Available online http://amq.aiqua.it
ISSN (print): 2279-7327, ISSN (online): 2279-7335

Alpine and Mediterranean Quaternary, 39 (2), 2026, 1-32 https://doi.org/10.26382/AMQ.2026.06

NEW INSIGHTS FROM PIRRO NORD (SOUTHERN ITALY) ON THE LONG DILEMMA OF EUROPEAN *STEPHANORHINUS ETRUSCUS* AND *STEPHANORHINUS HUNDSHEIMENSIS*

Dario Stefanelli[1], Beniamino Mecozzi[2], Maria Marino[1], Raffaele Sardella[3]

[1]Dipartimento di Scienze della Terra e Geoambientali, Università degli Studi di Bari Aldo Moro, Campus universitario, Bari, Italy.
[2]Independent Research, Roma, Italy.
[3]Dipartimento di Scienze della Terra, Laboratorio PaleoFactory, Università di Roma Sapienza, Roma, Italy

Corresponding author: Dario Stefanelli <dario.stefanelli@uniba.it >

ABSTRACT: This article describes the previously unpublished rhinoceros remains held at the University of Bari Aldo Moro and the University of Ferrara. The sample includes 29 specimens, and the particularly good preservation of a large part of teeth has allowed for a more in-depth investigation of the dental anatomy and inter- and intraspecific variability present in rhinoceroses of the genus *Stephanorhinus*. Previous studies on the Pirro Nord rhinoceros remains have led various authors to attribute them to *S. etruscus* or *S.* cf. *hundsheimensis*. This study uses unpublished remains to resolve this still-open taxonomic question and to better explore the variability present between two very similar species, which share numerous morphological traits, often making attribution difficult or uncertain. *Stephanorhinus etruscus*, a small-sized *S. hundsheimensis* specimen typical of southern Europe, and larger ones of the same species, typically present in northern Europe, have been identified. To interpret the complex taxonomic scenario that emerged from this study, we first evaluated the chronological constraints of the Pirro Nord site, which are partly based on earlier excavations lacking precise stratigraphic documentation. We then examined several evolutionary scenarios that could account for the high morphological and biometric variability observed in the sample: intraspecific variation, dispersal, coexistence, replacement, retention of ancestral traits, evolutionary changes, and hybridization.

Keywords: Dispersal, Early Pleistocene, southern Italy, *Stephanorhinus etruscus, Stephanorhinus hundsheimensis*.

1. INTRODUCTION

1.1. Early Pleistocene rhinoceroses from Europe

During the Early Pleistocene in Europe, different rhinoceros species occupied the European continent. One of these is *Stephanorhinus etruscus* Falconer, 1868, whose presence is documented from the Middle Villafranchian Faunal Unit (FU) of Saint Vallier (Guérin, 1980; Mazza, 1988; van der Made, 2010, 2015), to the Late Villafranchian FU of Tasso (van der Made, 2010, 2015). However, its biochronological limits, both first-and last-appearances have been repeatedly questioned. For example, Pandolfi et al. (2017) proposed to extend the range of *S. etruscus* up to the early Villafranchian, based on the record of Villarroya (La Rioja Province, MN16: de Villalta Comella, 1952; Guérin, 1980; Cerdeño & Alberdi, 2016). Nevertheless, the examined specimens lack sufficiently diagnostic morphological characters for an unequivocal identification therefore, the presence in Europe of *S. etruscus* in the Triversa FU must be considered with caution (Stefanelli et al., 2024).

Another aspect that needs to be considered is the spread of *Stephanorhinus hundsheimensis* Toula, 1902, if it occurred during the Early Pleistocene, and the possible coexistence of these two species during the Late Villafranchian. Historically, the earliest dispersal of *S. hundsheimensis* in Europe was placed around 1.5 Ma, based on the samples of the Italian localities of Pirro Nord (1.6-1.3 Ma) and Pietrafitta (ca. 1.5 Ma), and the almost coeval French sites of Ceyssaguet and Sainzelles (1.4 and 1.45 Ma) (Mazza et al., 1993; Fortelius et al., 1993; Lacombat, 2005). During the last two decades, the revision of the old collections and the description of new samples drew a different scenario, with most of the European records from the late Early Pleistocene sites attributed to *S. etruscus*. Examples are 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 & Erten, 2017), El Chaparral (ca. 1 Ma; Pacheco et al., 2011) and Huescar (ca. 0.9 Ma; Cerdeño, 1993; van der Made, 2010; Pandolfi & Erten, 2017), the French site of Bois-de-Riquet (1.3-1.1 Ma; Bourguignon et al., 2015), and the Italian sites of Imola Basin (latest Villafranchian; Pandolfi & Petronio, 2011), Madonna della Strada (ca. 1.2 Ma; Pandolfi & Petronio, 2011), Pietrafitta (1.6 Ma; van der Made, 2010; Pandolfi & Petronio, 2011; Pandolfi et al., 2015), as well as Pirro Nord (ca. 1.6-1.3 Ma; Pandolfi & Petronio, 2011).

The aim of this work is therefore to provide a comprehensive overview of the rhinoceros fossil material from Pirro Nord through a taxonomic assessment of the new finds from the “Dagostino Collection” housed at the University of Bari Aldo Moro, and the rhinoceros-related specimens housed at the University of Ferrara, both studied here in detail for the first time, and integrating them with data from previously known material studied by other authors. This fossil specimens were morphologically described and measured, and later compared with the main rhinoceros species of the European Pleistocene. The four species reported during the Pleistocene considered here are: the Etruscan rhinoceros, *Stephanorhinus etruscus* (Early Pleistocene); the Hundsheim rhinoceros (or Toula’s rhinoceros), *Stephanorhinus hundsheimensis* (latest Early Pleistocene to Late Pleistocene); the Merck’s rhinoceros (or forest rhinoceros), *Stephanorhinus kirchbergensis*

Jäger, 1835-39 (Middle to Late Pleistocene); the narrow-nosed rhinoceros (or steppe rhinoceros) and *Stephanorhinus hemitoechus* Falconer in Gaudin, 1859 (Middle to Late Pleistocene). Finally, the results of this work could improve our understanding of the biochronology and biogeography, as well as the ecological niches occupied by the different species of *Stephanorhinus* in Mediterranean Europe.

1.2. Remarks on Pirro Nord rhinoceroses

Pirro Nord, located north of the Apulian region (Fig. 1), dates back to the Early Pleistocene and is well known in the scientific community, both for the numerous excavation campaigns that have taken place over the last 50 years, even if discontinuously, and for the large number of vertebrate fossils that have been found and studied (Freudenthal, 1971; De Beaumont, 1979; De Giuli & Torre, 1984; De Giuli et al., 1986; Delfino & Bailon, 2000; Pavia et al., 2012; Petrucci et al., 2013; Duval et al., 2024; Iannucci et al., 2026; Stefanelli et al., 2026, among others). What the site is best known for, however, is the oldest evidence of human presence in Europe (Arzarello et al., 2007). Excavations are still in progress, more than forty years after its discovery and are currently coordinated by the University of Ferrara. Rhinoceros remains from the Pirro Nord have been studied over the past decades, and first attributed to *Stephanorhinus* cf. *hundsheimensis* by Mazza et al. (1993) and later reconsidered as *Stephanorhinus etruscus* by Pandolfi & Petronio (2011). Considering the extensive fieldwork activities conducted at Pirro Nord, coordinated by different universities over time, the fossil material has been dispersed among several institutions, including University of Florence, Sapienza University of Rome, the University Museum of Turin, and the University of Bari Aldo Moro. This aspect becomes important when mammal research is considered, since the results of these studies could be influenced by the fossils examined. Mazza et al. (1993) analysed 19 postcranial remains of Pirro Nord rhinoceroses preserved at the Museum of Geology and Paleontology of the University of Florence. The authors state that the remains of three or four individuals, one of which is a subadult and one a calf, are present in the sample. Despite the presence of some juvenile bones, Mazza et al. (1993) associated these remains with other small-sized rhinoceroses, with *S. etruscus* and *S. hundsheimensis* traits, from Westerhoven (The Netherlands), Pietrafitta (Italy) and Loreto (Italy). According to the authors, although morphologically similar to the limb bones of *S. etruscus*, the few specimens of Pirro Nord seem to be closer to *S. hundsheimensis* in terms of proportions, as also shown by the ratio diagrams included in their study. These small-sized forms with *S. etruscus* - *S. hundsheimensis* affinities lived in a rather restricted period between the Early and Middle Pleistocene (Mazza et al., 1993). Petrucci (2008), in his PhD thesis, examined a small and fragmentary specimen preserved at the University of Turin, consisting of 6 upper teeth, 1 lower tooth, and 1 third metapodial. The material was overall attributed to *S.* cf. *hundsheimensis*. Pandolfi & Petronio (2011) morphologically and biometrically analysed the rhinoceros remains of Pirro Nord preserved at the PaleoFactory Laboratory, Department of Earth Sciences, Sapienza University of Rome (indicated as MPUR), University Museums of Turin (MPUT) and Florence (MPUF). In particular, the small collection of Sapienza University contained a lower molar (MPUR s.n.), a fragmented mandible of a juvenile (MPUR s.n.) and a fourth metacarpal (MPUR s.n.). In the University of Turin, a D^3 (MPUT PU106664), a M^1 (MPUT PU123658), a P_2 (MPUT PU s.n.), and a third metacarpal (MPUT PU106398) were considered. Regarding the finds from the University of Florence and Turin, Pandolfi & Petronio (2011) revised the sample studied by Mazza et al. (1993) and Petrucci (2008) respectively, ascribing the material to the second evolutionary stage of the species *S. etruscus*. Although in a good state of preservation, the finds studied by these authors consist of a few remains and in some cases even of juvenile individuals. Even though the teeth present morphologies more indicative of *S. etruscus*, Pandolfi & Petronio (2011) note the presence of several dental characteristics in common with both *S. etruscus* and *S. hundsheimensis*. Concerning the morphologies of the third metacarpal, one of the most important bones for the taxonomic identification of Quaternary rhinoceroses, the shape of the anterior articular surface is not precisely described (and the images show only the cranial view of the specimen), the posterior one is instead described as sub-elliptical. Even if the Authors indicate this character as indicative of *S. etruscus*, this trait is also observed in *S. hundsheimensis* (Lacombat, 2005; Stefanelli et al., 2024). The size comparisons carried out by Pandolfi & Petronio (2011) show that deciduous lower molars and the third and fourth metacarpals were comparable with the minimum values of *S. etruscus*. Consequently, given the current state of knowledge, there is still uncertainty regarding the taxonomy of the Pirro Nord rhinoceroses and only the study of new remains from the same locality will perhaps be able to help resolve this taxonomic uncertainty. The rhinoceros finds from Pirro Nord studied and entirely listed in Mazza et al. (1993) and in Pandolfi & Petronio (2011) are reported in Supplementary Tab. 1. In light of the open issues on the taxonomic attribution of Pirro Nord rhinoceroses, it seems relevant to study the unpublished samples preserved at University of Bari Aldo Moro, called "Dagostino Collection" and collected during the early 1970s and at the University of Ferrara, collected during the last twenty years or so. The older fossil collections of Pirro Nord, named as “Pieri Collection” and the

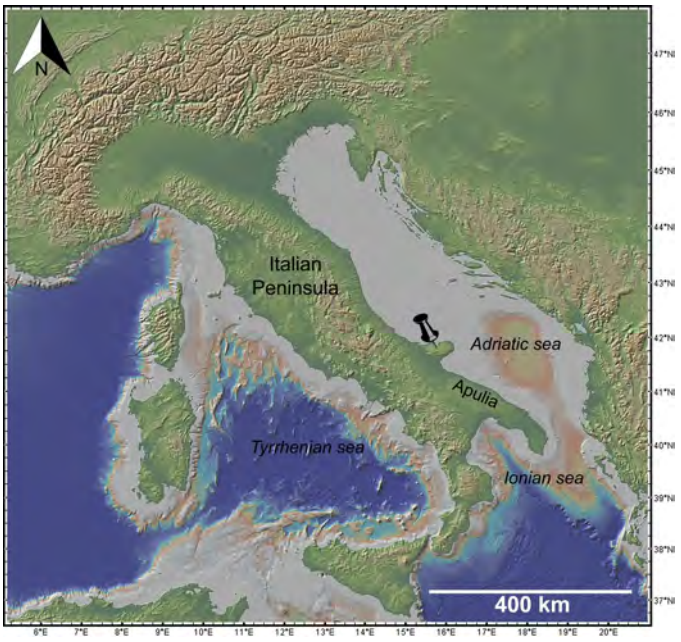


Fig. 1 - Geographic location of the Pirro Nord fossiliferous site (Apulia, southern Italy). The pin symbol indicates the location of the site. The map was produced using GeoMapApp 3.7.8 software.

"Dagostino Collection", were included only in some first works, for example De Giuli et al. (1986), which in a list of taxa found at Pirro Nord, indicate the presence of *Dicerorhinus etruscus* (=*Stephanorhinus etruscus*). Part of the "Pieri Collection" is currently preserved at the University of Florence, while there seems to be no trace of the "Dagostino Collection" until 2021, when it was found in the underground deposits of the Department of Earth and Geoenvironmental Sciences of the University of Bari Aldo Moro. The discovery of the "Dagostino Collection" was announced to the scientific community during the annual congress of the Italian Society of Paleontology (SPI) held in 2023 in Lecce (Stefanelli et al., 2023). The literature search conducted seems to indicate that nothing from this collection has ever been published before its rediscovery. The first two articles on testudinate fossils (Stefanelli et al., 2026) and some hyena fossils (Iannucci et al., 2026) have recently been published.

1.3. Stratigraphic context of the studied sample and chronological framework at Pirro Nord

The chronology of Pirro Nord has recently been called into question, based both on numerical dates obtained for fissure P13 (~0.8 Ma; Duval et al., 2024). In addition, the reported presence of the spotted hyena (*Crocuta crocuta*) in the "Dagostino Collection", associated with the karst fissure named Pirro 3, suggests the existence of presumably younger deposits in the quarry area (Iannucci et al., 2026). The fossil material from the University of Ferrara comes exclusively from P13, whereas the historical collection from the University of Bari Aldo Moro originates from Pirro 1 and Pirro 1c. It is unfortunately not possible to clarify with certainty the meaning of the labels Pirro 1 and Pirro 1c as applied to the specimens in the "Dagostino Collection." Dagostino (1972) describes the karst cavity Pirro 1 as being a few meters wide and 4-5 meters deep, consisting of a series of sub-horizontal sandy and pebbly lenses, each no more than 20-30 cm thick. Fossils were embedded in both types of sedimentary lenses and, in some areas, were sufficiently concentrated to form distinct bone-bearing layers. In general, regarding the rhinoceros specimens held at the University of Bari Aldo Moro, a few noteworthy observations can be made. The "Dagostino Collection" includes material from Pirro 1, Pirro 1b, Pirro 1c, and Pirro 1d; however, it remains unclear whether these labels refer to separate, adjacent fissures or to different stratigraphic levels within the same karst cavity. It is important to note that no rhinoceros specimen examined in this study comes from Pirro 3, a karst fissure deposit identified during the earlier stage of research and where the presence of *Crocuta crocuta* based on the fossil sample stored at University of Bari Aldo Moro has been reported. For the specimens housed at the University of Ferrara, the stratigraphic units of provenance are known, allowing a more detailed assessment of their distribution within P13. In particular, almost all the fossils studied here come from unit of group D, while only one comes from unit of group C. The P13 fissure has been one of the most extensively investigated within the Pirro Nord karst system, particularly from stratigraphic, depositional, and taphonomic perspectives (Arzarello et al., 2012, 2015; Cheheb et al., 2019; Berruti & Arzarello, 2020). The main aim of these studies was to understand the relationships between archaeological and paleontological remains, reconstruct the processes involved in the formation of the deposit, and assess its stratigraphic integrity. The results indicate that the formation of the deposit involved a sequence of interconnected events and do not support the hypothesis of substantial post-depositional reworking or mixing of materials within the fissure (Arzarello et al., 2012, 2015; Cheheb et al., 2019; Berruti & Arzarello, 2020). According to these reconstructions, interactions between humans and mammal carcasses initially took place on the surface, before the remains were subsequently transported into the fissure by gravity-driven sedimentary processes, such as mudflows or earthflows (Cheheb et al., 2019; Berruti & Arzarello, 2020). These events led to the infilling of the fissure with faunal remains, lithic artefacts, sediments, and rock fragments. The presence of trampling-related modifications on lithic artefacts and weathering features on vertebrate bones suggests that these materials may have remained exposed on the surface for some time before being incorporated into the fissure deposit (Cheheb et al., 2019; Berruti & Arzarello, 2020). Furthermore, chemical alterations observed on the remains indicate repeated episodes of water presence within the fissure, although these do not appear to have resulted in substantial reworking or mixing of the assemblages. The P13 fissure is also considered to be closely connected to P10, another important fissure within the Pirro Nord karst network (Pavia et al., 2012). This relationship suggests that different fissures may have been interconnected and potentially active during the same period. However, the limited stratigraphic information available for the fissures investigated during the earliest phases of research prevents this interpretation from being confidently extended to the aforementioned Pirro 1 complex (Pirro 1, Pirro 1b, Pirro 1c, and Pirro 1d). From a depositional perspective, the paleontological and archaeological assemblages of P13 are considered to have accumulated over a relatively short time span, without evidence of substantial subsequent reworking (Pavia et al., 2010, 2012; Arzarello et al., 2012, 2015; Cheheb et al., 2019; Berruti & Arzarello, 2020). As mentioned above, the faunal assemblage of P13 has been extensively studied and includes, according to among others, *Bison* (*Eobison*) *degiulii, Equus altidens, Pachycrocuta brevirostris,* and *Homotherium latidens* (Arzarello et al., 2012, 2015; Pavia et al., 2012; Cheheb et al., 2019). Similarly, fossil remains from Pirro 1 in the "Dagostino Collection", according to De Giuli et al. (1986), include *Ursus etruscus, Pachycrocuta brevirostris, Homotherium latidens, Mammuthus meridionalis, Equus altidens,* and *Bison* (*Eobison*) *degiulii*, as also recently confirmed by a systematic revision carried out by Stefanelli (2025). The broadly similar faunal composition documented in P13 and Pirro 1 suggests a substantial biochronological overlap between the assemblages, consistent with their traditional attribution to the Late Villafranchian (Pavia et al., 2010, 2012; Arzarello et al., 2012, 2015; Cheheb et al., 2019; Berruti & Arzarello, 2020). Nevertheless, the limited stratigraphic information available for the historical collections does not allow the contemporaneity of the depositional events in the different fissures to be firmly established. In this context, the possibility of a chronological discrepancy between the fossil remains and their enclosing sediments, recently proposed by Duval et al. (2024), deserves particular attention. These authors suggest that the dated sedimentary matrix may postdate an earlier accumulation of fossil remains. Importantly, this hypothesis is not necessarily inconsistent with the available taphonomic evidence from P13. Indeed, previous studies indicate that the archaeological and paleontological materials were initially exposed on the surface before being transported into the fissure through gravity-driven sedimentary processes. The relatively short duration inferred for the infilling events and the absence of substantial post-depositional reworking therefore support the stratigraphic integrity of the assemblage, but do not necessarily establish the chronological equivalence of the fossils and their enclosing sediments.

