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Stephanorhinus jeanvireti (Mammalia, Rhinocerotidae) from the early Pleistocene of Colțești (southwestern Romania)

Stephanorhinus jeanvireti *(Mammalia, Rhinocerotidae) du Pléistocène inférieur de Colteşti (Sud-Ouest de la Roumanie)*

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ABSTRACT

The Rhinocerotidae material from the early Pleistocene Tetoiu Formation of Colțești (southwestern Romania) is here described for the first time. The rhinoceros is documented by calcaneus and second, third, and fourth metatarsals, probably belonging to the same individual. The morphology and the dimensions of these specimens enable us to record the presence of *Stephanorhinus jeanvireti*, a relatively rare rhinoceros usually reported from late Pliocene European localities and recently considered a junior synonym of *S. elatus*. Nevertheless, the taxon *Rhinoceros elatus* is here regarded as a *nomen dubium* and the name *S. jeanvireti* is retained in order to maintain nomenclatural stability, being it based on much more diagnostic material. In Romania, *S. jeanvireti* has been listed within a few late Pliocene faunal assemblages, but the rhinoceros remains are fragmentary and isolated bones. The Colțești find is among the best documented records of *S. jeanvireti* in Romania. The biochronological distribution of *S. jeanvireti* is mainly confined within the MNQ16 (early and early middle Villafranchian), and its first occurrence is doubtfully reported in late MNQ15 faunas. The record of Colțești (MNQ17/MNQ18) represents, instead, the last occurrence of this taxon in Europe.

Mots clés :
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RÉSUMÉ

Le matériel de Rhinocerotidae du Pléistocène inférieur de la formation Tetoiu de Colteşti (Sud-Ouest de la Roumanie) est ici décrit pour la première fois. Le rhinocéros est documenté par le calcanéum et les deuxième, troisième et quatrième métatarses, appartenant probablement au même individu. La morphologie et les dimensions de ces spécimens permettent d'enregistrer la présence de *Stephanorhinus jeanvireti*, un rhinocéros relativement rare, signalé d'ordinaire dans des localités européennes du Pliocène terminal et récemment considéré comme un synonyme juvénile de *S. elatus*. Néanmoins, le taxon *Rhinoceros elatus* est ici considéré comme un *nomen dubium* et la dénomination *S. jeanvireti* est retenue pour maintenir la stabilité de la nomenclature, basée sur beaucoup plus de matériel diagnostique. En Roumanie, *S. jeanvireti* a été listé dans plusieurs assemblages fauniques du

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Pliocène tardif, mais les restes de rhinocéros sont des os fragmentaires et isolés. La découverte faite à Colteşti figure parmi les enregistrements les mieux documentés de *S. jeanvireti* en Roumanie. La distribution biochronologique de *S. jeanvireti* est majoritairement limitée au MNSQ16 (Villafranchien inférieur et inférieur-moyen) et sa première occurrence est rapportée de manière douteuse dans les faunes du MNQ15 terminal. L'enregistrement de Colteşti (MNQ17/MNQ18) représente, au contraire, la dernière occurrence de ce taxon en Europe.

1. Introduction

The occurrence of Rhinocerotidae during the Pliocene and early Pleistocene in eastern Europe is still poorly known, despite this area represents an important "bridge" between Western Europe and Asia. In this context, a revision of Plio-Pleistocene rhinoceroses from Eastern Europe has started in the last years and has contributed to improve knowledge of different fossil species such as *'Dihoplus' megarhinus* (de Christol, 1834), *Stephanorhinus etruscus* (Falconer, 1868) and *Stephanorhinus hundsheimensis* (Toula, 1906) (Boulbes et al., 2014; Konidaris et al., 2015; Pandolfi and Erten, 2017; Pandolfi et al., 2015a, 2016, 2017; Spassov, 2005 and references therein). However, Pliocene European rhinoceroses are still poorly investigated, and relatively poorly documented with respect to the late Miocene and early Pleistocene ones. During the Pliocene (MNQ14, MNQ15, MNQ16), at least four species are documented in Europe: *'D.' megarhinus*, considered a typical Pliocene species (Guérin, 1980; Pandolfi, 2013), but also recorded during the latest Miocene (Pandolfi and Rook, 2017; Pandolfi et al., 2015a, 2016); *'Stephanorhinus' miguelcrusafonti* (Guérin and Santafé-Llopis, 1978), reported at a few early Pliocene Spanish and French localities (Cerdeño, 1992; Guérin, 1980; Guérin and Santafé-Llopis, 1978); *Stephanorhinus jeanvireti* (Guérin, 1972: see note in Systematic Paleontology; Campanino et al., 1994; Pandolfi, 2013) documented from some late Pliocene localities; and *S. etruscus* that occurred in Europe at the end of the Pliocene and during the early Pleistocene (Cerdeño, 1993; Pandolfi et al., 2015b; Pandolfi et al., 2017 and references therein).

Starting with late Miocene in Romania as in other regions of Europe (Guérin, 1980; Heissig, 1996), Rhinocerotidae decreased their presence in the faunal communities in both diversity and abundance (Rădulescu and Samson, 2001; Rădulescu et al., 2003). *'Dihoplus' megarhinus* (Rădulescu and Samson, 2001; Rădulescu et al., 2003; therein as *Stephanorhinus leptorhinus* in partim), during the early Pliocene (Dacian; Andreescu et al., 2011, 2013; Rădulescu and Samson, 2001), *S. jeanvireti*, during the late Pliocene (Rădulescu and Samson, 2001; Rădulescu et al., 2003; therein as *Stephanorhinus elatus* in partim), and *S. etruscus*, during the early Pleistocene, (Pandolfi et al., 2017 and references therein) were listed within some faunal assemblages.

The aim of this paper is to describe postcranial rhinoceros remains collected from early Pleistocene deposits at Colţeşti (Oltenia Province, southwestern Romania; Fig. 1) and to discuss the biochronological implications of this finding.

Southwestern Romania is perhaps the most representative region where Pliocene and early Pleistocene sedimentary deposits are widely exposed in that country. These deposits have depositional histories related either to the peculiar sedimentary evolution of the western side of the Dacian Lake or to the fluvial system that replaced this lake after its warping, in the late Pliocene (Codrea, 1997; Codrea et al., 2006; Jipa, 2006).

For a long time and even hitherto, the Pliocene stratigraphy of Oltenia has been mainly based on mollusks (Andreescu et al., 2011, 2013 and references therein). Nevertheless, the fossil vertebrates—and overall mammal ones,—added useful details, leading to a better stratigraphy (Andreescu et al., 2013; Feru et al., 1983; Rădulescu and Samson, 1990, 2001; Rădulescu et al., 2003).

2. Geological and stratigraphic background

The vertebrate locality Colţeşti was found in April 1999. Colţeşti is a village located 51 km southeast from Târgu Jiu, nearby Hurezani, in the Gorj District (Fig. 1). The fossils were recovered in an unusual way, due to the works connective to a drilling rig-up carried out by the drillers from Drilling Boreholes Craiova (Foraj Sonde S.A. Craiova) Society. More precisely, the workers dug a pit mud using a bulldozer. A part of the scattered bones was donated by the drilling staff to the "Al. Stefulescu" Museum in Târgu Jiu and another part to the Oltenia Museum, Natural Sciences Branch in Craiova.

