2018. The birds from the Early Pleistocene of Ceyssaguet. Quaternarie. 29(3):183–194.

Orlova LA, Kuzmin YV, Dementiev VN. 2004. A review of the evidence for extinction chronologies for five species of upper Pleistocene megafauna in siberia. Radiocarbon. 46(1):301–314. doi: 10.1017/S0033822200039618.

Pacheco FG, Santiago A, Gutiérrez JM, López-García JM, Blain H-A, Cuenca-Bescós G, van der Made J, Cáceres I, García N. 2011. The Early Pleistocene paleontological site in the Sierra del Chaparral (Villaluenga del Rosario, Cádiz, Southwestern Spain). Quater Internat. 243(1):92–104. doi: 10.1016/j.quaint.2011.05.034.

Palombo MR. 2009. Biochronology of terrestrial mammals and Quaternary subdivisions: a case study of large mammals from the Italian peninsula. Il Quaternario. 22:291–306.

Pandolfi L. 2022. A critical overview on Early Pleistocene Eurasian *Stephanorhinus* (Mammalia, Rhinocerotidae): Implications for taxonomy and paleobiogeography. Quater Internat. 2022:109–120. doi: 10.1016/j.quaint.2022.11.008.

Pandolfi L, Bartolini-Lucenti S, Cirilli O, Bukhsianidze M, Lordkipanidze D, Rook L. 2021. Paleoecology, biochronology, and paleobiogeography of Eurasian Rhinocerotidae during the early Pleistocene: the contribution of the fossil material from Dmanisi (Georgia, southern Caucasus). J Hum Evol. 156:156–103013. doi: 10.1016/j.jhevol.2021.103013.

Pandolfi L, Cerdeño E, Codrea V, Kotsakis T. 2017. Biogeography and chronology of the Eurasian extinct rhinoceros *Stephanorhinus etruscus* (Mammalia, Rhinocerotidae). C R Palevol. 16(7):762–773. doi: 10.1016/j.crpv.2017.06.004.

Pandolfi L, Erten H. 2017. *Stephanorhinus hundsheimensis* (Mammalia, Rhinocerotidae) from the late Early Pleistocene deposits of the Denizli Basin (Anatolia, Turkey). Geobios. 50(1):65–73. doi: 10.1016/j.geobios.2016.10.002.

Pandolfi L, Fiore I, Gaeta M, Szabó P, Vennemann T, Tagliacozzo A. 2018. Rhinocerotidae (Mammalia, Perissodactyla) from the middle Pleistocene levels of Grotta Romanelli (Lecce, southern Italy). Geobios. 51(5):453–468. doi: 10.1016/j.geobios.2018.08.008.

Pandolfi L, Gaeta M, Petronio C. 2013. The skull of *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from the Middle Pleistocene of Campagna Romana (Rome, Central Italy): biochronological and paleobiogeographic implications. Bull Geosci. 88:51–62. doi: 10.3140/bull.geosci.1363.

Pandolfi L, Gasparik M, Piras P. 2015. Earliest occurrence of "*Dihoplus*" *megarhinus* (Mammalia, Rhinocerotidae) in Europe (Late Miocene, Pannonian Basin, Hungary): Palaeobiogeographical and biochronological implications. Ann Paleontol. 101(4):325–339. doi: 10.1016/j.annpal.2015.09.001.

Pandolfi L, Mannino MA, Talamo S, Salari L, Sansò P, Sublimi Saponetti S, Vacca E, Vicari D, Richards MP, Petronio C. 2017. A reassessment of the infills and faunal assemblages of karst cavities known as ventarole in Salento (Apulia, Southern Italy): a multidisciplinary investigation on Cava Donno (Corigliano d'Otranto Lecce). Alp Mediterr Quat. 30:25–40.

Pandolfi L, Marra F. 2015. Rhinocerotidae (Mammalia, Perissodactyla) from the chronostratigraphically constrained Pleistocene deposits of the urban area of Rome (Central Italy). Geobios. 48(2):147–167. doi: 10.1016/j.geobios.2015.02.003.

Pandolfi L, Petronio C. 2011a. The small-sized rhinoceroses from the Late Pleistocene of Apulia (Southern Italy). Rivista Italiana di Paleontologia e Stratigrafia. 117:509–520.