Catalogue numbers	Storage place	Anatomical indication	Portion or fragment	Age	Side	Karst cavity	Stratigraphic unit	Taxonomic assignment in this work
MSTB-PN 20723	University of Bari Aldo Moro	Mandibula	Both horizontal ramus with all teeth	Adult	All	Pirro 1	Unknown	*S. etruscus*
MSTB-PN 20724	University of Bari Aldo Moro	Tooth	P^3	Adult	Left	Pirro 1c	Unknown	*S. hundsheimensis*
MSTB-PN 20725	University of Bari Aldo Moro	Tooth	P^4	Adult	Right	Pirro 1c	Unknown	*S. hundsheimensis*
MSTB-PN 20726	University of Bari Aldo Moro	Tooth	M^2	Adult	Right	Pirro 1c	Unknown	*S. hundsheimensis*
MSTB-PN 20728	University of Bari Aldo Moro	Tooth	M^1	Adult	Left	Pirro 1c	Unknown	*S. hundsheimensis*
MSTB-PN 20729	University of Bari Aldo Moro	Tooth	P^2	Adult	Left	Pirro 1c	Unknown	*S. hundsheimensis*
MSTB-PN 20730	University of Bari Aldo Moro	Tooth	M^2	Adult	Left	Pirro 1c	Unknown	*S. hundsheimensis*
MSTB-PN 20731	University of Bari Aldo Moro	Tooth	P_4	Adult	Left	Pirro 1c	Unknown	*S. hundsheimensis*
MSTB-PN 20732	University of Bari Aldo Moro	Tooth	M_1	Adult	Left	Pirro 1c	Unknown	*S. hundsheimensis*
MSTB-PN 20733	University of Bari Aldo Moro	Tooth	P^4	Adult	Left	Pirro 1c	Unknown	*S. hundsheimensis*
MSTB-PN 20734	University of Bari Aldo Moro	Patella	Complete	Juvenile	Left	Pirro 1	Unknown	*S. etruscus*
MSTB-PN 20735	University of Bari Aldo Moro	Fourth metacarpal	1/2 proximal	Adult	Left	Pirro 1	Unknown	*S.* ex gr. *etruscus/ hundsheimensis*
MSTB-PN 20736	University of Bari Aldo Moro	Second metacarpal	1/2 proximal	Adult	Left	Pirro 1	Unknown	*S. hundsheimensis*
MSTB-PN 20737	University of Bari Aldo Moro	Third meta-carpal	1/2 proximal	Adult	Left	Pirro 1	Unknown	*S. hundsheimensis*
MSTB-PN 20738	University of Bari Aldo Moro	Tooth	M_1	Adult	Left	Pirro 1c	Unknown	*S. hundsheimensis*
P13USC6QB6S105	University of Ferrara	Tooth	Lower tooth fragment		Left	Pirro 13	C6	*Stephanorhinus* sp.
P13USD13QA5S33	University of Ferrara	Tooth	P_2, fragmentary	Adult	Left	Pirro 13	D13	*Stephanorhinus* sp.
P13USD18QB4S98	University of Ferrara	Tooth	$M(^1?)$, possibly part of S336	Adult	Left	Pirro 13	D18	*Stephanorhinus* sp.
P13USD19QB2S131	University of Ferrara	Second metacarpal	Proximal fragment	Adult	Left	Pirro 13	D19	*Stephanorhinus* sp.
P13USD20QC6S71	University of Ferrara	Tooth	D^3, slightly fragmentary	Juvenile	Right	Pirro 13	D20	*S. hundsheimensis*
P13USD22QB5S159	University of Ferrara	Tooth	M_1	Old adult	Left	Pirro 13	D22	*S. etruscus*
P13USD24QC6S241	University of Ferrara	Tooth	M_1	Old adult	Right	Pirro 13	D24	*S. hundsheimensis*
P13USD25QC6S175	University of Ferrara	Tooth	D^2, slightly fragmentary	Juvenile	Left	Pirro 13	D25	*S. hundsheimensis*
P13USD25QC6S336	University of Ferrara	Tooth	M^1, incomplete	Old adult	Left	Pirro 13	D25	*Stephanorhinus* sp.
P13USD26QC4S295	University of Ferrara	Tooth	D^3, fragmentary	Juvenile	Right	Pirro 13	D26	*Stephanorhinus* sp.
P13USD28QC4S437	University of Ferrara	Tooth	P^3, incomplete	Adult	Right	Pirro 13	D28	*Stephanorhinus* sp.
P13USD34QC2S157	University of Ferrara	Tooth	M_1, slightly fragmentary	Adult	Left	Pirro 13	D34	*S. hundsheimensis*
P13USD37QD3S115	University of Ferrara	Tooth	D_3, fragmentary	Juvenile	Right	Pirro 13	D37	*S. hundsheimensis*
P13USD41QD3S164	University of Ferrara	Pisiform	Slightly fragmentary	Adult	Right	Pirro 13	D41	*S. hundsheimensis*

Tab. 1 - List of fossil finds of Rhinocerotidae from Pirro Nord studied in this work.

2. MATERIALS AND METHODS

The rhinoceros sample from Pirro Nord belonging to the "Dagostino Collection" is preserved at the Museum of Earth Sciences of the University of Bari Aldo Moro. The sample consists of 15 remains that are labelled with progressive numbers preceded by the acronym MSTB-PN (Museo di Scienze della Terra Bari-Pirro Nord; Tab. 1). The rhinoceros sample from Pirro Nord, housed in the University of Ferrara and published in this work, consists of 14 dental and postcranial remains (Tab. 1). This material comes entirely from the karst cavity known as Pirro 13 and is studied here for the first time. The specimen ID for each of these finds contains information about the fissure (P13), the stratigraphic unit (e.g., USD19), and the square (e.g., QA5). Overall, the Pirro Nord specimen from the University of Bari Aldo Moro is in better condition and less fragmented than the one from the University of Ferrara, especially regarding the teeth. Therefore, morphological observations and biometric comparisons were mainly carried out on the Bari specimen because it's more complete and better preserved. The morphological descriptions of the dental and skeletal elements follow the nomenclature used in Lacombat (2005, 2006), Ballatore & Breda (2013), Stefanelli et al. (2024) and Kovalchuk et al. (2026). Measurements were taken with a digital calliper to 0.1 mm, following the methodology of Guérin (1980) and Lacombat (2005, 2006). Details of the measurements used here are reported in Supplementary Tabs. 2-9. As comparative material for teeth, biometric data of *Stephanorhinus* spp. was taken from the literature (Fortelius et al., 1993; Guérin, 1980; Handa & Pandolfi, 2016; Pandolfi & Erten, 2017; Pandolfi & Marra, 2015; Radovic et al., 2020). The most important meas-

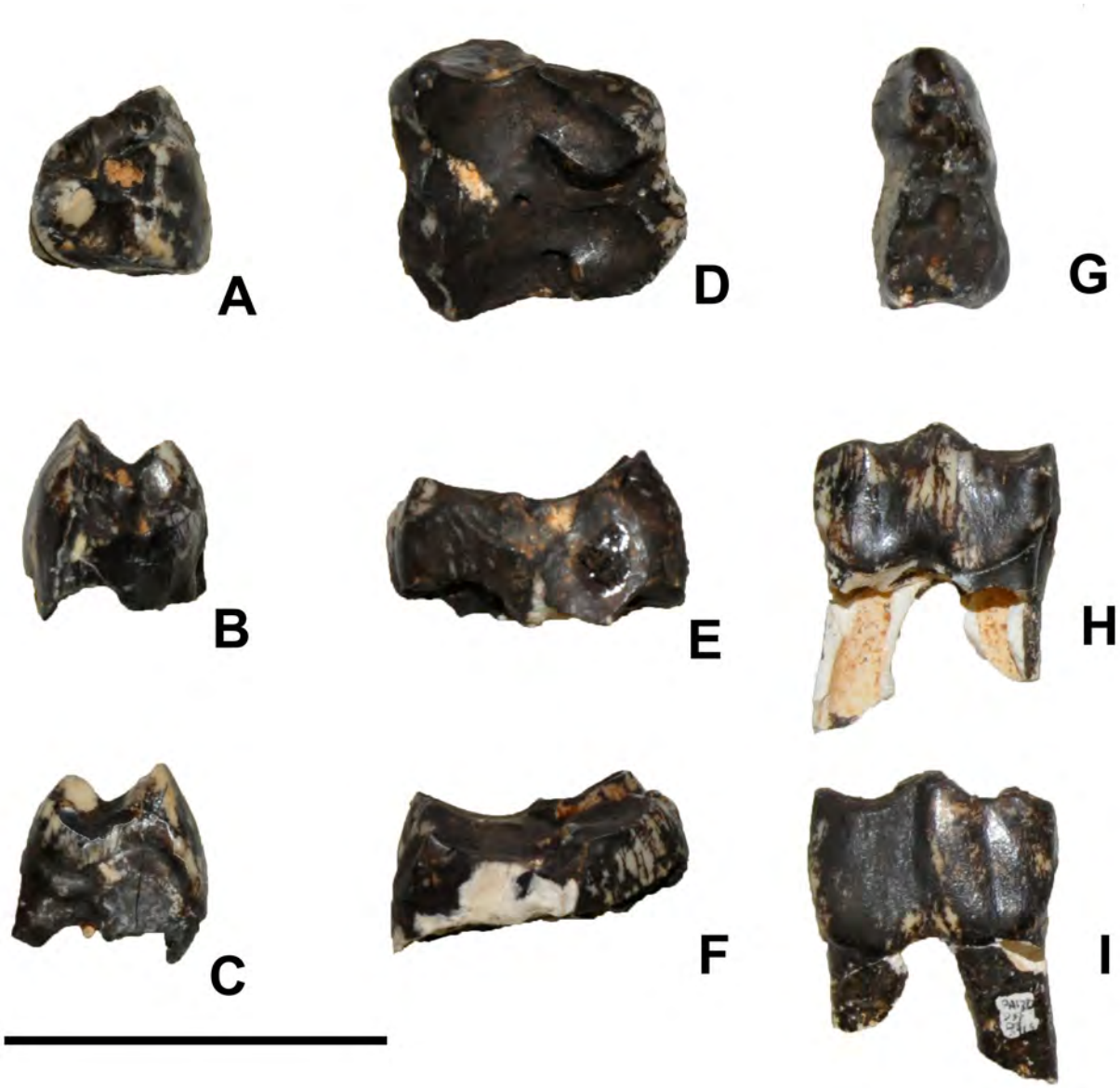


Fig. 2 - Dental remains of *Stephanorhinus hundsheimensis* from Pirro Nord: P13USD25QC6S175, left D^2 in occlusal (A), mesial (B) and distal (C) views; P13USD20QC6S71, right D^3 in occlusal (D), mesial (E) and distal (F) views; P13USD37QD3S115, right D_3 in occlusal (G),

urements for metacarpals have been plotted in scatter diagrams made with PAST v. 5.3 (Hammer et al., 2001). The data used to build the metacarpal scatter diagrams are shown in Supplementary Tabs. 10-12. Specimens affected by uncertain taxonomical attribution (*Stephanorhinus* sp.) have been excluded from the analyses, while the data relating to *Stephanorhinus* cf. *hundsheimensis* from Pietrafitta are reported isolated with their own symbol. This choice is linked both to the uncertain taxonomic identification of this sample and to investigate affinities between two samples (Pietrafitta and Pirro Nord) with a geographical/chronological and possibly taxonomic proximity. Due to the scarcity of comparative literature data, morphological and morphometric comparisons of the patella have been excluded.

3. RESULTS

3.1. Morphological descriptions

Deciduous teeth: P13USD25QC6S175 (Left D^2); P13USD20QC6S71 (Right D^3); P13USD37QD3S115 (Right D_3).

D^2 (P13USD25QC6S175, left; Fig. 2A-C): the tooth is rather well preserved, although slightly fragmented. In occlusal view, a double crochet and a single crista are present. The antecrochet is present and the mediofossetta is closed. A protocone constriction is present. Another notable feature is visible in the distal view (Fig. 2C), in which a hint of a continuous, wavy cingulum is present.

D^3 (P13USD20QC6S71, right; Fig. 2D-F): the tooth is in a fairly good state of preservation, but is significantly worn. In occlusal view, features such as the crochet and crista were not visible. The antecrochet is absent, and the mediofossetta is open. A constriction of the proto-

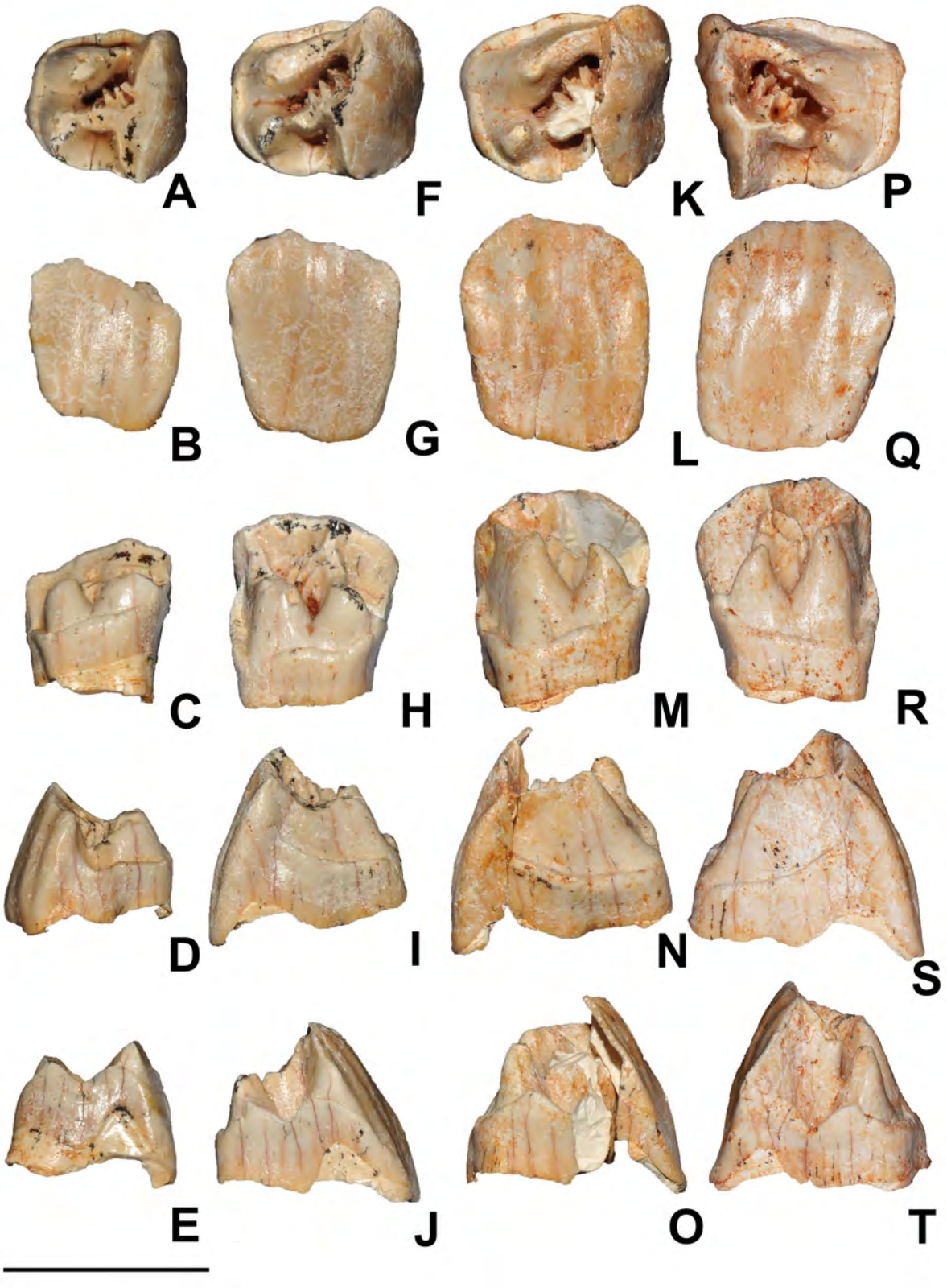


Fig. 3 - Dental remains of *Stephanorhinus hundsheimensis* from Pirro Nord: MSTB-PN 20729, right P^2 (A-E); MSTB-PN 20724, right P^3 (F-J); MSTB-PN 20733, left P^4 (K-O); MSTB-PN 20725, right P^4 (P-T) in occlusal (A, F, K, P), vestibular (B, G, L, Q), lingual (C, H, M, R), mesial (D, I, N, S) and distal (E, J, O, T) views. Scale bar: 5 cm.

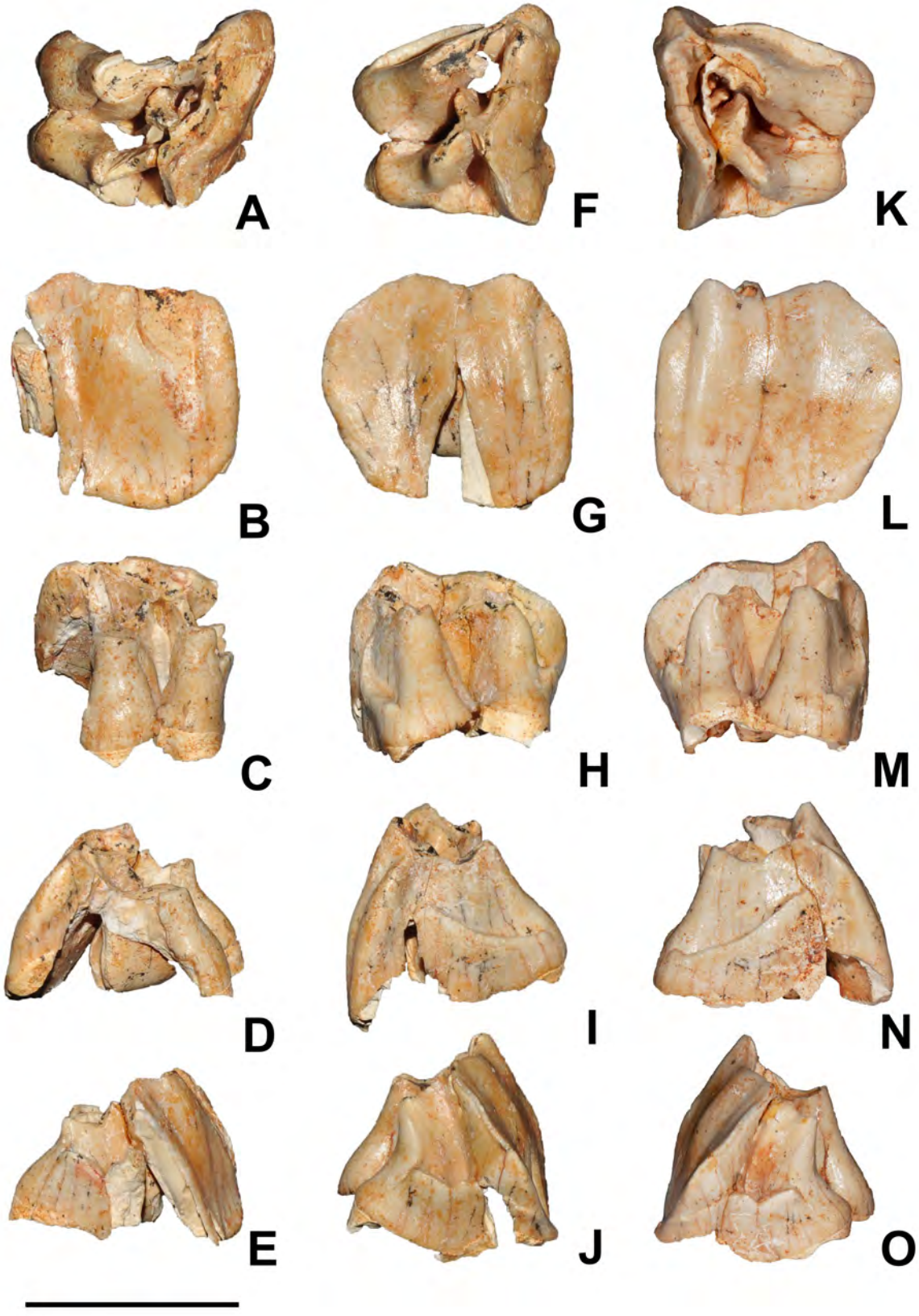


Fig. 4 - Dental remains of *Stephanorhinus hundsheimensis* from Pirro Nord: MSTB-PN 20728, left M^1 (A- E); MSTB – PN 20730, left M^2 (F-J); MSTB – PN 20726, right M^2 (K-O), in occlusal (A, F, K), vestibular (B, G, L), lingual (C, H, M), mesial (D, I, N) and distal (E, J, O) views. Scale bar: 5 cm.

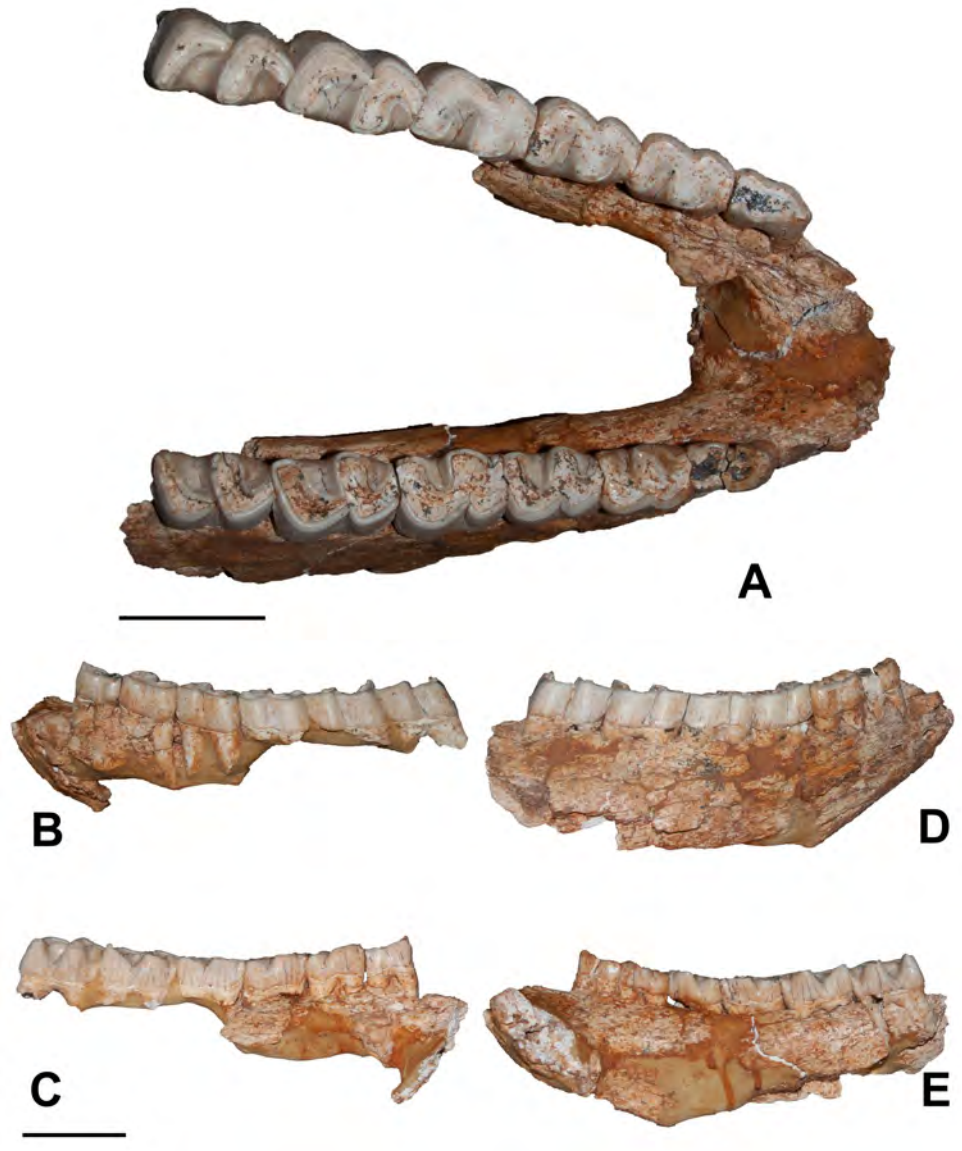


Fig. 5 - Complete mandible of *Stephanorhinus etruscus* from Pirro Nord MSTB-PN 20723 in occlusal (A), left (B) and right (D) vestibular, left (C) and right (E) lingual views. Scale bars: 5 cm.

cone is not present but there are a metacone rib and a short lingual cingulum.

