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A critical overview on Early Pleistocene Eurasian *Stephanorhinus* (Mammalia, Rhinocerotidae): Implications for taxonomy and paleobiogeography

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ABSTRACT

Isolated teeth and bones of rhinoceroses are sometimes difficult to identify at specific level because our poor knowledge of the morphological variability of fossil and, often, of extant species. During the past century, several studies have been devoted to highlight morphological and morphometric differences among the fossil Pleistocene species, but only a few of them considered the variability of the extant taxa, in particular *Dicerorhinus sumatrensis*, to support and interpret their results. *Dicerorhinus sumatrensis* is the closest extant relative of the Eurasian *Stephanorhinus*, as recently evidenced by molecular analyses, and it provides useful data to better understand the variability in extinct Pleistocene Eurasian taxa. Taking into account the observations on the extant Sumatran rhinoceros, the validity of some morphological traits, often used for specific attribution in Early Pleistocene fossil rhinoceroses, is revised. Sexual dimorphism and ontogenetic stage drive the development of some important features in Eurasian rhinoceroses and a detailed comparison among crania lead to new considerations on taxonomy, and, therefore, on paleobiogeography and biochronology of the different species.

1. Introduction

Early Pleistocene rhinoceroses are relatively well-documented in Eurasia and they are included within faunal lists from several fossiliferous localities (Bartolini-Lucenti et al., 2022; Kahlke et al., 2011; Rook and Martínez-Navarro, 2010; Wang et al., 2014). During that time, the family Rhinocerotidae is represented by four different genera of Rhinocerotini, *Stephanorhinus*, *Coelodonta*, *Dicerorhinus* and *Rhinoceros*, and only one genus of Elasmotheriini, *Elasmotherium* (Antoine et al., 2022). Among the Rhinocerotini, the genus *Stephanorhinus* occupies the widest area, being recorded from Iberian Peninsula to China (Guérin, 1980a, 1982a, 1982b; Lacombat, 2006; Martínez-Navarro, 2010; Pandolfi et al., 2017a, 2021a, 2021b; Pandolfi and Erten, 2017) with six species: *S. jeanvireti*, *S. etruscus* and *S. hundsheimensis* in Western Eurasia and *S. lantianensis*, *S. yunchuchenensis* and *S. kirchbergensis* in Eastern Eurasia. Although several studies have been devoted to highlight morphological and morphometric differences among the fossil Pleistocene species (Fortelius et al., 1993; Guérin, 1980a; Lacombat, 2006; Pandolfi et al., 2021b), isolated teeth and bones are sometimes difficult to identify at specific level because our poor knowledge of the morphological variability of fossil and, often, of extant species. Thus, the diversity of *Stephanorhinus* during the Pleistocene could be probably overestimated,

being the different species often erected on poorly diagnosed remains or being poorly compared among them. Only a few studies (Guérin, 1980b; Loose, 1975) considered the variability of the extant taxa, in particular *Dicerorhinus sumatrensis*, to support and interpret similarities and differences among the fossil *Stephanorhinus* species.

Dicerorhinus sumatrensis is the closest extant relative of the Eurasian *Stephanorhinus*, as recently evidenced by molecular analyses (Cappellini et al., 2019; Kirillova et al., 2017; Liu et al., 2021), and provides useful data to better understand the variability in the extinct Pleistocene Eurasian taxa. Accordingly, several crania belonging to the Sumatran rhino are here morphologically compared in order to highlight the intraspecific variability of this species and to detect morphological differences helpful to critically revise the cranial material of fossil Pleistocene rhinoceroses. In this paper, morphological comparisons are preferred to morphometrics, mainly because the latter has been extensively used in the past leading to a misidentification of the fossil material. Thus, Early Pleistocene *Stephanorhinus* species are compared among them, and their validity is confirmed or discarded, providing new insights on taxonomy and paleobiogeography.

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2. Material and methods

The material considered in this paper is housed in several Museums and Institutions and it is partially figured in published papers. The material was studied during visit to Paleontological Collections and represents the results of several years of researchers on Early Pleistocene rhinoceroses.

The classification above genus level follows [Antoine et al. \(2010\)](#) and [Pandolfi et al. \(2021b\)](#). The anatomical terminology follows [Antoine \(2002\)](#) and [Guérin \(1980a\)](#). The described anatomical features are reported in [Fig. 1](#).

Institutional Abbreviations - **GPIH**, Geologisch-Paläontologisches Institut der Universität Heidelberg, Germany; **HLMD**, Hessisches Landesmuseum Darmstadt, Germany; **HNHM**, Hungarian Natural History Museum, Budapest, Hungary; **IGF**, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MIL**, Milia Natural History Museum, Milia, Greece; **MNCN**, Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN**, Naturhistorisches Museum Mainz, Germany; **MNHNP**, Muséum National d'Histoire Naturelle, Paris, France; **MPI**, Museo Nazionale di Isernia, Isernia, Italy; **MPP**, Museo Paleontologico Parmense, Parma, Italy; **MZUF**, Museo di Storia Naturale sezione di Zoologia “La Specola”, Florence, Italy; **NHMUK**, Natural History Museum, London, England; **NHMW**, Naturhistorisches Museum, Vienna, Austria; **NMB**, Naturhistorisches Museum, Basel, Switzerland; **NMS**, National Museum of Scotland, Edinburgh, Scotland; **SMF**, Senckenberg Naturmuseum, Frankfurt, Germany; **SMNK**, Staatliches Museum für Naturkunde, Karlsruhe, Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Anatomical Abbreviations- **L**, length; **M/m**, upper/lower molar; **P/p**, upper/lower premolar.

3. Systematic paleontology

Class Mammalia Linnaeus, 1758
 Order Perissodactyla [Owen, 1848](#).
 Family Rhinocerotidae [Gray, 1821](#)
 Tribe Rhinocerotini [Gray, 1821](#)
 Genus *Stephanorhinus* [Kretzoi, 1942](#)

3.1. *Stephanorhinus kirchbergensis* ([Jäger, 1839](#))

Type material: isolated M2 (SMNS 34000.3), M3 (SMNS 34000.2) and p3 (SMNS34000.1) figured by [Jäger \(1839: Pl. 16, Figs. 31–33\)](#) are the lectotype of the species. The specimens are housed at Staatliches Museum für Naturkunde, in Stuttgart.

Type locality and horizon: Kirchberg, Baden-Württemberg, Germany, late Middle Pleistocene.

Temporal distribution: from the late Early Pleistocene to the latest Pleistocene. The oldest record of the species was in Eastern Asia, at Gongwangling (latest Early Pleistocene: [Liu et al., 2015](#)) and Tuozidong cave deposits (ca 1.6 Ma: [Dong et al., 2013](#)). These records are doubtful (see discussion section), but the species can be identified at Zhoukoudian Loc. 13 (Early/Middle Pleistocene boundary: [Tong, 2012](#)).

