



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Biogeography and chronology of the Eurasian extinct rhinoceros *Stephanorhinus etruscus* (Mammalia, Rhinocerotidae)



Biogéographie et chronologie du rhinocéros éteint Stephanorhinus etruscus (Mammalia, Rhinocerotidae) d'Eurasie

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ABSTRACT

Stephanorhinus etruscus is one of the most abundantly recorded and better known Eurasian Early Pleistocene rhinoceroses. Nevertheless, the first and last appearances of this species, as well as its paleogeographic distribution, are controversial and debated in literature. *S. etruscus* is documented since the latest Pliocene in Spain (Las Higuieruelas), Italy (Montopoli and Castelnuovo di Barardenga), France (Perrier–Les Étouaires) and Romania (Iarăș–Cariera Veche). During the Early Pleistocene, *S. etruscus* occurred in several Spanish, French and Italian localities, as well as in The Netherlands (e.g., Tegelen), Germany (e.g., Thiede), Greece (e.g., Aivaliki) and Israel (e.g., Ubeidiya). The last appearance of *S. etruscus* in Eurasia is debatable. Etruscan rhino populations survived till the Jaramillo subchrone (around 1.1 Ma) in France (Bois-de-Riquet), Romania (Betfia XII) and Hungary (Osztramos 2 and 8), and close to the early–middle Pleistocene transition in Spain (Cueva Victoria, Huéscar 1, Atapuerca TD4, TD6 and TD8), and Italy (Monte delle Piche).

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RÉSUMÉ

Stephanorhinus etruscus est une espèce de rhinocéros du Pléistocène inférieur d'Eurasie parmi les plus fréquemment rencontrées et les mieux connues. Néanmoins, la première et la dernière occurrence de cette espèce, tout comme sa répartition paléogéographique, sont controversées et débattues dans les références. *S. etruscus* est documentée à partir de la partie terminale du Pliocène en Espagne (Las Higuieruelas), en Italie (Montopoli et Castelnuovo di Barardenga), en France (Perrier–Les Étouaires) et en Roumanie (Iarăș–Cariera Veche). Pendant le Pléistocène inférieur, *S. etruscus* apparaît dans de nombreuses localités d'Espagne, de France et d'Italie et aussi aux Pays-Bas (e.g., Tegelen), en Allemagne (e.g., Thiede), en Grèce (e.g., Aivaliki) et en Israël (e.g., Ubeidiya). La dernière présence de *S. etruscus* en Eurasie fait l'objet de discussions. Les populations de rhinocéros étrusques

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ont survécu jusqu'au subchrone Jaramillo (environ 1,1 Ma) en France (Bois-de-Riquet), en Roumanie (Betfia XII) et en Hongrie (Osztramos 2 et 8), et à la transition Pléistocène inférieur/moyen en Espagne (Cueva Victoria, Huéscar 1, Atapuerca TD4, TD6 et TD8) et en Italie (Monte delle Piche).

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1. Introduction

During the Plio-Pleistocene, several mammal species were widespread throughout Eurasia and have undertaken a considerable importance for paleoclimatic and paleogeographic reconstructions, chronological correlation of continental deposits and evolutionary history of taxa. Among other mammals, rhinoceroses represent a common element of the Eurasian Plio-Pleistocene faunas, but the identification of the different species, as well as determining their paleobiogeographic and chronological distribution, is sometimes very difficult. Among the Eurasian rhinoceroses, *Stephanorhinus etruscus* (Falconer, 1868) is one of the most recorded and widespread extinct species. It was generally recorded from early Pleistocene localities (e.g., Cerdeño, 1993; Falconer, 1868; Fortelius et al., 1993; Guérin, 1980; Lacombat, 2005; Mazza, 1988; Pandolfi and Erten, 2017; Pandolfi and Petronio, 2011). Nevertheless, the first and last occurrences of the so-called Etruscan rhino as well as its geographic distribution are controversial and debated in recent literature (Cerdeño, 1993; Fortelius et al., 1993; Lacombat, 2005; van der Made, 2010; Mazza et al., 1993; Pandolfi and Erten, 2017; Pandolfi and Petronio, 2011).

A critical review of the most important findings of *Stephanorhinus etruscus* in continental Eurasia is reported in this paper together with the re-determination and description of several specimens. The aim of this work is to provide a comprehensive updated overview of *S. etruscus* in Eurasia and to well-define the biogeography and the chronology of this species.

2. Material and methods

Specimens referred to the Etruscan rhinoceros are housed in several institutions; the significant material discussed in this text and collected from selected localities is listed in Table 1.

The considered specimens were morphologically compared with the rhinocerotid material collected in numerous fossiliferous localities and referred to several Plio-Pleistocene species. The comparisons were based on direct observations by one of us (LP) of the material housed in different institutions as well as on published data. The supra-generic classification follows Antoine (2003); the dental terminology and the morphometric methodology follow Antoine (2002) and Guérin (1980), respectively. The measurements of postcranial remains assigned to *Stephanorhinus etruscus* are reported in Supplementary Material. The collected data, however, are too poor for a detailed statistical analysis and are not sufficient to evaluate evolutionary trends within the species.

Institutional abbreviations – **HNHM**: Hungarian Natural History Museum, Budapest, Hungary; **IGF**: Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy; **MAFI**: Magyar Földtani és Geofizikai Intézet (Geological and Geophysical Institute of Hungary), Budapest, Hungary; **MfN**: Museum für Naturkunde, Berlin, Germany; **MGGC**: Museo di Geologia “Giovanni Capellini”, Bologna, Italy; **MNCN**: Museo Nacional de Ciencias Naturales, Madrid, Spain; **MNHN**: Muséum national d'histoire naturelle, Paris, France; **MPCR**: Museo Provincial de Ciudad Real, Ciudad Real, Spain; **MPLBP**: Museo Paleontologico “Luigi Boldrini” di Pietrafitta, Perugia, Italy; **MPUR**: Museo di Paleontologia, Sapienza Università di Roma, Rome, Italy; **MRSN**: Museo Regionale di Scienze Naturali, Torino, Italy; **MSNAF**: Museo di Storia Naturale, Accademia dei Fisiocritici, Siena, Italy; **NHML**: Natural History Museum, London, U.K.; **NHMW**: Naturhistorisches Museum, Wien, Austria; **NMB**: Naturhistorisches Museum, Basel, Switzerland.

Anatomical Abbreviations – **APD**: antero-posterior diameter; **L**: length; **M/m**: upper/lower molar; **Mc**: metacarpal; **Mt**: metatarsal; **P/p**: upper/lower premolar; **TD**: transversal diameter.

3. Systematic paleontology

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Gray, 1821
Subfamily RHINOCEROTINAE Gray, 1821
Tribe RHINOCEROTINI Gray, 1821
Genus *Stephanorhinus* Kretzoi, 1942a

Type species: *Stephanorhinus etruscus* (Falconer, 1868).

