



Morphological and morphometric variability in Quaternary rhinoceroses as revealed by a small-sized adult *Stephanorhinus etruscus* skeleton from Poggio Rosso in Upper Valdarno (Early Pleistocene, Italy)

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ABSTRACT

A nearly complete skeleton of *Stephanorhinus etruscus* from the Upper Valdarno Basin (Italy) provides a rare opportunity to investigate the morphological and morphometric variability of Early Pleistocene rhinoceroses. The specimen, IGF8212V, is here described and compared with *S. etruscus*, *S. hundsheimensis*, and *S. jeanvireti* from several European localities. A detailed analysis of the postcranial remains shows that several characters previously proposed as diagnostic among these species are more variable than traditionally assumed. Because IGF8212V preserves cranial, dental and postcranial elements belonging to a single adult individual, it provides a rare test case for evaluating the reliability of isolated postcranial characters. The skeleton shows features consistent with an assignment to *S. etruscus*, but also displays some features previously regarded as typical of *S. hundsheimensis* or *S. jeanvireti*. These characters do not form a coherent diagnostic association with either of these taxa, suggesting that part of the morphological overlap among Early Pleistocene *Stephanorhinus* species reflects intraspecific variability. The hypothesized size-reduction trend in western European *S. etruscus* is not supported by the data considered here. Instead, the observed variability may reflect a combination of sexual dimorphism, ontogeny, geographic variability and possibly local ecological factors.

1. Introduction

Rhinoceroses, once widespread across Eurasia and Africa during the Quaternary period, have nowadays retreated to limited regions of the Old World. These large mammals were a common sight during both glacial and interglacial periods, playing a significant role in ancient ecosystems. Since the mid-19th century, the Eurasian species belonging to this group of mammals have been the subject of numerous papers and revisions, with the monumental works by Cuvier (1822), Falconer (1868), Osborn (1900) and other eminent palaeontologists. Despite this long history of research, chronological distribution and occurrences of the Quaternary Eurasian species are still a matter of debate. This is largely related to the fragmentary, isolated and poorly identifiable nature of fossil specimens and with the minor morphological and morphometric differences in closely related taxa, such as the species belonging to the genus *Stephanorhinus* (Guérin, 1980; Fortelius et al., 1993; Lacombe, 2005; van der Made, 2010; Pandolfi et al., 2017, 2021; Chitoglou et al., 2025). Furthermore, the scarcity of complete

skeletons, especially those preserving both cranial and postcranial elements, limits comprehensive studies of morphological variation and the correlation between cranial and postcranial features, thus leading to misidentification of isolated and/or fragmented specimens. The taxonomic identification of Early Pleistocene rhinoceroses is particularly problematic when based on isolated postcranial remains, because many of the characters traditionally used to distinguish *S. etruscus*, *S. hundsheimensis* and *S. jeanvireti* are subtle, partly overlapping and potentially affected by individual, ontogenetic, sexual or geographic variability. Accordingly, associated skeletons are crucial for testing whether postcranial characters commonly regarded as diagnostic are actually consistent with the cranial and dental evidence of a single individual.

The Upper Valdarno Basin, the type locality of *Stephanorhinus etruscus*, yielded considerable amount of fossil rhinoceros remains for over a century (Falconer, 1868; Guérin, 1980; Fortelius et al., 1993; Pandolfi et al., 2017), but no previously reported specimen preserves the same degree of associated cranial and postcranial completeness as

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IGF8212V. The latter skeleton was discovered from a clay quarry at Poggio Rosso and represents one of the most complete *S. etruscus* skeletons ever found in western Europe. It enables new insights into the morphological and morphometric variability of fossil rhinoceroses, and it is relevant for reassessing the taxonomic significance of Early Pleistocene small-sized *Stephanorhinus* remains. This relevance is rooted in the long-standing taxonomic debate surrounding the *Stephanorhinus etruscus*-*S. hundsheimensis* group. The Etruscan rhinoceros was traditionally treated within *Dicerorhinus*, and Guérin (1980) distinguished the nominal Villafranchian subspecies *Dicerorhinus etruscus etruscus* from a more evolved post-Villafranchian form, *Dicerorhinus etruscus brachycephalus*. In this framework, *D. e. etruscus* was regarded as a small-to medium-sized rhinoceros with slender limb bones and elongated metapodials, whereas *D. e. brachycephalus* was considered a less gracile, early Middle Pleistocene derivative, differing mainly in proportions and minor anatomical features. Guérin (1980) also proposed evolutionary trends within *D. e. etruscus*, including changes in cranial proportions, gracilisation of the mandible, reduction in cheek-tooth size, and shortening or narrowing of several limb bones and metapodials. However, this model was later revised by Fortelius et al. (1993), who transferred most western European Plio-Pleistocene “dicerorhines” to *Stephanorhinus* and recognized *S. hundsheimensis* as a species distinct from *S. etruscus*. Furthermore, they applied the name *S. hundsheimensis* to most of the material formerly included within *D. e. brachycephalus*, while excluding the type specimen of *brachycephalus* from this concept because the Daxlanden skull was considered closer to *S. kirchbergensis*. Accordingly, part of the morphology previously interpreted as representing an evolved stage of *D. etruscus* was reassigned to a distinct species, *S. hundsheimensis*, whereas *S. etruscus* sensu stricto became more restricted to latest Pliocene and Early Pleistocene forms. The status of small latest Villafranchian and latest Early Pleistocene rhinoceroses further complicated this scenario. Mazza et al. (1993) interpreted the small rhinoceros from Pietrafitta (latest Early Pleistocene, Italy) as *S. cf. hundsheimensis* and suggested that similar small-sized forms from western Europe could represent intermediate populations between *S. etruscus* and *S. hundsheimensis*. Conversely, later reassessments emphasized that these small rhinoceroses may overlap morphologically and morphometrically with *S. etruscus*, and that *S. etruscus* and *S. hundsheimensis* may have partially overlapping chronological ranges (van der Made, 2010; Pandolfi and Petronio, 2011; Chitoglou et al., 2025). Therefore, once *D. e. brachycephalus* sensu Guérin is excluded from *S. etruscus*, the available evidence does not support a simple directional body-size trend within *S. etruscus* during the Early Pleistocene. Instead, the problem concerns the extent of intraspecific variability, the reliability of isolated postcranial characters, and the taxonomic meaning of small-sized *Stephanorhinus* remains. In this context, the associated skeleton from Poggio Rosso provides an important test case for assessing whether small size and selected postcranial traits can be accommodated within the variability of *S. etruscus*.