From a structural viewpoint, Colţeşti is situated in the southern Carpathians Foredeep. This unit started its evolution next to the Latest Cretaceous ('Laramian') tectonic phase, finally thrusting the Moesian Platform (Săndulescu, 1984). The geological history began in the earliest Cenozoic. Between the Oligocene and the early Miocene, this region was part of the Proto- (Rusu, 1977) and Eo-Paratethys Sea realms, followed in the middle Miocene by the Meso-Paratethys (Popov et al., 2004). Paleogene and Miocene formations accumulated in marine and brackish realms until the Maeotian, when sectors of the riparian areas became emerged and large herbivores occurred on these terrestrial environments (Mihăilă, 1971). In Pontian, the marine and brackish waters were replaced by almost freshwater environments (Vasiliev et al., 2005).

At the beginning of the Pliocene (Dacian), this area was covered by the Dacian Lake, where a large diversity of mollusks lived, many of them endemic. In the late Pliocene (Romanian), the lake vanished in the Colţeşti area, replaced by a fluvial system with associated coal forming swamps.

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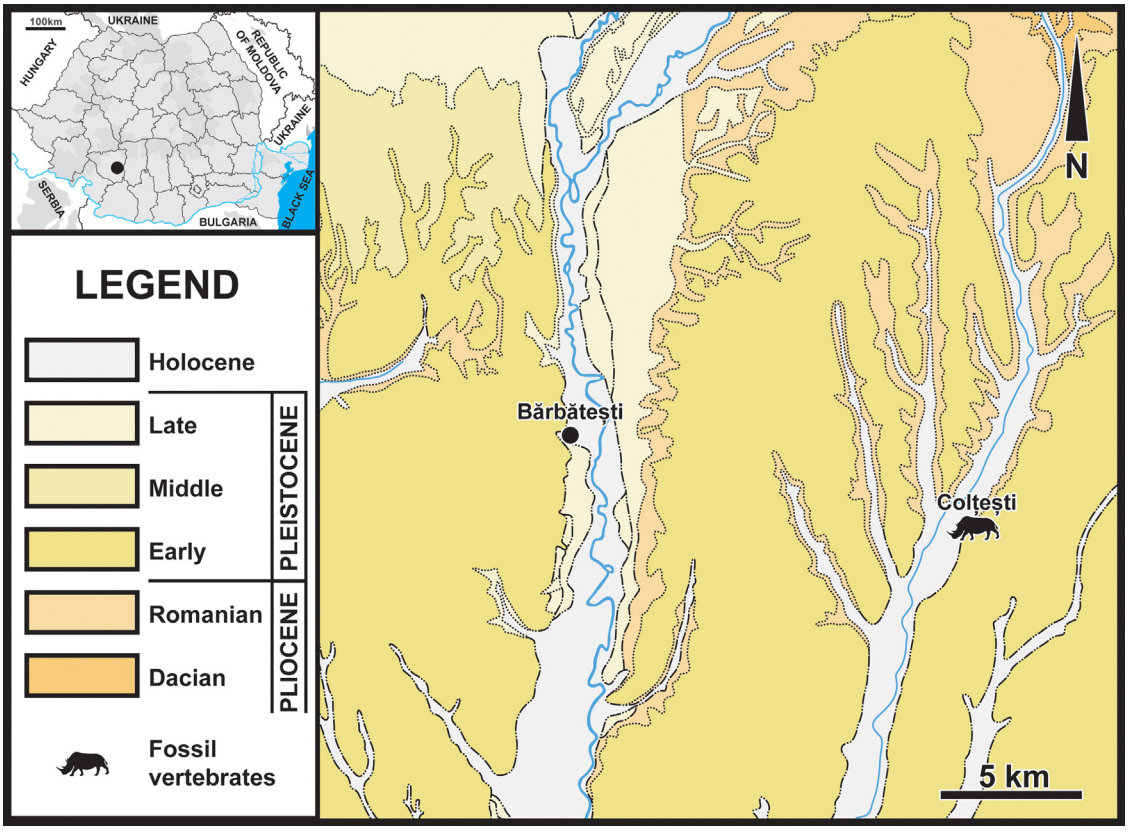

Fig. 1. Location of the locality Colțești (southwestern Romania) on the geological map.
Fig. 1. Situation de la localité de Colteşti (Sud-Ouest de la Roumanie) sur la carte géologique.

Various land vertebrates lived in these environments. In the Quaternary, this area was completely emerged.

Large herbivores, including rhinoceros remains, were also found mainly due to the coal mining works in the numerous open pits of this region. The vertebrate remains from Colțești were unearthed from yellowish, medium, and rough sand and sandstone concretions, belonging to the Tetoiu Formation (Andreescu et al., 2011, 2013), in particular to the so-called T-1 complex. The fossil mammals delivered by the Tetoiu Fm. are to be considered among the richest, most diverse and interesting ones in the early Pleistocene of the eastern Paratethys. The sequences of the early Pleistocene deposits, represented by the Tetoiu Fm., containing several fossiliferous levels rich in larger mammals, are to be found at Tetoiu in the middle valley of the Olteţ River. Paleontological investigations carried out in this area have detected a number of mammal-bearing deposits that can be assigned to three successive fossiliferous complexes named T1, T2, and T3 (Feru et al., 1983; Rădulescu and Samson, 1990), corresponding to: MNQ17 (final part) or first half of MNQ18, first half of MNQ19 and second half of MNQ19, respectively (Andreescu et al., 2011: fig. 4; Andreescu et al., 2013: fig. 4; Nomade et al., 2014: fig. 7). The fossil localities from T-1 have yielded the selected following mammalian species: *Mammuthus meridionalis*, *Trogontherium dacicum*, *S. etruscus*, *Stephanorhinus* sp., *Allohippus athanasiui* (= *Equus stenonis* or *E. sussenbornensis* see Forsten, 1999), *Eucladoceros* sp., *Pliotragus ardeus*, *Nyctereutes megamastoides*, *Lynx issiodorensis*, *Mitilanotherium inexpectatum*, *Ursus etruscus*, *Pliocrocuta perrieri*, *Homotherium crenatidens*, *Megantereon cultridens*, *Manis* cf. *hungarica* (Bolomey, 1965; Feru et al., 1983; Rădulescu and Samson, 1990, 2001; Samson and Rădulescu, 1963, 1966, 1973). An important biostratigraphic event in the Tetoiu area is indicated at ~1.7–1.8 Ma by the possible appearance of a *Homo erectus* lineage documented through the discovery of a few flint pebbles (Rădulescu and Samson, 1990, 1995; Samson and Rădulescu, 1963).

3. Material and methods

The revised Quaternary time scale of Gibbard et al. (2010) for chronological references is used in this text. The bottom and top boundaries of the Pliocene are placed at 5.4 Ma and 2.6 Ma, respectively.

The postcranial elements analyzed here include a left calcaneus and second, third, and fourth metatarsals belonging to a same individual. The material is currently housed at OMNSC. The specimens were morphologically compared with the rhinoceros material collected at several Pliocene and early Pleistocene localities of Eurasia and housed in several institutions, as well as with published data (Appendix 1). The anatomical descriptions follow

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Guérin (1980) and Antoine (2002), whereas the morphometric approach follows Guérin (1980). The comparative tables are reported in Appendix 1.