D_3 (P13USD37QD3S115, right; Fig. 2G-I): the tooth is generally in good condition and partially preserved. Both the anterior and posterior valleys are V-shaped, and the difference in height between the valleys is small. No cingulum is present, and the vestibular syncline is open and shallow.

Isolated upper teeth: MSTB-PN 20729 (Left P^2); MSTB-PN 20724 (Left P^3); MSTB-PN 20733 (Left P^4); MSTB-PN 20725 (Right P^4); MSTB-PN 20728 (Left M^1); MSTB-PN 20730 (Left M^2); MSTB-PN 20726 (Right M^2); P13USD28QC4S437 (Right P^3); P13USD25QC6S336 (Left M^1).

P^2 (MSTB-PN 20729, left; Fig. 3A-E): the tooth has a slightly worn crown. In occlusal view, it has a rather square shape with strong and continuous mesial and lingual cingulum. The protocone and hypocone have a conical shape, whereas the vestibular cones form a robust and regular wall. The protocone is free of constriction and the fold of the paracone is slightly marked. The crochet is multiple, the crista and the antecrochet are absent. In vestibular view, the wall is regular in P^2. In lingual view, closed lingual valleys and the inclination of the lingual cingulum can be observed, particularly evident in MSTB-PN 20729. In mesial view, it is clear how the mesial cingulum, always continuous, maintains a horizontal inclination and then curves upward and ends at the paracone. In distal view, the posterior wall closes in a V-shape behind the postfossette. In general, mesial and distal views show a widened base that then progressively narrows towards the end of the crown, with the vestibular and mesial sides tending to converge upwards.

P^3 (MSTB-PN 20724, left; Fig. 3F-J; P13USD28QC4S437, right): the tooth has a very minimally worn crown. In occlusal view, it has a rather square shape with strong and continuous mesial and lingual cingulum. The protocone and hypocone have a conical shape, while the vestibular cones form a wavy wall. The protocone is de-

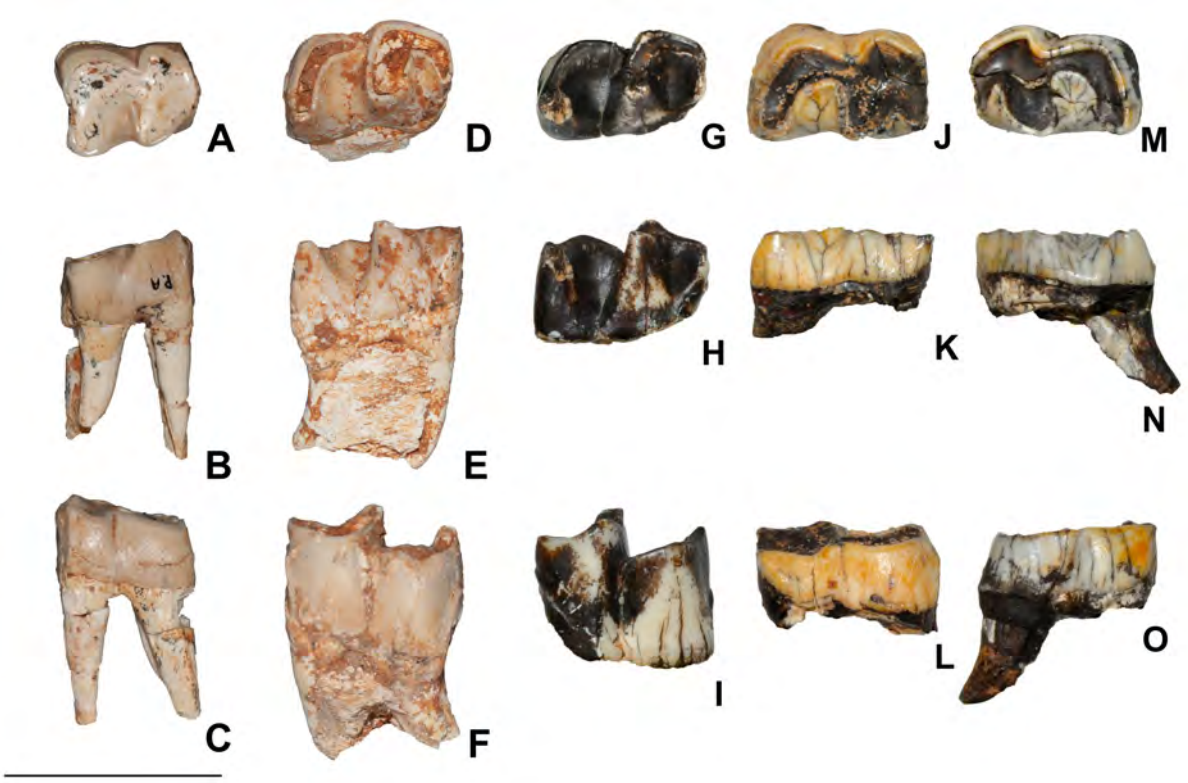


Fig. 6 - Dental remains of *Stephanorhinus etruscus* P13USD22QB5S159, left M_1 (J-L) and *Stephanorhinus hundsheimensis* from Pirro Nord MSTB-PN 20731, left P_4 (A-C), MSTB-PN 20732, left M_1 (D-F), P13USD34QC2S157, left M_1 (G-I), P13USD24QC6S241, right M_1 (M-O), in occlusal (A, D, G, J, M), lingual (B, E, H, K, N) and vestibular (C, F, I, L, O) views. Scale bar: 5 cm.

void of constriction, and the fold of the paracone is slightly marked. The crochet is multiple and both the crista and the antecrochet are absent. The mediofossetta is open. In vestibular view, the wall is wavy in P^3. In lingual view, the closed lingual valleys and the inclination of the lingual cingulum can be observed. In mesial view, it is clear how the mesial cingulum, always continuous, maintains a horizontal inclination and then curves upward and ends at the paracone. In distal view, the posterior wall closes in a V-shape behind the postfossetta. In general, mesial and distal views show a widened base that then progressively narrows towards the end of the crown, with vestibular and mesial sides tending to converge upwards.

P^4 (MSTB-PN 20733, left; Fig. 3K-O; MSTB-PN 20725, right; Fig. 3P-T): the tooth has a very minimally worn crown. In occlusal view, it has a rather square shape with strong and continuous mesial and lingual cingulum. The protocone and hypocone have a conical shape, while the vestibular cones form a wavy wall. The protocone is devoid of constriction, and the paracone fold is marked. The crochet is multiple and both the crista and the antecrochet are absent. The mediofossetta is open. In vestibular view, the wall is wavy in P^4. In lingual view, the closed lingual valleys and the inclination of the lingual cingulum can be observed, particularly evident in MSTB-PN 20733. In mesial view, it is clear how the mesial cingulum, always continuous, maintains a horizontal inclination, then curves upward, and ends on the paracone. In distal view, the posterior wall closes in a V-shape behind the postfossetta. In general, mesial and distal views reveal a broad base that then progressively narrows towards the end of the crown, with the vestibular and mesial sides tending to converge upward. MSTB-PN 20725 presents interesting peculiarities such as a large secondary mid-pouch (see Ballatore & Breda, 2013) and multiple crochets, of which the one closest to the side wall is bifid.

M^1 (MSTB-PN 20728, left; Fig. 4A-E; P13USD25Q-C6S336, left): the tooth is in fair condition, with fractured mesial and distal portions and slight wear on the chewing surface. In occlusal view, the teeth are trapezoidal in shape, with a broader base on the vestibular side. In contrast to the premolars, the protocone and hypocone are well connected to the vestibular cones (toward which they tend to be inclined), while remaining clearly separated from each other. The mesial cingulum is present, and the lingual and vestibular ones are absent and the distal one could not be evaluated. The vestibular wall appears wavy, and the paracone fold is marked. The crochet and crista are present and single, while the antecrochet is absent (MSTB-PN 20728) or present (P13USD25Q C6S336). The anterior fossa and postfossetta are quite wide and deep. The mediofossetta is closed in M^1, while the protocone constriction is absent. In vestibular view, the external wall is wavy. In lingual view, MSTB-PN 20728 has an open lingual valley, unlike what is observed in premolars. In mesial and distal view, M^1 shows, similarly to what was found in premolars, a widening of the base and a convergence of the vestibular and lingual sides towards the end of the crown.

M^2 (MSTB-PN 20730, left; Fig. 4F-J; MSTB-PN 20726, right; Fig. 4K-O): the teeth are in a fairly good state of preservation, with a slight degree of wear on the chewing surface. In occlusal view, the teeth are trapezoidal in shape, with a broader base on the vestibular side. The protocone and hypocone are well connected to the vestibular cones (toward which they tend to be inclined), while remaining clearly separated from each other. The vestibular wall appears wavy, and the paracone fold is marked. The crochet is present as single (MSTB-PN 20730) or multiple (MSTB-PN 20726). The crista is single (MSTB-PN 20726) or absent (MSTB-PN 20730) and

the antecrochet is absent. The anterior fossa and postfossetta are rather wide and deep. The mediofossetta is open, and the protocone constriction is present. In vestibular view, the outer wall is wavy. In lingual view, the lingual valley is open. In mesial and distal view, M^2 shows, similarly to what was found in premolars, a widening of the base and a convergence of the vestibular and lingual sides towards the end of the crown.

Mandible: MSTB-PN 20723 (Left: P_2-M_3; Right: P_2-M_3).

Overall, the mandible (Fig. 5) has a complete lower dentition and is in excellent condition. On the vestibular side of each tooth, the enamel surface is very weakly wrinkled. The mandibular body is incomplete and fractured: the ascending branches are not present, and the corpus ends behind the M_3. The mandibular symphysis is present rostrally, even if its most anterior part is missing. Its rear edge is located below P_2, but in a rather rearward position, almost near the P_2-P_3 interval.

The teeth (left and right) are described below:

P_2: due to its wear, the shape of the posterior valley cannot be observed. There are no cingula. The vestibular synclinal is open and very shallow.

P_3: due to its wear, the shape of the anterior valley cannot be observed. The posterior valley is V-shaped rather wide, but with the anterior branch clearly more inclined than the posterior one. There are no cingula. The vestibular synclinal is closed and shallow.

P_4: the anterior valley is in a very advanced position, and the base is barely visible, given its wear. The posterior valley is V-shaped. The difference in height between the bases of the lingual valleys is slight. There are no cingula. The vestibular synclinal is closed and shallow.

M_1: due to its wear, only the presence of the base of the anterior valley can be seen. The posterior valley is V-shaped. The difference in height between the valley bases is medium-high. There are no cingula. The vestibular synclinal is closed and shallow.

M_2: both the anterior and posterior valleys are U-shaped. The difference in height between the bases of the lingual valleys is medium. There is a weak vestibular cingulum in mesial position; other cingula are not present. The vestibular synclinal is closed and shallow.

M_3: both the anterior and posterior lingual valleys are rather narrow U-shaped. The difference in height between the bases of the valleys is medium. There is a vestibular cingulum nod in mesial position and a weak but continuous distal cingulum. The vestibular synclinal is deep and almost right-angled.

Isolated lower teeth: MSTB-PN 20731 (Left P_4); MSTB-PN 20732 (Left M_1); MSTB-PN 20738 (Left M_1); P13USD34QC2S157 (Left M_1); P13USD22QB5S159 (Left M1); P13USD24QC6S241 (Right M_1).

P_4 (MSTB-PN 20731, left; Fig. 6A-C): the tooth is in excellent condition, and the root is almost completely preserved. The enamel is entirely present, and it completely envelops the tooth, except in its mesial part, in correspondence with which it runs out. The overall wear is quite high and the anterior lingual valley is not visible, while the posterior valley is shaped like a narrow U. On the side, the surface of the enamel is rough, and there is a discontinuous but rather marked lateral cingulum. The vestibular synclinal is deep and closed.

M_1 (MSTB-PN 20732, left; Fig. 6D-F; MSTB-PN 20738, left; P13USD34QC2S157, left; Fig. 6G-I; P13USD22QB5S159, left; Fig. 6J-L; P13USD24QC6S241, right; Fig. 6M-O): the anterior lingual valley is visible only in MSTB-PN 20732 and has a wide V shape, while the posterior one is V-shaped (MSTB-PN 20732 and P13USD24QC6S241) or wide V (MSTB-PN 20738 and P13USD22QB5S159). The difference in height between the valley bases is medium (P13USD22QB5S159) or high (MSTB-PN 20732, MSTB-PN 20738 and P13USD24QC6S241). The mesial cingulum is present (MSTB-PN 20732, MSTB-PN 20738 and P13USD24QC6S241) or absent (P13USD22QB5S159), the lingual cingulum is always absent, the vestibular cingulum is absent (MSTB-PN 20732, MSTB-PN 20738 and P13USD24QC6S241) or present (P13USD22Q-B5S159) and the distal cingulum is present (MSTB-PN 20732, MSTB-PN 20738 and P13USD24QC6S241) or absent (P13USD22QB5S159). The vestibular synclinal is at 90° and shallow (MSTB-PN 20732 and MSTB-PN 20738) or open and deep (P13USD22QB5S159 and P13USD24QC6S241).

Pisiform: P13USD41QD3S164, right (Supplementary Fig. 1)

The bone is in a fairly good state of preservation, although some surfaces, such as the medial one, are quite abraded. In proximal view, the bone displays a markedly arched shape with a subtrapezoidal articular surface and a triangular one. In lateral view, the posterior margin is widened, giving the bone a racket-like shape with well-rounded edges. No further significant details are found in the other views.

Second metacarpal: MSTB-PN 20736, left (Fig. 7A-C); P13USD19QB2S131, left.

Only the proximal half of the bone is preserved, with a good state of conservation. In proximal view, the articular surface for the trapezius exhibits a trapezoidal shape and is elongated anteroposteriorly and larger in the posterior half than in the anterior. At the posterior end of the epiphysis there is a well-developed tuberosity. In lateral view, the articular surface for the magnum has the appearance of a long straight band with the anterior portion widening to a sub-circular shape. On this last surface in MSTB-PN 20736, some small signs of osteopathology, especially exostoses, are visible. Exostoses are new bone formations on the surface of a bone, caused by inflammation of the periosteum and appear as bumps or protuberances on an area that is expected to be smooth or relatively flat and can be caused by conditions related to mechanical stress (Stilson et al., 2016). Arthritis can cause the formation of bony exostoses. The proximal edge that separates it from the articular surface for the trapezius is marked and slightly convex. The articular lateral surface with the third metacarpal is subelliptical, large and elongated in a proximal-distal direction. The surface of the diaphysis shows a marked crest, and the section of the diaphysis is trapezoidal.

Third metacarpal: MSTB-PN 20737, left (Fig. 7D-F).

The preserved portion of bone (the proximal half) is in a good state of preservation. In proximal view, the articular surface for the magnum is sub-trapezoidal in shape and has a marked lateral indentation. The anterior margin of the proximal epiphysis is slightly convex. In cranial view, the proximal-lateral tuberosity is not very marked, so much so that the angle between its lower edge and the diaphysis is almost flat. Laterally, there are two articular surfaces to the fourth metacarpal: the anterior one is trapezoidal in shape and is higher than the posterior one, which is semi-circular in shape. The two articular surfaces are similar in size and well separated from each other. In medial view, near the proximal edge of the epiphysis, in a rather backward position, a small surface, semilunar in shape, for the second metacarpal occurs. The diaphysis has an elliptical section.

Fourth metacarpal: MSTB-PN 20735, left (Fig. 7G-I).

In this case too, the proximal half of the bone has been preserved and is in a good state of preservation. In



Fig. 7 - Postcranial remains of *Stephanorhinus hundsheimensis* from Pirro Nord: MSTB – PN 20736, left second metacarpal (A-C); MSTB – PN 20737, left third metacarpal (D-F) and *Stephanorhinus* ex gr. *etruscus*/*hundsheimensis* MSTB – PN 20735, left fourth metacarpal (G-I) in anterior (A, D, G), occlusal (B, E, H), lateral (C, F) and medial (I) views. Scale bar: 5 cm.

P^2					
Species / Character	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20729
Crochet	Single, rarely double (Guérin, 1980); Single (Lacombat, 2006; Kovalchuk et al., 2026)	Single or double (Lacombat, 2006); Single or double, rarely absent (Ballatore & Breda, 2013); Single (Kovalchuk et al., 2026)	Single, more rarely double or absent (Guérin, 1980); Single (Lacombat, 2006; Kovalchuk et al., 2026)	Single (Guérin, 1980); Single or double (Lacombat, 2006); Single or multiple (Kovalchuk et al., 2026)	Multiple
Crista	Single, more rarely absent (Guérin, 1980); Absent or single (Lacombat, 2006)	Absent or single, rarely multiple (Lacombat, 2006); Double, more rarely single or multiple (Ballatore & Breda, 2013)	Absent or single (Guérin, 1980); Single (Lacombat, 2006)	Single (Guérin, 1980; Lacombat, 2006)	Absent
Antecrochet	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent, more rarely present (Lacombat, 2006); Absent (Ballatore & Breda, 2013)	Absent, rarely present (Guérin, 1980; Lacombat, 2006)	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent
Mesial cingulum	Present (Lacombat, 2006)	Present (Lacombat, 2006; Ballatore & Breda, 2013)	Present (Lacombat, 2006)	Present (Lacombat, 2006)	Present
Lingual cingulum	Present (Guérin, 1980; Lacombat, 2006)	Present (Lacombat, 2006; Ballatore & Breda, 2013)	Present, more rarely absent (Guérin, 1980); Present (Lacombat, 2006)	Present (Guérin, 1980; Lacombat, 2006)	Present
Vestibular cingulum	Absent (Lacombat, 2006)	Absent (Lacombat, 2006; Ballatore & Breda, 2013)	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent
Distal cingulum	Absent (Lacombat, 2006)	Absent (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent
Medio-fossetta	Open, rarely closed (Guérin, 1980); Open (Lacombat, 2006)	Slightly open or slightly closed (Lacombat, 2006); Open, more rarely closed (Ballatore & Breda, 2013)	Open, rarely closed (Guérin, 1980); Open or closed (Lacombat, 2006)	Open, rarely closed (Guérin, 1980); Slightly open or slightly closed (Lacombat, 2006)	Open
Constriction of the protocone	Absent (Guérin, 1980; Lacombat, 2006; Kovalchuk et al., 2026)	Absent (Lacombat 2006; Ballatore & Breda 2013; Kovalchuk et al., 2026)	Absent (Guérin, 1980; Lacombat, 2006; Kovalchuk et al., 2026)	Absent (Guérin, 1980; Lacombat, 2006; Kovalchuk et al., 2026)	Absent
Paracone fold	Little marked (Guérin, 1980); Absent (Lacombat, 2006)	Little marked (Lacombat 2006; Ballatore & Breda 2013)	Marked (Guérin, 1980; Lacombat, 2006)	Little marked (Guérin, 1980)	Little marked
External wall profile	Convex (Guérin, 1980); Regular (Lacombat, 2006)	Regular (Lacombat, 2006)	Regular (Lacombat, 2006)	Slighty convex (Guérin, 1980); Regular (Lacombat, 2006)	Regular

Tab. 2 - Main morphological characters of P^2 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

proximal view, the articular surface for the hamate is very broad, highly irregular and wavy in shape, with a clear rise in the lateral part. The anterior margin of the epiphysis is rather straight. In cranial view, three clear longitudinal grooves parallel to the major axis of the bone are visible on the proximal lateral part. In medial view, the two articular surfaces for the third metacarpal are visible: the anterior one is wide and sub-triangular in shape with rounded corners; the posterior one is reduced and sub-elliptical in shape. The two surfaces are well separated from each other.

Patella: MSTB-PN 20734, left (Supplementary Fig. 2).

The bone is complete and in excellent condition. The cranial surface is convex and irregular. On the side, the front edge is straight. Caudally, the two articular surfaces are present with the femur in a rather high and slightly concave position. They are separated by a marked sinuous crest.

3.2. Morphological comparison

D^2: the typical morphology of this tooth reveals rather distinctive details. In fact, according to Lacombat (2006), the crochet is normally single in Pleistocene species of *Stephanorhinus*; however in *S. hundsheimensis* it can appear in different forms, just like in this case of P13USD25QC6S175 where it is double. The presence of the antecrochet is also indicative; in fact, it is typically absent, but can be observed on *S. hundsheimensis*. The presence of a faintly hinted posterior cingulum is quite peculiar.