1.1. Geological and stratigraphical framework of the Poggio Rosso site in Upper Valdarno

The Pliocene and Pleistocene Upper Valdarno sedimentary succession represents the infilling of an intermontane basin of tectonic origin and comprises richly fossiliferous palustrine, lacustrine, and alluvial deposits formed under varying climatic and environmental conditions (Ghinassi and Sagri, 2013; Ghinassi et al., 2013, 2025). The Upper Valdarno is renowned for the occurrence of mammal fossil bones since Renaissance times, and Upper Valdarno fossil vertebrates from this basin have been observed, collected, discussed, and kept in different private collections of early naturalists. The rich Upper Valdarno collections are nowadays an invaluable archive of the palaeobiology, palaeoecology and biochronology of the basin and, even more important, they are a reference for Plio-Pleistocene western European large mammal chronology (Rook et al., 2013).

The stratigraphic scheme of Upper Valdarno has been revised and refined with the basin-fill partition into four Synthems based on the scheme adopted by the CARG project (Sagri et al., 2012; Ghinassi et al., 2025): Castelnovo dei Sabbioni (CSB), Montevarchi (VRC), Fosso Salceto (OLC) and Torrente Ciuffenna (UFF) Synthems, in turn subdivided into sedimentary units on the basis of their lithology and/or sedimentary facies (see Fig. 5 in Ghinassi et al., 2025).

The locality of Poggio Rosso, which had been known for having yielded fossil vertebrate remains since early 1960s, is situated in the North-East of the Upper Valdarno Basin, on the right bank of the Arno River, near the town of Matassino (Fig. 1). In this area widely crops out the Early Pleistocene Montevarchi Synthem (VRC), made up of a succession of 40–50 m of grey sandy-silty clays alternating with lenticular or tabular grey-yellow sands (Unit VRCd, or “Limi di Terranuova” Auctorum). These are overlapped by 15–20 m of grey-green clay laminated with clayey levels rich in organic matter, representing unit VRCE (“Argille del Torrente Ascione”, Auctorum). Unit VRCE is in turn covered by about 10 m of Unit VRCf made up of grey silty clays with lenses and levels of yellow-grey sands (“Limi and Sabbie del Torrente Oreno” Auctorum). The transition between the VRCE and VRCf is well-evident in the quarry front of the SOLAVA quarry (Mazzini et al., 2000), where the studied skeleton has been recovered. Magnetostratigraphic samplings carried out between 1995 and 1999 revealed that the sequence is characterized by a single palaeomagnetic signal attributable to the Olduvai Subchron. The Poggio Rosso sequence has been compared with the successions outcropping at Matassino and Poggio al Pero, where the historical skeleton of *S. etruscus* discovered by Nesti in 1811 was recovered, and calibrated against the Faella type section (Cioppi and Napoleone, 2001; Napoleone et al., 2003). The Olduvai Subchron is currently calibrated between ca. 1.934 and 1.775 Ma; therefore, the broader interval reported in Fig. 1 refers to the duration of the subchron, whereas the age of ca. 1.8 Ma indicated for Poggio Rosso reflects the local magnetostratigraphic correlation of the fossiliferous interval within the Upper Valdarno succession. This correlation allowed a high-resolution study of Milankovitch-scale cycles, suggesting that the succession exposed at Poggio Rosso represents an interval of approximately 70 kyr (Napoleone et al., 2003).

2. Material and methods

The study focuses on an almost complete rhinoceros skeleton (IGF8212V), recovered in August 1999 from a clay quarry owned by SOLAVA brick factory. This specimen is currently housed at the Museum of Natural History, Geology and Palaeontology Section, University of Florence (IGF). While the skull and mandible are significantly damaged, retaining only M2-M3 and the right m3, the postcranial skeleton is largely intact. Missing elements include the left scapula, left pyramidal, left trapezoid, both trapezii, the first right cuneiform, and several anterior and posterior phalanges. A detailed description of the studied anatomical elements is reported in Supplementary File 1.