Institutional abbreviations

OMNSC, Oltenia Museum Natural Sciences Department Craiova; HNHM, Magyar Természettudományi Múzeum (Hungarian Natural History Museum), Budapest, Hungary; IGF, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MPLBP, Museo di Paleontologia Luigi Boldrini di Pietrafitta, Perugia, Italy; MPUR, Museo di Paleontologia, Sapienza, Università di Roma, Rome, Italy; NHMW, Naturhistorisches Museum, Wien, Austria; NMB, Naturhistorisches Museum, Basel, Switzerland.

Other abbreviations

ca, *circa* (about); *L*, maximal length; M, upper molar; MC, metacarpal; MNQ, mammal zones; MT, metatarsal.

4. Systematic paleontology

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Gray, 1821
Tribe Rhinocerotini Gray, 1821
Genus ***Stephanorhinus*** Kretzoi, 1942

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

Note. The debate on the taxonomic status of the European Pleistocene fossil rhinoceroses has been recently summarized by Pandolfi and Tagliacozzo (2015). Nevertheless, some issues concerning the paraphyly of the genus have been raised. Geraads (1988) suggested that *Stephanorhinus* is a paraphyletic group and *Coelodonta* represents the name for the monophyletic group that includes the species characterized by loss of anterior teeth, firmly closed external auditory pseudomeatus and backward-movement of the nasal notch. Heissig (1999) suggested a paraphyly of *Stephanorhinus*, recognizing two evolutionary lineages, one from *Dihoplus schleiermacheri* to *S. jeanvireti* through *'D'. megarhinus*, and the other one from *Stephanorhinus pikermiensis* to *S. etruscus* and other species. The Pikermi rhinoceros was later included into *Stephanorhinus* also by Antoine and Saraç (2005). Recent paleogenomic studies on this genus, however, revealed that *Stephanorhinus* is strictly related to *Coelodonta* (Kirillova et al., 2017; Cappellini et al., 2019). In the light of these results, the diagnostic characters of *Stephanorhinus* need to be re-discussed, as well as the validity of this genus (Cappellini et al., 2019). These issues, however, are beyond the contribution of this work and, in this paper, we consider *Stephanorhinus* as a monophyletic group as defined by diagnostic characters yet reported in past literature.

Stephanorhinus jeanvireti (Guérin, 1972)

Synonymy list: 1895 *Rhinoceros etruscus* var. *astensis* Sacco, 1–31, pl. I–IV; *nomen oblitum*.

2003 *Stephanorhinus elatus* (non Croizet and Jobert, 1828); Rădulescu et al., 3, 4, 8.

2010 *Stephanorhinus elatus* (non Croizet and Jobert, 1828); Rook and Martínez-Navarro, 136.

2019 *Stephanorhinus elatus* (non Croizet and Jobert, 1828); Ballatore and Breda, 205, tab. 2, in partim.

See Guérin (1972; *in partim*), Guérin and Tsoukala (2013; *in partim*) and Ballatore and Breda (2016; *in partim*) for a complete synonymy list.

Note: llatore and Breda (2016) recently suggested that *S. jeanvireti* (Guérin, 1972) is a junior synonym of *S. elatus* (Croizet and Jobert, 1828). Ballatore and Breda (2016) reported that the name *S. elatus* is not a *nomen oblitum* (being used in a few papers during the past century) and that *S. jeanvireti* should be replaced in force of ICZN rules. Nevertheless, the specimens of *Rhinoceros elatus* figured and described by Croizet and Jobert (1828) do not display diagnostic morphological features to distinguish them among the Pliocene and early Pleistocene rhinoceroses (including *'D.' megarhinus* and *'S.' miguelcrusafonti*). Ballatore and Breda (2016) briefly re-described those specimens but did not find exhaustive diagnostic characters. The anterior leg erected as a lectotype has been not collected in articulation and, except for the radius and humerus (but with some doubts), the bones reported by Croizet and Jobert (1828) cannot be confidently interpreted as belonging to the same individual (necessary to be included together as holotype/lectotype). The humerus and radius, which possibly constitute the articulated partial leg, are poorly preserved and do not display diagnostic characters (as also reported by Ballatore and Breda, 2016). In summary, the type specimens on which *Rhinoceros elatus* was established by Croizet and Jobert (1828) cannot be distinguished from other Pliocene and early Pleistocene taxa, and the lectotype erected by Ballatore and Breda (2016) is not properly defined. The name *Rhinoceros elatus* is here regarded as a *nomen dubium* and therefore *S. jeanvireti* is retained in order to maintain nomenclatural stability; furthermore, *S. jeanvireti* is based on well-preserved material such as skull and mandible. Despite this, some remains recovered posteriorly to Croizet and Jobert's work from Les Étouaires do actually correspond to *S. jeanvireti*, as it is reflected in the synonymy list (see also Pandolfi et al., 2017).

Type material: skull and mandible (No. Vt 627) described and figured by Guérin (1972), stored at Natural History Museum Basel.

Type locality and horizon: Vialette (Haute-Loire, France), late Pliocene.

Diagnosis: see Guérin (1972, 1980) and Guérin and Tsoukala (2013).

Referred material: associated left calcaneus (OMNSC 44635) and left second (OMNSC 44640), third (OMNSC 44616), and fourth (OMNSC 44624) metatarsals, fitting together, evidencing that they belong to the same individual (Fig. S1).

Description and comparison: *Calcaneus (44635)*. In lateral view, the plantar border of the bone is rather straight, the beak protrudes a little bit beyond the tuber calcanei, the proximal profile shows a marked concavity, and the posterior part of the tuber calcanei is higher and more convex than the anterior part (Fig. 2A).

In plantar view, the sustentaculum talii is perpendicular to the main axis of the bone, forming a right angle with the corpus of the bone (Fig. 2B). The articular surface

Fig. 2. *Stephanorhinus jeanvireti* from Colțești, calcaneus: lateral view (**A**); plantar view (**B**); medial view (**C**); distal view (**D**). The scale bar equals 5 cm.
Fig. 2. *Stephanorhinus jeanvireti* de Colteşti, calcaneum : vue latérale (**A**) ; vue plantaire (**B**) ; vue médiale (**C**) ; vue distale (**D**). La barre d'échelle représente 5 cm.