D^3: the distinguishable morphological characters in P13USD20QC6S71 are quite indicative for a taxonomic attribution. The antecrochet, absent in P13USD20QC6S71, is typically absent also in other Pleistocene *Stephanorhinus* species, except in *S. etruscus*, which may exhibit this character (Lacombat, 2006). The lingual cingulum is present, as is typical for *S. hundsheimensis* and *S. hemitoechus*, whereas it is absent in *S. etruscus*

P^3						
Species / Character	***S. etruscus***	***S. hundsheimensis***	***S. hemitoechus***	***S. kirchbergensis***	**MSTB-PN 20724**	**P13USD28 QC4S437**
Crochet	Single, rarely double (Lacombat, 2006); Single, rarely double, sometimes multiple (Guérin, 1980; Ballatore & Breda, 2013); Single (Kovalchuk et al., 2026)	Double, rarely single (Lacombat, 2006); Single, double, rarely multiple (Ballatore & Breda, 2013); Single (Kovalchuk et al., 2026)	Multiple or single (Guérin, 1980); Single, rarely double (Lacombat, 2006); Single (Kovalchuk et al., 2026)	Single or double (Guérin, 1980); Multiple (Lacombat, 2006); Single (Kovalchuk et al., 2026)	Multiple	–
Crista	Single or absent (Guérin, 1980); Absent or single (Lacombat, 2006; Kovalchuk et al., 2026)	Single or double (Lacombat, 2006); Single, double, rarely multiple or absent (Ballatore & Breda, 2013); Single (Kovalchuk et al., 2026)	Single or absent, rarely multiple (Guérin, 1980); Absent, more rarely single (Lacombat, 2006); Single (Kovalchuk et al., 2026)	Single or absent (Guérin, 1980); Absent (Lacombat, 2006); Single (Kovalchuk et al., 2026)	Absent	–
Antecrochet	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent, rarely present (Lacombat, 2006); Absent (Ballatore & Breda, 2013)	Absent, rarely present (Guérin, 1980); Absent or present (Lacombat, 2006)	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent	–
Mesial cingulum	Present (Lacombat, 2006)	Present (Lacombat 2006; Ballatore & Breda, 2013)	Present (Lacombat, 2006)	Present (Lacombat, 2006)	Present	–
Lingual cingulum	Present, rarely absent (Guérin, 1980); Present (Lacombat, 2006)	Present (Lacombat, 2006; Ballatore & Breda, 2013)	Present, more rarely absent (Guérin, 1980); Present (Lacombat, 2006)	Present or absent (Guérin, 1980); Present (Lacombat, 2006)	Present	–
Vestibular cingulum	Absent (Lacombat, 2006)	Absent (Lacombat, 2006; Ballatore & Breda 2013)	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent	Absent
Distal cingulum	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent	Absent
Medio-fossetta	Open, rarely closed (Guérin, 1980); Open (Lacombat, 2006)	Open or closed (Lacombat, 2006); Open, rarely closed (Ballatore & Breda 2013)	Open, rarely closed (Guérin, 1980); Open or closed (Lacombat, 2006)	Open, rarely closed (Guérin, 1980); Open (Lacombat, 2006)	Open	–
Constriction of the protocone	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Ballatore & Breda, 2013; Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent, rarely present (Guérin, 1980); Present (Lacombat, 2006); Absent (Kovalchuk et al., 2026)	Absent	–
Paracone fold	Little marked (Guérin, 1980; Lacombat, 2006)	Little marked (Lacombat, 2006) Little marked, rarely marked (Ballatore & Breda, 2013)	Marked (Guérin, 1980; Lacombat, 2006)	Little marked (Guérin, 1980); Absent (Lacombat, 2006)	Little marked	Little marked
External wall profile	Slightly convex (Guérin, 1980; Lacombat, 2006)	Wavy (Lacombat, 2006)	Wavy (Guérin, 1980); Highly irregular (Lacombat, 2006)	Slightly convex (Guérin, 1980; Lacombat, 2006)	Wavy	Wavy

Tab. 3 - Main morphological characters of P^3 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

and may be present in *S. kirchbergensis* (Kovalchuk et al., 2026). The metacone rib is present, as seen in *S. etruscus* and *S. hundsheimensis*, while it may be present in *S. kirchbergensis* and is absent in *S. hemitoechus* (Kovalchuk et al., 2026).

D_3: The morphological characters recognized on P13USD37QD3S115, such as the V-shaped morphology of the valleys, the small difference in height between their bottoms and the open and shallow vestibular synclinal, make this tooth related to *S. hundsheimensis* based on the characteristics described by Lacombat (2006). Also, in this case *S. etruscus* has rather similar morphologies; however, the difference in height between the valley bottoms in this species is clear.

P^2: the overall morphology of this tooth does not present particularly significant differences between the

P^4						
Species / Character	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20725	MSTB-PN 20733
Crochet	Single, rarely multiple (Guérin, 1980); Single (Lacombat, 2006; Kovalchuk et al., 2026)	Single, rarely double (Lacombat, 2006); Single, double or rarely multiple (Ballatore & Breda, 2013); Single (Kovalchuk et al., 2026)	Single, rarely absent (Guérin, 1980); Single, rarely double (Lacombat, 2006); Single (Kovalchuk et al., 2026)	Single or double (Guérin, 1980; Lacombat, 2006); Single (Kovalchuk et al., 2026)	Multiple	Multiple
Crista	Single, rarely multiple, or absent (Guérin, 1980); Single (Lacombat, 2006)	Single, rarely absent (Lacombat, 2006); Single, double, more rarely multiple or absent (Ballatore & Breda, 2013)	Single or absent (Guérin, 1980); Single, rarely absent (Lacombat, 2006)	Single, more rarely absent (Guérin, 1980); Single or absent (Lacombat, 2006)	Absent	Absent
Antecrochet	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent, rarely present (Lacombat, 2006); Absent (Ballatore & Breda, 2013)	Absent, more rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent	Absent
Mesial cingulum	–	Present, more rarely absent (Lacombat, 2006)	Present, more rarely absent (Lacombat, 2006)	–	Present	Present
Lingual cingulum	Present, rarely absent (Guérin, 1980; Lacombat, 2006)	Present, rarely absent (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Present, more rarely absent (Guérin, 1980); Present or absent (Lacombat, 2006)	Present, more rarely absent (Guérin, 1980); Absent (Lacombat, 2006)	Present	Present
Vestibular cingulum	Absent (Kovalchuk et al., 2026)	Absent (Ballatore & Breda, 2013; Kovalchuk et al., 2026)	Absent (Kovalchuk et al., 2026)	Absent (Kovalchuk et al., 2026)	Absent	Absent
Distal cingulum	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent	Absent
Medio-fossetta	Absent or closed (Guérin, 1980); Open (Lacombat, 2006)	Open, rarely closed (Lacombat, 2006; Ballatore & Breda, 2013)	Open, rarely closed (Guérin, 1980; Lacombat, 2006)	Open, rarely closed (Guérin, 1980); Open (Lacombat, 2006)	Open	Open
Constriction of the protocone	Present or absent (Guérin, 1980; Lacombat, 2006)	Absent, rarely present (Lacombat, 2006); Generally absent or weak (Ballatore & Breda, 2013)	Absent, rarely present (Guérin, 1980)	Absent, more rarely present (Guérin, 1980); Present (Lacombat, 2006)	Absent	Absent
Paracone fold	Little marked (Guérin, 1980; Lacombat, 2006) Little marked or absent (Kovalchuk et al., 2026);	Marked (Lacombat, 2006); Little marked, rarely marked (Ballatore & Breda, 2013); Little marked (Kovalchuk et al., 2026)	Marked (Lacombat, 2006); Little marked (Kovalchuk et al., 2026)	Little marked (Guérin, 1980); Absent (Lacombat, 2006); Marked or little marked (Kovalchuk et al., 2026)	Marked	Marked
External wall profile	Regular (Guérin, 1980); Slightly convex (Lacombat, 2006)	Wavy (Lacombat, 2006)	Highly wavy (Guérin, 1980; Lacombat, 2006)	Slightly wavy (Guérin, 1980); Wavy (Lacombat, 2006)	Wavy	Wavy

Tab. 4 - Main morphological characters of P^4 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

four Pleistocene species of *Stephanorhinus* (Tab. 2). However, in the case of MSTB-PN 20729, the presence of a weakly developed paracone fold occurred mostly in *S. hundsheimensis* and *S. kirchbergensis* according to Lacombat (2006) and Ballatore & Breda (2013). However, Guérin (1980) associates a weakly developed paracone fold also with *S. etruscus*. The presence of a multiple crochet in MSTB-PN 20729 appears to be quite particular. Indeed, according to Kovalchuk et al. (2026), this trait has been documented in both *S. kirchbergensis* and the newly described Pliocene species *Scythicorhinus vekua*.

P^3: the morphology differs slightly between the four *Stephanorhinus* species (Tab. 3). MSTB-PN 20724 generally exhibits morphologies more associated with *S. hundsheimensis* and *S. etruscus*. In this case too, a multiple crochet is present, a rather rare feature in the two species mentioned.

P^4: the morphological characters of P^4s tend to be quite similar between the various species (Tab. 4), except for *S. kirchbergensis,* which shows major differences such as the absence of the lingual cingulum, the

M^1						
Species / Character	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20728	P13USD25 QC6S336
Crochet	Single, rarely absent (Guérin, 1980); Single (Lacombat, 2006; Kovalchuk et al., 2026)	Single (Lacombat, 2006; Kovalchuk et al., 2026); Single, rarely double (Ballatore & Breda, 2013)	Single, rarely multiple (Guérin, 1980); Single or double (Lacombat, 2006); Single (Kovalchuk et al., 2026)	Single, rarely multiple (Guérin, 1980); Single (Lacombat, 2006; Kovalchuk et al., 2026)	Single	–
Crista	Absent, rarely single (Guérin, 1980); Absent, rarely double (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent, single or rarely double (Lacombat, 2006); Ballatore & Breda, 2013); Absent (Kovalchuk et al., 2026)	Single or absent (Guérin, 1980); Absent, single or double (Lacombat, 2006); Absent (Kovalchuk et al., 2026)	Single or absent (Guérin, 1980); Absent, rarely single (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Single	–
Antecrochet	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent, rarely present (Lacombat, 2006; Ballatore & Breda, 2013)	Absent, more rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent, more rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent	Present
Mesial cingulum	Present (Lacombat, 2006)	Present, rarely absent (Lacombat, 2006)	Present (Lacombat, 2006)	Present (Lacombat, 2006)	–	Present
Lingual cingulum	Present, more rarely absent (Guérin, 1980); Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent, rarely present (Lacombat, 2006); Present (Ballatore & Breda, 2013; Kovalchuk et al., 2026)	Absent, more rarely present (Guérin, 1980); Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent, more rarely present (Guérin, 1980); Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent	Absent
Vestibular cingulum	Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Kovalchuk et al., 2026); Absent, rarely single (Ballatore & Breda, 2013)	Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent	–
Distal cingulum	Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent (Lacombat, 2006); Present (Ballatore & Breda, 2013; Kovalchuk et al., 2026)	Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	–	–
Mediofossetta	Open, rarely closed (Guérin, 1980); Open (Lacombat, 2006)	Open, rarely closed (Lacombat, 2006; Ballatore & Breda, 2013)	Open, rarely closed (Guérin, 1980); Open (Lacombat, 2006)	Open, rarely closed (Guérin, 1980); Open (Lacombat, 2006)	Closed	Closed
Constriction of the protocone	Present, rarely absent (Guérin, 1980); Present (Lacombat, 2006; Kovalchuk et al., 2026)	Absent, rarely present (Lacombat, 2006); Absent or present (Ballatore & Breda, 2013); Present (Kovalchuk et al., 2026)	Present or absent (Guérin, 1980); Absent, rarely present (Lacombat, 2006); Absent (Kovalchuk et al., 2026)	Present or absent (Guérin, 1980); Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent	Absent
Paracone fold	Little marked (Guérin, 1980; Lacombat, 2006); Little marked or absent (Kovalchuk et al., 2026)	Marked (Lacombat, 2006; Ballatore & Breda, 2013); Little marked (Kovalchuk et al., 2026)	Highly marked (Guérin, 1980; Lacombat, 2006); Little marked (Kovalchuk et al., 2026)	Marked or little marked (Kovalchuk et al., 2026)	Marked	Marked
External wall profile	Little wavy (Guérin, 1980)	–	Highly wavy (Guérin, 1980)	Little wavy (Guérin, 1980); Wavy (Lacombat, 2006)	Wavy	–

Tab. 5 - Main morphological characters of M^1 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

presence of the protocone constriction and the absence of the paracone fold (according to Lacombat, 2006).

MSTB-PN 20725 and MSTB-PN 20733 are completely consistent with each other and show a certain affinity especially with *S. hundsheimensis*, although they present a multiple crochet, found only rarely in the sample from Isernia La Pineta by Ballatore & Breda (2013). The absence of the crista in both P^4s from Pirro Nord is a trait that has been found rather rarely in other Pleistocene *Stephanorhinus* species.

M^1: among the four *Stephanorhinus* species considered, there are some slight differences that distin-

M^2						
Species / Character	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20726	MSTB-PN 20730
Crochet	Single, rarely absent (Guérin, 1980); Single (Lacombat, 2006; Kovalchuk et al., 2026)	Single, rarely double (Lacombat, 2006; Ballatore & Breda, 2013); Single (Kovalchuk et al., 2026)	Single, rarely multiple (Guérin, 1980); Single (Lacombat, 2006; Kovalchuk et al., 2026)	Single (Guérin, 1980; Lacombat, 2006; Kovalchuk et al., 2026)	Multiple	Single
Crista	Absent, rarely single (Guérin, 1980); Absent, rarely double (Lacombat, 2006); Single (Kovalchuk et al., 2026)	Absent or single (Lacombat, 2006); Single, more rarely absent or multiple (Ballatore & Breda, 2013); Absent (Kovalchuk et al., 2026)	Single, more rarely absent (Guérin, 1980); Absent or single (Lacombat, 2006); Absent (Kovalchuk et al., 2026)	Single, more rarely absent (Guérin, 1980); Single (Lacombat, 2006); Absent or single (Kovalchuk et al., 2026)	Single	Absent
Antecrochet	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Absent, rarely present (Lacombat, 2006); Absent or present (Ballatore & Breda, 2013)	Absent, more rarely present (Guérin, 1980); Absent or present (Lacombat, 2006)	Absent, more rarely present (Guérin, 1980); Present (Lacombat, 2006)	Absent	Absent
Mesial cingulum	Present (Lacombat, 2006)	Present (Lacombat, 2006; Ballatore & Breda, 2013)	Present (Lacombat, 2006)	Present (Lacombat, 2006)	Present	Present
Lingual cingulum	Absent or present (Guérin, 1980); Absent (Lacombat, 2006)	Present (Lacombat, 2006; Ballatore & Breda, 2013)	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006)	Present, more rarely absent (Guérin, 1980); Absent (Lacombat, 2006)	Absent	Absent
Vestibular cingulum	Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Kovalchuk et al., 2026); Absent, rarely present (Ballatore & Breda, 2013)	Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent	Absent
Distal cingulum	Absent (Lacombat, 2006)	Absent, rarely present (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent	Absent
Mediofossetta	Open, rarely closed (Guérin, 1980)	Open (Ballatore & Breda, 2013)	Open, rarely closed (Guérin, 1980)	Open, rarely closed (Guérin, 1980)	Open	Open
Constriction of the protocone	Present, rarely absent (Guérin, 1980); Present (Lacombat, 2006); Present or absent (Kovalchuk et al., 2026)	Absent or present (Lacombat, 2006); Present (Ballatore & Breda, 2013); Absent (Kovalchuk et al., 2026)	Present, more rarely absent (Guérin, 1980); Absent, rarely present (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Present, more rarely absent (Guérin, 1980); Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Present	Present
Paracone fold	Marked (Guérin, 1980); Little marked (Lacombat, 2006; Kovalchuk et al., 2026)	Marked (Lacombat, 2006; Ballatore & Breda, 2013); Little marked (Kovalchuk et al., 2026)	Highly marked (Lacombat, 2006); Little marked (Kovalchuk et al., 2026)	Little marked (Guérin, 1980); Marked or little marked (Kovalchuk et al., 2026)	Marked	Marked
External wall profile	Little wavy (Guérin, 1980)	–	Highly wavy (Guérin, 1980)	Little wavy (Guérin, 1980); Wavy (Lacombat, 2006)	Wavy	Wavy

Tab. 6 - Main morphological characters of M^2 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

guish *S. etruscus* and *S. hundsheimensis* from *S. hemitoechus* and *S. kirchbergensis* that are very similar to each other (Tab. 5). MSTB-PN 20728 exhibits characteristics more typical of *S. hundsheimensis*. However, MSTB-PN 20728 has a closed mediofossetta, while in *S. hundsheimensis* it is typically open and only rarely closed, as is also the case for the other Pleistocene species. P13USD25Q-C6S336 has an antecrochet, a feature rarely seen in other comparison species of *Stephanorhinus*. It is also interesting to note, in the sample studied here, that the absence of a lingual cingulum on M^1, a feature observed by various authors to be variably present or absent in the *Stephanorhinus* species compared here, is a characteristic also found in *Scythicorhinus vekuai* which also presents a crochet and an antecrochet, but the crista is absent (Kovalchuk et al., 2026).

M^2: some differences can be found between the four *Stephanorhinus* species (Tab. 6). The most obvious are at the level of the constriction of the protocone and the paracone fold. MSTB-PN 20726 and MSTB-PN 20730 present differences between them only relating to the crochet, multiple in the first case and single in the second, and to the presence/absence of the crista. The multiple crochet of MSTB-PN 20726 is explicitly reported (and as rare) only in *S. hemitoechus* by Guérin (1980). In general, the M^2s from Pirro Nord are morphologically closer to *S. etruscus* and *S. hundsheimensis*, however, their association is rather controversial. In fact, the ab-

P_2					
Character \ Species	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20723
Shape of the anterior lingual valley	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	V-shaped (Guérin, 1980; Lacombat, 2006)	U-shaped (Lacombat, 2006)	–
Shape of the posterior lingual valley	V-shaped (Lacombat, 2006); Undefinite shape (Kovalchuk et al., 2026)	V-shaped or broad V (Lacombat, 2006); U or V-shaped (Kovalchuk et al., 2026)	V-shaped (Guérin, 1980; Lacombat, 2006; Kovalchuk et al., 2026)	U-shaped (Guérin, 1980; Kovalchuk et al., 2026); Broad V-shaped (Lacombat, 2006)	–
Height difference between the bases of the valleys	Not determinable (Lacombat, 2006)	Not determinable (Lacombat, 2006)	Small (Guérin, 1980); High (Lacombat, 2006)	Small (Guérin, 1980); High (Lacombat, 2006)	–
Mesial cingulum	Absent (Lacombat, 2006)	Absent (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent
Lingual cingulum	Present or absent (Guérin, 1980); Absent (Lacombat, 2006)	Absent (Lacombat, 2006); Absent, rarely present (Ballatore & Breda, 2013)	Absent (Lacombat, 2006)	Present (Lacombat, 2006)	Absent
Vestibular cingulum	Present or absent (Guérin, 1980; Kovalchuk et al., 2026); Absent (Lacombat, 2006)	Absent, rarely present (Lacombat, 2006); Absent or present (Ballatore & Breda, 2013; Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent (Guérin, 1980; Kovalchuk et al., 2026); Absent or present (Lacombat, 2006)	Absent
Distal cingulum	Absent (Lacombat, 2006)	Absent (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Present (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent
Vestibular synclinal	Open and shallow (Lacombat, 2006)	Open and shallow (Lacombat, 2006)	Open and shallow (Lacombat, 2006)	Open and shallow (Lacombat, 2006)	Open and shallow

Tab. 7 - Main morphological characters of P_2 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

sence of the lingual cingulum in both MSTB-PN 20726 and MSTB-PN 20730 contrasts with what has been found in *S. hundsheimensis*, in which this cingulum is present (Lacombat, 2006; Ballatore & Breda, 2013). The constriction of the protocone is reported quite variably by different authors; specifically, in *S. hundsheimensis*, it is noted as present or absent by Lacombat (2006), present by Ballatore & Breda (2013), and absent by Kovalchuk et al. (2026).

P_2: the morphological differences between *Stephanorhinus* species are very slight (Tab. 7), in particular *S. etruscus* and *S. hundsheimensis* are almost indistinguishable. However, Ballatore & Breda (2013) report that the mesial and distal cingula are always present on the lower teeth from Isernia La Pineta, even though Lacombat (2006) reports that the mesial cingulum is absent in all the Pleistocene species of the genus *Stephanorhinus*. The P_2 of MSTB-PN 20723 shows characteristics more closely associated with *S. etruscus*, although not clearly.

P_3: presents very slight differences between the typical morphologies of *Stephanorhinus* species (Tab. 8). Also in this case, the correlation between *S. etruscus* and *S. hundsheimensis* it is almost full. As for P_2, also in this case Ballatore & Breda (2013) report that the mesial and distal cingula are always present on the lower teeth from Isernia La Pineta, even though Lacombat (2006) reports that it may be absent or present. The P_3 of MSTB -PN 20723 shows a greater number of characters shared with those typical of *S. kirchbergensis* and *S. etruscus*.

P_4: the differences between *Stephanorhinus* species are slightly more marked in the P_4 than in the other premolars (Tab. 9). The Pirro Nord premolars of the studied specimen exhibit some variability. The P_4 of MSTB-PN 20723 displays, for the most part, a series of characteristics shared among all Pleistocene *Stephanorhinus* species, except with *S. kirchbergensis*. MSTB-PN 20731 shows a slightly greater affinity with the typical characteristics of *S. hundsheimensis*. The different presence of the cingula clearly distinguishes the P_4 of MSTB-PN 20723 from MSTB-PN 20731: in the first case, in fact, only the vestibular cingulum is present, while in the second case all of them are present except the lingual cingulum.