Pandolfi L, Petronio C. 2011b. Stephanorhinus etruscus (Falconer, 1868) from Pirro Nord (Apricena, Foggia, Southern Italy) with notes on the late Early Pleistocene rhinoceroses of Italy. Riv Ital Paleontol S. 117:173–187.

Pandolfi L, Tagliacozzo A. 2015. *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from the Late Pleistocene of Valle Radice (Sora, Central Italy) and re-evaluation of the morphometric variability of the species in Europe. Geobios. 48(2):169–191. doi: 10.1016/j.geobios.2015.02.002.

Pavia M, Zunino M, Coltorti M, Angelone C, Arzarello M, Bagnus C, Bellucci L, Colombero S, Marcolini F, Peretto C, et al. 2012. Stratigraphical and palaeontological data from the Early Pleistocene Pirro 10 site of Pirro Nord (Puglia, south eastern Italy). Quater Internat. 267:40–55. doi: 10.1016/j.quaint.2010.12.019.

Petronio C, Pandolfi L. 2008. *Stephanorhinus hemitoechus* (Falconer, 1868) del Pleistocene superiore dell'area di Melpignano-Cursi e San Sidero (Lecce, Italia). Geol Rom. 41:1–12.

Pieruccini P, Forti L, Mecozzi B, Iannucci A, Yu T-L, Shen C-C, Bona F, Lembo G, Muttillo B, Sardella R, et al. 2022. Stratigraphic reassessment of Grotta Romanelli sheds light on Middle-Late Pleistocene palaeoenvironments and human settling in the Mediterranean. Sci Rep. 12(1):13530. doi:10.1038/s41598-022-16906-9.

Radović P, Radonjić M, Billia E. 2020. Pleistocene rhinoceros from Bogovina Cave: The first report of *Stephanorhinus hundsheimensis* Toula, 1902 (Mammalia, Rhinocerotidae) from Serbia. Palaeontol Electronica. 23(2):a34. doi: 10.26879/985 .

Ricchetti G, Ciaranfi N, Luperto Sinni E, Mongelli F, Pieri P. 1988. Geodinamica ed evoluzione sedimentaria e tettonica dell'avampaese apulo. Memorie Società Geologica Italiana. 41:57–82.

Ros-Montoya S, Martínez-Navarro B, Espigares M-P, Guerra-Merchán A, García-Aguilar JM, Piñero P, Rodríguez-Rueda A, Agustí J, Oms O, Palmqvist P. 2017. A new Ruscinian site in Europe: Baza-1 (Baza basin, Andalusia, Spain). C R Palevol. 16(7):746–761. doi: 10.1016/j.crpv.2017.05.005.

Ruddiman WF, Raymo M, McIntyre A. 1986. Matuyama 41,000-year cycles: North Atlantic Ocean and northern hemisphere ice sheets. Earth and Planetary Science Letters. 80(1–2):117–129.

Ryder OA, Friese C, Greely HT, Sandler R, Saragusty J, Durrant BS, Redford KH. 2020. Exploring the limits of saving a subspecies: The ethics and social dynamics of restoring northern white rhinos (*Ceratotherium simum cottoni*). Conserv Sci Pract. 2(8):e241. doi: 10.1111/csp2.241.

Schvyreva AK. 2015. On the importance of the representatives of the genus *Elasmotherium* (Rhinocerotidae, Mammalia) in the biochronology of the Pleistocene of Eastern Europe. Quater Internat. 379:128–134. doi: 10.1016/j.quaint.2015.03.052.

Sorbelli L, Cherin M, Kostopoulos DS, Sardella R, Mecozzi B, Plotnikov V, Prat-Vericat M, Azzarà B, Bartolini-Lucenti S, Madurell-Malapeira J. 2023. Earliest bison dispersal in Western Palearctic: Insights from the Eobison record from Pietrafitta (Early Pleistocene, central Italy). Quat Sci Rev. 301:107923. doi: 10.1016/j.quascirev.2022.107923.