The anatomical description and morphological comparisons follow those proposed by Guérin (1980), Antoine (2002), and Pandolfi (2023). The ontogenetic stage follows Groves (1967) and Pandolfi et al. (2025): 1, first permanent molar not visible; 2, first permanent molar erupting; no trace of a second molar; 3, second molar erupting; second and third premolars in process of replacement; 4, second molar in wear; fourth premolar in process of replacement; 5, third molar in evidence: all milk teeth replaced; 6, third molar fully erupted; 7, third molar in wear; 8, third molar in advanced wear.

The studied specimen was morphologically compared with individuals from various European localities belonging to *S. etruscus*, *S. jeanvireti* and *S. hundsheimensis* (Supplementary File 2). Direct comparisons were performed with *S. etruscus* housed at IGF (Olivola Val di Magra, Upper Valdarno, Pirro Nord, Montopoli), NMB (Senèze, Saint Vallier, Perrier-Etouaires, Upper Valdarno), MGPLBP (Pietrafitta), MPUR (Capitone, Pirro Nord) and MNCN (Huéscar, El Rincon, Upper

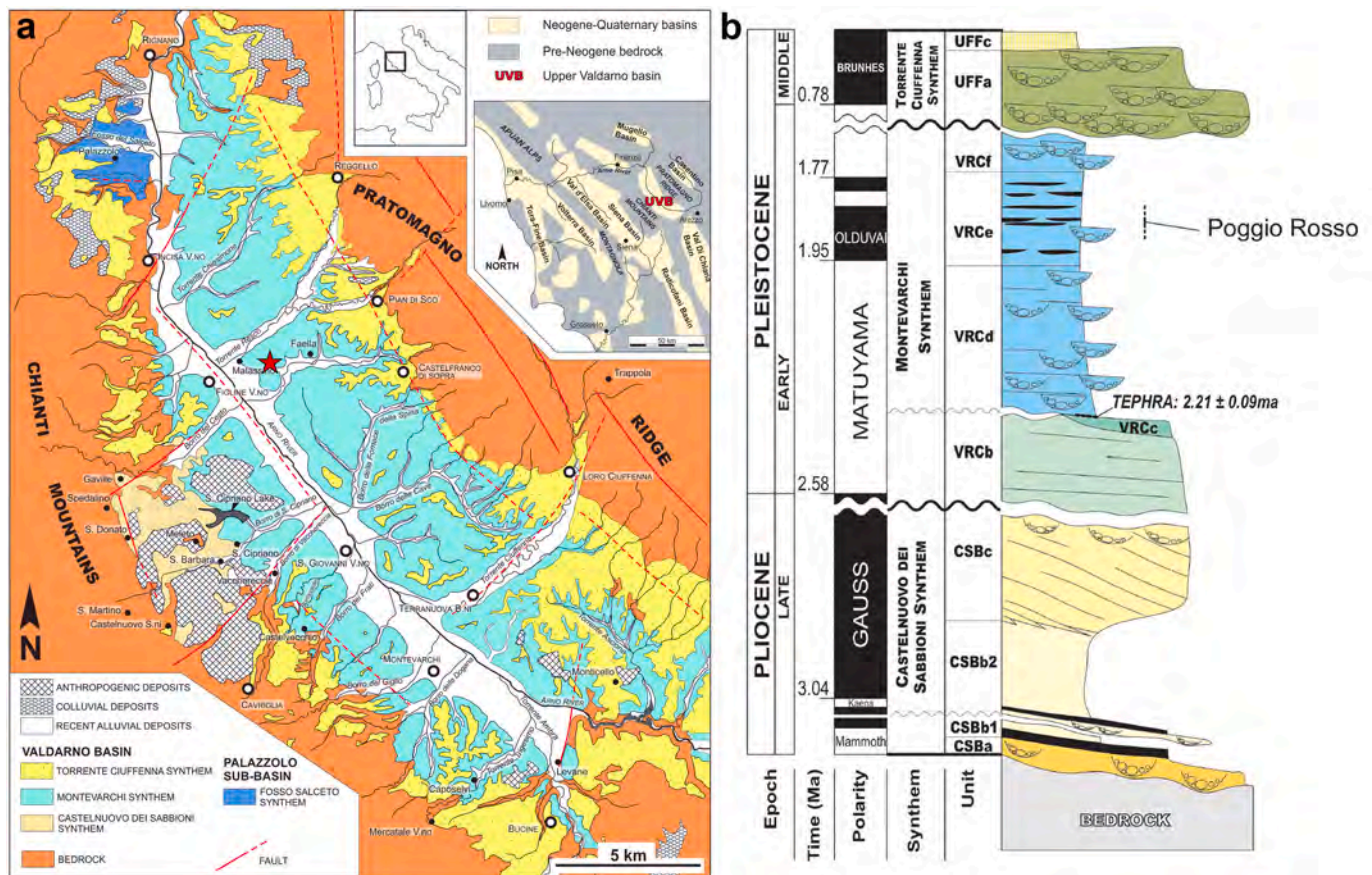


Fig. 1. Location of the Poggio Rosso site, Upper Valdarno Basin, Italy and stratigraphic position of the Poggio Rosso rhinoceros skeleton (modified from Ghinassi et al., 2013).