Included species: *Stephanorhinus kirchbergensis* (Jäger, 1839), *Stephanorhinus hemitoechus* (Falconer, 1859), *Stephanorhinus hundsheimensis* (Toula, 1902), *Stephanorhinus yunchuchenensis* (Chow, 1963), *Stephanorhinus jeanvireti* (Guérin, 1972), *Stephanorhinus lantianensis* (Hu and Qi, 1978), maybe “*Stephanorhinus*” *miguelcрусafonti* (Guérin and Santafé-Llopis, 1978) and with uncertainty *Stephanorhinus africanus* (Arambourg, 1970).

Occurrence: From the early Pliocene to the latest Pleistocene in Eurasia and during the late Pleistocene in Africa. The genus was reported from the early middle Pliocene of Tunisia with uncertainty (*S. africanus*) and also in Chad at about 3–3.5 Ma (Geraads, 2010).

Revised diagnosis: Large to medium-sized two-horned rhinoceros. Dolichocephalic skull. Presence of a rostrally ossified nasal septum connecting the intermaxilla with the nasal bones. Moralized premolars. Strongly reduced or absent incisors. Brachyodont to semi-hypsodont cheek teeth.

Table 1

List of selected localities discussed in the text (where identifications are based on direct observations and figured specimens), ages, selected references and institutions where the material of *Stephanorhinus etruscus* is stored.

Tableau 1

Liste des localités sélectionnées dans le texte, âges, références sélectionnées et institutions où est conservé le matériel de *Stephanorhinus etruscus*.

Area	Locality	Institution	Age (chronology in Ma/biochronology)	Selected References
Iberian Peninsula	Las Higueraelas	MPCR	ca. 3.3	Mazo, 1995
Iberian Peninsula	Piedrabuena	MNCN	ca. 3.0	Mazo and Torres, 1991
Iberian Peninsula	El Rincón-1	MNCN	MN16	Alberdi et al., 1997
Iberian Peninsula	Villarroya		MN16	de Villalta Comella, 1952; Cerdeño and Alberdi, 2016
Iberian Peninsula	Huélago		MNQ17	Cerdeño, 1989
Iberian Peninsula	La Puebla de Valverde	MNCN	MNQ18	Guérin and Heintz, 1971
Iberian Peninsula	Fonelas P-1		MNQ18	Garrido, 2006
Iberian Peninsula	Huésca	MNCN	ca. 0.9	Cerdeño, 1993
Iberian Peninsula	Atapuerca TD4, TD6 and TD8		Brunhes–Matuyama transition	van der Made, 1998, 1999, 2010
Iberian Peninsula	El Chaparral		ca. 1	Pacheco et al., 2011
Italian Peninsula	Villafranca d'Asti	NMB	MN16	Guérin, 1972
Italian Peninsula	Montopoli	IGF	MN16	Azzaroli, 1962
Italian Peninsula	Castelnuovo di Barardenga Scalo	MSNAF	MN16	Cusani Politi, 1963, 1971
Italian Peninsula	Pirro Nord	IGF, MPUR, MRSN	latest Villafranchian	Mazza et al., 1993; Pandolfi and Petronio, 2011
Italian Peninsula	Madonna della Strada	MPUR	ca. 1.3–1.1	Pandolfi and Petronio, 2011
Italian Peninsula	Imola Basin	IGF, MGGC	latest Villafranchian	Pandolfi and Petronio, 2011
Italian Peninsula	Pietrafitta	MPLBP	late Villafranchian	Mazza et al., 1993; Pandolfi and Petronio, 2011
Italian Peninsula	Lefte		ca. 1.1	Vialli, 1956
Italian Peninsula	Monte delle Piche	MPUR	ca. 0.9	Pandolfi and Marra, 2015
France	Perrier–Les Étouaires	NMB	ca. 2.78	Guérin, 1972
France	Saint-Vallier	NMB	middle Villafranchian	Guérin, 2004
France	Senèze	NMB, MNHN	ca. 2.2–2	Guérin, 1980
France	Blassac–La-Girondie		ca. 2.2–2.3	Boivin et al., 2010
France	Bois-de-Riquet		ca. 1.3–1.1	Bourguignon et al., 2015
The Netherlands	Tegelen	MfN	?early Pleistocene	Bernsen, 1927
Germany	Thiede	MfN	?early Villafranchian	Dietrich, 1953
Greece	Tourkovounia 4		MN16–MNQ17	Symeonidis and De Vos, 1976
Greece	Aivaliki		late early Pleistocene	Symeonidis et al., 2006
Romania	Pralea 1		MN16a	Andrescu et al., 2013
Romania	Curtea de Argeş		MN16a	Andrescu et al., 2013
Romania	Betfia XII	HNHM, MAFI	ca. 1.1	This work
Hungary	Osztramos 2 and 8	HNHM, MAFI	ca. 1.2	Jánossy, 1986
Georgia	Akhalkalaki		early–middle Pleistocene transition	Vekua, 1986
Israel	Ubeidiya		ca. 1.6–1.2	Guérin, 1986

Taxonomic remarks: The taxonomic status of the European Pleistocene fossil rhinoceroses has been discussed in several contributions (e.g., Fortelius et al., 1993; Groves, 1983; Guérin, 1980, 1982, 1989, 2004; van der Made, 2010; McKenna and Bell, 1997; Pandolfi and Petronio, 2011; Pandolfi and Tagliacozzo, 2015). As noted by Pandolfi and Tagliacozzo (2015), the works of Kretzoi (1942a, 1942b) satisfy the Articles 8, 11.8, 13.1, 13.3, 42 of the ICZN (1999) and the name *Stephanorhinus* is a valid genus. Ballatore and Breda (2016) recently suggested replacing the name

S. jeanvireti with *S. elatus*. The motivations proposed by Ballatore and Breda (2016) are reasonable as well as those reported by Guérin (1972) and Guérin and Tsoukala (2013). Pending a decision of the ICZN Commission, we prefer to retain the name erected by Guérin (1972), because it was largely used in literature after the description of the species.

Stephanorhinus etruscus (Falconer, 1868)

Type material: Skull (IGF 756) figured and described by Falconer (1868), stored at Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy.

Type horizon: early Pleistocene.

Type locality: Upper Valdarno Basin (Tuscany, Italy).

Diagnosis: Guérin (1980) reported an exhaustive diagnosis of the species, despite he considered the species as belonging to genus *Dicerorhinus*, subgenus *Brandtorhinus*.

4. The continental Eurasian records of *Stephanorhinus etruscus*

Stephanorhinus etruscus has been recorded in a lot of Eurasian fossiliferous localities (Table 1; Fig. 1). It is well known at the type locality, the upper Valdarno Pleistocene levels (Florence Province; Italy), as well as at French localities such as Senèze (Haute-Loire). Here, those localities with paleogeographic or chronological importance are reported (Table 1; Fig. 1), following a roughly regional geographic distribution. The occurrence of *S. etruscus* in the Pleistocene deposits of Great Britain (Stuart, 1982) needs to be confirmed. Breda et al. (2010) excluded the presence of this species from the faunas from Fresh Water beds at West Runton and coeval deposits along the Norfolk and Suffolk coast, which are not herein considered, also because the material from this area displays some peculiar features (see also Ballatore and Breda, 2013) and should be deeply revised in an independent paper. A deeper revision should be also performed on specimens collected in older localities, such as East Runton and coeval deposits, which might contain this species.