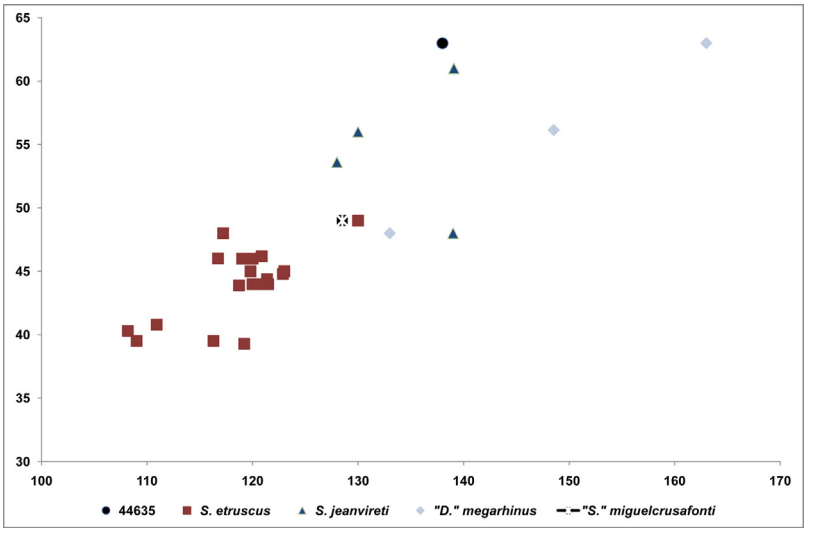

Fig. 3. Scatterplot of greatest length (GL) and greatest width of the tuber calcanei (GWt) of the calcaneus from Colțești, *S. etruscus*, *S. jeanvireti*, *'S.' miguelcrusafonti* and *'D.' megarhinus* (data from the Appendix 1).
Fig. 3. Nuage de points représentatifs de la plus grande longueur (GL) et de la plus grande largeur (GWt) du tubercule calcanéen du calcanéum de Colteşti, *S. etruscus*, *S. jeanvireti*, *'S.' miguelcrusafonti* et *'D.' megarhinus* (données de l'Annexe 1).

located on the sustentaculum talii is wide, but separated from the latero-proximal articular surface and connected with the distal articular surface for the astragalus (Fig. 2C). In distal view, the latero-proximal articular surface for the astragalus is relatively broad, proximo-distally convex in the proximal half and concave in the distal one (Fig. 2D). The distal border of this surface extends distally, joining the distal articular surface for the astragalus. The latter is elongated, relatively high and connected distally with the articular surface for the cuboid. The latter is subtrapezoidal in shape; it is latero-medially depressed, with a slightly convex posterior border. This surface extends proximally, almost reaching the sustentaculum talii, and it is well evident in plantar view.

The studied calcaneus is larger than those of *S. etruscus* (Appendix 1; Fig. 3); in this species, the tuber calcanei protrudes well over the beak, the posterior border of the bone is slightly concave, and the sustentaculum talii shows an obtuse angle with the corpus of the bone. The calcaneus of *'S.' miguelcrusafonti* differs from 44635 by being less massive and smaller and by having a concave posterior profile of the bone. The calcanei of *S. jeanvireti* and *'D.' megarhinus* are rather similar in morphology, with a wide overlapping in size (Fig. 3). The main diagnostic feature in the calcaneus seems to be the development of the sustentaculum talii; *S. jeanvireti* is characterized by a long sustentaculum talii with a medial border wider than in *'D.' megarhinus*. This feature is evident in the calcaneus 44635. In plantar view, in *S. jeanvireti* and in the studied specimen, the lateral border is slightly concave, while in *'D.' megarhinus* it is irregular.

MTII (44640). The bone is rather slender (Fig. 4A). In proximal view, the articular surface is damaged on its dorso-medial side, but it seems rather elliptical, with a concave lateral border. The proximal epiphysis is more developed dorso-plantarly than the proximal articular surface (Fig. 5C). In lateral view, two articular surfaces are present (Fig. 4B): the dorsal one is elliptical and

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Fig. 4. *Stephanorhinus jeanvireti* from Colțești, MTII: dorsal view (**A**); lateral view (**B**); plantar view (**C**); medial view (**D**). The scale bar equals 5 cm.
Fig. 4. *Stephanorhinus jeanvireti* de Colteşti, MT II : vue dorsale (**A**) ; vue latérale (**B**) ; vue plantaire (**C**) ; vue médiale (**D**). La barre d'échelle représente 5 cm.

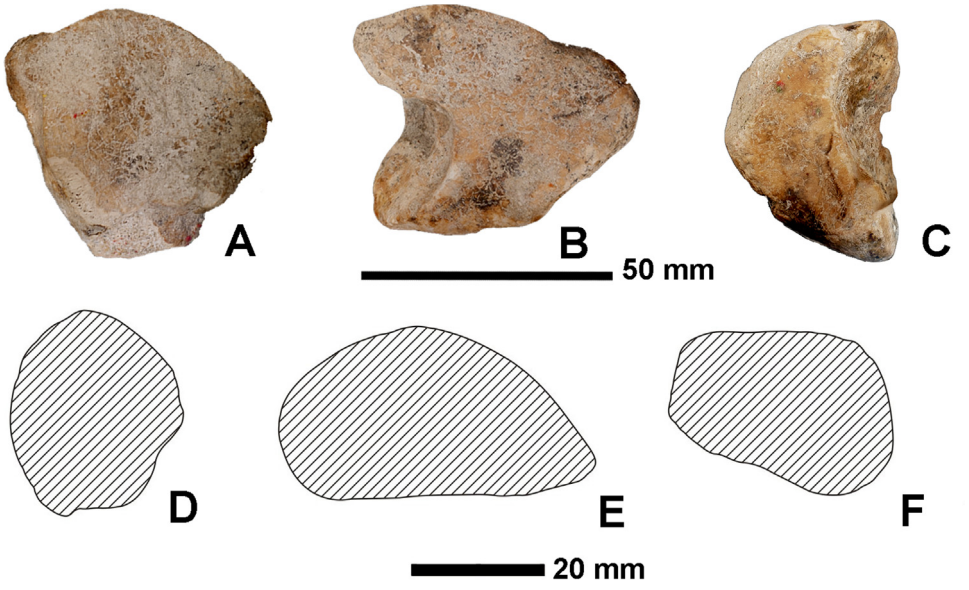

Fig. 5. *Stephanorhinus jeanvireti* from Colțești, proximal articular surface of metatarsals in proximal view (A-C) and cross section of metatarsal diaphyses (**D-F**): MTII (**A**); MTIII (**B,E**); MTIV (**C,F**).
Fig. 5. *Stephanorhinus jeanvireti* de Colteşti, vues proximale de métatarse (**A-B**) et section transversale de diaphyses de métatarse (**D-F**) : MTII (**A**) ; MTIII (**B**) ; MTIV (**C**).

proximo-distally elongated, whereas the plantar one (poorly preserved) is sub-trapezoidal, but higher than the dorsal one. In posterior view (Fig. 4C), a poorly preserved articular surface for the first cuneiform is present. The section of the diaphysis is rather rounded with a marked and wide posterior carena (Figs. 4C–D and 5F).

The bone is larger than the MTIIs of *S. etruscus* and *'S.' miguelcrusafonti*. The specimen differs from *'D.*

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Fig. 6. *Stephanorhinus jeanvireti* from Colţeşti, MTIII: dorsal view (**A**); lateral view (**B**); plantar view (**C**); medial view (**D**). The scale bar equals 5 cm.
Fig. 6. *Stephanorhinus jeanvireti* de Colteşti, MTIII : vue dorsale (**A**) ; vue latérale (**B**) ; vue plantaire (**C**) ; vue médiale (**D**). La barre d'échelle représente 5 cm.

' megarhinus, in which the proximal articular surface reaches the dorsal border of the proximal epiphysis and the latter is not much higher than the plantar border. In *'D.' megarhinus*, the section of the diaphysis is more irregular than that of the studied specimen. The morphology of the MT 44640 resembles in its features the MTIIs of *S. jeanvireti* (Guérin, 1972: fig. 18; Guérin, 1980: fig. 80).