Valdarno, Villanueva de Pitamo), as well as based on published data (Guérin and Heintz, 1971; Guérin, 1972, 2004; Ruiz Bustos, 1976; Santafé-Llopis and Casanovas-Cladellas, 1987; Mazza, 1988; Lacomat, 2005; Pandolfi and Petronio, 2011; Pandolfi et al., 2017; Tsoukala, 2018; Stefanelli et al., 2025; Chitoglou et al., 2025). The specimens of *S. jeanvireti* considered in the comparative section are from Viallette, Villafranca d'Asti and Les Etouaires (NMB), Pradalbino and Monte Tiffi (MGCC), Hajnacka (NHMW), Montopoli (IGF), Colțești (Pandolfi et al., 2019) and Milia (Guérin and Tsoukala, 2013). The specimens of *S. hundsheimensis* considered in the comparative section are from Hundsheim (NHMW), Isernia La Pineta (MPI), Voigtstedt, Sussenborn (IQW), Mosbach (MfN, NHMUK, NMB), Soleilhac (NMB), Untermassfeld (Kahlke, 2001) and Vallonnet (Lacomat, 2005; Lacomat and Moullé, 2005). In addition, the postcranial characters traditionally used to distinguish *S. etruscus*, *S. hundsheimensis* and *S. jeanvireti* were assessed in light of the diagnostic features summarized in the literature, including the recent synthesis by Stefanelli et al. (2025), in order to evaluate their consistency within the associated skeleton IGF8212V.

Morphometric comparison follows the protocols reported by Guérin (1980), Lacomat (2005), van der Made (2010), Pandolfi et al. (2017, 2021), and is performed using the software R version 1.4.103 and RStudio (R Core Team, 2019). The hypsodonty index is calculated as the ratio of the crown height (H) to the maximal diameter (DTmax) of the tooth. Body mass was estimated using the postcranial regression equations proposed by Fortelius and Kappelman (1993) for Rhinocerotidae. These equations are based on log-transformed relationships between body mass and selected limb-bone measurements, including the humerus, radius, tibia and femur, and provide estimates in kilograms after back-transformation from log10 values. For each anatomical element, all available measurements suitable for the application of the

corresponding equations were used to calculate separate body-mass estimates; these values were then averaged to obtain a single element-specific estimate. For IGF8212V, final body-mass estimates (Table 1) were based on the radius and tibia, which preserve suitable dimensions for the application of the selected equations, and on humeral length. Femora were used only for the comparative sample because the femora of IGF8212V do not preserve the measurements required by the available formulas. The distal diameters of the humeri were excluded from the final estimate because they appear affected by diagenetic deformation. In particular, the distal humeral width produced an estimate exceeding 2000 kg, more than 1000 kg higher than all other estimates obtained for the same individual. The exclusion of this value is further supported by the relatively low coefficient of determination and high prediction error associated with some humeral regressions in Fortelius and Kappelman (1993).

The measurements of postcranial remains used for comparisons and analyses, and assigned to *Stephanorhinus etruscus*, *Stephanorhinus jeanvireti* and *Stephanorhinus hundsheimensis*, are provided in Supplementary File 2.

Anatomical abbreviations: DTD, distal transverse diameter; DAPD, distal antero-posterior diameter; HI, hypsodonty index; Hm, medial height of the astragalus; L, maximal length; M/m, upper/lower molars; MC, metacarpal; MT, metatarsal; TDmax, maximal transverse diameter of the astragalus; TDDmax, distal maximal diameter of the astragalus.

Institutional abbreviations: FSL, Faculté des Sciences et Technologies, Université Claude Bernard, Lyon 1, Lyon, France; HNHM, Hungarian Natural History Museum, Budapest, Hungary; IGF, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Università di Firenze, Florence, Italy; IQW, Institut für Quartärpaläontologie, Weimar, Germany; MCLP, Musée Crozatier, Le Puy-en-Velay, France; MfN,

Table 1

Statistical summary of the body mass estimates for the considered *Stephanorhinus etruscus* samples. BM, Body Mass; min, minimum; max, maximal; sd, standard deviation; cv, coefficient of variation.

Locality	N	min BM	max BM	mean BM	median BM	sd BM	cv %	note
Capitone	7	1121.	1234.	1181.	1186.	45.2	3.83	same individual
El Rincon	1	1490.	1490.	1490.	1490.	NA	NA	
La Puebla de Valverde	4	1040.	1192.	1114.	1111.	70.6	6.34	
Olivola Val di Magra	8	892.	1252.	1014.	966.	112.	11.1	
Pietrafitta	12	894.	1312.	1074.	1016.	130.	12.1	same individual
Pirro Nord	2	755.	942.	848.	848.	132.	15.6	
Poggio Rosso	5	904.	954.	930.	927.	18.6	2.00	
Saint Vallier	7	1032.	1276.	1140.	1108.	87.1	7.64	
Senéze	4	1089.	1243.	1168.	1169.	66.5	5.69	
Upper Valdarno	18	890.	1253.	1067.	1041.	108.	10.1	
Venta Micena	1	696.	696.	696.	696.	NA	NA	

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; MPI, Museo Paleontologico di Isernia La Pineta, Isernia, Italy; MPLBP, Museo Paleontologico "Luigi Boldrini" di Pietrafitta, Perugia, Italy; MPUR, Museo Paleontologico dell'Università di Roma, Rome, Italy; MSNAF, Museo di Storia Naturale, Accademia dei Fisiocritici, Siena, Italy; MSTB, Museo di Scienze della Terra dell'Univeristà di Bari, Bari, Italy; NHMUK, Natural History Museum, London, United Kingdom; NHMW, Naturhistorisches Museum, Wien, Austria; NMB, Naturhistorisches Museum, Basel, Switzerland; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

2.1. Systematic palaeontology

Order PERISSODACTYLA Owen, 1848.