Geographic distribution: *S. kirchbergensis* was present in Eastern Asia from the latest Early Pleistocene to the latest Late Pleistocene ([Tong et al., 2014](#); [Kirillova et al., 2021](#); [Kosintsev et al., 2020](#); [Lobachev et al., 2021](#); [Chen et al., 2012](#); [Tong and Wu, 2010](#); [Tong and Moigne, 2000](#); [Turvey et al., 2013](#)). The species reached Western Europe during the early Middle Pleistocene ([Guérin, 1980a](#); [Lacombat, 2006](#); [Pandolfi and Marra, 2015](#)), where it became extinct during the Late Pleistocene ([Guérin, 1980a](#); [Lacombat, 2005a](#); [Marciszak et al., 2019](#); [Pandolfi et al., 2017b](#); [Sobczyk et al., 2020](#)), and reached the Japanese islands during the Middle Pleistocene ([Handa and Pandolfi, 2016](#)). At present, *S. kirchbergensis* is unknown in Iberian Peninsula and Greece ([Billia, 2011](#); [Cerdeño, 1990](#); [Chitoglou, 2022](#); [Giaourtsakis, 2022](#); [van der Made, 2010](#)) whilst the records from the Levant are uncertain ([Pandolfi et al., 2020](#)).

3.2. *Stephanorhinus etruscus* ([Falconer in Ansted, 1859](#))

Type material: cranium (IGF 756) stored at Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy. Figured in [Falconer \(1868: pp. 355–358, pl. XXVI, Figs. 1–3, pl. XXVII, Figs. 1 and 5\)](#). Concerning the authorship, see discussion in [Giaourtsakis \(2022\)](#).

Type locality and horizon: Upper Valdarno Basin (Tuscany, Italy), Lower Pleistocene.

Temporal distribution: from the latest Pliocene of Western Europe to the early Middle Pleistocene.

Geographic distribution: the species is recorded in several localities of Iberian Peninsula and Italian Peninsula, central Europe and

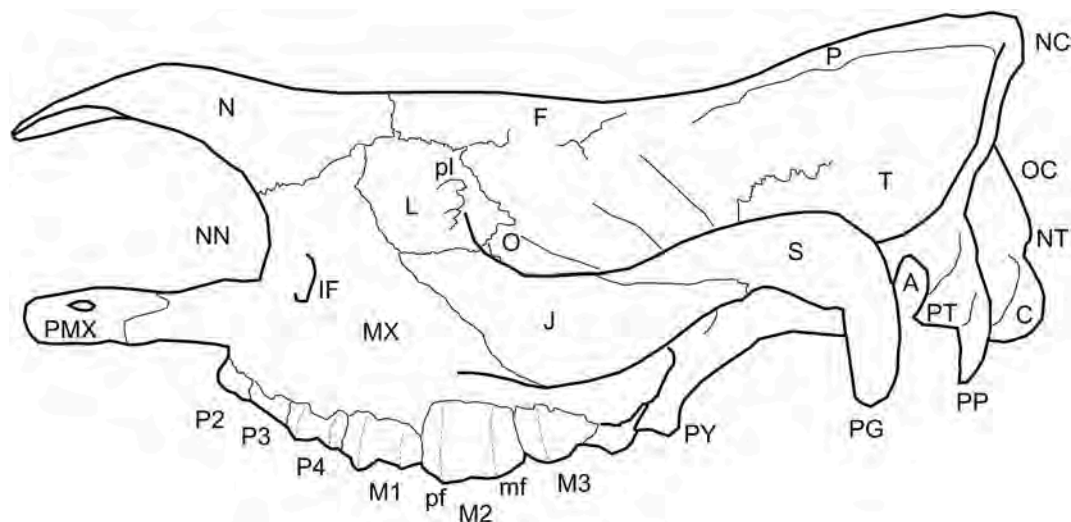


Fig. 1. Anatomical features of the cranium described in the text. A, external auditory pseudomeatus; C, occipital condyle; F, frontal; IF, infraorbital foramen; J, jugal; L, lacrymal; mf, metacone fold; MX, maxilla; N, nasals; NC, nuchal crest; NN, nasal notch; NT, nuchal tubercle; O, orbit; OC, occipital face; P, parietal; pf, paracone fold; PG, processus post-glenoidalis; pl, processus lacrymalis; PMX, praemaxilla; PP, processus paraoccipitalis; PT, processus post-tympanicus; PY, pterygoid; S, squamosal; T, temporal. P2–P4, upper premolars; M1–M3, upper molars.



Fig. 2. Crania of *Dicerorhinus sumatrensis* in lateral view. A, NHMUK 1952-4-1-2, male, M3 not erupted; B, NHMUK 1948-12-20-1, unknown sex, erupting M3; C, NHMUK 68-4-15-1, unknown sex, M3 fully erupted; D, NHMUK 1921-2-8-2, male, M3 fully erupted; E, NHMUK 1921-2-8-3, female, M2 only half erupted; F, NHMUK 1921-2-8-4, female, M3 fully erupted. Scale bar equals 10 cm.



Fig. 3. Crania of *Dicerorhinus sumatrensis* in dorsal view. A, NHMUK 1879-6-14-2, unknown sex, M3 fully erupted; B, NHMUK 1921-2-8-4, female, M3 fully erupted; C, NHMUK 1894-9-24-1, male, M3 fully erupted; D, NHMUK 68-4-15-1, unknown sex, M3 fully erupted; E, NHMUK 1931-5-28-1, male, erupting M3. Scale bar equals 10 cm.

Eastern Europe (Cerdeño, 1993; Chitoglou, 2022; Falconer, 1868; Fortelius et al., 1993; Giaourtsakis, 2022; Guérin, 1980a; Lacombat, 2005a; Mazza, 1988; Pandolfi et al., 2017a, 2019, 2022; Pandolfi and Erten,

2017; Pandolfi and Petronio, 2011; Sanisidro and Cantalapiedra, 2022). The occurrence in the Levant is at present doubtful (Pandolfi et al., 2020) as well as its occurrence in the famous site of Dmanisi in Georgia



Fig. 4. Crania of Pleistocene *Stephanorhinus* in lateral view. A, *S. kirchbergensis* SMNK PAL 4254, M3 fully erupted; B, *S. kirchbergensis* SMNS 6617.2.12.67.3, M3 fully erupted; C, *S. yunchuchenensis* IVPP V2879, M3 fully erupted?; D, *S. etruscus* IGF 756, M3 fully erupted; E, *S. etruscus* IGF 889, M3 fully erupted; F, *S. etruscus* NMB Se1703, M3 fully erupted; G, *S. hundsheimensis* NHMW 2013/0282/0001, M3 fully erupted; H, *S. hundsheimensis* IQW 1965–2513 (Suss. 9615); I, *S. hundsheimensis* MNHN PW 1958–764; L, *S. etruscus* MNHN 1923-4; M, *S. lantianensis* IVPP V5413; N, *S. jeanvireti* NMB Vt 621.

(Cappellini et al., 2019; Pandolfi et al., 2021a).

3.3. *Stephanorhinus hundsheimensis* (Toula, 1902)

Type material: an almost complete skeleton, including partial cranium and mandible (NHMW, 2013/0282/0001), housed at Naturhistorisches Museum, Vienna (Austria). Figured in Toula (1902: Pls. I–III, IV Figs. 1–3, V–XII).

Type locality and horizon: Hundsheim (Lower Austria, Austria), early Middle Pleistocene (Marine Isotopic Stage 15 or 13).