M_1: the lower first molar presents some interspecific variability among the four species of *Stephanorhinus* (Tab. 10). However, variability is also present in the specimens from Pirro Nord, such as the presence/absence of the various cingula. Among the 6 M_1s examined in this work, two different typologies can be distinguished: in four cases, both the mesial and distal cingulum are present, and in two cases, these are absent. Overall, there are therefore three specimens showing greater affinity to *S. hundsheimensis* (MSTB-PN 20732, MSTB-PN 20738, P13USD24QC6S241 and P13USD34QC2S157) and two to *S. etruscus* (the M_1 of MSTB-PN 20723 and P13USD22QB5S159).

M_2: the morphological differences between the M_2s of the four *Stephanorhinus* species are not very marked and are substantially concentrated in the presence/absence of the cingula (Tab. 11). The M_2 of MSTB-PN 20723 shows a greater affinity with the typical characteristics of *S. kirchbergensis* and *S. etruscus*, especially

P_3					
Species / Character	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20723
Shape of the anterior lingual valley	V-shaped (Guérin, 1980); V-shaped or broad V (Lacombat, 2006)	V-shaped or rarely broad V (Lacombat, 2006)	V-shaped, rarely closed (Guérin, 1980); V-shaped or rarely broad V (Lacombat, 2006)	V-shaped, rarely closed (Guérin, 1980); U-shaped (Lacombat, 2006)	–
Shape of the posterior lingual valley	V-shaped (Guérin, 1980; Lacombat, 2006; Kovalchuk et al., 2026)	V-shaped or rarely broad V (Lacombat, 2006; Ballatore & Breda, 2013); V-shaped (Kovalchuk et al., 2026)	V-shaped (Guérin, 1980; Lacombat, 2006; Kovalchuk et al., 2026)	V-shaped or broad V (Guérin, 1980); Broad V-shaped (Lacombat, 2006); V-shaped (Kovalchuk et al., 2026)	Broad V-shaped
Height difference between the bases of the valleys	High (Guérin, 1980; Lacombat, 2006)	Small (Lacombat, 2006)	Small, medium or high (Guérin, 1980); High (Lacombat, 2006)	Small (Guérin, 1980; Lacombat, 2006)	–
Mesial cingulum	Absent or present (Lacombat, 2006)	Absent or present (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Absent, rarely present (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent
Lingual cingulum	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent, rarely present (Lacombat, 2006); Absent (Ballatore & Breda, 2013); Absent or present (Kovalchuk et al., 2026)	Present, more rarely absent (Guérin, 1980); Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent, more rarely present (Guérin, 1980); Absent (Lacombat, 2006); Absent or present (Kovalchuk et al., 2026)	Absent
Vestibular cingulum	Present or absent (Guérin, 1980); Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent, rarely present (Lacombat, 2006); Absent or present (Ballatore & Breda, 2013; Kovalchuk et al., 2026)	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent, more rarely present (Guérin, 1980); Absent or present (Lacombat, 2006; Kovalchuk et al., 2026)	Absent
Distal cingulum	Absent, rarely present (Lacombat, 2006)	Absent or present (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Absent or present (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent
Vestibular synclinal	Open or closed and shallow (Lacombat, 2006)	Open, rarely at 90° and deep, rarely shallow (Lacombat, 2006)	Open or closed and shallow, rarely null (Lacombat, 2006)	Closed and shallow (Lacombat, 2006)	Closed and shallow

Tab. 8 - Main morphological characters of P_3 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

regarding the shape of the lingual valleys.

M_3: the M_3s of the four *Stephanorhinus* species present some rather relevant morphological differences (Tab. 12). The M_3 of MSTB-PN 20723 appears very similar to *S. kirchbergensis* and to *S. hundsheimensis*, whereas the affinity with *S. etruscus* is less marked, except for the discontinuous vestibular cingulum that shares with *S. etruscus*, as well as with *Scythicorhinus vekuai* (see Kovalchuk et al., 2026).

Pisiform: the morphology fits better with the description that Lacombat (2005) presents for *S. hundsheimensis*, with its massive appearance, rounded edges, and marked curvature. Guérin (1980) underlines how in *S. etruscus* the racket shape is less pronounced than in *S. hundsheimensis*.

Second metacarpal: the morphological characters observed on the proximal end of the second metacarpal suggest a closer affinity with *S. hundsheimensis* (see table 5 in Stefanelli et al., 2024), in particular for the well-developed posterior tuberosity and the trapezoidal shape of the articular surface to the trapezium. The combined presence of these two characteristics is in fact common in this species. Furthermore, in Kovalchuk et al. (2026), the articular facet for the trapezium on the second metacarpal is absent in *S. etruscus* and *S. hemitoechus* (as well as in *Scythicorhinus vekuai*), whereas its presence is consistent with *S. hundsheimensis* and *S. kirchbergensis*.

Third metacarpal: characters associating this specimen with the species *S. hundsheimensis* have been observed in third metacarpal (see table 6 in Stefanelli et al., 2024), in particular for the sub-trapezoidal articular surface to the magnum, the slightly convex anterior margin of the proximal epiphysis and the shape of the articular surfaces to the fourth metacarpal, trapezoidal (anterior) and semi-circular (posterior).

Fourth metacarpal: the morphological characters observed on the proximal end of fourth metacarpal do not show a clear affinity with one of the main rhinoceros species of the European Pleistocene (see table 7 in Stefanelli et al., 2024). In fact, the main characters of this metapodial are rather shared, especially for *S. etruscus* and *S. hundsheimensis*. The evaluation of the morphologies of this bone therefore does not allow a clear attribu-

P_4						
Species / Character	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20723	MSTB-PN 20731
Shape of the anterior lingual valley	V-shaped, rarely closed (Guérin, 1980); V-shaped or broad V (Lacombat, 2006)	V-shaped (Lacombat, 2006; Ballatore & Breda, 2013)	V-shaped, rarely closed (Guérin, 1980); V-shaped (Lacombat, 2006)	V-shaped, rarely U (Guérin, 1980); U-shaped (Lacombat, 2006)	–	Broad V-shaped
Shape of the posterior lingual valley	V-shaped (Guérin, 1980; Lacombat, 2006; Kovalchuk et al., 2026)	V-shaped, rarely broad V (Lacombat, 2006); U-shaped (Kovalchuk et al., 2026)	V-shaped, rarely closed (Guérin, 1980); V-shaped (Lacombat, 2006; Kovalchuk et al., 2026)	V-shaped, rarely U (Guérin, 1980); Broad V-shaped (Lacombat, 2006); V-shaped (Kovalchuk et al., 2026)	V-shaped	U-shaped
Height difference between the bases of the valleys	Small or medium (Guérin, 1980); High, rarely small (Lacombat, 2006)	Small, rarely high (Lacombat, 2006)	Small, medium or high (Guérin, 1980); Small, rarely null or high (Lacombat, 2006)	Small, medium or high (Guérin, 1980); High (Lacombat, 2006)	Small	Medium
Mesial cingulum	Present, rarely absent (Lacombat, 2006)	Present, rarely absent (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Absent, rarely present (Lacombat, 2006)	Present, rarely absent (Lacombat, 2006)	Absent	Present
Lingual cingulum	Absent (Guérin, 1980; Kovalchuk et al., 2026); Absent, rarely present (Lacombat, 2006)	Absent or present (Lacombat, 2006); Absent (Ballatore & Breda, 2013; Kovalchuk et al., 2026)	Present, more rarely absent (Guérin, 1980); Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent, rarely present (Guérin, 1980); Absent or present (Lacombat, 2006; Kovalchuk et al., 2026)	Absent	Absent
Vestibular cingulum	Present or absent (Guérin, 1980; Kovalchuk et al., 2026); Absent, rarely present (Lacombat, 2006)	Absent or present (Lacombat, 2006; Kovalchuk et al., 2026); Absent, rarely present (Ballatore & Breda, 2013)	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent, rarely present (Guérin, 1980); Absent or present (Lacombat, 2006; Kovalchuk et al., 2026)	Present	Present
Distal cingulum	Absent or present (Lacombat, 2006)	Absent or present (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Absent (Lacombat, 2006)	Absent or present (Lacombat, 2006)	Absent	Present
Vestibular synclinal	Closed, rarely open and shallow (Lacombat, 2006)	Closed and shallow or deep (Lacombat, 2006)	Open or closed and shallow or deep (Lacombat, 2006)	Closed and deep (Lacombat, 2006)	Closed and shallow	Closed and deep

Tab. 9 - Main morphological characters of P_4 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

tion.

Patella: The morphological characteristics observed on this very well-preserved bone reveal a fairly clear affinity. Specifically, the convex and irregular cranial surface, the straight anterior margin (in lateral view), and the articular surfaces for the femur, which are positioned superiorly and are slightly concave, correspond quite well to those described by Lacombat (2005) for *S. etruscus*. The author describes the patella of *S. hundsheimensis* as being very similar to that of *S. etruscus*; however, in lateral view, the margin exhibits a sinuous contour.

3.3. Biometric comparison

Among the four species of *Stephanorhinus* that lived in Europe during the Pleistocene, as far as the size of the lower teeth is concerned, only *S. kirchbergensis* clearly stands out for its larger size. The comparison with the dental remains of Pirro Nord from the "Dagostino Collection" gave different results. The mandible with complete dentition MSTB-PN 20723 shows very small dimensions (Tab. 13), almost always corresponding to the minimum values found for the other three species and, in some cases, even slightly smaller, as in P_4 and M_1. The upper teeth of the four species of *Stephanorhinus* considered here show, as in the case of the lower ones, clearly larger dimensions for *S. kirchbergensis*. In this case, however, the other three species present more marked differences in size between them: *S. hundsheimensis* and *S. hemitoechus* seem rather similar, especially with regard to the dimensions of P^4 and M^1. However, the two are mainly distinguished by P^3 and M^2, in which ranges with larger values were observed respectively in *S. hundsheimensis* and *S. hemitoechus*. The latter species therefore presents a greater dimensional development of the molars to the detriment of the premolars, which instead appear smaller. *S. etruscus* is instead the species that always shows ranges with smaller values. The isolated upper teeth from Pirro Nord studied here fall well within the ranges of *S. hundsheimensis* and *S. hemitoechus*, with a slightly greater

M_1										
Species / Character	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20723	MSTB-PN 20732	MSTB-PN 20738	P13US D34Q C2S157	P13US D22Q B5S159	P13US D24Q C6S241
Shape of the anterior lingual valley	V or U-shaped (Guérin, 1980; Kovalchuk et al., 2026); Broad V, V or U-shaped (Lacombat, 2006)	V-shaped (Lacombat, 2006); V or U-shaped (Kovalchuk et al., 2026)	V-shaped, more rarely broad U or V (Guérin, 1980); V-shaped (Lacombat, 2006); V or U-shaped (Kovalchuk et al., 2026)	V-shaped, more rarely U (Guérin, 1980); U-shaped (Lacombat, 2006); V or U-shaped (Kovalchuk et al., 2026)	–	Broad V-shaped	–	Broad V-shaped	–	–
Shape of the posterior lingual valley	V or U-shaped, rarely closed (Guérin, 1980); V-shaped, broad V or U (Lacombat, 2006); V or U-shaped (Kovalchuk et al., 2026)	V-shaped, rarely broad V (Lacombat, 2006; Ballatore & Breda, 2013); V-shaped (Kovalchuk et al., 2026)	V-shaped, rarely U (Guérin, 1980); V-shaped, rarely broad V (Lacombat, 2006); V or U-shaped (Kovalchuk et al., 2026)	U-shaped, more rarely V (Guérin, 1980); Broad V-shaped (Lacombat, 2006); V or U-shaped (Kovalchuk et al., 2026)	V-shaped	V-shaped	Broad V-shaped	V-shaped	Broad V-shaped	V-shaped
Height difference between the bases of the valleys	Medium (Guérin, 1980); High, rarely small (Lacombat, 2006)	High, rarely small (Lacombat, 2006)	Small, medium or high (Guérin, 1980); Small, high or null (Lacombat, 2006)	Small, medium or high (Guérin, 1980); High (Lacombat, 2006)	Medium	High	High	High	Medium	High
Mesial cingulum	Present or absent (Lacombat, 2006)	Present (Lacombat, 2006; Ballatore & Breda, 2013)	Present or absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent	Present	Present	Present	Absent	Present
Lingual cingulum	Absent, rarely present (Guérin, 1980; Lacombat, 2006); Absent or present (Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Ballatore & Breda, 2013; Kovalchuk et al., 2026)	Absent, rarely present (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Present or absent (Guérin, 1980; Kovalchuk et al., 2026); Absent (Lacombat, 2006)	Absent	Absent	Absent	Absent	Absent	Absent
Vestibular cingulum	Present or absent (Guérin, 1980; Kovalchuk et al., 2026); Absent, rarely present (Lacombat, 2006)	Present or absent (Lacombat, 2006; Kovalchuk et al., 2026); Absent, rarely present (Ballatore & Breda, 2013)	Absent, rarely present (Guérin, 1980); Present or absent (Lacombat, 2006); Absent (Kovalchuk et al., 2026)	Present or absent (Guérin, 1980; Lacombat, 2006; Kovalchuk et al., 2026)	Absent	Absent	Absent	Absent	Present	Absent
Distal cingulum	Absent, rarely present (Lacombat, 2006)	Present (Lacombat, 2006; Ballatore & Breda 2013)	Present or absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent	Present	Present	Present	Absent	Present
Vestibular synclinal	Open or closed and shallow (Lacombat, 2006)	Open and deep (Lacombat, 2006)	Open and shallow (Lacombat, 2006)	Closed or at 90° and deep (Lacombat, 2006)	Closed and shallow	At 90° and shallow	At 90° and and deep	At 90° and and deep	Open and deep	Open and deep

Tab 10 - Main morphological characters of M_1 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

affinity with the first (Tab. 14). Almost always lower and even much lower than the minimum values of *S. kirchbergensis*, the upper teeth are high for *S. etruscus*, especially in the premolars, where they are close to the maximum values. The lower isolated teeth show remarkable peculiarities in size. Regarding the M_1s of the "Dagostino Collection", while MSTB-PN 20731 is only slightly larger than the P_4 of MSTB-PN 20723, the two isolated M_1s (MSTB-PN 20732 and MSTB-PN 20738) are clearly larger, close to maximum values for maximum vestibular-lingual diameter of *S. etruscus*. The three M_1s from the University of Ferrara collection (P13USD22QB5S159, P13USD34QC2S157 and P13USD24QC6S241) are slightly smaller in size than the two large isolated M_1s from Bari, but still clearly larger than the M_1s from the small mandible (MSTB-PN 20723).

The pisiform (P13USD41QD3S164, Supplementary Fig. 1) is characterized by its very short maximum length (1) (51.92 mm, see Supplementary Tab. 9). This measurement is clearly lower than the minimum values for

M_2					
Species / Character	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20723
Shape of the anterior lingual valley	V-shaped, broad V, or rarely U (Guérin, 1980; Lacombat, 2006); U or V-shaped (Kovalchuk et al., 2026)	V-shaped, U, or rarely broad V (Lacombat, 2006); V-shaped (Ballatore & Breda, 2013); U or V-shaped (Kovalchuk et al., 2026)	V-shaped, rarely broad V or U (Guérin, 1980); V-shaped, rarely broad V (Lacombat, 2006); V-shaped (Kovalchuk et al., 2026)	V or U-shaped (Guérin, 1980; Kovalchuk et al., 2026); U or broad V-shaped (Lacombat, 2006)	U-shaped
Shape of the posterior lingual valley	Broad V-shaped, V, or rarely U (Guérin, 1980; Lacombat, 2006); U or V-shaped (Kovalchuk et al., 2026)	Broad V-shaped, V, or rarely U (Lacombat, 2006); U or V-shaped (Kovalchuk et al., 2026)	V-shaped, rarely broad V or U (Guérin, 1980); V-shaped, rarely broad V (Lacombat, 2006); U-shaped (Kovalchuk et al., 2026)	U or V-shaped (Guérin, 1980; Kovalchuk et al., 2026); Broad V or U-shaped (Lacombat, 2006)	U-shaped
Height difference between the bases of the valleys	Medium (Guérin, 1980); High or small (Lacombat, 2006)	High, rarely small (Lacombat, 2006)	Small, more rarely high (Lacombat, 2006)	High, medium or small (Guérin, 1980); High (Lacombat, 2006)	Medium
Mesial cingulum	Present or absent (Lacombat, 2006)	Present, rarely absent (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Present or absent (Lacombat, 2006)	Absent (Lacombat, 2006)	Absent
Lingual cingulum	Absent, rarely present (Guérin, 1980; Lacombat, 2006); Absent (Kovalchuk et al., 2026)	Present or absent (Guérin, 1980; Kovalchuk et al., 2026); Absent (Lacombat, 2006; Ballatore & Breda, 2013)	Present or absent (Guérin, 1980); Absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent
Vestibular cingulum	Present or absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Present or absent (Lacombat, 2006; Kovalchuk et al., 2026); Absent, rarely present (Ballatore & Breda, 2013)	Present, more rarely absent (Guérin, 1980); Present or absent (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Present or absent (Guérin, 1980; Lacombat, 2006); Present (Kovalchuk et al., 2026)	Present
Distal cingulum	Present or absent (Guérin, 1980; Lacombat, 2006)	Present, rarely absent (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Present or absent (Lacombat, 2006)	Present (Lacombat, 2006)	Absent
Vestibular synclinal	Closed, open or at 90° and shallow (Lacombat, 2006)	Closed, open, more rarely at 90° and deep, more rarely shallow (Lacombat, 2006)	At 90°, more rarely open and shallow or deep (Lacombat, 2006)	Closed or at 90° and shallow or deep (Lacombat, 2006)	Closed and shallow

Tab 11 - Main morphological characters of M_2 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

both *S. etruscus* (58 mm, see table 97 in Guérin, 1980) and *S. hundsheimensis* (56 mm, see table 40 in Lacombat, 2005). The other measurements are in line with what was found on average by other authors: maximum width (2) and maximum height (3) differ very little between *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus*. The measurements of *S. kirchbergensis* are significantly larger than those of the previous ones.

The second metacarpal (MSTB-PN 20736) shows a proximal epiphysis with extremely reduced diameters compared to the comparison species (Fig. 8A) so much so that it stands out as the smallest value. The second metacarpal of *Stephanorhinus* cf. *hundsheimensis* from Pietrafitta, however, although smaller in size, falls within the minimum variability of *S. etruscus*. The third metacarpal (MSTB-PN 20737) displays a similar pattern (Fig. 8B); however, the dimensions are relatively closer to the smaller values found in *S. etruscus* and *S. hundsheimensis*. The two third metacarpals of *Stephanorhinus* cf. *hundsheimensis* from Pietrafitta, as well as the third metacarpal from Pirro Nord from Florence (IGF 2909), despite being small in size, fall within the overlapping variability of *S. etruscus* and *S. hundsheimensis*. Even the fourth metacarpal (MSTB-PN 20735) shows the smallest dimensions compared to the entire sample analysed (Fig. 8C), as the second and third metacarpal. The fourth metacarpal of *Stephanorhinus* cf. *hundsheimensis* from Pietrafitta falls within the low values of the variability of *S. etruscus*.

The measurements for the patella reported by authors such as Mazza (1988), Mazza et al. (1993), and Lacombat (2005) are, in all cases, significantly larger than those of the patella from the "Dagostino Collection" (MSTB-PN 20734; see Supplementary Tab. 9). Therefore, given the previously noted presence of juvenile individuals among the rhinoceroses from Pirro Nord,

M_3					
Species / Character	*S. etruscus*	*S. hundsheimensis*	*S. hemitoechus*	*S. kirchbergensis*	MSTB-PN 20723
Shape of the anterior lingual valley	Broad V-shaped, rarely V or U (Lacombat, 2006); Broad U or U-shaped (Kovalchuk et al., 2026)	V-shaped or broad V (Lacombat, 2006); U-shaped, more rarely V or broad V (Ballatore & Breda, 2013); Broad U or U-shaped (Kovalchuk et al., 2026)	V-shaped, rarely broad V or U (Guérin, 1980); V-shaped, rarely broad V (Lacombat, 2006); Broad U-shaped (Kovalchuk et al., 2026)	U-shaped or broad V (Guérin, 1980; Lacombat, 2006); Broad U or U-shaped (Kovalchuk et al., 2026)	U-shaped
Shape of the posterior lingual valley	V-shaped, rarely broad V (Lacombat, 2006); U or V-shaped (Kovalchuk et al., 2026)	U-shaped or more rarely broad V (Lacombat, 2006); U-shaped, more rarely V or broad V (Ballatore & Breda, 2013); U or V-shaped (Kovalchuk et al., 2026)	V-shaped, rarely broad V, U or closed (Guérin, 1980); V-shaped or broad V (Lacombat, 2006); V-shaped (Kovalchuk et al., 2026)	U-shaped, rarely V (Guérin, 1980); U-shaped or broad V (Lacombat, 2006); U-shaped (Kovalchuk et al., 2026)	U-shaped
Height difference between the bases of the valleys	High, medium or small (Guérin, 1980); High, rarely small (Lacombat, 2006)	Small, rarely high (Lacombat, 2006)	Small, high or null (Guérin, 1980); Small, more rarely high (Lacombat, 2006)	High, more rarely small (Lacombat, 2006)	Medium
Mesial cingulum	Present or absent (Lacombat, 2006)	Present or absent (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Present or absent (Lacombat, 2006)	Present or absent (Lacombat, 2006)	Absent
Lingual cingulum	Absent, rarely present (Guérin, 1980); Present (Lacombat, 2006); Absent (Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Kovalchuk et al., 2026); Absent, rarely present (Ballatore & Breda, 2013)	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent, rarely present (Guérin, 1980); Absent (Lacombat, 2006; Kovalchuk et al., 2026)	Absent
Vestibular cingulum	Present, more rarely absent (Guérin, 1980); Absent or present (Lacombat, 2006); Present (Kovalchuk et al., 2026)	Absent (Lacombat, 2006; Ballatore & Breda, 2013; Kovalchuk et al., 2026)	Absent, rarely present (Guérin, 1980; Lacombat, 2006); Absent (Kovalchuk et al., 2026)	Absent, rarely present (Guérin, 1980); Absent or present (Lacombat, 2006); Absent (Kovalchuk et al., 2026)	Present
Distal cingulum	Present or absent (Lacombat, 2006)	Present or absent (Lacombat, 2006); Present (Ballatore & Breda, 2013)	Present or absent (Lacombat, 2006)	Present or absent (Lacombat, 2006)	Present
Vestibular synclinal	At 90°, open or closed and shallow, more rarely deep (Lacombat, 2006)	Closed, open, more rarely at 90° and deep, rarely shallow (Lacombat, 2006)	Closed or at 90° and shallow or deep (Lacombat, 2006)	At 90° and deep (Lacombat, 2006)	At 90° and deep

Tab. 12 - Main morphological characters of M_3 from Pirro Nord (northern Apulia) compared with those of the main four European species of the genus *Stephanorhinus* during Pleistocene.

we may assume that this bone belongs to an immature specimen.