Family RHINOCEROTIDAE Gray, 1821.

Subfamily RHINOCEROTINAE Gray, 1821.

Tribe RHINOCEROTINI Gray, 1821.

Subtribe RHINOCEROTINA Gray, 1821.

Genus *Stephanorhinus* Kretzoi, 1942.

Assigned species: Several Plio-Pleistocene Eurasian rhinoceroses have traditionally been referred to *Stephanorhinus*, including *S. etruscus* (Falconer, 1868), *S. jeanvireti* (Guérin, 1972), *S. hundsheimensis* (Toula, 1902), *S. hemitoechus* (Falconer, 1868) and *S. kirchbergensis* (Jäger, 1839), although the composition and phylogenetic relationships of the genus remain debated. The validity of the two Chinese species *Stephanorhinus lantianensis* (Hu and Qi, 1978) and *Stephanorhinus yunchuchenensis* (Chow, 1963) has recently been questioned, and they have been interpreted as junior synonyms of *S. etruscus* and *S. kirchbergensis*, respectively. Little is known about the putative African species *Stephanorhinus africanus* (Arambourg, 1970), which Pandolfi (2015) regarded as a possible junior synonym of *S. etruscus*.

Stephanorhinus etruscus (Falconer, 1868).

Type material: skull (IGF756) stored at Museo di Storia Naturale, sezione di Geologia e Paleontologia, Università di Firenze.

Type age and horizon: Early Pleistocene, ca. 1.8 Ma.

Type locality: Poggio al Pero, 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*. A recent diagnosis has been published by Pandolfi (2023) and Chitoglou et al. (2025).

2.2. Short description and comparison

Skull, mandible, scapula, humerus, radius, MCIII, femur, tibia, calcaneus, astragalus and MTIII are used for the morphological comparison because these elements include characters traditionally considered relevant for distinguishing species of *Stephanorhinus* (Guérin,

1980; Fortelius et al., 1993; Lacombat, 2005; Stefanelli et al., 2025; Chitoglou et al., 2025). Morphometric graphical comparison was carried out for MCIII, astragalus and MTIII, which are among the best represented postcranial elements in fossil collections. The comparison below is intended not only to support the taxonomic attribution of IGF8212V, but also to test the reliability of characters commonly used for identifying isolated postcranial remains.

2.3. Skull

IGF8212V is morphologically similar to *S. etruscus* from Upper Valdarno. The shared characters are: a slightly flat dorsal profile of the skull, a small and round orbital cavity and a slender and sinuous zygomatic arch. Fortelius et al. (1993) reported that in *S. etruscus* the anterior border of the orbit lies above M3, however, in IGF8212V the orbit extends above M2 as well as in several other skulls belonging to this species (Pandolfi, 2023). The frontal horn-base rugosity of IGF8212V is far less developed than in other individuals from Valdarno and from Senéze, but this character is affected by sexual dimorphism and ontogeny in some extant rhinoceros species such as *Dicerorhinus sumatrensis* (Groves, 1967; Pandolfi, 2022). The studied specimen differs from *S. jeanvireti* for its different dimensions. The skull of an adult individual of *S. jeanvireti* is far larger than IGF8212V (Fig. 2). Regarding the morphological comparison, IGF8212V skull is less massive than *S. jeanvireti* from Vialette and Milia. In *S. jeanvireti* the shape of the orbital cavity is more dorsoventrally compressed, and the zygomatic arch is more massive than IGF8212V (Fig. 2). The skull of IGF8212V and those of *S. hundsheimensis* show many similarities such as the shape of the orbital cavity and the shape of the occipital face in lateral view (Fig. 2). Nevertheless, the orbital cavity of *S. hundsheimensis* is positioned lower than in IGF8212V. Mazza (1988) and Fortelius et al. (1993) suggested that the zygomatic arch of *S. hundsheimensis* is thicker and straighter than in *S. etruscus* but the skull from Poggio Rosso displays a zygomatic arch that is very similar in thickness and curvature to that of the skull from Hundsheim (Fig. 2). Both in IGF8212V and in some specimens belonging to *S. hundsheimensis* the orbit extends well over M2 (see Pandolfi, 2023). The teeth of IGF8212V are unworn and the hypsodonty index is relatively low: 0.8 for both M2 and M3.

2.4. Mandible

The morphology of the ascending branch of the mandible IGF8212V is very similar to both *S. etruscus* and *S. hundsheimensis*, resulting an unreliable element for a useful distinction between the two species. IGF8212V bears a less developed neck of the condyle than some specimens of *S. etruscus*. The ascending branch in *S. jeanvireti* is morphometrically larger than IGF8212V and its anterior border is more backward inclined. Further, in *S. jeanvireti* the angle of the mandible has a lower arching than in IGF8212V.