Temporal distribution: from the late Early Pleistocene to the early Middle Pleistocene in Europe. *S. hundsheimensis* (= *Dicerorhinus etruscus brachycephalus* in partim) is reported in Caucasus during the late Middle Pleistocene (Bona and Sala, 2016; Breda et al., 2010; Chitoglou, 2022; Fortelius et al., 1993; Guérin and Baryshikov, 1987; Kahlke et al., 2011; Konidaris et al., 2015; Kotowski et al., 2020; Lacombat, 2006; Madurell-Malapeira et al., 2010; Moullé et al., 2006; Pandolfi, 2013; Pandolfi et al., 2018; Pandolfi and Erten, 2017; Pandolfi and Marra, 2015; Radović et al., 2020; van Asperen and Kahlke, 2015; Vislobokova and Agadjanian, 2015).

Geographic distribution: the specie is documented from Iberian Peninsula to Anatolia, including central Europe, United Kingdom, Balkan Peninsula and Caucasus (Bona and Sala, 2016; Breda et al., 2010; Chitoglou, 2022; Fortelius et al., 1993; Kahlke et al., 2011; Konidaris et al., 2015; Kotowski et al., 2020; Lacombat, 2006; Madurell-Malapeira et al., 2010; Moullé et al., 2006; Pandolfi, 2013; Pandolfi et al., 2018; Pandolfi and Erten, 2017; Pandolfi and Marra, 2015; Radović et al., 2020; van Asperen and Kahlke, 2015; Vislobokova and Agadjanian, 2015).

3.4. *Stephanorhinus yunchuchenensis* (Chow, 1963)

Type material: an almost complete cranium, IVPP V2879, housed at Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. Figured in Chow (1963: Pl. I).

Type locality and horizon: Yunchuchen, Yushe, Shanxi, China; the exact location is uncertain.

Temporal distribution: late Early Pleistocene?, the age is estimated on regional geological information (Tong, 2012).

Geographic distribution: only from the type area.

3.5. *Stephanorhinus lantianensis* (Hu and Qi, 1978)

Type material: an almost complete cranium of a very old individual, IVPP V5413, housed at Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. Figured in Hu and Qi (1978: Pl. XI).

Type locality and horizon: Gongwangling, Lantian, Shanxi, China, late Early Pleistocene, ca. 1.6 Ma (Zhu et al., 2015).

Temporal distribution: only from the type locality.

Geographic distribution: only from the type locality. A *Dicerorhinus* sp., possibly *S. lantianensis*, is reported at Longgupo by Liu et al. (2015).

3.6. *Stephanorhinus jeanvireti* (Guérin, 1972)

Type material: cranium and mandible partially restored (NMB 627), housed at Naturhistorisches Museum in Basel. Figured in Guérin (1972: Pl. I).

Type locality and horizon: Viallette (Haute-Loire, France), Uppermost Pliocene.

Temporal distribution: from the latest Pliocene (MN16a) to the first half of Early Pleistocene (MNQ18).

Geographic distribution: mainly recorded from France, Italy, Slovakia, Romania (Campanino et al., 1994; Cirilli et al., 2020; Codrea, 2000; Guérin, 1972, 1980a; Guérin and Tsoukala, 2013; Lacombat and Mörs, 2008; Pandolfi et al., 2015, 2019; Sabol et al., 2006; Szabó et al., 2022; Tsoukala, 2018; Vlačíky et al., 2008). A few records are from Germany (Lacombat and Mörs, 2008), Hungary (Pandolfi et al., 2015), Greece (Guérin and Tsoukala, 2013; Tsoukala, 2018). The species is dubitatively present in Spain where a detailed systematic study of the specimens from Camp dels Ninots is needed (Gómez De Soler et al., 2012; Pandolfi et al., 2022). The uncertain MN15 record from Musse-lievo (Spasov, 2005), based on two scanty and fragmented remains, is here considered not reliable.

4. Observation on the cranial morphological variability in the Sumatran rhinoceros

Dicerorhinus sumatrensis is characterized by a relatively wide morphological variability in several features of the cranium, as evidence by Groves (1982). Morphometric data on this taxon were reported by Groves (1967, 1982), Loose (1975), Guérin (1980a). Normally, male