4.1. Iberian Peninsula

The Iberian record of *S. etruscus* corresponds so far to Spanish localities, mostly summarized by Cerdeño (1993). The first occurrence of *S. etruscus* in Spain corresponds to Las Higuieruelas (Ciudad Real Province, ca. 3.3 Ma; Mazo, 1995). The skull (MPCR LHG84, IV, C-1 No. 60; Mazo, 1995; fig. 1) collected from this locality displays morphological characters (e.g., squared shape of the occipital face, straight dorsal border of the nuchal crest in occipital view) that are evident on some skulls of *S. etruscus* from Senèze, France, housed at MNHN and NMB. In respect to the Italian specimens from Upper Valdarno housed at IGF, the skull from Las Higuieruelas has the occipital face slightly inclined forward and the dorsal profile less straight. The dimensions of the skull from Las Higuieruelas are consistent with an attribution to the Etruscan rhino. The mandible from Las Higuieruelas (MPCR LHG84, IV, C-1, No. 23 and No. 44; Mazo, 1995; fig. 2) slightly resembles *S. jeanvireti* from Viallette (France; Guérin, 1972) and Milia (Greece; Guérin and Tsoukala, 2013) in having a rather irregularly convex ventral border, a long symphysis and four alveoli for the lower incisors. However, the anterior border of the vertical ramus is straight as in *S. etruscus* and the maximal width of symphysis is at the level of its anterior border, whereas in *S. jeanvireti* the maximal width of symphysis is at the back of the incisor alveoli (see also Guérin and Tsoukala, 2013; Fig. 7C, E); in contrast, the total length of the mandible

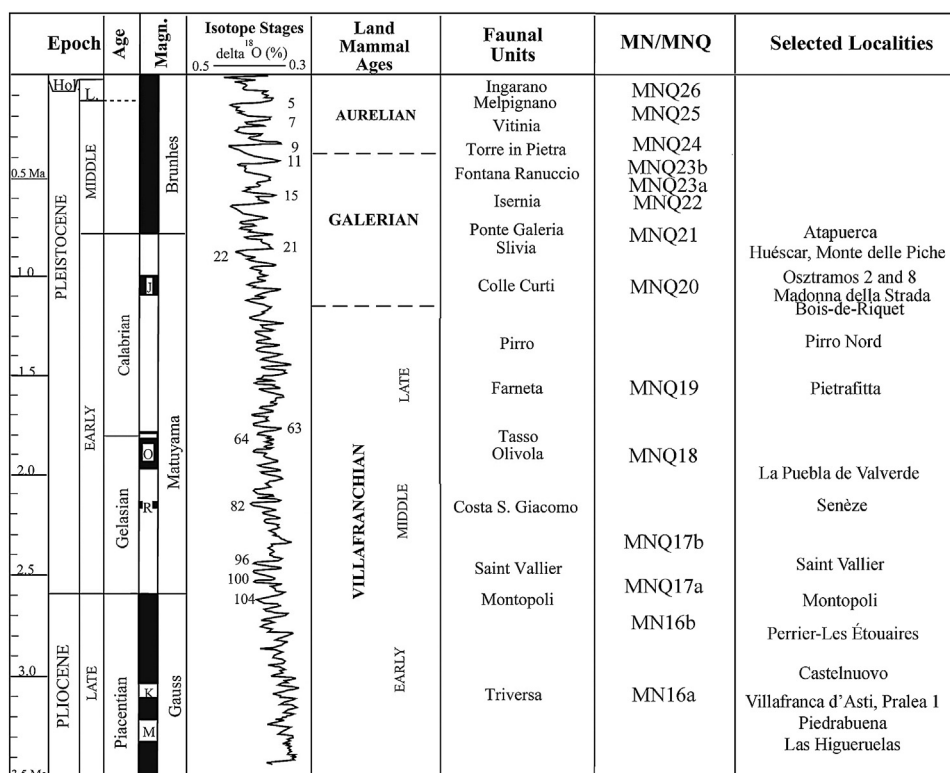


Fig. 1. Chronological and biochronological position of selected Eurasian localities which yielded remains of *Stephanorhinus etruscus* (Table 1).

Fig. 1. Position chronologique et biochronologique des localités eurasiatiques sélectionnées qui ont fourni des restes de *Stephanorhinus etruscus* (voir le texte pour plus de détails sur les localités et les âges).

and of the symphysis are consistent with the dimensions of *S. jeanvireti*. The presence of the lower incisors can be interpreted as a plesiomorphic feature retained by the earliest representatives of the species; lower incisors are completely absent on the mandibles of *S. etruscus* from younger localities.

Stephanorhinus etruscus was also reported at Piedrabuena (Ciudad Real Province), referred to an age earlier than 3.0 Ma (MN15–MN16 transition) (Mazo, 1999; Mazo and Torres, 1991) and to MN16 by Madurell-Malapeira et al. (2014 and references therein). A distal humerus (MNCN 41574) from this locality is quite small, the medial border of the distal trochlea is convex, similar to some specimens of *S. etruscus* from Upper Valdarno, and the medial tuberosity appears less evident in anterior view than in *S. jeanvireti* from Vialette (France; Guérin, 1972, 1980) and Monte Pastore (Italy; Pandolfi, 2013). The material collected at El Rincón-1 (Albacete Province) has been described by Alberdi et al. (1997) and the fossiliferous locality has been recently referred to MN16 (Madurell-Malapeira et al., 2014). The direct revision of the specimens at MNCN by one of us (LP) confirms their attribution to the Etruscan rhino. This species is also documented in the early Villafranchian of Villarroya (La Rioja Province, MN16: Cerdeño and Alberdi, 2016; Guérin, 1980; de Villalta Comella, 1952) and in the middle Villafranchian of Crespì (Girona Province, MN16–MNQ17 transition; García-Fernández et al., 2001) as published by one of us (EC). The presence of *S. etruscus* can be also confirmed at La Puebla de Valverde (Teruel Province, MNQ18 according to Nomade et al., 2014 and discussion therein), Huélago and Felones P-1 (Guadix-Baza Basin, Granada Province, MNQ18: Cerdeño, 1989, 1992, 1993; Garrido, 2008), based on direct observations and figured material.

S. etruscus was reported during the early Galerian (early–middle Pleistocene transition) in Spain, where it seems to be a long-lived species (Cerdeño, 1993; van der Made, 2010). The presence of the Etruscan rhino can be confirmed at Huéscar (Granada Province; around 0.9 Ma: Cerdeño, 1993; van der Made, 2010) where, among other specimens, the distal epiphysis of a humerus (MNCN 19206) has a massive and protruding lateral epicondyle as in *S. etruscus* from Upper Valdarno, and the astragalus (MNCN 19214) displays morphological similarities with those collected from Upper Valdarno and Senèze, being different from those of *S. hundsheimensis* (e.g., medial lip of the trochlea more oblique in the latter). Moreover, the Etruscan rhino was also reported at Atapuerca TD4, TD6 and TD8 (Burgos Province, Brunhes–Matuyama transition) by van der Made (1998, 1999, 2010). The astragalus from TD6 figured by van der Made (1999: fig. 3, 1a–f) resembles several astragali of *S. etruscus* collected from Upper Valdarno, Tiberino Basin and Senèze.