MTIII (44616). In anterior view, the medial and lateral borders of the diaphysis are rather straight (Fig. 6A). In proximal view, the MTIII displays a rather convex anterior border of the proximal epiphysis; the plantar articular surface for the MTIV is partially visible (Fig. 5B). In lateral view (Fig. 6B), the dorsal articular surface for MTII is partially preserved and it seems to be trapezoidal, whereas the plantar articular surface for MTII is elliptical. These two surfaces are rather similar in size and are separated by a wide groove. In plantar view, the diaphysis is rather flat (Fig. 6C), the plantar tuberosity is well evident. In medial view (Fig. 6D), the proximal epiphysis is poorly preserved, but traces of two small articular surfaces are present, with the dorsal one larger than the plantar one. In this view, the plantar tuberosity is evident, but it is not much developed. The section of the diaphysis is sub-triangular with rounded angles, a rather flat plantar border and a medial border much narrower than the lateral one (Fig. 5E).

The proximal epiphysis in 44616 is longer than wide, contrary to the case of *'D.' megarhinus*, and similarly to *S. jeanvireti*. The anterior border of the proximal epiphysis in 44616 displays a little concavity in the medial side, but this feature is less marked than in *'D.' megarhinus* (even though some specimens display a little concavity in the middle of the anterior border, e.g., NMB Mp59) and it is usually absent in *S. jeanvireti*. Contrary to the studied specimen, the dorsal articular surface for MTIV is wider than in *'D.' megarhinus*. The section of the diaphysis in *'D.' megarhinus* is medio-laterally longer and dorso-plantarly narrower than that of the studied specimen and *S. jeanvireti*; in addition, the plantar border in *'D.' megarhinus* is usually concave or slightly concave. The studied bone is longer than *S. etruscus* and *'S.' miguelcrusafonti* (Fig. 7).

MTIV (44624). In anterior view, the two proximo-medial articular surfaces are partially evident (Fig. 8A). In lateral view, the proximal tuberosity is little developed (Fig. 8B). In proximal view, the articular surface is pentagonal, with relatively marked angles. The surface is concave medio-laterally. Its dorso-plantar length is similar to its medio-lateral one. The plantar border of the proximal articular surface is rather sinuous and the proximal epiphysis is a little more plantarly developed than the articular surface. In proximal view, the medial tuberosity, on which the plantar articular surface for MTIII is located, is well developed and much more medially projected than the proximal articular surface (Fig. 5A). In posterior view (Fig. 8C), the articular surface projects proximally over the rest of the proximal epiphysis. On the medial side of the bone (Fig. 8D), two articular surfaces for the MTIII are present. The dorsal one is poorly preserved, but seems to be less developed than the posterior one, which is rather elliptical. The section of the diaphysis is sub-rectangular in shape, with rounded angles and the medial border shorter than the lateral one (Fig. 5D).

The proximal articular surface is more irregular in shape and medio-distally longer in *'D.' megarhinus* than in 44624 and *S. jeanvireti*. The section of the diaphysis is much more rounded in *'D.' megarhinus* than in *S. jeanvireti*

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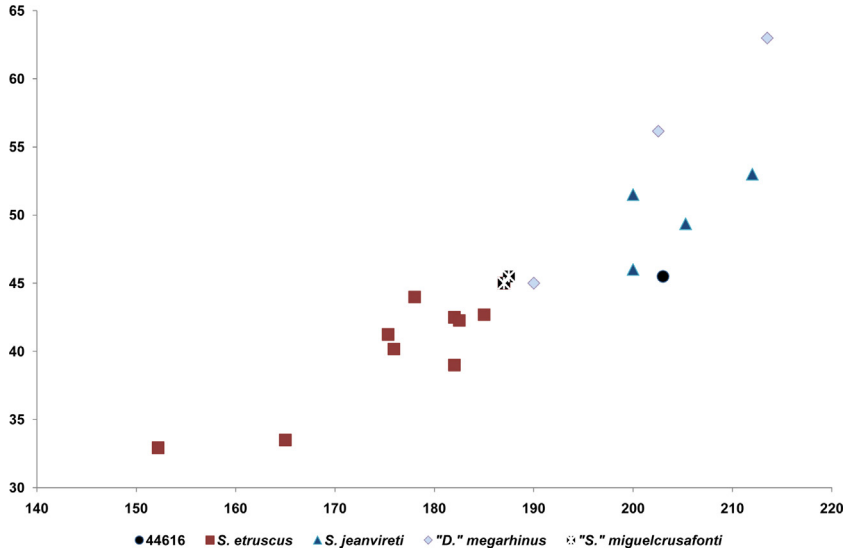

Fig. 7. Scatterplot of greatest length (GL) and width of the diaphysis (WD) of the MTIII from Colțești, *S. etruscus*, *S. jeanvireti*, *'S.' miguelcrusafonti* and *'D.' megarhinus* (data from Appendix 1).
Fig. 7. Nuage de points représentatifs de la plus grande longueur (GL) et de la largeur (WD) de la diaphyse du MTIII de Colteşti. *S. etruscus*, *S. jeanvireti*, *'S.' miguelcrusafonti* et *'D' megarhinus* (données de l'Annexe 1).

Fig. 8. *Stephanorhinus jeanvireti* from Colțești, MTIV: dorsal view (**A**); lateral view (**B**); plantar view (**C**); medial view (**D**). The scale bar equals 5 cm.
Fig. 8. *Stephanorhinus jeanvireti* de Colteşti, MTIV : vue dorsale (**A**) ; vue latérale (**B**) ; vue plantaire (**C**) ; vue médiale (**D**). La barre d'échelle représente 5 cm.

and the studied specimen. The MTIV 44624 is longer than in *S. etruscus* and *'S.' miguelcrusafonti*.

5. Discussion

Stephanorhinus jeanvireti seems to be a relatively rare taxon with respect to other European Plio-Pleistocene rhinoceroses (except for *'S.' miguelcrusafonti*). The species was defined at Vialette (ca 3 Ma, MNQ16a), in France, but also recorded at Perrier–Les Étouaires (ca 2.78 Ma, MNQ16b; Pandolfi et al., 2017), Vincent and Desnes (both MNQ16) (Guérin, 1972, 1980). *Stephanorhinus jeanvireti* was reported in only one locality in Spain, Camp dels Ninots, with an age around 3.2 Ma (MNQ15-MNQ16 transition, Soler et al., 2012; Fig. 9). In Italy, it was recorded in several localities (MNQ16 or generally referred as