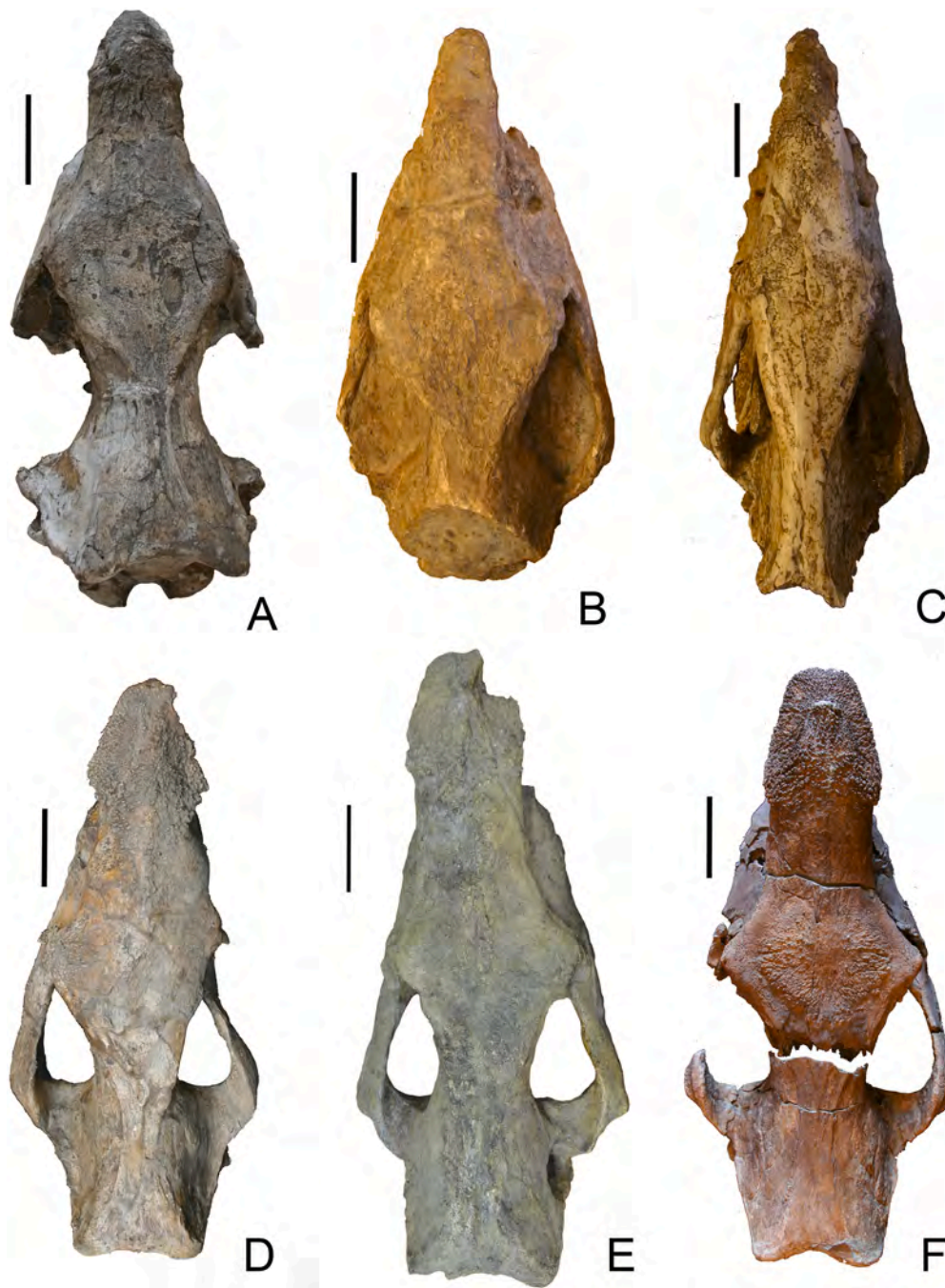


Fig. 5. Crania of Pleistocene *Stephanorhinus* in dorsal view. A, *S. lantianensis* IVPP V5413; B, *S. etruscus* IGF 889; C, *S. etruscus* IGF 12488; D, *S. etruscus* MNHNP 1923-4; E, *S. etruscus* IGF 756; F, *S. etruscus* IGF 8660v.

individuals are somewhat larger than female (Fig. 2) and are characterized by wider nasal bones (see Groves, 1982). By the way, relatively young male individuals can display narrow nasal bones similarly to females (Figs. 2–3). A few characters of the cranium are reliable observable in all the studied specimens: the ventrally opened external auditory pseudomeatus, the un-ossified nasal septum, the long contact between the lachrymal and the nasal bones (Fig. 2). The development of the nuchal crest is a little bit variable; it differs in individuals at different ontogenetic stage, but the shape of the occipital face in adult individuals (M3 fully erupted) is relatively constant (Fig. 2). The occipital face, in lateral view, is slightly forwardly to vertically inclined and the nuchal crest protrudes a little bit over the face; the condyles are downwards oriented, and the nuchal tubercle is relatively well-developed (Fig. 2).

According to Groves (1967) the subspecies from Borneo (*D. s. harrissoni*) has a forwardly inclined occipital face, but I cannot validate this character because only juveniles from this area are retrieved from the studied collections. The shape of the nasals, in lateral view, varies from being dorsally hard-edged to rounded (Fig. 2). The dorsal profile of the cranium, in lateral view, is generally gently concave, but the parietal bones can be flattened or slightly convex. The position of the rear border of the nasal notch, of the rear border of the infraorbital foramen and of the anterior border of the orbit are strongly affected by the ontogenetic stage of the animal. Some differences in the position of these features can be evidenced between individuals with erupting M3 and with erupted or worn M3 (Table 1). In very old individuals, the anterior border of the orbit lies above the mid of M2 or just above its anterior half; the same

Table 1Position of the nasal notch, infraorbital foramen and orbit in *Stephanorhinus etruscus*, *S. hundsheimensis* and *Dicerorhinus sumatrensis* crania.

Specimen number	Locality	Rear border of the nasal notch	Rear border of the infraorbital foramen	Anterior border of the orbit	Species	Sex	Stage
IGF 756	Valdarno	mid of P4	mid of P4	mid of M2	<i>S. etruscus</i>		8
MNHNP AC1872-n214	Valdarno	between P3–P4	mid of P4	mid of M2	<i>S. etruscus</i>		8
IGF 889	Olivola	anterior of P4	anterior of P4	mid of M2	<i>S. etruscus</i>		8
IGF 12488	Olivola	mid of P4	between P4-M1	mid of M2	<i>S. etruscus</i>		8
IGF8660	Poggio Rosso	mid of P4	mid of P4	mid of M2	<i>S. etruscus</i>		8
NMB Se107	Sèneze	mid of P4	mid of P4	mid of M2	<i>S. etruscus</i>		8
MNHN PW 1977-13	Sèneze	mid of P4	mid of P4	anterior of M2	<i>S. etruscus</i>		6
MNHNP 1922-15	Sèneze	posterior of DP3	mid of DP3	posterior of DP4	<i>S. etruscus</i>		2
MNHNP 1923-4	Sèneze	anterior of P4	between P4-M1	mid of M2	<i>S. etruscus</i>		8
NHMW 2013/0282/0001	Hundsheim	between P4-M1?	?	mid of M2	<i>S. hundsheimensis</i>		7
IGF 12 728	Mugello	mid of P4	?	between M1-M2	<i>S. hundsheimensis</i>		6
MPP nn	Torrente	posterior of P4	posterior of P4	anterior of M2	<i>S. hundsheimensis</i>		7
	Stirone						
MNHN PW 1945-172	Mosbach	mid of P4	mid of P4	mid of M2	<i>S. hundsheimensis</i>		8
MNHN PW 1958-764	Mosbach	between P4-M1	mid of P4	between M2-M3	<i>S. hundsheimensis</i>		8
SMNK M389	Mauer	mid of P4	posterior of P4	?	<i>S. hundsheimensis</i>		?
MPI 33085	Isernia	M1		between M2-M3	<i>S. hundsheimensis</i>		?
HLMD Mau85	Mauer	posterior of P4		mid of M2	<i>S. hundsheimensis</i>		7
HLMD M.298	Mauer	posterior of P4		mid of M2	<i>S. hundsheimensis</i>		?
HLMD M.350	Mauer	between P4-M1		between M2-M3	<i>S. hundsheimensis</i>		?
NMB 10529	Zoo	mid of P2	mid of P3	posterior of M1	<i>D. sumatrensis</i>		7
MNHNP A7965 BVI-192	Sumatra	mid of P2	mid of P3	between M1-M2	<i>D. sumatrensis</i>		6
NHMUK 1894-9-24-1	Sumatra	anterior of P2	mid of P3	mid of M2	<i>D. sumatrensis</i>	male	8
NHMUK 1952-4-1-2	Sumatra	anterior of P2	anterior of P3	anterior of M1	<i>D. sumatrensis</i>	male	5
NMS Z1994.131	Sumatra	anterior of P2	mid of P3	between M1-M2	<i>D. sumatrensis</i>	female	7
NHMUK 79-3-11-1	Borneo	posterior of DP1	posterior of DP2	between DP4-M1	<i>D. sumatrensis</i>		2
NHMUK 1901-8-15-1	Borneo	anterior of P2	between P2–P3	anterior of M1	<i>D. sumatrensis</i>	female	3
NHMUK 72-12-31-1	Malaya	mid pf P2	mid of P3	between M1-M2	<i>D. sumatrensis</i>	female	7
NHMUK 1921-2-8-2	Malaya	mid of P2	mid of P3	anterior of M2	<i>D. sumatrensis</i>	male	7
NHMUK 1921-2-8-3	Malaya	anterior of DP2	anterior of DP3	anterior of M1	<i>D. sumatrensis</i>	female	3
NHMUK 1921-2-8-4	Malaya	mid of P3	anterior of P4	mid of M2	<i>D. sumatrensis</i>	female	8
NHMUK 68-4-15-1	Burma	mid of P2	posterior of P3	between M1-M2	<i>D. sumatrensis</i>		7
NHMUK 1931-5-28-1	Burma	posterior of P2	mid of P3	posterior of M1	<i>D. sumatrensis</i>	female	5
NHMUK 1901-1-22-1	Bangladesh	?	mid of P3	anterior of M2	<i>D. sumatrensis</i>	female	8
NHMUK 1948-1-14-2	Rothschild coll.	mid of P2	anterior of P3	posterior of M1	<i>D. sumatrensis</i>		3
NHMUK 1948-12-20-1	Rothschild coll.	mid of P2	mid of P3	posterior of M1	<i>D. sumatrensis</i>		5
NHMUK 1949-1-11-1	Rothschild coll.	posterior of P2	mid of P3	posterior of M1	<i>D. sumatrensis</i>		6
SMF ZIH 184		mid of P2	mid of P3	posterior of M1	<i>D. sumatrensis</i>		6
MZUF 735		mid of P2	mid of P3	posterior of M1	<i>D. sumatrensis</i>		5
NHMUK 1948-1-14-1		posterior of DP1	posterior of DP2	anterior of M1	<i>D. sumatrensis</i>		4
NHMUK 1986-12-20-8		posterior of P2	posterior of P3	?	<i>D. sumatrensis</i>		?
NHMUK 1879-6-14-2		mid of P2	posterior of P3	anterior of M2	<i>D. sumatrensis</i>		8
NHMUK 72-720		anterior of P2	anterior of P3	anterior of M1	<i>D. sumatrensis</i>	female	6