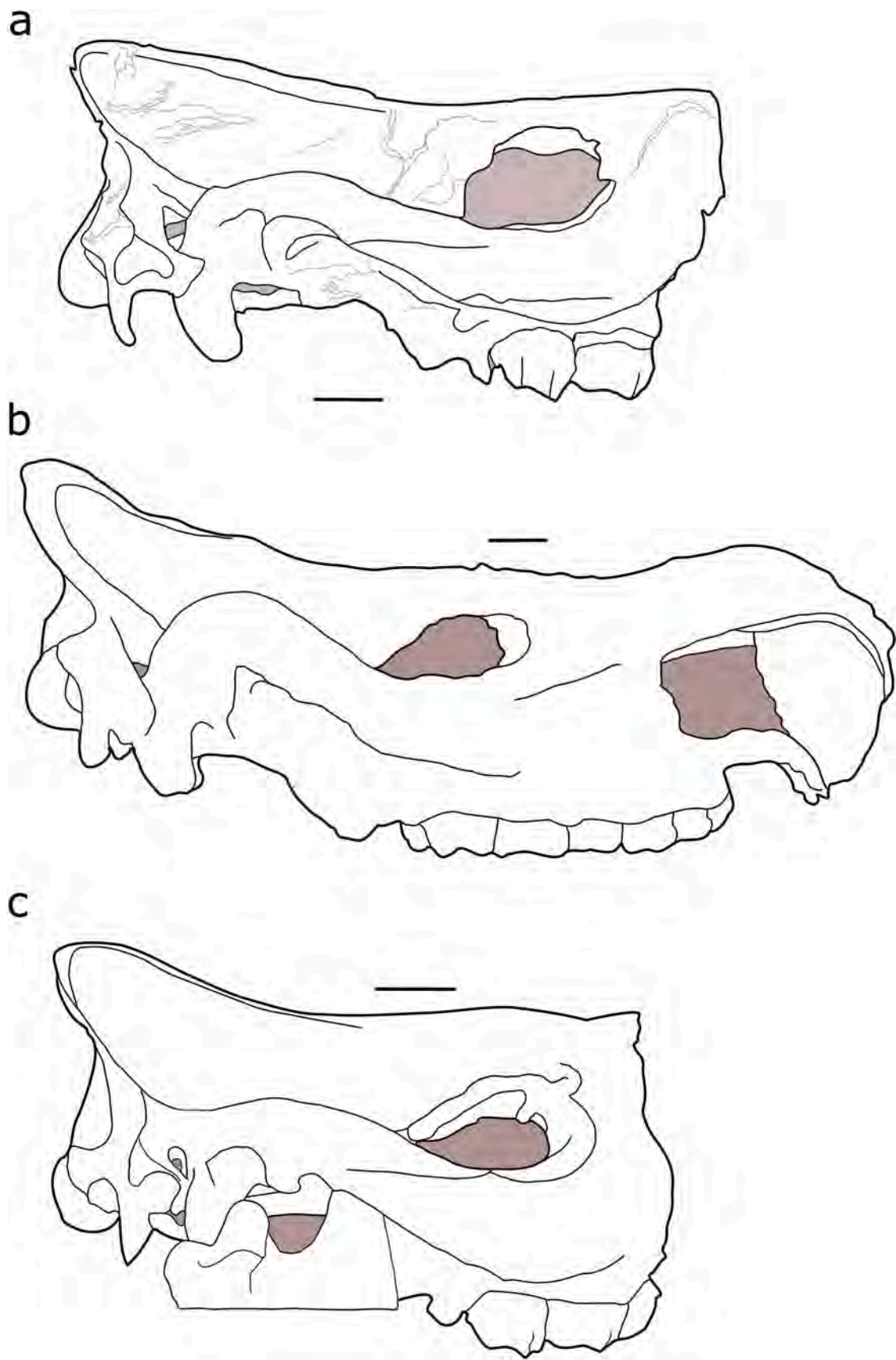


Fig. 2. Comparative drawing of the skull in lateral view: (a) *Stephanorhinus etruscus* IGF8212V, (b) *Stephanorhinus jeanvireti* from Milia (Guérin and Tsoukala, 2013), (c) *Stephanorhinus hundsheimensis* from Hundsheim NHMW 2013/0282/0001.

2.5. Scapula

The morphology of the glenoid cavity and of the supraglenoid tubercle in IGF8212V (Fig. 3) strongly resembles that of *S. etruscus* from Upper Valdarno. The elliptical outline of the glenoid cavity of IGF8212V in distal view is also very similar to that of *S. hundsheimensis*, while *S. jeanvireti* shows a rounder cavity. The supraglenoid tubercle of IGF8212V strongly differs from *S. hundsheimensis* and *S. jeanvireti*: both these latter species show a more transversely developed tubercle with a strongly pronounced coracoid process, while in IGF8212V and *S. etruscus* the supraglenoid tubercle is stubbier and rounded.