4. DISCUSSION

4.1. Morphological and biometric considerations

In general, the rhinoceros premolars from Pirro Nord of the Dagostino and Ferrara universities Collections have a multiple crochet, a crista and antecrochet always absent. Furthermore, the mesial and lingual cingula are always present, while the vestibular and distal ones are always missing. In the premolars (Fig. 3), the hypocone is free from the protocone, connecting only at the base (see Fig. 3C, H, M, R); however, it is connected to the metaloph in P^2 and P^3 by a dentine bridge (see Fig. 3A, F), whereas it is completely free in P^4 (see Fig. 3K, P). It is particularly interesting to note that the presence of multiple crochets on P^3-P^4 (while observed) is not especially common among the four *Stephanorhinus* species considered; however, it is regarded as a diagnostic character of *Scythicorhinus vekuai*, according to Kovalchuk et al. (2026). This perhaps suggests a closer affinity of the latter species to the *Stephanorhinus* lineage than to that of *Coelodonta*. Indeed, although the unique combination of cranial, dental, and postcranial characters in *Scythicorhinus vekuai* places it phylogenetically outside both *Coelodonta* and *Stephanorhinus*, the authors do not rule out alternative placements within the initial radiation of *Coelodonta* and *Stephanorhinus*. The molars (Fig. 4) of the studied sample show a greater morphological variability than the premolars: the crochet is single (2/3) or multiple (1/3), the crista can be single (2/3) or absent (1/3) and the antecrochet is present only on one M^1 (P13USD25QC6S336). Furthermore, the mediofossetta is closed in M^1 and open in M^2 and the constriction of the protocone is present only on M^2s. By analysing the comparison morphological tables developed here, it emerges that the authors who have previously evaluated in detail the dental morphology of Pleistocene *Stephanorhinus* species, the same considered here (Guérin, 1980; Lacombat, 2006; Ballatore & Breda, 2013; Kovalchuk et al., 2026), generally agree regarding the value of dental morphological characters for taxonomic identification. In the case of Guérin (1980) and

Tooth	Measurements	*S. etruscus* (min. - max.)	*S. hundsheimensis* (min. - max.)	*S. hemitoechus* (min. - max.)	*S. kirchbergensis* (min. - max.)	MSTB-PN 20723
P_2	1	25- 36.4	25.2- 39	23- 31	26- 34	25.19 - 27.92*
	8	16- 21.5	16- 33	14.5- 21	19- 21.5	16.63 - 16.75
P_3	1	31.3- 39.7	30- 42.5	27- 40	35- 46	28.63 - 31.06
	8	21.5- 30	21- 37	21- 28	27- 35.5	21.87 - 23.61
P_4	1	34.4- 43	33- 45	35- 43	38- 51	30.96 - 32.05
	8	24- 31	23- 35	24- 32	28.5- 38.5	23.63 - 24.01
M_1	1	35.2- 49	37- 57	36.5- 52	43- 59	35 - 34.64
	8	26- 33	25- 37	26- 35	33- 42	24.58 - 25.09
M_2	1	40- 49	39- 57.5	41- 55	53- 63	39.67 - 40.05
	8	25- 33.5	23.5- 35	28- 36	32- 40	26.06 - 26.91

Tab. 13 - Comparison of the main dental measurements taken on MSTB – PN 20723 from Pirro Nord with those relating to the four species of rhinoceros of the genus *Stephanorhinus* that lived in the Pleistocene in Europe. Data from Fortelius et al. (1993), Guérin (1980), Handa & Pandolfi (2016), Pandolfi & Erten (2017), Pandolfi & Marra (2015), Radovic et al. (2020). Abbreviations: 1: Maximum mesio-distal diameter; 8: Maximum vestibular-lingual diameter. Measurements are in mm; those marked with * are estimated.

Lacombat (2005, 2006), they often studied the same rhinoceros remains from the same sites in their works. Often one confirms and expands the variability detected by the other, but they rarely clearly disagree. A particular case concerns P^3, in which Guérin (1980) and Lacombat (2006) do not agree in reporting the presence/absence and number of crochet and crista in the various species. Other cases concern P^4 and M^2, in which the previous authors do not agree on many characters of *S. kirchbergensis* (see Tables 4 and 6). Ballatore & Breda (2013) instead based their analyses on a sample of rhinoceroses from Isernia La Pineta (229 studied teeth), which differed from the one analysed by previous authors for the same site. Kovalchuk et al. (2026) diverge most significantly from previous authors, as they employ an expanded morphological dataset which only partially overlaps with that of the previous authors and phylogenetic analyses. Regarding the morphologies of the lower teeth, the authors are generally more in agreement, except in the cases of P_2 and P_3, in which the disagreement on several characters of *S. kirchbergensis* is repeated (see Tables. 7 and 8). The dimensions of the isolated upper teeth studied here fall well within the ranges of *S. hundsheimensis*, while they are high for *S. etruscus*, especially that of the premolars, where they are close to the maximum values (Tab. 14). Overall, from the morphological and biometric analyses performed here, the isolated upper teeth (MSTB-PN 20724, MSTB-PN 20725, MSTB-PN 20726, MSTB-PN 20728, MSTB-PN 20729, MSTB-PN 20730 and MSTB-PN 20733) considering the variability and also the many morphological characters shared between *S. etruscus* and *S. hundsheimensis*, the sample shows a stronger affinity with the latter species. Other isolated upper teeth from Pirro Nord have been examined by Petrucci (2008) who, in addition to several fragmentary remains, analyses a dental fragment of an upper molar (M^1/M^2, MPUT PU106664), which the Author attributed to *S.* cf. *hundsheimensis* as similar to the specimens from the French site of Vallonet. However, the same tooth was later identified as D^3 by Pandolfi & Petronio (2011). The mandible (MSTB-PN 20723, Fig. 5) shows morphologies that are more similar to those of *S. etruscus*, such as the absence of the mesial cingulum in P_4, of the mesial and distal cingula in M_1 as well as the close and shallow vestibular synclinal. M_2 and M_3 both present U-shaped lingual valleys, the distal cingulum is absent in the former and present in the latter; furthermore, the M_3 also presents the vestibular cingulum. This series of characters is typically found in *S. etruscus* and also distinct from those of the similar *S. hundsheimensis*. Among the *Stephanorhinus* species examined, only *S. kirchbergensis* exhibits a mandibular symphysis extending posteriorly to

Upper teeth				
Specimen	Tooth	1	2	Storage place
MSTB-PN 20724	P^3	40.89	48.95	University of Bari Aldo Moro
MSTB-PN 20725	P^4	42.34	50.65	University of Bari Aldo Moro
MSTB-PN 20733	P^4	43.08	52.96	University of Bari Aldo Moro
MSTB-PN 20728	M^1	_	55.74	University of Bari Aldo Moro
MSTB-PN 20730	M^2	53.91	53.43	University of Bari Aldo Moro
MSTB-PN 20726	M^2	54.02	54.46	University of Bari Aldo Moro
P13USD28QC4S437	P^3	40.73	_	University of Ferrara
P13USD25QC6S336	M^1	52.55	_	University of Ferrara
Lower teeth				
Specimen	**Tooth**	**1**	**8**	**Storage place**
MSTB-PN 20731	P_4	37.33	27	University of Bari Aldo Moro
MSTB-PN 20732	M_1	45.8	32.09	University of Bari Aldo Moro
MSTB-PN 20738	M_1	45.78	32.15	University of Bari Aldo Moro
P13USD13QA5S33	P_2	28.21	19.71	University of Ferrara
P13USD30QC6S392	P_3 or P_4	37.06	22.44	University of Ferrara
P13USD22QB5S159	M_1	43.55	28.70	University of Ferrara
P13USD34QC2S157	M_1	43.8	27.78	University of Ferrara
P13USD24QC6S241	M_1	42	26	University of Ferrara

Tab. 14 - Comparison of the main dental measurements taken on various isolated teeth from Pirro Nord with those relating to the four species of rhinoceros of the genus *Stephanorhinus* that lived in the Pleistocene in Europe. Data from Fortelius et al. (1993), Guérin (1980), Handa & Pandolfi (2016), Pandolfi & Erten (2017), Pandolfi & Marra (2015), Radovic et al. (2020). Abbreviations: 1: Maximum mesio-distal diameter; 2 and 8: Maximum vestibular-lingual diameter. Measurements are in mm.

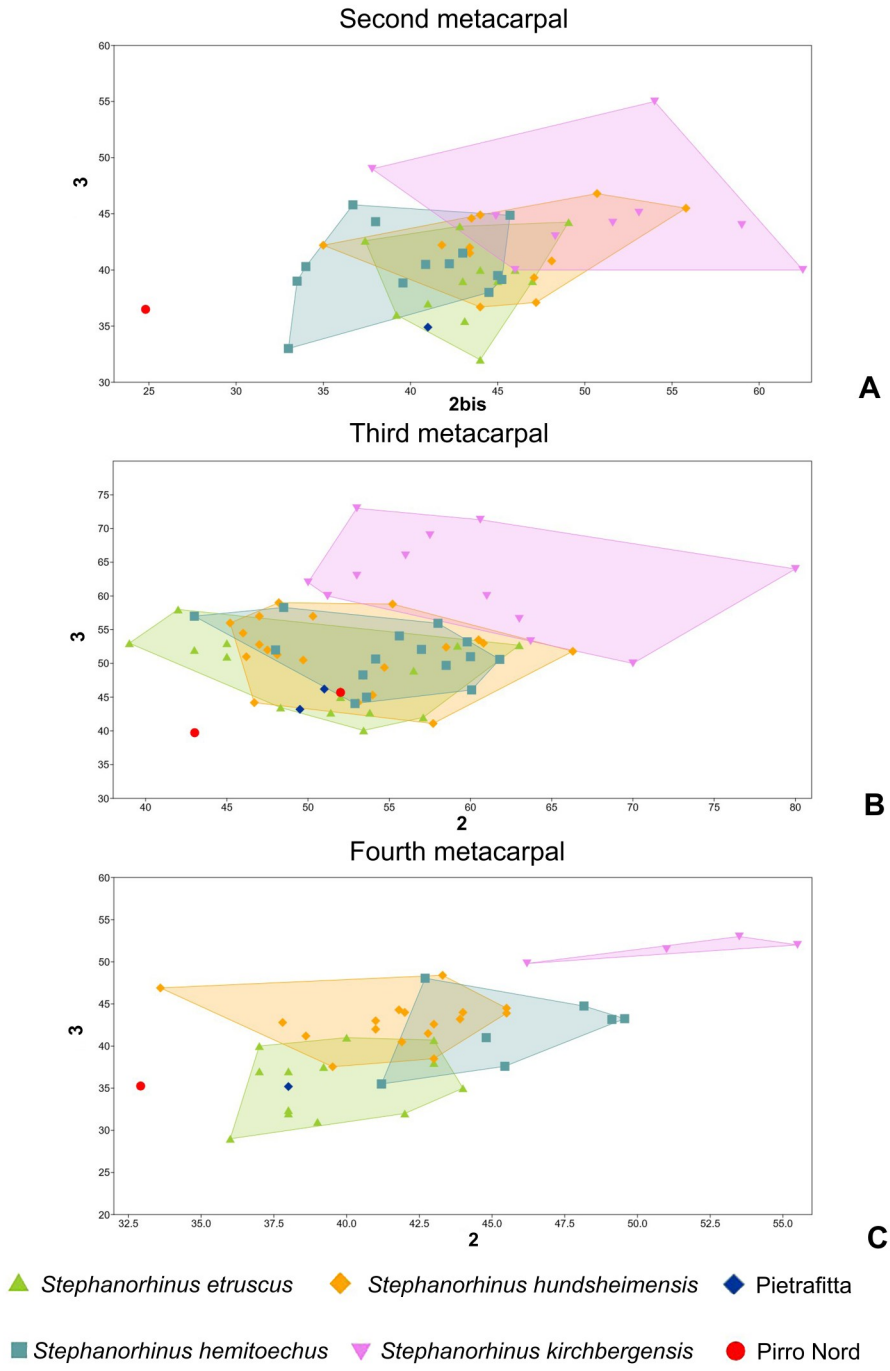


Fig. 8 - Scatter diagrams of the transverse diameter of the proximal articular surface (2bis) and maximum transverse diameter of the proximal end (3) of the second metacarpal (A) and of the transverse diameter of the proximal articular surface (2) and antero-posterior diameter of the proximal end (3) of the third (B) and fourth (C) metacarpal. All measures used and their relative reference are reported in Supplementary Tabs. 10-12.

beneath P_3, whereas the other three display a configuration similar to that observed in MSTB-PN 20723. From a biometric point of view, MSTB-PN 20723 shows very low values, even in some cases, below the minimum values of the P_4 and the M_1 (Tab. 13). The morphological and biometric characteristics therefore suggest an attribution to a small-sized adult specimen of *S. etruscus* for the mandible with complete dentition MSTB-PN 20723. This is in line with the results emerged in Pandolfi & Petronio (2011) for the Pirro Nord rhinoceroses from the collections of Rome, Turin and Florence Universities. Regarding most of the isolated lower teeth (MSTB-PN 20731, MSTB-PN 20732, MSTB-PN 20738, P13USD34Q-C2S157 and P13USD24Q-C6S241), these show greater morphological affinity with *S. hundsheimensis*. In particular, the P_4 (MSTB-PN 20731, Tab. 9), exhibit both the mesial and distal cingula, and also presents a U-shaped posterior valley as seen in *S. hundsheimensis*. Among

the six M_1s, the presence/absence of the cingula appears to be particularly interesting, as two different typologies seem to emerge, namely those of MSTB-PN 20732, MSTB-PN 20738, P13USD34QC2S157 and P13USD-24QC6S241, which exhibit mesial and distal cingula, while on the contrary they are absent in the M_1 of MSTB-PN 20723 and P13USD22Q-B5S159. Regarding the latter, it showed morphological affinities with the M_1 of the small mandible MSTB-PN 20723, attributable above all to the absence of both the mesial and distal cingula, a characteristic associated with *S. etruscus* and not with *S. hundsheimensis* (see Tab. 10). This morphological affinity, however, is not reflected in its dimensions; in fact, P13USD22Q-B5S159 appears to be significantly larger and generally in line with the other M_1s examined here (see Supplementary Tab. 6). The isolated lower teeth show significant differences in size; in fact while MSTB-PN 20731 (P_4) is only slightly larger than the P_4 of MSTB-PN 20723, MSTB-PN 20732 and MSTB-PN 20738 (both M_1) are clearly larger, close to the maximum values for the maximum vestibulo-lingual diameter of *S. etruscus* (Tab. 14). Therefore, the morphological and biometric analysis carried out on the isolated lower teeth suggests an attribution to full-sized *S. hundsheimensis* (MSTB-PN 20731, MSTB-PN 20732, MSTB-PN 20738, and P13U-SD24QC6S241) and full-sized *S. etruscus* (P13US-D22QB5S159). The morphologies of three isolated deciduous teeth from the University of Ferrara collection (P13USD25QC6S175, P13USD20-QC6S71 and P13U-SD37QD3S115; Fig. 2) showed similarities with the typical features of *S. hundsheimensis* described by Lacombat (2006) and Kovalchuk et al. (2026) for the deciduous teeth of Pleistocene rhinoceroses. In other cases, given the fragmentary nature and the scarcity of recognizable morphological and biometric characteristics in certain isolated teeth, a more cautious attribution to *Stephanorhinus* sp. has been adopted (P13USC6QB6S105, P13USD13QA5S33, P13USD18Q-B4S98, P13USD25Q-C6S336, P13USD26Q-C4S295 and P13USD28QC4S437). The pisiform (P13USD-41QD3S164, Supplementary Fig. 1) presents morphological characteristics closer to *S. hundsheimensis*. However, it appears to be particularly reduced in terms of maximum length, even lower than the minimum values found for *S. etruscus* and *S. hundsheimensis*. Regarding the metacarpals of the “Dagostino Collection” (Fig. 7), the second (MSTB-PN 20736) and third (MSTB-PN 20737) exhibit morphological characters more similar to *S. hundsheimensis*, such as the well-developed posterior tuberosity and the trapezoidal shape of the articular surface to the trapezium for the second metacarpal and the sub-trapezoidal articular surface to the magnum, the slightly convex anterior margin of the proximal epiphysis and the shape of the articular surfaces to the fourth metacarpal, trapezoidal (anterior) and semi-circular (posterior) for the third metacarpal. In the fourth metacarpal (MSTB-PN 20735), it was not possible to evaluate characters that allow a clear attribution; in fact, both *S. etruscus* and *S. hundsheimensis* can show very similar morphologies for this bone. A similar situation applies to the proximal fragment of the second metacarpal from the University of Ferrara (P13USD19QB2S131); indeed, the poor preservation of this specimen has precluded a reliable assessment of its morphological characteristics. Consequently, in this instance, it was preferred more prudent to assign the specimen to *Stephanorhinus* sp. Biometric analysis of the metacarpals was limited to the diameters of the proximal ends, the only parts that were preserved. This comparison gave very low results for the Pirro Nord specimen examined; in particular, the transverse diameters of the proximal ends were particularly small (Fig. 8). Overall, the metapodials from Pietrafitta and Pirro Nord (Florence) were also found to be small in size and, especially in the case of Pietrafitta, often closer to *S. etruscus* than to *S. hundsheimensis*. Another rhinoceros metapodial from Pirro Nord was described by Pandolfi & Petronio (2011); it is a fourth metacarpal with a transverse diameter greater than MSTB-PN 20735, but slightly smaller than the antero-posterior one. Overall, the measurements compared here show that the Pirro Nord specimen of the "Dagostino Collection" is clearly the smallest compared to all the other *Stephanorhinus* at least based on the few remains available. Guérin (1980) reports that in rhinoceroses such as *Rhinoceros sondaicus* and *Ceratotherium simum*, the metacarpals complete their epiphysis when the second molars (M^2) erupt. Morphological and biometric analyses performed on the patella (MSTB-PN 20734) have shown notable affinities with *S. etruscus*; however, the measurements are significantly smaller, even when compared to the "small" specimens from Pietrafitta (see Mazza et al., 1993; Lacombat, 2005). These results suggest that this bone belonged to a juvenile individual of *S. etruscus*. However, it is important to note that taxonomic assignments involving such similar rhinoceros species require caution, particularly regarding postcranial and/or fragmentary remains. Indeed, findings from recent years have highlighted significant evidence. Stefanelli et al. (2024) observed extensive morphological variability in the rhinoceroses from Contrada Monticelli, characterized by various distinctive traits and a strong morphological affinity between *S. etruscus* and *S. hundsheimensis*, suggesting that the latter exhibits a high degree of intraspecific variability. Subsequently, Chitoglou et al. (2025) discussed the limited diagnostic value of various isolated or fragmentary postcranial elements. More recently, Pandolfi et al. (2026) examined a well-preserved specimen from Poggio Rosso in the Upper Valdarno (1.8 Ma) and provided a detailed description of the postcranial anatomy of a single *S. etruscus* individual. The authors further highlighted how several traits traditionally considered diagnostic may overlap across species or even vary within the morphology of a single skeleton. Therefore, a coherent combination of morphological and biometric data may be an effective system for a taxonomic assignment of *Stephanorhinus* based on dental remains, isolated or not.