Institutional abbreviations are reported in Material and methods. DP, deciduous; P, premolar; M, molar. “Anterior” is used when the character lies between the mesial side of the tooth and the paracone fold; “mid” is used when the character lies between the paracone and metacone folds; “posterior” is used when the character lies between the metacone fold and distal side of the tooth. The ontogenetic stage is after Groves (1967): 1, first permanent molar not visible; 2, first permanent molar erupting; no trace of a second molar; 3, second molar erupting; second and third premolars in process of replacement; 4, second molar in wear: fourth premolar in process of replacement; 5, third molar in evidence: all milk teeth replaced; 6, third molar fully erupted; 7, third molar in wear; 8, third molar in advanced wear.

feature lies above M1-M2 or the anterior half of M1 in individuals with erupting M3. This evidence suggests considering with caution these features to distinguish among the different fossil species, in particular when it is not possible to evaluate the tooth-eruption sequence. In dorsal view (Fig. 3), several morphological differences can be detected: the crania of adult individuals vary from relatively short and wide to long and narrow. The wide of the nasals is evident and clearly different between sexes. The posterior border of the nuchal crest is normally slightly concave, but it can be also straight in some individuals or even well-concave in some young individuals, thus suggesting an ontogenetic control on this character. The studied sample (Table 1) is too small to be distinct among subspecies of the Sumatran rhinoceros but, of course, clearly highlights some critical morphological differences within the same species. The wide variability of this taxon in respect to the other

extant rhinoceroses was also detected by Guérin (1980b). As evidenced by Pocock (1945), the maximal width of the nasals is reached when M3 start to be worn. A similar pattern is also recognized in the studied sample. In addition, specimens belonging to individual grown up in optimal environmental conditions display relatively larger size even if belonging to female individual (i.e., specimen NHMUK 1.1.22.1, type of *D. lasiotis*; see discussion in Groves, 1982). The shape of the otic region, in particular the development and morphology of the processus post-glenoidalis, processus post-tympanicus and processus paroccipitalis is somewhat different in different individuals. The anterior border of the processus post-glenoidalis can be straight (Fig. 2E) or rather concave (Fig. 2D), the processus post-tympanicus varies from poorly developed (Fig. 2A) to anteriorly forwarded (Fig. 2C), thus affecting the opening of the auditory pseudomeatus. The

processus-paraoccipitalis is normally narrow and slender (Fig. 2B and C), but it can be also more robust (Fig. 2A). The development of the zygomatic arch displays a few differences not related with sex, but probably with age. Adult males and females (Fig. 2D, F) has a thick jugal with the presence of an evident processus post-orbitalis and the development of rugosities on the ventral side of the squamosal. Juvenile individuals and subadults with not fully erupted M3 has a slender jugal area, with the absence or a poorly developed processus-postorbitalis and the absence or poorly developed rugosities on the squamosal. The increasing of cranial surface rugosity with the increasing in age of the individual was also observed by Kitchener (1997). The latter author also reported the (partial) ossification of the nasal septum in mature individuals from Malay Peninsula (2 specimens), Burma (1 specimen) and Sumatra (1 specimen). Presence of a partially ossified nasal septum is detected on the specimen NHMUK 1901-1-22-1, 1921-2-8-4 and 1872-12-31-1, NMS Z1994.131 with M3 fully erupted and in an advanced stage of wear. These specimens are from Malayan Peninsula, Burma and Sumatra, thus representing the nominal subspecies and the mainland *D. s. lasiotis*, and are females, suggesting that this character is not related to sexual dimorphism.

5. Discussion

5.1. *Stephanorhinus etruscus* and *S. hundsheimensis*: cranial differences and similarities

Differences in cranial morphology between the Etruscan' and the Hundsheim' rhinoceroses have been discussed in several papers. Guérin (1980b) considered the Toulou's species as a synonym of *Dicerorhinus etruscus brachycephalus* Schroeder (1903), but the latter name was used to designate the cranium from Daxlander, later referred as *S. kirchbergensis* (Azzaroli, 1962a). The type material from Hundsheim is represented by a mounted skeleton with a partial cranium housed at the NHMW and described and figured by Toulou (1902). The cranium preserves the neurocranial portion, frontals and orbits, including the zygomatic arches (Fig. 4). The individual is an adult, with M3 fully erupted and slightly worn. Looking at the preserved neurocranial portion, in lateral view (Fig. 4), it is possible to detect some similarities with *S. etruscus*, in particular in the shape of the nuchal crest and in the orientation of the occipital condyle. The different elevation of the occipital face can be included within the intraspecific variability of a species (see *D. sumatrensis*) and cannot be used as discriminant between the Etruscan' and Hundsheim rhinoceroses. The shape of the zygomatic arches displays a relatively wide variability in the extant Sumatran rhinoceros and this character cannot be considered, within a certain degree, as indicative of a specific difference. The development of the nasal bosses and of the ossification of the septum are both characters affected by sexual dimorphism and age, at least in *D. sumatrensis*, and must be considered with caution. However, *S. etruscus* and *S. hundsheimensis* differ in the length of the cranium (Lacombat, 2005a) and in the concavity of the dorsal profile of frontal-parietal bones (that reflects in the Zeuner' angle; Lacombat, 2005a); this character is relatively constant in adults of *D. sumatrensis*. The position of the rear border of the nasal notch and the anterior border of the orbit displays a wide variability within the same species (Table 1), and it is affected by the ontogenetic stage of the individual. The positions of these characters described by Guérin (1980b) for *D. etruscus brachycephalus* cannot be considered as indicative for *S. hundsheimensis*, being those descriptions based on crania that were later assigned to different species, as in the case of the Daxlander specimen. Within the studied sample, *S. hundsheimensis* individuals with fully erupted M3 display an anterior border of the orbit above the mid of M2 or just above the posterior half of M2, the infraorbital foramen above P4 and the rear border of the nasal notch above the mid of P4 or at the contact between P4 and M1 (Table 1). Only the cranium from Mugello with erupted, but un-worn M3, has the anterior border of the orbit above the M1-M2 contact, so