A small-sized *S. etruscus* has been recently recorded at El Chaparral (around 1 Ma, Villaluenga del Rosario, Cádiz Province: Pacheco et al., 2011). According to Pacheco et al. (2011), *S. etruscus* with small-sized postcranial elements occurred between 1.4 Ma and 0.78 Ma, first documented from Pietrafitta (Perugia, Italy) and last from Atapuerca TD8. An almost coeval occurrence to that from El Chaparral

is at Cueva Victoria (Murcia Province, around 1 Ma: Cerdeño, 1993).

4.2. Italian Peninsula

According to Guérin (1980) and Pandolfi (2013), *Stephanorhinus etruscus* occurred in Italy during the latest Pliocene (MN16a) in the site of Villafranca d'Asti (Asti Province) and during the Plio-Pleistocene transition (MN16b) at Montopoli (Pisa Province). Mazza (1988) considered both records to be too poorly documented and gave scant credit to them. The Etruscan rhino is represented only by one astragalus (IGF1452V, Fig. 2A) and a fragmentary metatarsal (IGF4688V) in the site of Montopoli (where also *S. jeanvireti* is present: see Pandolfi, 2013); although the species is represented only by two remains, they testified the presence of the Etruscan rhino in the early Villafranchian of Italy. The isolated remains from Villafranca d'Asti (housed at NMB), instead, come from an undefined stratigraphic level and an attribution to an age younger than the early Villafranchian cannot be excluded.

S. etruscus is also reported in latest Pliocene deposits of Castelnuovo di Baradenga Scalo (Siena Province) (Cusani Politi, 1963, 1971), represented by several forelimb bones of the same individual housed at MSNAF (specimens 7124–7130 and 7138–7141; Fig. 2D–E). Among them, the Mc III (MSNAF 7138; Fig. 2E) displays a sub-triangular proximal epiphysis, with a straight anterior border, a rather convex medial border and a narrower lateral border compared with that of *S. jeanvireti* from Vialette. In lateral view, the anterior articular surface for the Mc IV is narrow and sub-rectangular whereas the posterior one, slightly covered by sediment, is sub-elliptical, morphology that coincides with several specimens of *S. etruscus* from Upper Valdarno (Florence Province) (Fig. 2B) and Tiberino Basin (Perugia and Terni Provinces).

Fortelius et al. (1993) also reported the presence of the Etruscan rhino in the late Pliocene (early Villafranchian) localities of Palaia (Pisa Province) and Città della Pieve (Perugia Province). Nevertheless, the fragmentary nasal bone IGF5566v (without nasal septum) and the mandible IGF13091 from Palaia display morphological and morphometric features closer to *D. megarhinus* and were referred to this species by Azzaroli (1962), Guérin (1980) and Pandolfi (2013). In turn, the attribution of the specimen from Città della Pieve cannot be confirmed, unfortunately, because it is part of a non-defined Private Collection (Fortelius et al., 1993, p. 67), it was not figured by Fortelius et al. (1993) and information about the stratigraphic level was not reported.

The last occurrence of *S. etruscus* in Italy was relatively controversial. Several small-sized remains from the latest early Pleistocene of Europe were usually ascribed to *S. etruscus*, *S. cf. hundsheimensis* or to *S. hundsheimensis*. According to Pandolfi and Petronio (2011), the latest Villafranchian Italian rhinoceroses from Pirro Nord (Foggia Province, southern Italy), Madonna della Strada (L'Aquila Province, central Italy) and Imola Basin (Imola Province, northern Italy) can be ascribed to *S. etruscus*. The remains from Pietrafitta (Perugia Province; latest early Pleistocene, Farneta Faunal Unit; Fig. 2C; Fig. 3A–B) were assigned to *Stephanorhinus cf. S. hundsheimensis* by Mazza et al. (1993),

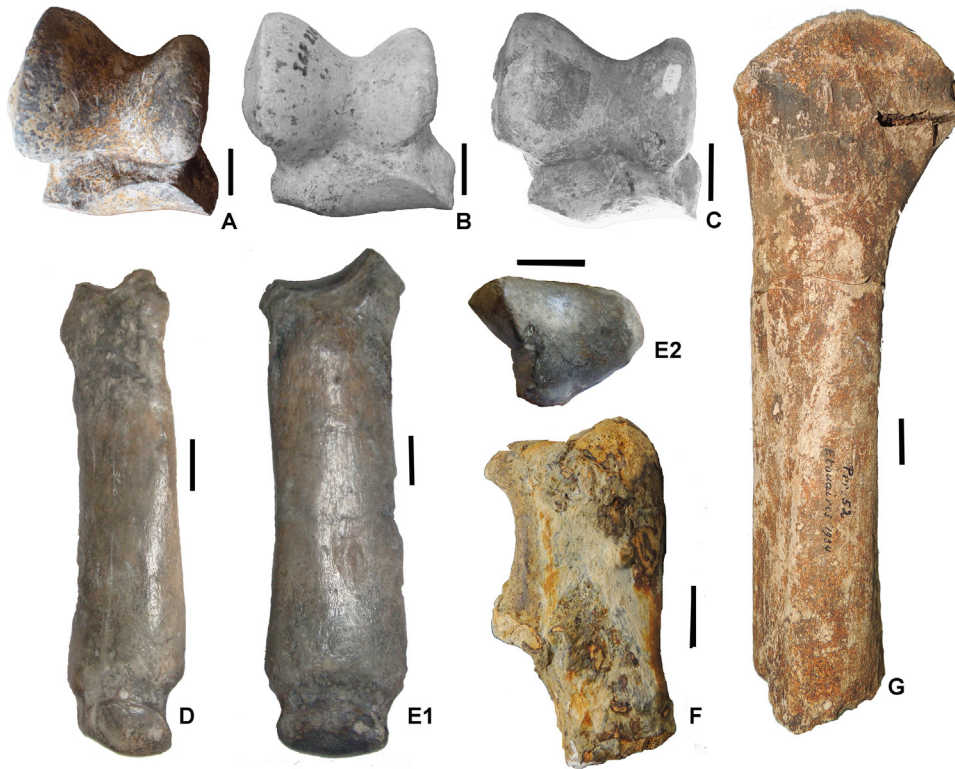


Fig. 2. Fossil remains of *Stephanorhinus etruscus* from latest Pliocene and early Pleistocene European localities. **A.** Right astragalus IGF1452V from Montopoli (Italy) in anterior view. **B.** Right astragalus IGF 2243v from Upper Valdarno (Italy) in anterior view. **C.** Right astragalus MPLBP 819 from Pietrafitta (Italy) in anterior view. **D.** Left McII MSNAF 7130 from Castelnuovo di Barardenga Scalo (Italy) in anterior view. **E.** Left McIII MSNAF 7138 from Castelnuovo di Barardenga Scalo (Italy). **1:** anterior view, **2:** proximal view. **F.** Left calcaneus NMB Prr54 from Perrier–Les Étouaires (France) in lateral view. **G.** Left radius NMB Prr52 from Perrier–Les Étouaires (France) in anterior view. Scale bar = 2 cm.