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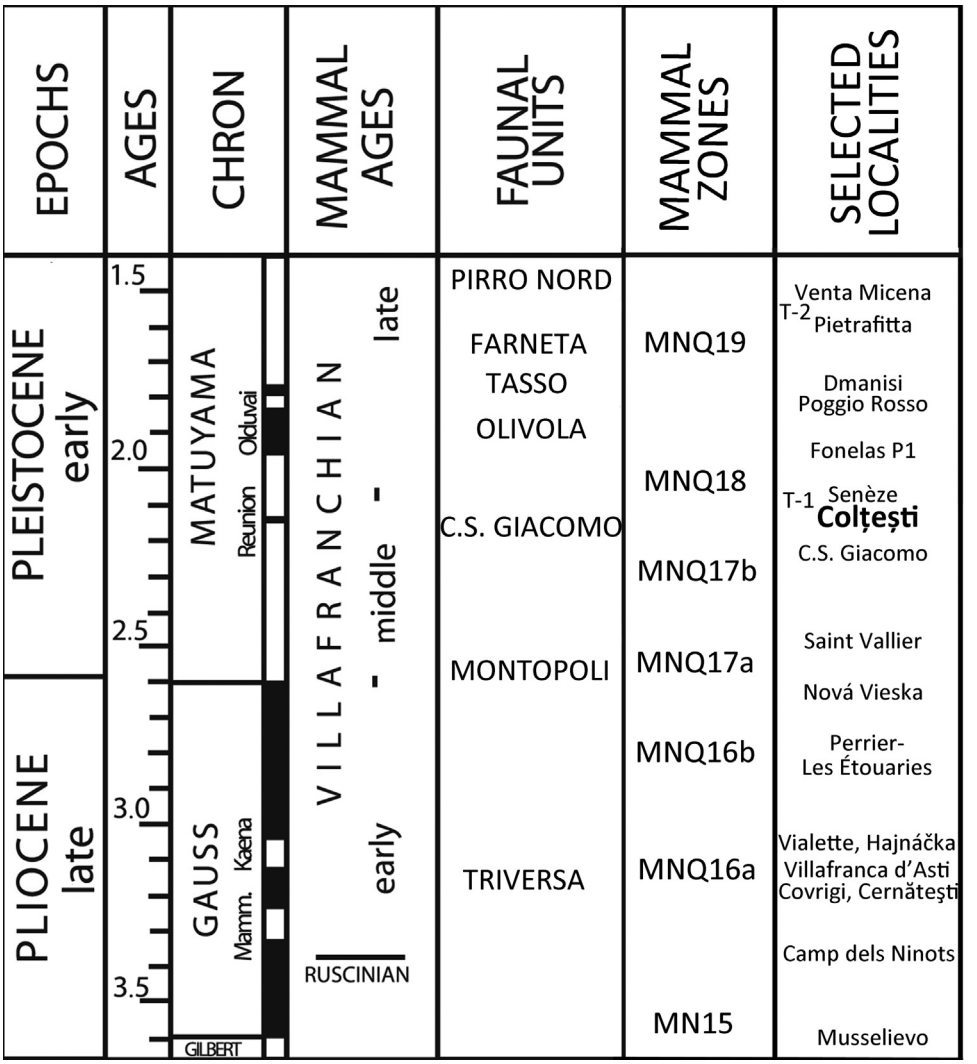

Fig. 9. Biochronological occurrence of *Stephanorhinus jeanvireti* from Colțești and chronological position of selected European localities (see text for details on localities and ages). Scheme modified from Rook et al. (2017). T-1 and T-2 refer to the first two T-faunal horizons reported by Andreescu et al. (2013).
Fig. 9. Distribution biochronologique de *Stephanorhinus jeanvireti* de Colțești et position chronologique de localités européennes sélectionnées (voir le texte pour les localités et les âges). Schéma de Rook et al. (2017) modifié. T-1 et T-2 se réfèrent aux deux premiers horizons fauniques rapportés par Andreescu et al. (2013).

Pliocene), in particular from the northern area: in Piedmont (Dusino, Villafranca d'Asti, Roatto), Emilia-Romagna (Monte Pulgnasco, Pradalbino, Monte Pastore, Monte San Pietro), and Tuscany (Montopoli, Capannoli) (Simonelli, 1897; Guérin, 1980; Pandolfi, 2013 and references therein). In Germany, *S. jeanvireti* was recorded in the Hambach lignite mine (MNQ16) (Lacombat and Mörs, 2008) and scanty material from the Netherlands was doubtfully referred to this species (De Vos et al., 1998; Hooijer, 1981, 1985; Scager et al., 2017); our revision confirms that the tooth remains are too fragmentary for a confident determination. In Slovakia, *S. jeanvireti* was documented at least at Hajnáčka (MNQ16a), Nová Vieska (MNQ16b or 17a), and Strekov (MNQ16a) (Ďurišová, 2004; Šujan et al., 2013; Vlačiky et al., 2008; Pandolfi, pers. observ. at NHMW; Fig. 9), and in Bulgaria it was recorded at Musselievo (second half of MNQ15; Spassov, 2005). In Hungary, *S. jeanvireti* was present at Rákoscsaba (early Villafranchian), where it is documented by isolated teeth partially published by Pandolfi et al. (2015a) and by an unpublished mandible. In Russia, *S.* ex gr. *jeanvireti* was mentioned in the Khapry faunal complex from the Sea Azov Region by Bajgusheva et al. (2001), but this record has been reported as *Stephanorhinus* sp. or *S.* ex gr. *megarhinus-kirchbergensis* by Titov (2008). Recently, *S. jeanvireti* was reported in Greece at Milia (MNQ16; Guérin and Tsoukala, 2013). According to Lacombat and Mörs (2008), the species could be present at Kvabebi (Georgia), Udunga and Nizhnavodyanoy (Russia). The material from Georgia represents a large and massive rhinoceros and it is at present under review by one of us (LP). The rhinoceros from Udunga has been referred by Fukuchi et al. (2009) as *S. megarhinus* (*recte* '*D.*' *megarhinus*, Pandolfi et al.,

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2015a, 2016), whereas the material from the Azov Region (Alekseeva, 1977; Bajgusheva et al., 2001) should be deeply revised.

In Romania, Rădulescu and Samson (1985 and references therein), Codrea (2000) and Rădulescu et al. (2003) reported *S. jeanvireti* (= *Dicerorhinus elatus* in Rădulescu and Samson, 1995 or *Stephanorhinus elatus* in Rădulescu and Samson, 2001) in the Covrigi fauna (MNQ16a), Cernăteşti (MNQ16a), Iarăş 2 and Araci–Fântâna Fagului (early Gauss, MNQ16), Cernatu (early–middle Villafranchian) and *S.* cf. *S. jeanvireti* at Ilieni "Basin" (in fact, a sub-basin of the Bârsei Basin; early Villafranchian, MNQ16a). Most of the rhinoceros remains collected from these localities are represented by fragmentary and isolated bones.

Apart from the rhinoceros, the faunal assemblage recovered from Colţeşti includes *Ursus etruscus* (Stiucă et al., 2000), *Pliotragus ardeus*, *Allohippus* cf. *athanasiui* (= *E. stenonis* or *E. sussenbornensis*) and *Eucladoceros* sp. (Costin Rădulescu, *personal communication* to one of us, AP), and it is correlated with the faunal assemblage of the T-1 faunal complex (Andreescu et al., 2011: fig. 4; Andreescu et al., 2013: fig. 4 and references therein), corresponding to the final part of MNQ17 or the first half of MNQ18. Thus, the Colţeşti record represents the youngest occurrence of *S. jeanvireti* in Eurasia.

Stephanorhinus jeanvireti is usually associated with *Anancus arvernensis* and *Tapirus arvernensis*, in a woodland environment with humid climate (Guérin, 1980; Szabó et al., 2017), related to MNQ16 localities (Fig. 9). At Colţeşti, the presence of *Pliotragus* and an equid would be indicative of a savannah with small forested interleaved areas, whereas *Ursus etruscus* could indicate the proximity of higher altitudes.