a little bit forwardly located than in other specimens. Further, on the cranium from Isernia, the rear border of the nasal notch and the anterior border of the orbit are located respectively above M1 and above the M2-M3 contact (Sala and Fortelius, 1993); this cranium was probably of an old individual. The same features observed on the specimen from Isernia, can be detected on individuals from Mosbach and Mauer with an advanced stage of wear on M3. In *S. etruscus* the position of the anterior border of the orbit lies above the mid of M2 for individuals with advanced stage of wear on M3, and above the anterior half of M2 for individuals with erupted but unworn M3 (Table 1), whilst the infraorbital foramen lies above the mid of P4, or above the P4-M1 contact. The rear border of the nasal notch in *S. etruscus* lies above the mid of P4, or above the anterior half of P4, and in one case above the P3-P4 contact (Table 1). Considering the differences observed on adult individuals, and the intraspecific variability depicted for *D. sumatrensis*, *S. etruscus* and *S. hundsheimensis* can be considered as valid taxa, but preventing the morphological considerations reported by Guérin (1980b) on *D. etruscus brachycephalus*. The teeth of *S. etruscus* and *S. hundsheimensis* have been extensively treated and discussed in several papers (Fortelius et al., 1993; Lacombat, 2005a; Pandolfi and Erten, 2017), and the main differences between these species can be observed on the premolar-row, with the presence in *S. hundsheimensis* of a developed lingual cingulum and a more complex enamel foldings.

5.2. *Stephanorhinus etruscus* and *S. lantianensis*: intraspecific variability or different species?

The Chinese species *S. lantianensis* has been erected on a cranium of an adult individual (Figs. 4–5). The cranium is characterized by being smaller than *S. kirchbergensis* and by having sharply tapered nasal bone (Fig. 5), and a long toothrow (L P2-M3 = 250 mm). The morphological characters of the teeth (Tong, 2012) such as protoloph and metaloph parallel, and smooth ectoloph, are probably related with the advanced stage of wear. The nasal bone of the cranium strongly resembles that of the specimen IGF889 belonging to *S. etruscus*, and this character can be interpreted as sexually dimorphic (Fig. 5). The dorsal profile of the cranium, and the general shape of the neurocranial portion, strongly resembles the specimen NMB Se107 from Senèze. The length of the toothrow is similar to those observed in *S. etruscus* (Guérin, 1980a) and its value can be related with the age of the animal. The anterior border of the orbit lies above the mid of M2 and the rear border of the nasal notch lies above the mid of P4, as observed on adult individuals of *S. etruscus*. It cannot be excluded that *S. lantianensis* represents an old female individual of *S. etruscus*. The latter species probably reached the Eastern Asia during the late Early Pleistocene, or, at least, *S. lantianensis* could be a taxon (subspecies? geographic morphotype?) strongly related with the Upper Valdarno species.

5.3. Differences among *Stephanorhinus kirchbergensis*, *S. hundsheimensis* and *S. yunchuchenensis*

At present, *S. yunchuchenensis* is recorded only in one locality in Yushe Basin (Shanxi Province, Early Pleistocene), and, even if the exact location is uncertain, the age is estimated on regional geological information (Tong, 2012). Anyway, the morphology of the cranium and teeth closely resembles *S. kirchbergensis* (as also noted by Chow, 1963). The expanded nasal bones (Fig. 6) are similar in shape and size to that observed in *S. kirchbergensis* cranium SMNS 6617.2.12.67.3 and *S. hundsheimensis* cranium MNHN PW 1958-764, and can be regarded as a sexual dimorphic trait. The latter specimen, an old individual with worn-out M2 (and presumably with fully erupted M3), also displays a mid-vertical groove on the tip of the nasals. The latter character is documented in males of *D. sumatrensis*. The morphology of the nasals represents the only character used to discriminate *S. yunchuchenensis* from other taxa and, basing on the evidence reported for the extant *D. sumatrensis* and the observations of fossil Eurasian species, it is

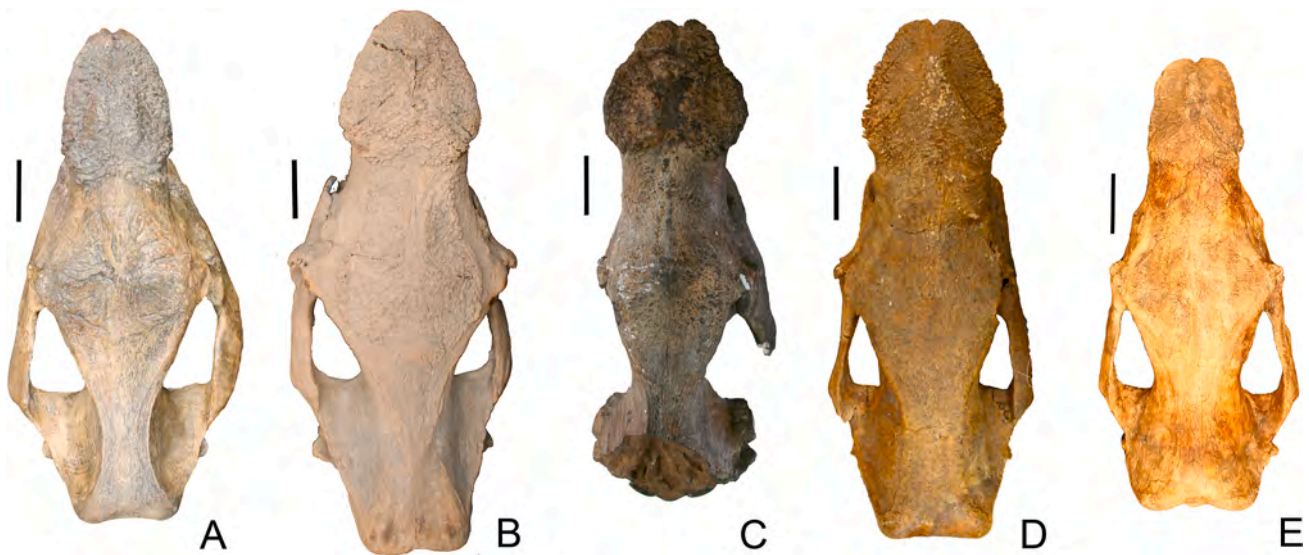


Fig. 6. Crania of Pleistocene *Stephanorhinus* in dorsal view. A, *S. kirchbergensis* SMNK PAL 4254, M3 fully erupted; B, *S. kirchbergensis* SMNS 6617.2.12.67.3, M3 fully erupted; C, *S. yunchuchenensis* IVPP V2879, M3 fully erupted? D, *S. hundsheimensis* MNHN PW 1958–764, M3 fully erupted; E, *S. hundsheimensis* IGF 1931V, M3 fully erupted? Scale bar equals 10 cm.



Fig. 7. Location map of selected latest Pliocene and Pleistocene localities mentioned in the text.

possible that *S. yunchuchenensis* is a younger synonym of the Merck's rhinoceros.