Fig. 2. Restes fossiles de *Stephanorhinus etruscus* des localités européennes du Pliocène terminal et du Pléistocène inférieur. **A.** Astragale droit IGF1452V de Montopoli (Italie) en vue antérieure. **B.** Astragale droit IGF 2243v de Valdarno supérieur (Italie) en vue antérieure. **C.** Astragale droit MPLBP 819 de Pietrafitta (Italie) en vue antérieure. **D.** McII MSNAF 7130 gauche de Castelnuovo di Barardenga Scalo (Italie) en vue antérieure. **E.** McIII MSNAF 7138 gauche de Castelnuovo di Barardenga Scalo (Italie). **1 :** vue antérieure, **2 :** vue proximale. **F.** Calcanéus gauche NMB Prr54 de Perrier–Les Étouaires (France) en vue médiane. **G.** Radius gauche NMB Prr52 de Perrier–Les Étouaires (France) en vue antérieure. Échelle = 2 cm.

but their closer similarity with *S. etruscus* was later recognized by van der Made (2010), Pandolfi and Petronio (2011) and Pandolfi et al. (2015). The dorsal profile of a skull from Pietrafitta (MPLBP n585; Fig. 3A–B), which seems not to be deformed by fossilization, is very close to that of the lectotype of *S. etruscus* (Fig. 3C), while it is more concave in *S. hundsheimensis* (Fig. 3D). Besides, its dimensions are close to those of the specimen from Senèze and fall into the dimensional range of *S. etruscus* given by Guérin (1980). The mandibular rami from Pietrafitta display a slightly more convex ventral border and shorter height below the first molar than in *S. hundsheimensis*; moreover, the ascending ramus is less massive (Pandolfi et al., 2015). In the humeri from Pietrafitta, the medial border of the distal trochlea is more inclined than in *S. hundsheimensis*, while the proximal border is more regularly convex. In the Mc III, the lateral side of the proximal epiphysis is small and squared, being more massive and rounded in *S. hundsheimensis*. The astragali from Pietrafitta (Fig. 2C) differ from *S. hundsheimensis*; in the latter species, the medial face of the bone protrudes much more externally than the outline of the medial lip of the trochlea and the medial tuberosity is well

marked and rounded. These Etruscan-like characters can be observed on the rhinoceros specimens collected from the lignite beds of Pietrafitta; nevertheless, a mounted skeleton housed at MPLBP and collected from a clayey level of Pietrafitta displays some differences with *S. etruscus* and further investigations are needed. Therefore, the species present during the latest Villafranchian in Italy is *S. etruscus* and the presence of *S. hundsheimensis* is not confidently supported.

In contrast, some of the rhinoceros remains collected from the Lefte Basin (Bergamo Province) and referred as *Dicerorhinus etruscus* by Vialli (1956) show morphological characters that allow their attribution to *S. hundsheimensis* (Pandolfi and Erten, 2017). An adult individual (individual B in Vialli, 1956) was collected from a lignite bed chronologically close to the beginning of the Jaramillo subchron (level 5 in Vialli, 1956 = unit 7 of Ravazzi et al., 2009). The occurrence of *S. hundsheimensis* at Lefte represents the earliest record of this species in northern Italy (Pandolfi and Erten, 2017) whereas *S. etruscus* persisted in central Italy until the end of the early Pleistocene (e.g., Monte delle Piche, Rome: Pandolfi and Marra, 2015).

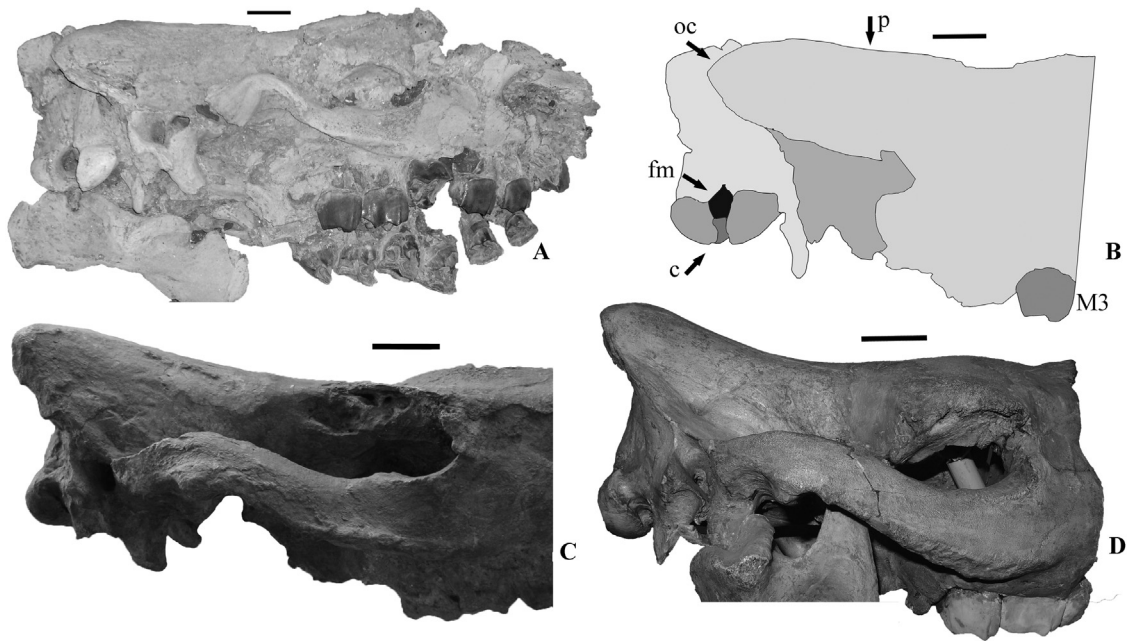


Fig. 3. A–B. Skull of *Stephanorhinus etruscus* from Pietrafitta (MPLBP n585), right lateral view. A. Original specimen. B. Redrawn. C. *S. etruscus* from Upper Valdarno IGF 756, left lateral view (reverse). D. *S. hundsheimensis* from Hundsheim NHMW 2013/0282/0001, right lateral view. Scale bar = 5 cm. oc: occipital crest; p: parietal bones; fm: foramen magnum; c: occipital condyles.

Fig. 3. A–B. Crâne de *Stephanorhinus etruscus* de Pietrafitta (MPLBP n585), vue latérale droite. A. Spécimen original. B. Le même, redessiné. C. Crâne de *S. etruscus* de Valdarno supérieur IGF 756, vue latérale gauche (retourné). D. Crâne de *S. hundsheimensis* de Hundsheim NHMW 2013/0282/0001, vue latérale droite. Échelle = 5 cm. oc : crête occipitale ; p : os pariétal ; fm : foramen magnum ; c : condyles occipitaux.