4.2. Reassessing the taxonomic status of the Pirro Nord rhinoceroses

On the rhinoceroses from the Pirro Nord site, a taxonomic issue still remained open. In fact, the results of previous studies have led some authors to report *Stephanorhinus* cf. *hundsheimensis* (e.g. Mazza et al., 1993) or *Stephanorhinus etruscus* (e.g. Pandolfi & Petronio, 2011) at the site. Pandolfi & Petronio (2011) analysed the rhinoceros material from Pirro Nord present in the universities of Rome, Turin and Florence: in the latter case, it coincided with that presented in Mazza et al. (1993), and which the authors attributed to *S.* cf. *hundsheimensis*. Mazza et al. (1993) had already identified the first forms of *S. hundsheimensis* in Pietrafitta and Pirro Nord, which he defined as the first evolutionary stage or *S.* aff. *hundsheimensis* 'small form'. However, this interpretation was subsequently challenged by van der Made (2010, 2015), who observed that the Pietrafitta material can be considered more similar to *S. etruscus* than to *S. hundsheimensis* in terms of size and proportions. Lacombat (2005) identifies two evolutionary stages for *S. hundsheimensis*. The first one, present during the Early Pleistocene, is characterized by smaller dimensions, comparable to those of *S. etruscus*. The second evolutionary stage is present mainly during the Middle Pleistocene and is characterized by larger dimen-

sions. However, the same author states that transposing these evolutionary stages to Northern Europe is impossible and that the larger Northern Pleistocene rhinoceroses require specific study. Lacombat (2009) then examined rhino populations in Western Europe to assess the possibility of general trends in size variation among different species of the genus *Stephanorhinus* (*S. hundsheimensis*, *S. kirchbergensis*, and *S. hemitoechus*) during the Middle and Late Pleistocene. Regarding *S. hundsheimensis*, in addition to a gradual increase in size over time, clear differences were observed between the southernmost sites (Le Vallonnet, Soleilhac, and Isernia) and those further north (Untermaßfeld, Süßenborn, Voigtstedt, Mosbach 2, and Mauer). Indeed, the *S. hundsheimensis* populations from southern Europe (Italy and France) are smaller in size than coeval populations from central Germany. This increase in size, present in two geographically close areas with different climatic conditions, is therefore constant throughout Europe and can be considered an evolutionary trend that can be used as a biochronological tool (Lacombat, 2009). This trend appears to be partially confirmed at the Pirro Nord site, where part of the sample exhibits characteristics similar to *S. hundsheimensis* and is particularly small in size. However, the scenario is more complicated: in addition to small-sized *S. hundsheimensis* (evolutionary stage a), there are also larger *S. hundsheimensis* (evolutionary stage 2) and specimens that can be associated with *S. etruscus* both in terms of morphology and size. Regarding the rhinoceros specimens held at the University of Bari Aldo Moro, a few observations can be made. Pirro 1 contains all the smaller specimens, associated to *S. etruscus*, *S. hundsheimensis*, and others of uncertain attribution, whereas Pirro 1c contains medium-to-large specimens, all attributed to *S. hundsheimensis* (see Tab. 1). In any case, despite the stratigraphic uncertainty described in paragraph 1.3., it is clear that specimens associated with both *S. etruscus* and *S. hundsheimensis* were found together within the same level or fissure of Pirro 1. As for the specimens from the University of Ferrara, the stratigraphic units from which they originated are known, and the following has emerged: units D13 through D22 yielded only specimens of uncertain attribution or, in one instance, *S. etruscus*. From unit D24 to D41, only *S. hundsheimensis* or doubtful specimens have been reported (see Tab. 1). In any case, there was a crucial period during which *S. etruscus* and *S. hundsheimensis* coexisted in Europe (Lacombat, 2005). For example, Lacombat (2005) studied the rhinoceroses from Le Vallonnet (south-eastern France, ca. 1.07-0.99 Ma), identifying affinities with *S*. cf. *hundsheimensis* (small form) described by Mazza et al. (1993). According to the author, the rhinoceroses from this site present a clear morphology of *S. hundsheimensis* with dimensions smaller than the typical form of the beginning of the Middle Pleistocene (or evolutionary stage 2). Lacombat (2005), who considers *S. hundsheimensis* a distinct species from *S. etruscus*, also associated the Untermaßfeld (Germany, ca. 1.0 Ma) rhinoceros with *S. hundsheimensis*, a species already present at that time. However, the same author emphasizes that the Untermaßfeld rhinoceros is significantly larger than the Le Vallonnet rhinoceros, which prevents the previously described evolutionary stages from being correlated with northern European rhinoceroses. The Durfort site (southern France) was placed by Brugal (1994) between Mosbach I and Süßenborn, i.e., and is currently considered late Early Pleistocene (ca. 0.9 Ma) in age. Rhinoceros remains from this site were associated with *Dicerorhinus etruscus brachycephalus* by Guérin (1980) and later with *S. hundsheimensis* by Lacombat (2005). In particular, the latter author reports that *S. hundsheimensis* from Durfort appears in its typical form (evolutionary stage 2). Another example is Isernia La Pineta site (southern Italy, ca. 0.6 Ma) represented by a very rich sample studied by various authors over the years (e.g. Sala & Fortelius, 1993; Lacombat, 2005; Ballatore & Breda, 2013) and has been associated with large-sized *S. hundsheimensis* (evolutionary stage 2), even if Ballatore & Breda (2013) indicate them as slightly smaller than the contemporary British populations of the same species. The same authors, however, emphasize that a comparison between the Isernia population and the British specimens suggests lower morphological variability for the latter. The proposed explanation is that Great Britain, being an island, experienced alternating periods of isolation from the continent, and thus a bottleneck effect, resulting in a reduction of the gene pool. However, this requires recognition of the timing of the reinvasion of the British Isles by continental stocks following any major glacial oscillation. The Italian peninsula, and in particular the Gargano promontory, also suffered the effects of glacial oscillations, resulting in periods of isolation in the area surrounding Pirro Nord (see De Giuli et al., 1987). The rhinoceroses from Pirro Nord might represent a transitional form between the morphologies of *S. etruscus* and *S. hundsheimensis* (almost a chronospecies, with *S. hundsheimensis* displaying more pronounced versions of certain *S. etruscus* traits), and their variability likely reflects intraspecific variation rather than the coexistence of two species.

However, in our opinion from both a morphological and biometric point of view, the variability found in the sample examined is remarkably high, making the scenario of a single rhinoceros species in Pirro Nord unlikely. One might consider sexual dimorphism as a possible cause for the size differences observed among the various specimens. In general, the family Rhinocerotidae exhibits a certain degree of sexual dimorphism in both extant and fossil species (Faggi & Pandolfi, 2022). However, most differences, when present, are found in the skull. Leveraging the notable abundance of *S. etruscus* in the fossil record, Faggi & Pandolfi (2022) investigated the presence of sexual dimorphism in the limb bones of this taxon. Analyses revealed relatively slight sexual dimorphism across all examined bones. The authors consider it likely that adult male *S. etruscus* specimens possessed slightly larger forelimbs and hindlimbs than females. While size differences between sexes-observed in both modern rhinoceroses and *S. etruscus*, might account for the presence of individuals of markedly different sizes at the same site, they certainly do not explain why *S. hundsheimensis* from the Early Pleistocene is smaller than that from the Middle Pleistocene. For this reason, combined with the fact that the size difference appears too pronounced (especially in the metacarpals), the study's authors consider it unlikely that the specimens at Pirro Nord exhibit size-based sexual dimorphism. The same situation as in Pirro Nord seems to have been present up to the early Middle Pleistocene site of Contrada Monticelli (Murge area, ca. 0.6 Ma), slightly further south.

The last study carried out on that rhinoceros (Stefanelli et al., 2024) concerned the postcranial remains and differences were highlighted both in morphology and size within the same sample, as also noted by Mazza & Varola (1999). The situation is, however, more complex, as the study of the cranial and dental remains initially led Luperto Sinni & Colucci (1985) to identify them as '*Rhinoceros mecki*' (= *Stephanorhinus kirchbergensis*) and subsequently Mazza & Varola (1999) reattributed them to *S. hundsheimensis*. In his PhD thesis, Stefanelli (2025) re-examined the cranial and dental remains of the Contrada Monticelli rhinoceros both from a

morphological and biometric point of view. In a part of the sample notable similarities with *S. kirchbergensis* emerged, thus supporting in part the previous attribution by Luperto Sinni & Colucci (1985). Recently Pandolfi et al. (2026) support this attribution. Since this is a different situation compared to what happens for Pirro Nord, the case of the Contrada Monticelli rhinoceros specimen cannot be considered connected and will then require a study dedicated to the cranial and dental remains. Bellucci et al. (2021) reported the last occurrence of *S. etruscus* at the Cúllar de Baza 1 site (southern Spain), a site attributed to the early Middle Pleistocene using faunal criteria (Ruiz-Bustos & Michaux, 1976; Ruiz-Bustos, 1984), while paleomagnetic data provide an estimated age of about 0.77-0.75 Ma (Gibert et al., 2007; Scott & Gibert, 2009). These are few remains belonging to a single individual and their morphological description is present in Cerdeño (1989). Pandolfi et al. (2017) indicated that the disappearance of *S. etruscus* is reported in the late Early Pleistocene in Central Europe, while it survived in the Italian and Iberian peninsulas until the transition between the Early and Middle Pleistocene. Therefore, a prolonged longevity of *S. etruscus* in Italy and Spain until the beginning of the early Middle Pleistocene is not so surprising. A speculative scenario could therefore be outlined, in which rhinoceros samples from approximately 1.5 to 0.8 Ma have traits of *S. hundsheimensis*, as if a population with evolved traits had arrived in Europe, but was capable of hybridizing with local *S. etruscus* populations, thus giving rise to samples with "mixed" traits, similarly to what was described for example by Lister (2022) for *Mammuthus trogontherii* and *M. primigenius*. Such events can also, in fact, lead to character reversals towards more plesiomorphic states (see Mishler & Theriot, 2000). Conversely, rhinoceros samples from post-0.8 Ma exhibit more stable morphological traits and sizes more typical of *S. hundsheimensis*, but morphotypes similar to *S. etruscus* may still be sporadically present. The disagreement on the oldest occurrences of *S. hundsheimensis* is in line with the peculiarity found in several taxa of large mammals 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 these, the appearance of the oldest praemegacerine, *Praemegaceros obscurus* (Abbazzi, 2004) and the oldest true-bison, *Bison* (*Eobison*) *degiulii* at 1.5 Ma (Sorbelli et al., 2023), suggests that the precursors of the long-lived *S. hundsheimensis* could have been already present at 1.5 Ma as stated by Mazza et al. (1993). Studies conducted on the Pirro Nord sample from University of Bari Aldo Moro (belonging to the "Dagostino Collection") and University of Ferrara seem to further confirm this hypothesis, with one of the first reports of *S. hundsheimensis* in the Italian peninsula. However, the presence of individuals with *etruscan*-like features among the analysed sample could suggest the hypothesis presented in Stefanelli et al. (2024), regarding the possible hybridization between the two species. This could also explain the presence, in a series of Early Pleistocene sites (e.g. Westerhoven, Pietrafitta and Loreto), of small-sized forms of rhinoceroses with *S. etruscus*-*S. hundsheimensis* affinities (Mazza et al., 1993). Furthermore, traces of the specimens described above are also present in Pirro Nord, as described in the previous paragraph. In any case, given the lack of direct evidence the hybridization hypothesis should be evaluated with caution. Indeed, the combination of traits associated with both taxa could be due to a greater degree of intraspecific variability than previously assumed, a point also recently highlighted by Pandolfi et al. (2026). Another possibility is that the Early Pleistocene *S. hundsheimensis* retained a larger number of ancestral traits shared with *S. etruscus* and, in some instances, even with *Scythicorhinus vekuai*. Furthermore, one cannot rule out the hypothesis that evolutionary changes occurred in *S. hundsheimensis* populations inhabiting areas subject to periodic isolation, such as the Italian Peninsula; this could account not only for the mixed morphological traits but also for the observed differences in body size. Pandolfi & Petronio (2011) hypothesize that *S. hundsheimensis* may have been an immigrant that replaced *S. etruscus* at the end of the Early Pleistocene. This is in line with the model of Fortelius et al. (1993), who did not derive *S. hundsheimensis* from *S. etruscus*, rather than with the model of Guérin (1980) who instead identified *S. hundsheimensis* as a subspecies of *S. etruscus*. The latter hypothesis could be supported by the presence in Dmanisi (ca. 1.8 Ma) of *Stephanorhinus* closely related to *S. hundsheimensis*, which is certainly recorded in Europe starting from ca. 1.2-1.1 Ma (Pandolfi et al., 2021 and references therein). However, Pandolfi et al. (2021) distinguish two different ecomorphotypes for the rhinoceroses found in Dmanisi, different in size and showing the presence of *etruscan*-like characters, so much so that the authors refer these remains to *S.* ex gr. *etruscus-hundsheimensis*. The set of clues analysed here could instead suggest an arrival in Europe of *S. hundsheimensis* from the East and that it progressively replaced *S. etruscus*, but not immediately, coexisting for a certain period during the Early Pleistocene (ca. 1.6-1.2 Ma). However, considering what has been discovered at the Cúllar de Baza 1 and Contrada Monticelli sites, this transition phase could have continued until the early Middle Pleistocene (ca. 0.6 Ma), perhaps also due to the isolation of the Apulia region.

4.3. *Stephanorhinus etruscus* and *Stepahnorhinus hundsheimensis*: dispersal and coexistence

According to Pandolfi (2022) *S. etruscus* probably dispersed eastwards, reaching the Gongwangling area where it is known as *S. lantianensis* (ca. 1.6 Ma) (Zhu et al., 2015) and it is possible that the last records of rhinoceroses from the Early Pleistocene in Europe represent local populations of *S. etruscus*, which became isolated during stressful climatic conditions and survived until the Early-Middle Pleistocene transition in favorable geographical areas such as southern Italy and the Iberian Peninsula (Pandolfi et al., 2017). However, records of the Etruscan rhinoceros or closely related forms from Tajikistan and Kazakhstan (Dmitrieva & Nesmeyanov, 1982; Forsten & Sharapov, 2000; Sharapov, 1986) could shed light on the dispersal and evolution of this species, but this needs critical review (Pandolfi, 2022). The dispersal of *S. hundsheimensis* in Europe and Italy could be related to the climatic deterioration of the latest Early Pleistocene (Pandolfi & Petronio, 2011). The same could also explain the variations in proportions and size of *S. etruscus* supposed by Guérin (1980). In fact, during this period, the transition to a phase characterized by shift from 41,000-year cycles to long glaciations with cycles of 100,000 years occurred and the difference between temperatures during the glacial and interglacial phases became more pronounced (see Leroy, 2007; Masini & Sala, 2007, among others). A Central Asian origin of *S. hundsheimensis* and a dispersal towards Western Europe cannot be completely excluded (Cerdeño, 1998). The particular conditions of isolation of the Apulian peninsula may therefore have provided a refuge area for *S. etruscus*, while it was progressively replaced (or perhaps merged) with the more generalist *S. hundsheimensis*. According to recent data on rhinoceroses from the late Early Pleistocene, *S. etruscus* and *S. hundsheimensis*

are both present in Europe, but probably occupied different habitats (Pandolfi, 2022), being documented in different localities and showing different results in meso-and microwear analyses (Kahlke & Kaiser, 2011; Rivals & Lister, 2016; Saarinen et al., 2016; van Asperen & Kahlke, 2017). The occupation of different niches between the two species and the highly flexible feeding traits found for *S. hundsheimensis* (see Kahlke & Kaiser, 2011), could explain their contemporary presence in Pirro Nord and in other approximately contemporary sites. Pandolfi et al. (2021), point out that the rhinoceros skulls from the Dmanisi site show some morphological differences that cannot currently be linked to intraspecific variability and sexual dimorphism, on the contrary the presence of two different types of feeding or ecomorphotypes can be deduced in the site. The same authors point out that a similar condition, although attested among extant taxa, is not documented in Europe during the Early Pleistocene, that area being occupied alternatively by *S. etruscus* (a grazer) and *S. hundsheimensis* (a highly flexible feeder), but is instead present in East Asia. Chitoglou et al. (2025) report that the study of rhinoceros material from the 1.78 Ma to ~1.5 Ma site (Konidaris et al., 2021) of Tsiotra Vryssi (Mygdonia Basin, northern Greece) indicates the presence of two morphotypes, likely representing two distinct species of *Stephanorhinus*. In particular, Chitoglou et al. (2025) argue that the Tsiotra Vryssi rhinoceros could represent a single species, differentiated from the typical *S. etruscus*, perhaps showing affinities towards *S. hundsheimensis*, or a local transitional population. However, further data and a thorough study of the Tsiotra Vryssi rhinoceroses will likely confirm the coexistence of two species during the late Early Pleistocene in Eurasia. In light of the results of the study of the undescribed rhinoceros specimen from Pirro Nord the "Dagostino Collection" (University of Bari Aldo Moro) and University of Ferrara, the two species may have coexisted within a fragmented environment such as that of Pirro Nord or that of Dmanisi during the late Early Pleistocene. The coexistence of the two species can be explained by the fact that they occupied different ecological niches and that the subsequent deterioration of climatic conditions led to the disappearance of the grazer *S. etruscus* in favor of the more generalist and highly flexible *S. hundsheimensis*. Furthermore, the presence of particularly small-sized *S. hundsheimensis* individuals (evolutionary stage 1) together with that of full-sized specimens (evolutionary stage 2) can be explained by the influx into the Italian Peninsula of larger-sized *S. hundsheimensis* populations from continental Europe that mixed with the smaller local populations of southern Europe during the Early Pleistocene. Perhaps it was the influx of these larger populations from the north that ultimately led to the disappearance of the smaller and less generalist *S.etruscus* and the smaller form of *S. hundsheimensis*, leading to the definitive affirmation of the larger form also in southern Europe during the early Middle Pleistocene.

5. CONCLUSION

The Pirro Nord rhinoceroses studied here include a sample of 29 cranial-dental and postcranial remains, including a complete mandible with teeth, several isolated upper and lower teeth, one pisiform and three metacarpals. It was important to study these highly diagnostic remains for this taxon, as they could contribute to the knowledge of the taxonomy of the Pirro Nord rhinoceroses. In fact, the rhinoceros remains from this site, preserved in the museum facilities of the Universities of Rome, Florence and Turin, studied in the last decades have been attributed to *S.* cf. *hundsheimensis* by some authors and, subsequently, other authors would have associated them with *S. etruscus*. Regarding the sample examined in this study, the isolated upper teeth and the deciduous often showed greater morphological and biometric affinities with *S. hundsheimensis*. The fully toothed mandible showed morphologies and dimensions more similar to those of *S. etruscus*, therefore this find is here attributed to a small-sized adult specimen of *S. etruscus*. Regarding the isolated lower teeth, morphological and biometric analyses suggest an attribution to *S. hundsheimensis* of medium or smaller size and to *S. etruscus* of medium size. The pisiform and metacarpals show morphologies similar to *S. hundsheimensis*, but they are particularly small in size. The patella is also notably small in size; however, it exhibits morphological features that can be associated with *S. etruscus*, probably a juvenile individual. Finally, other remains that were too fragmentary or lacked particularly diagnostic parts have been assigned to *S.* ex gr. *etruscus*/*hundsheimensis* or *Stephanorhinus* sp. The reliability of dental morphological characters among the four main species of *Stephanorhinus* from the European Pleistocene was also assessed. The comparison was made by cross-referencing data from the most detailed studies examining numerous specimens and evaluating their degree of concordance and their actual reliability in taxonomic assignments. The result was that, although previous authors were substantially in agreement in assessing the typical dental morphologies of the four comparison species (*S. etruscus*, *S. hundsheimensis*, *S. hemitoechus*, and *S. kirchbergensis*), significant intraspecific variation was nevertheless present. It follows that the numerous morphological characters observed on rhinoceros teeth, while very useful, cannot be sufficient to make a credible attribution. In fact, they need to be coordinated and confirmed by available biometric analyses and biochronological data, since, as demonstrated, dental morphologies can lead to apparently misleading results, especially in the case of isolated teeth. Furthermore, from the study conducted here on the sample from the Pirro Nord site and from its comparison with the literature on other rhinoceros finds from the same site and preserved in the university museums of Rome, Turin and Florence, evidence that, given that the rhinoceros specimens from Pirro Nord analyzed here are roughly contemporaneous to the late Villafranchian fauna associated with the Pirro Faunal Unit, the following possibilities arise: 1) the presence of a single species, albeit with high internal variability and morphologies intermediate between *S. etruscus* and *S. hundsheimensis* sensu stricto; 2) specimens of *S. etruscus* and specimens of *S. hundsheimensis* "small form" that are actually females, with those of *S. hundsheimensis* "large form" being males; 3) the coexistence of *S. etruscus* and one (“small form”) or two (primarily the "small form," but also “large form”) morphotypes of *S. hundsheimensis*. This latter case would be consistent with findings from studies of rhinos from the Early Pleistocene sites of Dmanisi (Georgia) and Tsiotra Vryssi (Greece), both biochronologically close to Pirro Nord. At the same time, the three sites are located in three different areas of Europe, of which Pirro Nord is the westernmost. This might suggest that the arrival of *S.hundsheimensis* occurred earlier than previously assumed and that it did not occupy the ecological niche vacated by *S. etruscus*, but coexisted with it for a time, eventually replacing it entirely, perhaps at the end of the Early Pleistocene or in the early Middle Pleistocene. Within this scenario, the different typologies of *S. hundsheimensis* found in the analysed sample can be explained by the presence at the site of a local population of small-sized *S. hundsheimensis* (evolutionary stage 1)

typical of southern Europe in the Early Pleistocene, to which was added an influx of northerners larger-sized *S. hundsheimensis* populations (evolutionary stage 2) coming from central-northern Europe. Furthermore, the extensive morphological and biometric variability observed in the Pirro Nord specimens associated with *S. hundsheimensis* may be attributed to: 1) greater intraspecific variability than previously assumed for this species; 2) the retention of ancestral traits shared with *S. etruscus*; 3) evolutionary changes that occurred in populations living in areas subject to periodic isolation; 4) the potential hybridization between *S. etruscus* and *S. hundsheimensis*.