2.6. Humerus

The overall morphology of the humeri of IGF8212V (Fig. 4), especially the distal epiphysis, resembles those of Capitone, Upper Valdarno and Senèze, all ascribed to *S. etruscus*. The distal trochlea is oblique, and the medial border of its medial lip is straight and oblique, similarly to *S. etruscus* from Tsiotra Vryssi and Apollonia-1 (Chitoglou et al., 2025; Greece). The distal epiphysis of *S. etruscus* from Pietrafitta shows a proportionally smaller trochlea than IGF8212V but similar morphology. The humerus of *S. jeanvireti* differs from Poggio Rosso by showing proportionally more massive epiphyses, rounder articular head, proportionally smaller lesser tubercle, and in proximal view a more concave bicipital groove. IGF8212V differs from *S. hundsheimensis* from Hundsheim which is characterised by a proportionally bigger lesser tubercle, a more rectangular head and, in distal view, a proportionally smaller lateral lip of the trochlea. The morphometrical comparison (Table S1) shows that the length of the humeri of the studied specimen is much smaller than *S. jeanvireti* and *S. hundsheimensis*, while it falls within the range of values given by Guérin (1980) for *S. etruscus*. The transverse diameters of the epiphyses are slightly smaller than the minimal values given by Guérin (1980) for *S. etruscus*.

2.7. Radius

The radii of IGF8212V and those of *S. etruscus*, *S. hundsheimensis* and *S. jeanvireti* are broadly similar (Fig. 5a–c, see Chitoglou et al., 2025). In anterior view, they show very similar proportions and a well-developed radial styloid process. In proximal view, glenoid cavities are strongly asymmetrical in all the three species. *Stephanorhinus jeanvireti* from Roatto shows a medial proximal articulation slightly more developed anteriorly and a proportionally wider lateral proximal articulation than in IGF8212V, *S. etruscus* and *S. hundsheimensis*. Similarly to *S. etruscus* from Upper Valdarno and from Tsiotra Vryssi and Apollonia-1 (Chitoglou et al., 2025), the studied specimens show a $\sim 120^\circ$ angle between the posterior borders of the proximal articulation. In distal view, the epiphysis of *S. jeanvireti* is stockier than IGF8212V and *S. hundsheimensis*. The length of studied radii is slightly smaller than the minimum values given by Guérin (1980) for *S. etruscus*, while the diameters of the epiphyses fall within the given dimensional ranges, but

very close to the minimum values. All the measurements reported for *S. jeanvireti* and *S. hundsheimensis* strongly exceed the values of IGF8212V.

2.8. MCIII

The two MCIIIs from Poggio Rosso (Fig. 6a–c) are compared with individuals from Upper Valdarno, Pietrafitta, Saint Vallier and Capitone. The overall morphology of IGF8212V is very similar to that of *S. etruscus*. In proximal view, the groove between the two articular surfaces for the fourth metacarpal is less deep in IGF8212V than in other *S. etruscus* specimens, while the morphology of the proximal articular surface in anterior view resembles that of the specimen from Tsiotra Vryssi (Chitoglou et al., 2025). The MCIII of *S. jeanvireti* differs from IGF8212V in having a proportionally more massive diaphysis, a proportionally bigger articular surface for the second metacarpal and a broader and more triangular proximo-lateral articular surface for the uncinat. In proximal view, the groove between the two articular surfaces for MCIV is more marked in *S. jeanvireti* than in IGF8212V. In *S. hundsheimensis* the lateral border of the diaphysis is thicker and slightly more bulging than in IGF8212V. In *S. hundsheimensis*, in proximal view, the articular surfaces for the uncinat and for the MCII are slightly broader than in IGF8212V, and, in anterior view, the angle between the lateral articular surface for the uncinat and that for the MCIV is slightly more acute. Fortelius et al. (1993) reported that in *S. hundsheimensis* the distal articular surface is broader than in *S. etruscus*, however, this difference is not relevant between IGF8212V and the specimen from Hundsheim. The length of IGF8212V (Fig. 7) is slightly smaller than the minimal values given by Guérin (1980) for *S. etruscus*, while the diameters of the epiphyses fall within the ranges, but very close to the minimal values. The length and the transversal diameters of IGF8212V are very similar to the values of *S. etruscus* from Pietrafitta.

2.9. Femur

The overall morphology of the femurs of IGF8212V (Fig. 8) resembles those of Capitone, Upper Valdarno, Pietrafitta and Senèze, all attributed to *S. etruscus*. The greater trochanter of IGF8212V is posteriorly and proximally more developed than most of the other *S. etruscus* specimens. The Pietrafitta femur shows, in anterior view, a greater trochanter and a lesser trochanter more developed than in IGF8212V. The femur of *S. jeanvireti* is morphologically very similar to IGF8212V: the proportions of the diaphysis and the epiphyses are very similar; the greater trochanter and the articular head have similar shape, and, in anterior view, the trochlea is strongly asymmetrical in both species. The only differences are that the third trochanter and the neck of *S. jeanvireti* are more massive than in IGF8212V. Guérin (1980) reported that in *S. etruscus* the lesser trochanter is less developed than in *S. jeanvireti*, and, in distal view, the axis of the trochlea is more oblique in *S. etruscus* than in *S. jeanvireti*. Such differences cannot be observed between IGF8212V and the specimens from Montopoli and Viallette. Compared