4.3. Central Europe (France, Netherlands, Germany, Austria)

Stephanorhinus etruscus was recorded by Guérin (1972, 1980, 2007) and Heintz et al. (1974) at Perrier–Les Étouaires (Puy-de-Dôme, France; MN16b), recently dated at ca. 2.78 Ma by Nomade et al. (2014). This record was questioned by Mazza (1988: p. 62), who suggested a careful verification. The rhinoceros specimens collected from Perrier–Les Étouaires (Fig. 2F–G), and housed at NMB, are represented by a humerus (Prr429), two radii (Prr52, Prr109), a magnum (Prr56), a Mc III (Prr55), two femuri (Prr nn, Prr323), a tibia (Prr321) and three calcanei (Prr53, Prr54, Prr327). The radii (Fig. 2G) differ from *S. jeanvireti* from Vialette (comparison based on direct observations) which has, in proximal view, a more marked concavity on the anterior border and a proportionally narrower medial articular surface. The humerus resembles *S. jeanvireti* in having a well-developed and marked lateral tuberosity and a less concave dorsal border of the trochlea. The maximal length of the magnum ($L = \text{ca. } 82 \text{ mm}$) is smaller than the minimal values reported for *S. jeanvireti* ($L = 94 \text{ mm}$; see Guérin, 1980) and the medial articular surface is more anteriorly placed than in *S. jeanvireti*. The third metacarpus has the proximal anterior border sinuous and the proximal transverse diameter is wider than in *S. etruscus*. The femuri are rather similar, but the specimen Prr323 displays more developed lateral and medial distal tuberosities. The two specimens differ from *S. jeanvireti* in having a relatively wider and shorter medial articular condyle. The tibia differs from *S. jeanvireti* in having a narrower distal lateral facet

and a wider and sub-quadrangular distal medial facet. The calcanei Prr327 and Prr53 (Fig. 2F) are slenderer than those of *S. jeanvireti* from Vialette, the tuber calcanei are less massive anteriorly and the anterior border of the cuboid facet is concave. The third calcaneum (Prr54) has a smaller tuber ($TD = 39.2$; $APD = 53$) than in *S. jeanvireti* (see Guérin, 1980: Tab. 108). This comparison supports the recognition of the Etruscan rhino at Les Étouaires.

The species is also recorded in numerous Villafranchian French localities (Guérin, 1980), which yielded a considerable number of remains. Among others, the specimens from Saint-Vallier (Drôme, middle Villafranchian) were revised by Guérin (2004) whereas those from Senèze were included in the Guérin's (1980) monumental work, but they have never been described or studied in detail, despite being one of the largest rhino samples of early Pleistocene age (2.2–2 Ma; Nomade et al., 2014). A few isolated teeth have been reported from Peyrolles (Haute-Loire; MNQ19, 1.47 Ma; Nomade et al., 2014) and figured by Dawkins (1868: pl. VIII). According to Guérin (1980), the specimens can be referred to *S. etruscus*, but the morphological characters of the teeth (e.g., presence of a strong lingual cingulum on the upper premolar, presence of a midfossette on the third upper molar) are common in both *S. etruscus* and *S. hundsheimensis*, and accordingly the specimens are here referred to *Stephanorhinus* sp. Several remains, including a juvenile skull, were referred to *S. etruscus* by Guérin (1980) from Blassac-La-Girondie (Haute-Loire, 2.2–2.3 Ma; Boivin et al., 2010; Nomade et al., 2014). Guérin (1980) referred to *D. etruscus brachycephalus* an isolated metapodial from La Sartanette (Garde; MNQ19; Bonnet and Malaval, 1976);

later, [Palombo and Valli \(2004\)](#) listed *S. etruscus* within the faunal assemblage of this locality, even though most European material previously recognized as *D. e. brachycephalus* was reassessed as *S. hundsheimensis* ([Fortelius et al., 1993](#)). *S. etruscus* is certainly recorded at Bois-de-Riquet (Hérault; [Bourguignon et al., 2015](#): fig. 6D; pictures kindly provided by Antoine P.-O., March 2015) dated around 1.3–1.1 Ma ([Bourguignon et al., 2015](#)), suggesting a persistence of this taxon in southern France during the latest early Pleistocene (Villafranchian–Galerian transition).

In the Netherlands, [Hooijer \(1981\)](#) reported the presence of a rhinoceros tooth belonging to *D. etruscus* or *D. jeanvireti* from the Pretiglian (early or middle Villafranchian) “black bones” fauna. Unfortunately, this tooth ([Hooijer, 1981](#): pl. I) is much worn and its morphological characters are not useful for an accurate taxonomic attribution. [Bernsen \(1927\)](#) described several rhinoceros remains from Tegelen (Limburg; Early Pleistocene, late Villafranchian) and ascribed them to *Rhinoceros etruscus* and *Rhinoceros mercki* (= *S. kirchbergensis*), but [Loose \(1960\)](#) referred the maxilla ascribed to the latter ([Bernsen, 1927](#): pl. III) to *R. etruscus*. Later, [Guérin \(1980\)](#) also reported the occurrence of two species at Tegelen: *D. e. brachycephalus* and *D. mercki*, but [van Kolfschoten \(1989\)](#) reported *D. etruscus* and, with doubts, *D. mercki*. More recently, [van der Made \(2010\)](#) stated that the remains from Tegelen resemble metrically *S. hundsheimensis*, but some specimens are morphologically different from it. The tooth series figured by [Bernsen \(1927: pl. I\)](#) shares with *S. hundsheimensis* from Mosbach (Karlsruhe), Voigsted (Kyffhäuserkreis) and Hundsheim (Buck an der Leitha) the following characters: presence of a continuous lingual cingulum on the premolars, presence of the crista on the premolars, presence of a complex crochet on the premolars, a constricted protoloph on P2, presence of a small crista on M1, presence of a slight lingual cingulum on M2, presence of a small and prominent paracone fold on M1–M2. These characters can be also observed in *S. etruscus*, but in different percentage and never occur on a single specimen. In agreement with [Loose \(1960\)](#), the tooth series figured by [Bernsen \(1927: pl. III\)](#) cannot be referred to *S. kirchbergensis* and are morphologically close to *S. hundsheimensis* or *S. etruscus*. The teeth are much worn and prevent a confident taxonomic attribution. The mandible figured by [Bernsen \(1927: pl. VI, fig. 4\)](#) resembles *S. hundsheimensis*; it is slenderer than in *S. etruscus* and the anterior border of the vertical ramus is inclined backwards whereas is rather vertical in *S. etruscus*. On the contrary, another specimen figured by [Bernsen \(1927: pl. V, fig. 4\)](#) is morphologically closer to *S. etruscus* than to *S. hundsheimensis*.