Stefanelli D, Mecozzi B, Francescangeli R, Girone A, Marino M, Montenegro V, Sardella R, Breda M. 2021. The Fallow deer from Contrada Monticelli (Bari, Southern Italy): the southernmost occurrence of a large *Dama* of the early Middle Pleistocene. Bollettino della Società Paleontologica Italiana. 60(1):55–60.

Stefanelli D, Mecozzi B, Marino M, Girone A, Sardella R, Breda M, Francescangeli R, Montenegro V. 2019. Contrada Monticelli (Castellana Grotte, southern Italy): the southernmost occurrence of the early Middle Pleistocene *Dama* cf. *roberti* (Cervidae, Mammalia). In: Rook L, and Paleodays PL. La Società Paleontologica Italiana a Benevento e Pietraroja. Parte 1: Volume dei riassunti della XIX Riunione annuale SPI (Società Paleontologica Italiana). Abstract volume. Modena: Società Paleontologica Italiana; p. 43.

Stuart AJ, Lister AM. 2007. Patterns of Late Quaternary megafaunal extinctions in Europe and northern Asia. Courier Forschungsinstitut Senckenberg. 259:287–297.

Stuart AJ, Lister AM. 2012. Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of late Quaternary megafaunal extinctions in northern Eurasia. Quat Sci Rev. 51:1–17. doi: 10.1016/j.quascirev.2012.06.007.

Toula F. 1902. Das Nashorn von Hundsheim *Rhinoceros* (Ceratorhinus, Osborn) *hundsheimensis* nov. form. Mit Ausführungen über die Verhältnisse von elf Schädeln von *Rhinoceros* (Ceratorhinus) *sumatrensis*. Abh der Kaiserlich-Königlichen, Geol Reichsanst. 19(1): 1–92. Wien.

Tunstall T, Kock R, Vahala J, Diekhans M, Fiddes I, Armstrong J, Paten B, Ryder OA, Steiner CC. 2018. Evaluating recovery potential of the northern white rhinoceros from cryopreservedsomatic cells. Genome Res. 28 (6):780–788. doi: 10.1101/gr.227603.117.

Uzunidis A, Antoine P-O, Brugal J-F. 2022. A Middle Pleistocene *Coelodonta antiquitatis* praecursor Guérin (1980) (Mammalia, Perissodactyla) from Les Rameaux, SW France, and a revised phylogeny of *Coelodonta* Bronn, 1831. Quat Sci Rev. 288:107594. doi: 10.1016/j.quascirev.2022.107594.

Uzunidis A, Brugal J-P. 2018. Les grands herbivores (Bovines, Equides, Rhinocerotides, Proboscidiens) de la fin du Pleistocene Moyen: la couche 9 de Coudoulous II (Lot, Quercy, Sud-Ouest France). Paleo. 29 (29):223–249. doi: 10.4000/paleo.4194.

Valduga A. 1965. Contributo alla conoscenza delle Murge baresi, Studi Geologici e Morfologici sulla regione pugliese. Bari: Istituto di Geologia e Paleontologia dell'Università di Bari.

Valkvander T, Pečnerová P, Díez-Del-Molino D, Bergström A, Oppenheimer J, Hartmann S, Xenikoudakis G, Thomas JA, Dehasque M, SağlıSağlıCan E, et al. 2021. Million-year-old DNA sheds light on the genomic history of mammoths. Nat. 591(7849):265–269. doi:10.1038/s41586-021-03224-9.

van der Made J. 1998. Ungulates from Gran Dolina (Atapuerca, Burgos, Spain) [La faune des ongulés de la séquence de Gran Dolina (Atapuerca, Burgos, Espagne)]. Quater. 9(4):267–281. doi: 10.3406/quate.1998.1609.

van der Made J. 1999. Ungulates from Atapuerca TD6. J Hum Evol. 37(3–4):389–413. doi: 10.1006/jhev.1998.0264.

van der Made J. 2010. The rhinos from the Middle Pleistocene of Neumark-Nord (Saxony-Anhalt). Veroffentlichungen des Landesamtes fur Archaeologie. 62:432–527.

van der Made J. 2015. The rhinoceros *Stephanorhinus* aff. *etruscus* from the latest Early Pleistocene of Cueva Victoria (Murcia, Spain). Mastia. 1:359–383.