5.4. New considerations on the crania of *S. jeanvireti*

Two crania are known from the type locality of Vialette, belonging to adult individuals (NMB Vt 621 and 627), and two others are from Milia (a complete cranium, MIL162, and an incomplete cranium without teeth MIL 1501: Guérin and Tsoukala, 2013). A cranium from Dusino, figured by Sacco (1895: Pl. II, Figs. 1–5, 7), was destroyed in the 1944 and

another one from Montopoli, figured by Azzaroli (1962b: Pl. VI Fig. 2, Pl. VIII, Fig. 5), belongs to a juvenile individual (IGF 14869). According to Guérin (1972, 1980b) the crania from Vialette, Vt 627 and Vt 621, show respectively the rear border of the nasal notch at the level of P3–P4 transition and P4–M1 transition, the infraorbital foramen above the mid of P4 and the mid of M1, and the anterior border of the orbit above the mid of M2. However, the specimen Vt 621 is almost entirely restored with plaster, in particular between the praemaxilla and the zygomatic arch, and the position of such features seems not to be reliable (Fig. 4N). In the specimen MIL 162, the position of the rear border of the nasal

notch is at the level of P3–P4 transition, the infraorbital foramen is above the mid of P4, and the anterior border of the orbit is between M2 and M3. The cranium from Dusino results severely damaged and nor the position of the infraorbital foramen, nor that of the nasal notch, can be properly detected on the plates reported by Sacco (1895). The anterior border of the orbit seems to lie above the M2–M3 transition (Sacco, 1895: Pl. II, Fig. 3) and the individual would have an estimated class of age of 8, similarly to the specimen from Milia. The differences in the position of the anterior border of the orbit between Vialette and Milia and Dusino fall within the intraspecific variability of Quaternary species, as observed in *D. sumatrensis*, and could be also related with sexual dimorphism. The considered crania of *D. sumatrensis* display some differences in the position of the orbit between males and females at the same ontogenetic stage (Table 1), with males having a slightly more posteriorly position of this feature with respect to females. Further, the cranium from Milia displays two small I1s that could be indicative of a male individual, and I1s were also present on the cranium from Dusino Sacco (1895: p. 6), whilst they are absent on the specimens from Vialette. The crania of *S. jeanvireti* are more massive than those of *S. etruscus* at the same estimated class of age; further, in *S. jeanvireti* the occipital face is higher, the orbit more posteriorly placed, and the foramen magnum is wider ventrally (in occipital face view). *S. hundsheimensis* and *S. jeanvireti* share several characters of the cranium, such as nuchal crest posteriorly projected, steeper parietal profile (see also Fortelius et al., 1993: p. 117), relatively low orbits, low zygomatic arches, ventrally wide foramen magnum. In *S. hundsheimensis*, the infraorbital foramen is more posteriorly located than in *S. jeanvireti* (class age 8), and the occipital face on the specimen from Hundsheim is lower than in those from Dusino and Milia. Similarly to the cranium from Dusino, the presence of alveolar cavities for I1s is documented in the cranium of *S. hundsheimensis* from Torrente Stirone (Cigala-Fulgosi, 1976). *S. hundsheimensis* and *S. jeanvireti* could be probably strongly related, and a detailed analysis of the postcranial material can be helpful to investigate this issue.

5.5. Critical remarks on the biochronology of Early Pleistocene rhinoceroses and paleobiogeographic implications

The first and last occurrences of *S. etruscus* and *S. hundsheimensis* have been revised in several recent papers (Cirilli et al., 2020; Giaourtsakis, 2022; Pandolfi et al., 2017a, 2019, 2021b; Pandolfi and Erten, 2017; Pandolfi and Marra, 2015; Pandolfi and Petronio, 2011; van der Made, 2010) and will be not deeply discussed here. Despite the revised framework on the biochronology of these two species, and the morphological and morphometric evidences provided during the last years, some authors continue to refer the latest Early Pleistocene rhinoceroses as *S. cf. hundsheimensis*, *S. aff. hundsheimensis* or to call them as small-form species without providing any justification. Bona and Sala (2016) reported that Italian authors signalize the presence of these forms in the late Villafranchian, in contrast with Pandolfi and Marra (2015) that instead reported *S. etruscus*. The papers cited by Bona and Sala (2016), however, included Gliozzi et al. (1997) or Masini and Sala (2007) that did not revise the fossil rhinoceroses from Italy but simply reported the identifications provided at the beginning of the '90s by Mazza et al. (1993), thus ignoring the extensive work of revision recently provided by other authors (Pandolfi and Marra, 2015; Pandolfi and Petronio, 2011; van der Made, 2010). According to the recent data on late Early Pleistocene rhinoceroses, *S. etruscus* and *S. hundsheimensis* are both present in Europe but probably they occupied different habitats (Fig. 7), being documented in different localities (Fig. 8) and displaying different results on meso- and microwear analyses (Kahlke and Kaiser, 2011; Rivals and Lister, 2016; Saarinen et al., 2016; van Asperen and Kahlke, 2015). The origin of *S. etruscus* is still poorly understood, and yet un-resolved in recent cladistic analyses (Deng et al., 2011; Guérin, 1980a, 1982b) but a relationship with *Dihoplus pikermiensis* seems to be probable (Antoine and Saraç, 2005; Pandolfi et al., 2021b; Uzunidis

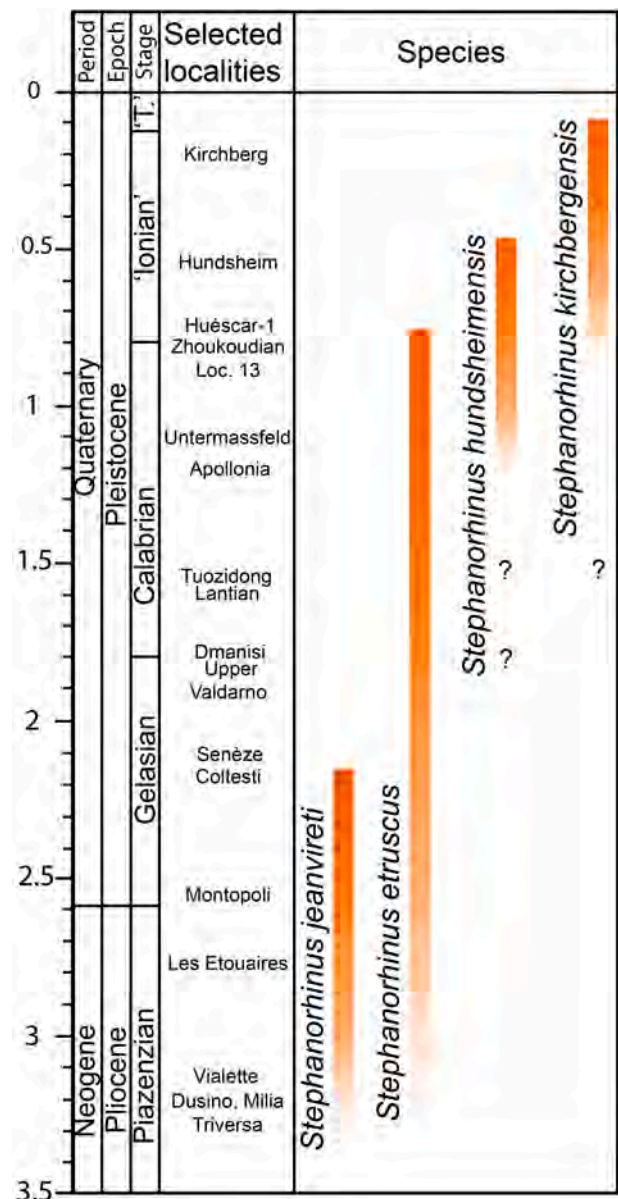


Fig. 8. Chronological distribution of the European *Stephanorhinus* species discussed in the text.