Among postcranial remains, the astragalus ([Bernsen, 1927](#): pl. XII, fig. 13) displays morphological characters coincident with *S. hundsheimensis* from Hundsheim (the medial face of the bone extends medially and the medial tuberosity is well marked and rounded; comparison based on direct observations); instead, an unpublished astragalus from Tegelen (MfN MbMa 26297) is closer to *S. etruscus*. In summary, at least two species are present at Tegelen, *S. etruscus* and *S. hundsheimensis*. However, the occurrence of a third species, *S. kirchbergensis*, was reported by [Guérin \(1980: 978\)](#) on the basis of two tooth rows,

some isolated teeth and some postcranial remains. This suggests that the Tegelen clay-pits are characterized by diachronic fossiliferous deposits referable to early and early middle Pleistocene, as raised by several authors ([Guérin, 1980](#); [van den Hoek Ostende, 2004](#); [O'Regan and Turner, 2004](#); [Schreuder, 1949](#)). The material ascribed to *S. etruscus* probably comes from the early Pleistocene levels, but any chronological detail is not currently available.

In Germany, *S. etruscus* is reported from a few Villafranchian localities ([Dietrich, 1953](#); [Guérin, 1980](#); [Lehmann, 1953](#)). The specimens collected at Thiede (Salzgitter; Villafranchian) are represented by M2–M3 (MfN MbMa26305) and p2–p4 (MfN MbMa26304). M2 displays a slightly marked paracone fold, a concave posterior side of the ectoloph, a single crochet, a continuous metaloph and a slightly marked lingual cingulum. M3 has a rather flat ectometaloph with slightly marked paracone fold, a single crochet, a mesial cingulum and a lingual cingulum on the protocone. In occlusal view, the lower premolars ($L_{p2-p4} = 103.9$ mm; $L_{p3-p4} = 72.2$ mm) display a rough enamel, a rounded trigonid, and a slightly marked and deep vestibular groove. The p2 has a long paralophid and a slightly developed mesial cingulum; p4 has a mesial cingulum, lacks labial and lingual cingula, and the lingual valleys are V-shaped. These specimens differ from *S. jeanvireti*, in which cheek teeth display rather smooth enamel, a slightly convex ectometaloph on M3, a reduced or absent cingulum on M2 and rather shorter distance between the bottoms of the lingual valleys and the base of the crown on lower molars.

No other records of *S. etruscus* are currently reported in Germany, considering that the specimens collected from the latest early and early middle Pleistocene localities of Untermassfeld (Schmalkalden–Meiningen), Süssenborn (Weimar) and Voigtstedt (Mansfeld–Südharz) were recently referred to *S. hundsheimensis* ([Kahlke, 1965, 1969, 2001](#); [Kahlke and Kaiser, 2011](#); [Kahlke et al., 2011](#)).

4.4. Balkans, eastern Europe and European Russia

Remains generally related to *S. etruscus* were reported in a few Villafranchian localities of Greece, but they consist of isolated teeth or fragmentary material ([Symeonidis et al., 2006](#): 444, and references therein).

[De Vos et al. \(2002: pl. IV, fig. C\)](#) described some badly preserved specimens from Vatera (Lesvos, Greece: ca. 2.5–2 Ma), determining them as *S. cf. etruscus*. The femur figured by [De Vos et al. \(2002: pl. IV, fig. C\)](#), as well as the other listed specimens ([De Vos et al., 2002](#): p. 55), does not display useful morphological characters to distinguish among the different species, but the authors stated that they are morphometrically closer to *S. etruscus* than to *S. jeanvireti* or “*Dihoplus*” *megarhinus*. [Symeonidis and De Vos \(1976\)](#) ascribed a p2 and a m1 to *Dicerohinus cf. etruscus* from Tourkovounia 4 (Athens, MN16-MNQ17; [Koufos, 2006](#)). The dimensions of these teeth fall within the respective ranges of *S. etruscus* ([Guérin, 1980](#): 468) with the exception of the width of m1, which is slightly smaller. [Symeonidis et al. \(2006: 443\)](#) described two fragmentary mandibles from Aivaliki (Serres, Greece: late early Pleistocene) and assigned them to *S. cf. etruscus*. According to [Symeonidis](#)

et al. (2006), the morphology of these specimens is closer to that of *S. etruscus* and they were tentatively correlated to the small-sized etruscoid populations *sensu* Mazza et al. (1993), including Pirro Nord and Pietrafitta, whose remains have been recently referred to *S. etruscus* (van der Made, 2010; Pandolfi and Erten, 2017; Pandolfi and Petronio, 2011; Pandolfi et al., 2015). A few isolated teeth, mandibular fragments and postcranial remains doubtfully assigned to the Etruscan rhino have been also reported from an undefined locality near the Aliakmonas river (Greek Macedonia) and from several early Pleistocene Greek localities (e.g., Libakos, Kozani Regional Unit; Krimmi, Halkidiki Regional Unit; Sesklo, Magnesia Regional Unit; Molykrio, Etoloakarnania Regional Unit; Psychiko, Athens Regional Unit; Symeonidis et al., 2006 and references therein).

The species has never been reported in Serbia (Dimitrijević, personal communication, December 2016). *Dicerorhinus etruscus* has been reported in Montenegro, at Trlica (Pljevlja; late early Pleistocene?) by Dimitrijević (1990), but the material assigned to this taxon has been revised by Codrea and Dimitrijević (1997) and identified as *S. cf. hundsheimensis*. Recently, Vislobokova and Agadjanian (2015) suggested the presence of *S. etruscus* in the lower levels (level TRL10 and TRL11) of the Trlica sequence based on a few isolated teeth. Nevertheless, the specimens figured by these authors, in particular the M2 (Vislobokova and Agadjanian, 2015: fig. 5b) morphologically resemble *S. hundsheimensis*. The age of the fauna is still discussed (see van der Made and Dimitrijević, 2015).

Several postcranial remains of rhinoceros from an early Pleistocene karst cavity near Split (Split, Croatia) were ascribed to *Dicerorhinus etruscus* by Malez (1961). This species has also been listed in the Villafranchian faunal assemblages from Strmica (Šibenik-Knin, Croatia) and Pula (Istria, Croatia; Malez, 1986), as well as from Novo Mesto (Jugovzhodna Slovenija, Slovenia; Malez, 1986).

Within the Dacian Basin (Romania), *S. etruscus* has been recorded at Pralea 1 and Curtea de Argeş area (Cândeşti Formation, MN16a; Andreescu et al., 2013) whereas an isolated M3 assigned to *S. ex gr. etruscus* has been reported at Leu (Craiova, around 1.6 Ma; Andreescu et al., 2013; Popescu, 2004). *Stephanorhinus cf. etruscus* has been reported from the MN 16a of Mătăsari-Brădeţu and Cernăteşti in association with the mastodon *Ananacus arvernensis* and in the latter site with *S. jeanvireti* (Rădulescu et al., 2003). The species was also reported from the MNQ17 at La Petriş (Rădulescu et al., 2003). In the Braşov Depression, *S. cf. etruscus* was cited at Iarăş (Late Pliocene; Rădulescu et al., 1965, 2003). The record of this species at Piteşti (Argeş; Stancu et al., 1969) could be wrong as it is based on a not diagnostic remain. *S. etruscus* occurred in several early Pleistocene localities of Romania; the latest records such as this from Betfia XII, Bihor Country (Codrea personal data, LP personal observation at HNHM) are close to the Jaramillo subchrone (Terzea, 2006; Venczel, 2000).