According to Heissig (1996), *S. jeanvireti* derived from *'D.' megarhinus* and replaced it during the late Pliocene. The two species have been never recorded from coeval localities. The cluster analysis (UPGMA) performed by Pandolfi and Maiorino (2016: fig. 9) placed the cranial shape of *S. jeanvireti* in an intermediate stage between *'D.' megarhinus* and *S. kirchbergensis*, whereas the upper-tooth row shape clustered together with that of *'D.' megarhinus* (Pandolfi and Maiorino, 2016: fig. 9B), with *D. sumatrensis* as their closest relative. The presence of vestigial incisors, which was considered as a distinctive character between *'D.' megarhinus* and *S. jeanvireti*, has been recently verified also on the latter species (Guérin and Tsoukala, 2013). Guérin (1980) suggested an Asian origin of *S. jeanvireti*, but Pliocene records of South-East Asia and East Asia are at present not exhaustive enough to support this hypothesis.

6. Conclusion

The study of the rhinoceros material collected from the locality of Colţeşti represents a contribution towards a revision of the mammal faunas from Romania.

The morphological comparison revealed that the studied specimens can be assigned to *S. jeanvireti*. The western limit of the geographic distribution of this species is at present located at the northeasternmost part of the Iberian Peninsula (Camp dels Ninots, Girona) whereas the Romanian findings represent the eastern limit. The biochronological distribution of *S. jeanvireti* is mainly confined to the MNQ16 (early and early middle Villafranchian; Rook and Martínez-Navarro, 2010), and its first occurrence is doubtfully reported in late MNQ15 faunas (Spassov, 2005). The record of Colţeşti (MNQ17/MNQ18) represents, at present, the last occurrence of this taxon in Eurasia (Fig. 9). A better understanding of late Pliocene and earliest Pleistocene western Asian and eastern European Rhinocerotidae (including the revision of the Balkan and Caucasian material) could deeply contribute to the investigation of the origin and phyletic affinities of *S. jeanvireti*, as well as of the temporal and spatial distribution of fossil rhinoceroses.

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Appendix 1. Comparative tables of the rhinoceros material from Colţeşti (southwestern Romania)

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Calcaneum	Locality	Museum	Specimen	Reference	Range value	Greatest length	Minimum posterior transversal diameter	Greatest width of the tuber	*Greatest breadth at sustentaculum tali*
	Colţeşti	OMNSC	44635	This paper		138	40.2	63	86.5
S. etruscus	Pietrafitta	MPLBP		Pandolfi et al., 2017		116.72	38.27	46.02	73.24
S. etruscus	Pietrafitta	MPLBP		Pandolfi et al., 2017		110.9	36.1	40.81	69.38
S. etruscus	Valdarno	NMB		Pandolfi et al., 2017		119.2	25.4	39.3	61.9
S. etruscus	Valdarno	MNCN		Pandolfi et al., 2017		116.28	27.6	39.5	60
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		121.47	31.31	44	
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017			32.71	45.9	63
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		108.17	32.28	40.3	69.9
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		122.86	35.13	44.8	66.08
S. etruscus	Olivola Val di Magra	IGF		Pandolfi et al., 2017		120	30	44	
S. etruscus	Olivola Val di Magra	IGF		Pandolfi et al., 2017			31	41	74.8
S. etruscus	Olivola Val di Magra	IGF		Pandolfi et al., 2017		120	31.3	46	68
S. etruscus	Capitone	MPUR		Pandolfi et al., 2017		119.8	34.5	45	72
S. etruscus	Capitone	MPUR		Pandolfi et al., 2017		119	37	46	73
S. etruscus	Venta Micena			Santafè-Llopis and Casanovas-Cladellas, 1987				45	
S. etruscus	El Rincon	MNCN		Pandolfi et al., 2017		122.62	33.5		76.19
S. etruscus	Les Etouaries	NMB		Pandolfi et al., 2017		121.7	35.6		75.2
S. etruscus	Les Etouaries	NMB		Pandolfi et al., 2017				39.2	
S. etruscus	Les Etouaries	NMB		Pandolfi et al., 2017		117.2	35.4	48	74.7
S. etruscus	Senèze			Lacombat, 2005		121.36	37.65	44.38	72.77
S. etruscus	Senèze			Lacombat, 2005		120.87	39.16	46.19	73.11
S. etruscus	Saint Vallier			Guérin, 2004		120.5	34.5	44	75.5
S. etruscus	Saint Vallier			Guérin, 2004		123	33	45	72
S. etruscus				Guérin, 1980	Min	109	31	39.5	60
S. etruscus				Guérin, 1980	Med	118.72	34.98	43.89	67.61
S. etruscus				Guérin, 1980	Max	130	39	49	75
S. jeanvireti	Milia			Guérin and Tsoukala, 2013		139	43	56	80
S. jeanvireti				Guérin, 1980	Min	128	35	48	75
S. jeanvireti				Guérin, 1980	Med	139.08	38.15	53.61	81.36
S. jeanvireti				Guérin, 1980	Max	149.5	43.5	61	89
"D." megarhinus				Guérin, 1980	Min	133	38.5	48	72
"D." megarhinus				Guérin, 1980	Med	148.54	43.72	56.14	84.4
"D." megarhinus				Guérin, 1980	Max	163	51	63	98
"S." miguelcrusafonti				Guérin, 1980		128.5		49	

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MTII	Locality	Museum	Specimen	Reference	Range value	Length	Breadth of the proximal epiphysis	Depth of the proximal epiphysis	Breadth of the shaft	Depth of the shaft	Breadth of the distal epiphysis	Breadth of the distal articular surface	Depth of the distal epiphysis
	Colțești	OMNSC	44640	This paper		187	33	45.3	26	23.5	42	34.3	41
S. etruscus	Montopoli	IGF		Pandolfi et al., 2017			27.9	35.85	26	21.1			
S. etruscus	Valdarno	NMB		Pandolfi et al., 2017		193.8			33.1	17.4	48.1	37	33.1
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017					29.3		37.1	30.7	
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017					27		39	30.5	
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017					27.19	24.35	37.71	30.25	36.35
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		145.71	29.74	36.15	24.42	20.85	33.67	26.12	32.66
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		148	28.9		23.3	23.51	36.04	29.87	35.17
S. etruscus	Capitone	MPUR		Pandolfi et al., 2017		156	27	40	22.5	23.5	34.7		34
S. etruscus	La Puebla de Valverde	MNCN		Pandolfi et al., 2017			25	41					
S. etruscus	La Puebla de Valverde			Guérin and Heintz, 1971			25	42					
S. etruscus	Saint Vallier	NMB		Pandolfi et al., 2017			28.08	39.44	22.78	24.97			
S. etruscus				Guérin, 1980	Min	145	21	32.5	22.5	21	34	31	32
S. etruscus				Guérin, 1980	Med	155.41	27.1	37.9	25.91	24.38	37.1	32.87	35.15
S. etruscus				Guérin, 1980	Max	162	31	42	29	27.5	41	35	39
S. jeanvireti				Guérin, 1980	Min	179	30	45	22	23	39	36	41
S. jeanvireti				Guérin, 1980	Med	182.43	35.12	46.21	30	28.81	43.07	38.72	43.44
S. jeanvireti				Guérin, 1980	Max	189	40	50	33	34	46	40	47
"D." megarhinus				Guérin, 1980	Min	174.5	31.5	41	27	24	43	36.5	37
"D." megarhinus				Guérin, 1980	Med	182.92	35.66	47.56	33.93	26.56	46.92	40.71	42.64
"D." megarhinus				Guérin, 1980	Max	191	42.5	53	38.5	33	52.5	45	46
"D." megarhinus	Çalta			Guérin and Sen, 1998		175.5	ca 43	ca 32	29	29.5	37.5	33	38.5
"S." miguelcrusafonti				Guérin and Santafé-Llopis, 1978		162	34.5	39	29.5	28.5	37	33	38.5
"S." miguelcrusafonti				Guérin and Santafé-Llopis, 1978		158.5	26.5	37.5					