et al., 2022). Similarly, the origin of *S. hundsheimensis* is controversial. Although related with *S. etruscus* (Pandolfi et al., 2021a), an origin in Central Asia and a dispersal towards Western Europe cannot be totally ruled out (Cerdeño, 1998). The latter hypothesis could be supported by the presence at Dmanisi (ca. 1.8 Ma) of *Stephanorhinus* closely related with *S. hundsheimensis*, which is certainly recorded in Europe starting from around 1.2–1.1 Ma (see discussion in Pandolfi et al., 2021a and cited references) (Figs. 7–8). The intriguing, but less parsimoniously, hypothesis of an evolutionary pattern from *S. etruscus* to *S. hundsheimensis* through small-sized “transitional forms” is discarded because not supported by objective evidence. It is instead possible that the latest Early Pleistocene rhinoceros records of Europe represent local populations of *S. etruscus*, that became isolated during climatic stressed conditions and survived till the Early-Middle Pleistocene transition in favorable geographic areas such as southern Italy and Iberian Peninsula (Pandolfi et al., 2017a). *S. etruscus* probably dispersed towards East, reaching the Gongwangling area where it is known as *S. lantianensis* (ca. 1.6 Ma) (Zhu et al., 2015). This framework can be supported by the presence of the Etruscan rhinoceros at Lebyazhye 2 (Kazakhstan), early

Early Pleistocene in age (Shpansky and Ilyina, 2020), identified on the basis of a fragmented third metatarsal, morphologically and morphometrically close to *S. etruscus*. The presence of this taxon at Moiseevka 1 (Western Siberian plain) is instead doubtful, being the lower teeth from this site characterized by wide lingual valleys and deep external grooves that reach the base of the crown (uncommon features for *S. etruscus*). Other records of the Etruscan rhinoceros or closely related forms from Tajikistan and Kazakhstan (Dmitrieva and Nesmeyanov, 1982; Forsten and Sharapov, 2000; Sharapov, 1986) should be critically revised and can shed light on dispersal and evolution of the species.

Stephanorhinus jeanvireti is generally reported from latest Pliocene/earliest Pleistocene sites (Guérin, 1972, 1980a; Lacombat and Mörs, 2008; Pandolfi et al., 2019, 2022), and it is recently documented in younger locality (MNQ18) of Romania (Pandolfi et al., 2019) thus suggesting a long persistence of this taxon in Europe (Fig. 8). Poorly is known about the evolution and phylogeny of this species, but, together with *S. etruscus*, it represents the first *Stephanorhinus*-rhinoceros in Eurasia. Fortelius et al. (1993) regarded *S. jeanvireti*, *S. etruscus* and *S. hundsheimensis* as unresolved sister group, but also noted that *S. jeanvireti* is highly similar in most characters to *S. hundsheimensis*. If this similarity is related with morphological convergence or suggests a phylogenetic relationship between these two taxa is difficult to support at present, and both hypotheses will be object of a future paper.

A synonymy between *S. yunchuchenensis* and *S. kirchbergensis* confirms the presence of the latter rhinoceros in the Early Pleistocene of China; the uncertain age of the cranium IVPP V2879 does not help to discuss any paleobiogeographic or phyletic hypothesis.

S. kirchbergensis is reported in several localities of East Asia (Fortelius et al., 1993; Tong, 2000, 2012). The record of the species at Gongwangling (latest Early Pleistocene: Liu et al., 2015) is reported, at my known, only within a faunal list and, at present, it is not possible to verify this occurrence. The same locality yielded the type-specimen of *S. lantianensis*. The juvenile right maxilla from Tuozidong cave deposits (ca 1.6 Ma) (Dong et al., 2013), assigned to *S. kirchbergensis*, should be considered with caution. Juvenile teeth of Pleistocene rhinoceroses are highly conservative both from morphometric and morphological point of views (Lacombat, 2005a). *S. kirchbergensis*, however, is for certain documented at Zhoukoudian Loc. 13 (Early/Middle Pleistocene boundary: Tong, 2012) and, starting from the early Middle Pleistocene, in Western Europe (Guérin, 1980a; Lacombat, 2005a, 2005b, 2009). *S. kirchbergensis* was previously related with *Pliorhinus megarhinus* (Deng et al., 2011; Fortelius et al., 1993; Guérin, 1980a; Pandolfi et al., 2021b) but an origin from this latest Miocene-early Pliocene species is at present discarded, or, at least, should be supported by a better investigation of the phylogeny of the group. Recent molecular evidences showed that *S. kirchbergensis* is the sister taxon of *Coelodonta antiquitatis* (Cappellini et al., 2019; Kirillova et al., 2017; Welker et al., 2017) and that it is more closely related with the woolly rhinoceros than with *Stephanorhinus* from Dmanisi. An origin of *S. kirchbergensis* in Asia, similarly to *Coelodonta*, can be therefore plausible, and a deep analysis of the Udung material (Fukuchi et al., 2009) can be helpful to solve this issue.

6. Conclusion

The Early Pleistocene *Stephanorhinus* species of Eurasia are here critically reviewed in order to provide a comprehensive overview of their main cranial features, and to highlight similarities and differences in comparison with the variability observed on the extant Sumatran rhinoceros. The cranium is the most distinctive anatomical element within the fossil rhinoceroses and it is relatively well-known for all the taxa included in this paper. The diversity of the genus *Stephanorhinus* in Eurasia is overestimated and the two East Asian species, *S. lantianensis* and *S. yunchuchenensis*, are here considered synonyms of *S. etruscus* and *S. kirchbergensis* respectively. A new paleobiogeographic assessment of the Early Pleistocene *Stephanorhinus* rhinoceroses is therefore provided, suggesting a dispersal from West to East of *S. etruscus* and from East to

West of *S. kirchbergensis*. *S. hundsheimensis* probably dispersed from Central Asia to Western Europe during the climatic deterioration of the late Early Pleistocene and no strong evidences are at present available to support a direct origin from the Etruscan species. *S. etruscus* most probably became extinct in Europe after the isolation in several local populations, with late survivors in southern Italy and Iberian Peninsula. Future phylogenetic analysis, including postcranial remains from partial or complete skeletons, can be probably resolute to depict a more clear framework on evolution and dispersal of Pleistocene rhinoceroses.

Author contributions

Conceptualization, methodology, data acquisition, analysis, discussion, writing, funding acquisition, LP.

Data availability

All the specimens described in this paper are available in the selected Museums and Institutions. The collection number is reported for all the mentioned specimens.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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