A well-preserved skull of rhinoceros referred as *Dicerorhinus etruscus* was collected from the gravels of Tiraspol (early middle Pleistocene, Moldova) together with several other remains (Beliajeva and David, 1975). The dorsal profile of the skull (Beliajeva and David, 1975: pl. 1), as well as the presence of a well-developed lingual

cingulum on the premolars, resembles *S. hundsheimensis* from Hundsheim rather than *S. etruscus* from Upper Valdarno; therefore, we recognize the rhinoceros from Tiraspol as *S. hundsheimensis* and discard its previous assignment to *S. etruscus*.

In the Czech Republic, Fejfar (1995) referred to *Dicerorhinus etruscus* a few teeth from the Middle Pleistocene site of Přezletice (Prague eastern district), but van der Made et al. (2017) recently suggested a probable attribution to *S. hundsheimensis*.

In the Slovak Republic, the Etruscan rhino has been reported at Strekov, Nová Vieska (Nové Zámky, early Villafranchian in age, MNQ 17: Holec, 1986, 1996; Vlačický et al., 2008), represented only by isolated teeth. Remains of rhinoceros labeled as *Opsiceros etruscus* come from Gombasek (Rožňava, latest early–early middle Pleistocene; Wagner and Gasparik, 2014). However, these specimens, housed at HNHM, morphologically resemble *S. hundsheimensis* according to Pandolfi and Erten (2017). In Hungary, Kretzoi (1954) reported *S. etruscus* at Kisláng (Fejér country, MNQ 17 or 18: see Janossy, 1986) and Villány loc. 3 (Baranya country, MNQ 17 or 18: see Jánossy, 1986; Kretzoi, 1956) on the basis of a few specimens not described or figured. The material has not been found in the visited Hungarian institutions and this taxonomic attribution cannot be confirmed, as well as that from Tarkó (Borsod–Abaúj–Zemplén country; early middle Pleistocene; Jánossy, 1986). *Stephanorhinus etruscus* is represented by a small-sized radius (HNHM v.67.277) at Süttő freshwater limestone (Komárom–Esztergom country, MNQ 17). The species has been also reported at Osztramos 2 and 8 (Borsod–Abaúj–Zemplén country, around 1.2 Ma; Jánossy, 1986; personal observation at HNHM and MFGI), whereas uncertain determinations of Etruscan rhino are reported at Somssich Hill 2 (Baranya country, aff. “*Rhinoceros etruscus*” around 0.9 Ma), Ürömhegy (*Dicerorhinus cf. etruscus*, latest early Pleistocene) and Budakalász (Pest country, *D. aff. etruscus*, latest early Pleistocene). “*Rhinoceros etruscus*” has been listed in the faunal assemblage of Vértesszőlős (Komárom–Esztergom country; early middle Pleistocene; Jánossy, 1986), but a few unpublished teeth housed at MFGI (v.17724–33, v.17738–47, v.17759–67) closely resemble *S. hundsheimensis* rather than *S. etruscus*.

Two fragmentary mandibles were referred to *Rhinoceros etruscus* from the alluvial deposit of the Dnestr River, near Kamianets–Podilskyi (Kamianets–Podilskyi district, western Ukraine; Leybman, 1960: fig. 1). These specimens are too badly preserved for an accurate determination.

In Caucasus, *Dicerorhinus etruscus*, *Dicerorhinus cf. etruscus* or *Stephanorhinus etruscus* has been reported from the early Pleistocene of Kotsakhuri Dedoplistsqaro district, Georgia and the famous site of Dmanisi (Dmanisi district, Georgia, Vekua and Lordkipanidze, 2008 and references therein), but the material was not figured or described. The specimens from Akhalkalaki (Tbilisi district, Georgia, early–middle Pleistocene transition) figured by Vekua (1986: pl. 6) morphologically resemble the Etruscan rhino. *Stephanorhinus etruscus* has also been listed within the mammal assemblage from Psekups (Adygea Republic, Russia), chronologically dated between the Reunion and

Olduvai subchrones (Vislobokova, 2005 and references therein), but the systematic attribution of the material has not been verified.

4.5. Turkey and Near East

The presence of a small form of Plio-Pleistocene rhinoceros (*Dicerorhinus* sp., probably *Stephanorhinus*) in Turkey was firstly reported at Yokuri-Sögütönü (Eskisehir; MN 17a) by Becker-Platen and Sickenberg (1968) and Sickenberg et al. (1975). However, this material has never been published and seems to be missing (Mayda pers. comm., March 2017). *Stephanorhinus* cf. *etruscus* has been recently reported from the Denizli Basin (Denizli Province, southwestern Turkey, late Villafranchian: Boulbes et al., 2014). Unfortunately, the conservation status of the specimens figured by Boulbes et al. (2014) does not allow an adequate appreciation of their morphologies to get a more precise determination. New remains collected from this Basin have been instead assigned to *S. hundsheimensis* (Pandolfi and Erten, 2017).

The occurrence of the Etruscan rhino at Ubeidiya (Bethlehem governorate, 1.6–1.2 Ma; Belmaker, 2009) is here confirmed through the observation of the remains reported by Guérin (1986: pl. 1). A second record in Israel corresponds to Bethlehem (Bethlehem governorate, Hooijer, 1958; ca. 2.5 Ma; Bar-Yosef and Belmaker, 2010). Nevertheless, the crushed skull from this locality, housed at NHML, displays morphological characters that have not been observed in *S. etruscus* (e.g., absence of nasal septum, presence of medifossette in molars and premolars). The rhinoceros from Bethlehem needs a careful revision and a detailed comparison to establish a confident taxonomic determination.

5. Conclusions

Stephanorhinus etruscus is recorded at several early Pleistocene Eurasian localities and it appears to be the sole rhinoceros species in Europe from ca. 2.5 to ca. 1.3 Ma (Fig. 1). The first occurrence of *S. etruscus* is attested at around 3.5–3 Ma in Spain, Italy and the Dacian Basin, and the species also co-occurs with *S. jeanvireti* in localities such as Montopoli and Perrier–Les Étouaires. The origin of the species is still unknown. According to Heissig (1996), *S. etruscus* probably derived from the Turolian *Dihoplos pikermiensis*. New Pliocene findings from the Near East and Anatolia would be probably crucial to investigate this hypothesis. The last occurrence of *S. etruscus* is diachronic in the different Eurasian areas; indeed the species disappeared in central Europe at the end of the Villafranchian Mammal Age (late Early Pleistocene) whereas it survived in Italy and the Iberian Peninsula until the early–middle Galerian transition (early–middle Pleistocene transition). The morphometric values of the specimens collected in late early Pleistocene deposits are close to those from older localities (Supplementary Material); accordingly, the presence of late Villafranchian small-sized forms of *S. etruscus* is not confirmed here. Further investigations should be performed and further material need to be added to investigate this issue.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2017.06.004>.

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