MTIII	Locality	Museum	Specimen	Reference	Range value	Length	Breadth of the proximal epiphysis	Depth of the proximal epiphysis	Breadth of the shaft	Depth of the shaft	Breadth of the distal epiphysis	Breadth of the distal articular surface	Depth of the distal epiphysis
	Colţeşti	OMNSC	44616	This paper		203	55.6	47	45.5	24.3	61.4	46.7	40
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		182	51.5		42.5		55	42.9	
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		185	51.8		42.7		53	43.1	
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		182.5	47.96	44.02	42.28	23.11	53.77	41.3	37.57
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		175.34	49.83	39.37	41.24	21.36	53.51	41.1	37.31
S. etruscus	Capitone	MPUR		Pandolfi et al., 2017		182	47.5		39	25	51.75	45	
S. etruscus	Villanueva de Pitamo	MNCN		Pandolfi et al., 2017		152.18	40.36		32.92	16.68	41.01	36.66	27.71
S. etruscus	La Puebla de Valverde			Guérin and Heintz, 1971			51	46					
S. etruscus	La Puebla de Valverde			Guérin and Heintz, 1971					39	24	49	40	32
S. etruscus	Saint Vallier	NMB		Pandolfi et al., 2017			46.36	35.16					
S. etruscus	Saint Vallier	NMB		Pandolfi et al., 2017			49.11	40.46	40.3	22.8			
S. etruscus	Saint Vallier	NMB		Pandolfi et al., 2017			44.75	40.12					
S. etruscus	Várhegy	HNHM		Pandolfi et al., 2017		178			44	25	52	45.5	39
S. etruscus				Guérin, 1980	Min	165	43	38	33.5	21.5	48	39	32
S. etruscus				Guérin, 1980	Med	175.92	48.54	41.86	40.18	22.9	52.13	42.28	36.86
S. etruscus				Guérin, 1980	Max	187	56	47	45	25	59	46	40
S. jeanvireti	Milia			Guérin and Tsoukala, 2013		200	58	48	51.5	27	59.5	50	46
S. jeanvireti	Milia			Guérin and Tsoukala, 2013			57.5						
S. jeanvireti				Guérin, 1980	Min	200	53	44	46	21	58	45	40
S. jeanvireti				Guérin, 1980	Med	205.29	57	47.83	49.36	24.06	61.83	50.17	43.44
S. jeanvireti				Guérin, 1980	Max	212	60.5	52	53	25	65.5	54	45
"D." megarhinus				Guérin, 1980	Min	190	53	42.5	45	22	57	46.5	37.5
"D." megarhinus				Guérin, 1980	Med	202.53	60.03	47.93	56.16	25.55	65.47	53.26	43.92
"D." megarhinus				Guérin, 1980	Max	213.5	65	55	63	34	72	59	48
"S." miguelcrusafonti	Layna			Guérin and Santafé-Llopis, 1978		186	52	41			60	47.5	38.5
"S." miguelcrusafonti	Layna			Guérin and Santafé-Llopis, 1978		187.5	51.5		45.5	25	58.5	47	40
"S " miguelcrusafonti	Layna			Guérin and Santafé-Llopis, 1978		187	52	40.5	45	24.5	56	45	38

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MTIV	Locality	Museum	Specimen	Reference	Range value	Length	Breadth of the proximal epiphysis	Depth of the proximal epiphysis	Breadth of the shaft	Depth of the shaft	Breadth of the distal epiphysis	Breadth of the distal articular surface	Depth of the distal epiphysis
	Colțești	OMNSC	44624	This paper		176.5	49	44.5	32	21.3	37.5	36	42
S. etruscus	Capitone	MPUR		Pandolfi et al., 2017		145	37	34.5	23	24	34.5		37.5
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		155			32		37.5	29	
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		154					37		
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017		156.07	38.61	35.1	25.44	22.42	36.53	30.06	36.04
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017			38.77	35.18	29.24	19.5			
S. etruscus	Valdarno	IGF		Pandolfi et al., 2017			41.33	35.9					
S. etruscus	El Rincon	MNCN		Pandolfi et al., 2017			41.84	36.1	32.07	24.03			
S. etruscus	La Puebla de Valverde	MNCN		Pandolfi et al., 2017			42.44	35.01					
S. etruscus	La Puebla de Valverde			Guérin and Heintz, 1971		153	40	35	24	25			
S. etruscus	Saint Vallier	NMB		Pandolfi et al., 2017			40.45	32.76					
S. etruscus	Saint Vallier	NMB		Pandolfi et al., 2017			38.96	33.8					
S. etruscus	Senèze	NMB		Pandolfi et al., 2017		165.6			33.3	19.9	40.8	37.9	
S. etruscus	Senèze			Lacombat, 2005		151	40.92	35.37	28.3	23.34	32.34	30.2	35.37
S. etruscus				Guérin, 1980	Min	146	30	33	22	20	29	28.5	33
S. etruscus				Guérin, 1980	Med	153.69	37.58	36.32	26.25	24.03	33.32	32.1	35.93
S. etruscus				Guérin, 1980	Max	163	42	41	31	28	41.5	35	39
S. jeanvireti	Milia			Guérin and Tsoukala, 2013		178.5	56	51.5	36.5	35.5	43	43	45
S. jeanvireti	Hajnacka I			Durisova, 2004		188	49	44.2	34	27	40	38.5	40.5
S. jeanvireti	Hajnacka I			Durisova, 2004		186	50	44	37	32	46	43	43
S. jeanvireti				Guérin, 1980	Min	168	44	40.5	31	23	40	37	41
S. jeanvireti				Guérin, 1980	Med	180.43	49	44.15	35	28.56	41.6	39.86	45
S. jeanvireti				Guérin, 1980	Max	188.5	52	49	38	36	44	45	49.5
"D." megarhinus				Guérin, 1980	Min	164	42	38	32	22	39	35.5	40.5
"D." megarhinus				Guérin, 1980	Med	176.19	49.65	47.55	34.29	31.08	40.22	38.72	44.81
"D." megarhinus				Guérin, 1980	Max	182	55	53.5	37	35	42	42	47
"S." miguelcrusafonti	Layna	MNCN		This work		156.5	37	35	29	29.5	35	33.5	34.5
"S." miguelcrusafonti	Layna	MNCN		This work			38.5						

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.crpv.2019.07.004.

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