ACKNOWLEDGEMENTS

The authors thank the Museum of Earth Sciences and the Department of Earth and Geoenvironmental Sciences (University of Bari Aldo Moro, Italy) and Dr Nicola Venisti for facilitating access to the Museum and for studying the fossil specimen of the "Dagostino Collection". The authors thank Prof. Marta Arzarello, Prof. Benedetto Sala, and Dr Julie Arnaud for facilitating access to the Pirro Nord specimen held at the University of Ferrara. This study was financially supported by Geoscience PhD scholarship to DS (University of Bari-Italy), and by fund "FrancescangeltCTCAVAPONT2022" to MM (University of Bari-Italy). RS acknowledges the Italian Ministry of University and Research, PRIN 2022 scorrimento Prot. 2022JWFEKE "The evolution of mammals in changing ecosystems of the Middle Pleistocene of Italy". The authors thank Thijs van Kolfschoten and the other anonymous reviewer for their insightful and useful comments and suggestions which improved the first draft of our manuscript. Images of the fossil material from the University of Ferrara are used with the permission of the Ministry of Culture-Superintendency of Archaeology, Fine Arts and Landscape for the provinces of BAT and FG.

Author contributions

DS: investigation (dental, cranial and postcranial remains), paleontological analysis (description, comparison and taxonomic discussion), writing: original draft preparation, writing: review and editing. BM: writing: original draft preparation, writing-review and editing. MM and RS: writing: review and editing.

The authors have declared that no competing interests exist.

No ethical statement was reported.

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI. No AI tools were used in the preparation of this manuscript.

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. Rendiconti Lincei Scienze Fisiche e Naturali, 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: 10.1007/s00114-006-0173-3

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

Arzarello M., Pavia G., Peretto C., Petronio C., Sardella R. (2012) - Evidence of an early Pleistocene hominin presence at Pirro Nord (Apricena, Foggia, southern Italy): P13 site. Quaternary International, 267, 56-61.
Doi: 10.1016/j.quaint.2011.01.042

Arzarello M., Peretto C., Moncel M.H. (2015) - The Pirro Nord site (Apricena, Fg, Southern Italy) in the context of the first European peopling: convergences and divergences. Quaternary International, 389, 255- 263.
Doi: 10.1016/J.QUAINT.2014.08.051

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. Quaternary International, 302, 169-183.
Doi: 10.1016/j.quaint.2013.02.002

Bellucci L., Palombo M.R., DeMiguel D., Strani F., Alberdi M.T. (2021) - New taxonomical, biochronological and palaeoenvironmental data from the Middle Pleistocene site of Cúllar de Baza 1 (Granada, Spain). Quaternary Science Reviews, 261,106932.
Doi: 10.1016/j.quascirev.2021.106932

Berruti G.L.F., Arzarello M. (2020) - Talking stones: Taphonomy of the lithic assemblage of Pirro Nord 13 (Apricena, FG, Italy). A new approach to the study of the post depositional alterations on lithics tools. Journal of Archaeological Science: Reports 31, 102282.
Doi: 10.1016/j.jasrep.2020.102282

Bourguignon L., Crochet J.-Y., Capdevila R., Ivorra J., Antoine P.-O., Agustí J., Barsky D., Blain H.A., Boulbes N., Bruxelles L., Claude J., Cochard D., Filoux A., Firmat C., Lozano-Fernandez I., Magniez P., Pelletier M., Rios-Garaizar J., Testu A., Valensi P., Louis De Weyer L. (2015) - Bois-de-Riquet (Lézignan-la- Cèbe, Hérault): A late Early Pleistocene archeological occurrence in southern France. Quaternary International, 393, 24-40.
Doi: 10.1016/j.quaint.2015.06.037

Brugal J.-P. (1994) - Le bison (Bovidae, Artiodactyla) du Pleistocene moyen ancien de Durfort (gard, France). Bulletin - Museum National d'Histoire Naturelle Section C: Sciences de la Terre, 16C (2-4), 349-381.

Cerdeño E. (1989) - Rhinocerotidae (Mammalia, Perissodactyla) de la cuenca de Guadix-Baza. In: Alberdi, Maria Teresa, Bonadonna, Francesco Paolo (Eds.), Geologia y Paleontologia de la cuenca de Guadix-Baza. Museo Nacional de Ciencias Naturales, CSIC, Madrid, 273-287.

Cerdeño E. (1993) - Remarks on the Spanish Plio-Pleistocene *Stephanorhinus etruscus* (Rhinocerotidae). Comptes Rendus Academie des Sciences, 317, 1363-1367.

Cerdeño E. (1998) - Diversity and evolutionary trends of the family Rhinocerotidae (Perissodactyla). Palaeogeography, Palaeoclimatology, Palaeoecology, 141, 13-34.

Cerdeño E., Alberdi M.T. (2016) - Los perisodáctilos de Villarroya: équidosy rinocerótidos. In: Alberdi M.T., Azanza B., Cervantes E. (Eds.), Elyacimiento de Villarroya, una joya paleontológica riojana. Institutode Estudios Riojanos, Rioja, 143-158.

Cheheb R.C., Arzarello M., Arnaud J., Berto C., Cáceres I., Caracausi S., Colopi F., Daffara S., Canini G.M., Huguet R., Karambatsou T., Sala B., Zambaldi M., Berruti G.L.F. (2019) - Human behavior and *Homo*-mammal interactions at the first Euro-

pean peopling: new evidence from the Pirro Nord site (Apricena, Southern Italy). The Science of Nature, 106, 16.
Doi: 10.1007/s00114-019-1610-4

Chitoglou K., Pandolfi L., Konidaris G.E., Kostopoulos D.S. (2025) - Early Pleistocene rhinoceroses (Mammalia, Perissodactyla, Rhinocerotidae) from Northern Greece: biochronological and paleobiogeographic implications. PalZ, 99, 407-434.
Doi: 10.1007/s12542-025-00739-8

Dagostino G. (1972). Studi sui resti fossili di *Equus stenonis* COCCHI rinvenuti nel giacimento pleistocenico di Pirro (Apricena, Foggia). Università degli Studi di Bari. Unpublished thesis, pp. 188.

De Beaumont G. (1979) - Note sur quelques carnivores (Mammiferes) du Quaternaire ancien de la province de Foggia (Italie). Bulletin de la Societé Vaudoise des Sciences Naturelles, 74, 217-226.

De Giuli C., Torre D. (1984) - Species interrelationships and evolution in the Pliocene endemic faunas of Apricena (Gargano Peninsula-Italy). Geobios, 17 (1), 379-383.

De Giuli C., Masini F., Torre D. (1986) - The latest Villafranchian faunas of Italy. The Pirro Nord Fauna (Apricena, Gargano). Palaeontographia Italica, 74, 51-62.

De Giuli C., Masini F., Valleri G. (1987) - Paleogeographic evolution of the Adriatic area since Oligocene to Pleistocene. Rivista Italiana di Paleontologia e Stratigrafia, 93(1), 109-126.

Delfino M., Bailon S. (2000) - Early Pleistocene Herpetofauna from cava dell'Erba and cava Pirro (Apulia, Southern Italy). Herpetological Journal, 10, 95-110.

Dmitrieva E.L., Nesmeyanov S.A. (1982) - Mammals and Stratigraphy of Tertiary Continental Deposits in Southeastern Middle Asia. Nauka, Moskow, pp. 140 ([in Russian]).

Duval M., Arnold L.J., Bahain J.-J., Parés J.M., Demuro M., Falguères C., Shao Q., Voinchet P., Arnaud J., Berto C., Berruti G.L.F., Daffara S., Sala B., Arzarello M. (2024) - Reexamining the earliest evidence of human presence in Western Europe: new dating results from Pirro Nord (Italy). Quaternary Geochronology, 82, 101519.
Doi: 10.1016/j.quageo.2024.101519

Faggi A., Pandolfi L. (2022) - Evaluating sexual dimorphism in postcranial elements of eurasian extinct *Stephanorhinus etruscus* (Falconer, 1868) (Mammalia, Rhinocerotidae). Geosciences, 12, 164.
Doi: 10.3390/geosciences12040164

Falconer H. (1868) - On the European Pliocene and Postpliocene species of the genus Rhinoceros. Paleontological and Notes, 2, 309-403.

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

Forsten A., Sharapov S. (2000) - Fossil equids (Mammalia, Equidae) from the Neogene and Pleistocene of Tadzhikistan. Geodiversitas, 22, 293-314.

Freudenthal M. (1971) - Neogene vertebrates from the Gargano Peninsula, Italy. Scripta Geologica, 3, 1-10.

Gaudin C.-T. (1859) - Modifications apportées par Mr. Falconer à la faune du Val d'Arno. Bulletin des Séances de la Société Vaudoise des Sciences Naturelles, 44, 130-131.

Gibert L., Scott G., Martin R., Gibert J. (2007) - The Early to Middle Pleistocene boundary in the Baza Basin (Spain). Quaternary Science Reviews, 26, 2067-2089.
Doi: 10.1016/j.quascirev.2007.06.012

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.

Hammer Ø., Harper D.A., Ryan P.D. (2001) - PAST: paleontological statistics software package for education and data analysis. Paleontologia Electronica, 4, 1-9.

Handa N., Pandolfi L. (2016) - Reassessment of the middle Pleistocene Japanese rhinoceroses (Mammalia, Rhinocerotidae) and paleobiogeographic implications. Paleontological Research, 20(3), 247-260.
Doi: 10.2517/2015PR034

Iannucci A., Stefanelli D., Conti J., Marino M., Sardella R. (2026) - Occurrence of *Crocuta* (Carnivora, Hyaenidae) from a potential Middle Pleistocene site at Pirro Nord (Apricena, southern Italy). Journal of Quaternary Science, 41(4), 552-557.
Doi: 10.1002/jqs.70065

Jäger G.F. (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., Kaiser T.M. (2011) - Generalism as a subsistence strategy: advantages and limitations of the highly flexible feeding traits of Pleistocene *Stephanorhinus hundsheimensis* (Rhinocerotidae, Mammalia). Quaternary Science Reviews, 30, 2250-2261.

Konidaris G.E., Kostopoulos D.S., Maron M., Schaller M., Ehlers T.A., Aidona E., Marini M., Tourloukis V., Muttoni G., Koufos G.D., Harvati K. (2021) - Dating of the Lower Pleistocene vertebrate site of Tsiotra Vryssi (Mygdonia Basin, Greece): Biochronology, magnetostratigraphy, and cosmogenic radionuclides. Quaternary, 4(1), 1.
Doi: 10.3390/quat4010001

Kovalchuk O., Borrani A., Mackiewicz P., Barkaszi Z., Capalbo C., Davydenko S., Dubikovska A., Ratajczak-Skrzatek U., Sinitsa M., Stefaniak K., Krajcarz M.T., Mazza P.P.A. (2026) - *Scythicorhinus vekuai* gen. nov. et comb. nov. (Mammalia, Rhinocerotidae) from the Pliocene of Georgia and its implications for the early evolution of *Coelodonta* and *Stephanorhinus*. Scientific Reports, 16, 21401.
Doi: 10.1038/s41598-026-57113-0

Lacombat F. (2005) - Les rhinocéros fossiles des sites préhistoriques de l'Europe méditerranéenne et du Massif central. Paléontologie et implications biochronologiques. British Archaeological Reports, 1419, 1-175.
Doi: 10.30861/9781841718583

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, 274, 71-111.
Doi: 10.1127/pala/274/2006/71

Lacombat F. (2009) - Biochronologie et grand Mammifères au Pléistocène Moyen et Superiéur en Europe Occidentale: l'apport des Rhinocerotidae (genre *Stephanorhinus*). Quaternaire, 20(4), 429-435.
Doi: 10.4000/quaternaire.5302

Leroy S.A.G. (2007) - Progress in palynology of the Gelasian-Calabrian Stages in Europe: ten messages. Revue de Micropaléontologie, 50, 293-308. Doi: 10.1016/j.revmic.2006.08.001

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

Masini F., Sala B. (2007) - Large and small mammal distribution patterns and chronostratigraphic boundaries from the Late Pliocene to the Middle Pleistocene of the Italian peninsula. Quaternary International, 160, 43-56. Doi: 10.1016/j.quaint.2006.09.008

Mazza P. (1988) - The Tuscan Early Pleistocene rhinoceros *Dicerorhinus etruscus*. Paleontographia Italica, 75, 1-87.

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., 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. Palaeontographia Italica, 80, 25-50.

Mishler B.D., Theriot E.C. (2000) - The phylogenetic species concept (sensu Mishler and Theriot): monophyly, apomorphy, and phylogenetic species concepts. In Wheeler Q.D., Meier R. (eds), Species Concepts and Phylogenetic Theory: A Debate. Columbia University Press, 44-54.

Pacheco F.G., Santiago A., Gutiérrez J.M., López-García J.M., 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). Quaternary International, 243(1), 92-104. Doi: 10.1016/j.quaint.2011.05.034

Pandolfi L. (2022) - A critical overview on Early Pleistocene Eurasian *Stephanorhinus* (Mammalia, Rhinocerotidae): Implications for taxonomy and paleobiogeography. Quaternary International, 674-675, 109-120. Doi: 10.1016/j.quaint.2022.11.008

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., 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. (2011) - *Stephanorhinus etruscus* (Falconer, 1868) from Pirro Nord (Apricena, Foggia, Southern Italy) with notes on the late Early Pleistocene rhinoceroses of Italy. Rivista Italiana di Paleontologia e Stratigrafia, 117, 173-187. Doi: 10.13130/2039-4942/5969

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. Annales de Paléontologie, 101(4), 325-339. Doi: 10.1016/j.annpal.2015.09.001

Pandolfi L., Cerdeño E., Codrea V., Tassos K. (2017) - Biogeography and chronology of the Eurasian extinct rhinoceros *Stephanorhinus etruscus* (Mammalia, Rhinocerotidae). Comptes Rendus Palevol, 16, 762-773. Doi: 10.1016/j.crpv.2017.06.004

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). Journal of Human Evololution, 156, 103013. Doi: 10.1016/j.jhevol.2021.103013

Pandolfi L., Faggi A., Bartolini-Lucenti S., Rook L. (2026) - Morphological and morphometric variability in Quaternary rhinoceroses as revealed by a small-sized adult *Stephanorhinus etruscus* skeleton from Poggio Rosso in Upper Valdarno (Early Pleistocene, Italy). Quaternary International, 785, 110483. Doi: 10.1016/j.quaint.2026.110483

Pavia G., Bertok C., Ciampo G., Di Donato V., Martire L., Masini F., Santangelo N., Taddei Ruggiero E., Zunino M. (2010) - Depositional events in the Pliocene to Lower Pleistocene succession of the Apricena- Lesina-Poggio Imperiale mining district (western Gargano, Foggia, southern Italy). Bollettino della Società Geologica Italiana, 129, 132-155. Doi: 10.3301/IJG.2009.11

Pavia M., Zunino M., Coltorti M., Angelone C., Arzarello M., Bagnus C., Bellucci L., Colombero S., Marcolini F., Peretto C., Petronio C., Petrucci M., Pieruccini P., Sardella R., Tema E., Villier B., Pavia G. (2012) - Stratigraphical and palaeontological data from the early Pleistocene Pirro 10 site of Pirro Nord (Puglia, South eastern Italy). Quaternary International, 267, 40-55. Doi: 10.1016/j.quaint.2010.12.019

Petrucci M. (2008) - Analisi sistematica dei Macromammiferi di Pirro Nord (Apricena, Foggia, Puglia). PhD thesis, University of Turin, Turin, Italy, pp. 201.

Petrucci M., Cipullo A., Martínez-Navarro B., Rook L., Sardella R. (2013) - The late Villafranchian (Early Pleistocene) carnivores (Carnivora, mammalia) from Pirro Nord (Italy). Palaeontographica Abteilung, 298, 113-145. Doi: 10.1127/pala/298/2013/113

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

Rivals F., Lister A.M. (2016) - Dietary flexibility and niche partitioning of large herbivores through the Pleistocene of Britain. Quaternary Science Reviews, 146, 116-133. Doi: 10.1016/j.quascirev.2016.06.007

Ruiz-Bustos A. (1984) - El yacimiento paleontológico de Cúllar de Baza I. Investigación y Ciencia, 91, 20-28.

Ruiz-Bustos A., Michaux J. (1976) - Le site préhistorique nouveau de Cullar de Baza -I (Province de Grenade, Espagne) d'âge Pléistocène moyen. Etude préliminaire et analyse de la faune des Rongeurs. Géologie Méditerranéenne, 3(3), 173-182.

Saarinen J., Eronen J., Fortelius M., Seppä H., Lister A.M. (2016) - Patterns of diet and body mass of large ungulates from the Pleistocene of Western Europe, and their relation to vegetation. Palaeontologia Electronica, 19, 1-58. Doi: 10.26879/443

Sala B., Fortelius M. (1993) - The rhinoceroses of Isernia la Pineta (early Middle Pleistocene, southern Italy). Palaeontographia Italica, 80, 157-174.

Scott G.R., Gibert L. (2009) - The oldest hand-axes in Europe. Nature, 461, 82-85.
Doi: 10.1038/nature08214

Sharapov S. (1986) - *Kuruksayskiy Kompleks Pozdnepliocenovich Mlekopitayuzhih Afgano-Tadjikskoy Depressii* [Kuruksay Complex of Late Pliocene Mammals from Afgan-Tadjik Depression]. Dushanbe, Donish, pp. 270 (in Russian).

Sorbelli L., Cherin M., Kostopoulos D.S., 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). Quaternary Science Reviews, 301, 107923.
Doi: 10.1016/j.quascirev.2022.107923

Stefanelli D. (2025) - The evolution of terrestrial ecosystems in the Quaternary: Pleistocene mammals from Apulia in the Museum of Earth Sciences (UniBa). Unpublished PhD thesis, Università degli Studi di Bari Aldo Moro, Bari, Italy, pp. 304.
Handle: http://hdl.handle.net/11586/539200

Stefanelli D., Mecozzi B., Breda M., Girone G., La Perna R., Maiorano P., Marino M., Sardella R. (2023) - Rediscovering the fossil collection from the late Early Pleistocene site of Pirro Nord. (Foggia, Southern Italy) at the Bari University. Paleodays 2023. La Società Paleontologica Italiana a Lecce. Volume dei riassunti & Guida all'Escursione della XXIII riunione annuale SPI (Società Paleontologica Italiana). Abstract book: p. 76.
Doi: 10.1285/i9788883051968

Stefanelli D., Mecozzi B., Marino M., Sardella R., Breda M. (2024) - The postcranial variability of Quaternary European rhinoceroses: the case study of *Stephanorhinus hundsheimensis* from the Middle Pleistocene site of Contrada Monticelli (Apulia, southern Italy). Historical Biology, 37(4), 758-777, (2025).
Doi: 10.1080/08912963.2024.2328276

Stefanelli D., La Perna R., Delfino M. (2026) - Turtle remains of the “Dagostino Collection” from the Pleistocene of Pirro Nord (Apulia, southern Italy). Annales de Paléontologie, 112, 102914.
Doi: 10.1016/j.annpal.2026.102914

Stilson K.T., Hopkins S.S.B., Davis E.B. (2016) - Osteopathology in Rhinocerotidae from 50 Million Years to the Present. PLoS ONE, 11(2), e0146221.
Doi: 10.1371/journal.pone.0146221

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, Geologischen Reichsanstalt, 19(1), 1-92.

van Asperen E.N., Kahlke R.-D. (2017) - Dietary traits of the late Early Pleistocene *Bison menneri* (Bovidae, Mammalia) from its type site Untermaßfeld (Central Germany) and the problem of Pleistocene ‘wood bison’. Quaternary Science Reviews, 177, 299-313.
Doi: 10.1016/j.quascirev.2017.10.002

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)]. Quaternarie, 9(4), 267-281.

van der Made J. (1999) - Ungulates from Atapuerca TD6. Journal of Human Evolution, 37(3- 4), 389-413.

van der Made J. (2010) - The rhinos from the middle Pleistocene of Neumark-Nord (Saxony-Anhalt). Veroffentlichungen des Landesamtes für Denkmalpflege und Archaologie, 62, 433-500.

van der Made J. (2015) - The rhinoceros *Stephanorhinus* aff. *etruscus* from the latest Early Pleistocene of Cueva Victoria (Murcia, Spain). Mastia, 10, 345-369.

de Villalta Comella J.F. (1952) - Contribución al conocimiento de los mamíferos fósiles del Plioceno de Villaroya (Logrõno). Boletín del Instituto Geológico y Minero de España, 64, 1-203.

Zhu Z.-Y., Dennell R., Huang W.-W., Wu Y., Rao Z.-G., Qiu S.-F., Xie J.-B., Liu W., Fu S.-Q., Han J.-W., Zhou H.-Y., Ou Yang T.-P., Li H.-M. (2015) - New dating of the *Homo erectus* cranium from Lantian (Gongwangling), China. Journal of Human Evolution, 78, 144-157.
Doi: 10.1016/j.jhevol.2014.10.001

Ms. received: September 2, 2026 Revised: October 18, 2026
Accepted: November 7, 2026 Available: November 18, 2026