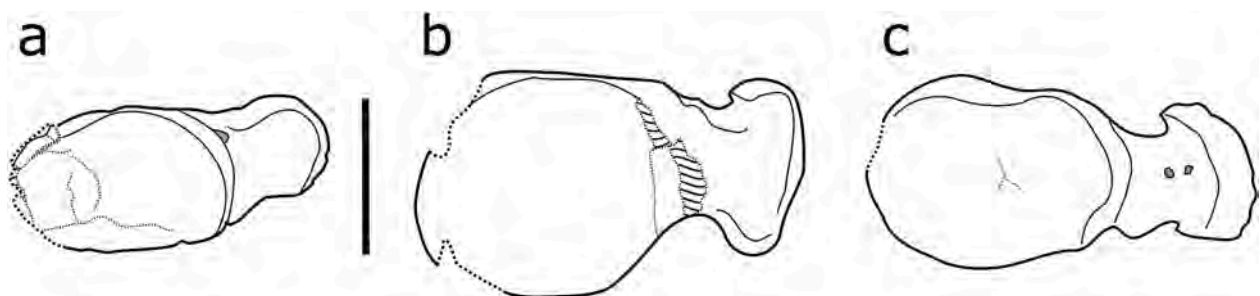


Fig. 3. Comparative drawing of the distal articular surface of the scapula: (a) *Stephanorhinus etruscus* IGF8212V, (b) *Stephanorhinus jeanvireti* from Roatto (Campanino et al., 1994), (c) *Stephanorhinus hundsheimensis* from Hundsheim NHMW 2013/0282/0001.

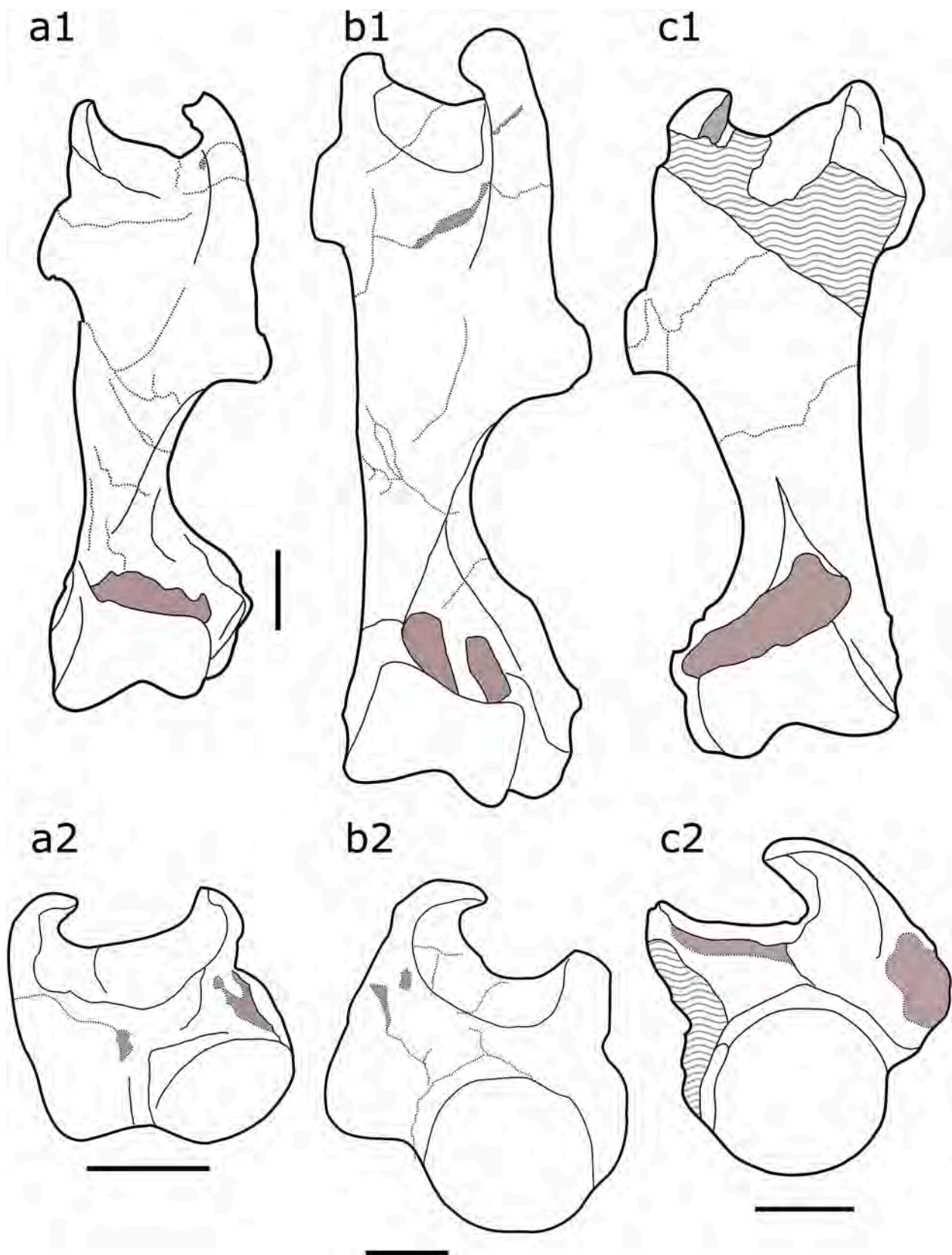


Fig. 4. Comparative drawing of the humerus: (a) *Stephanorhinus etruscus* IGF8212V, (b) *Stephanorhinus jeanvireti* from Roatto (Campanino et al., 1994), (c) *Stephanorhinus hundsheimensis* from Hundsheim, NHMW 2013/0282/0001, in anterior view (1) and proximal view (2).

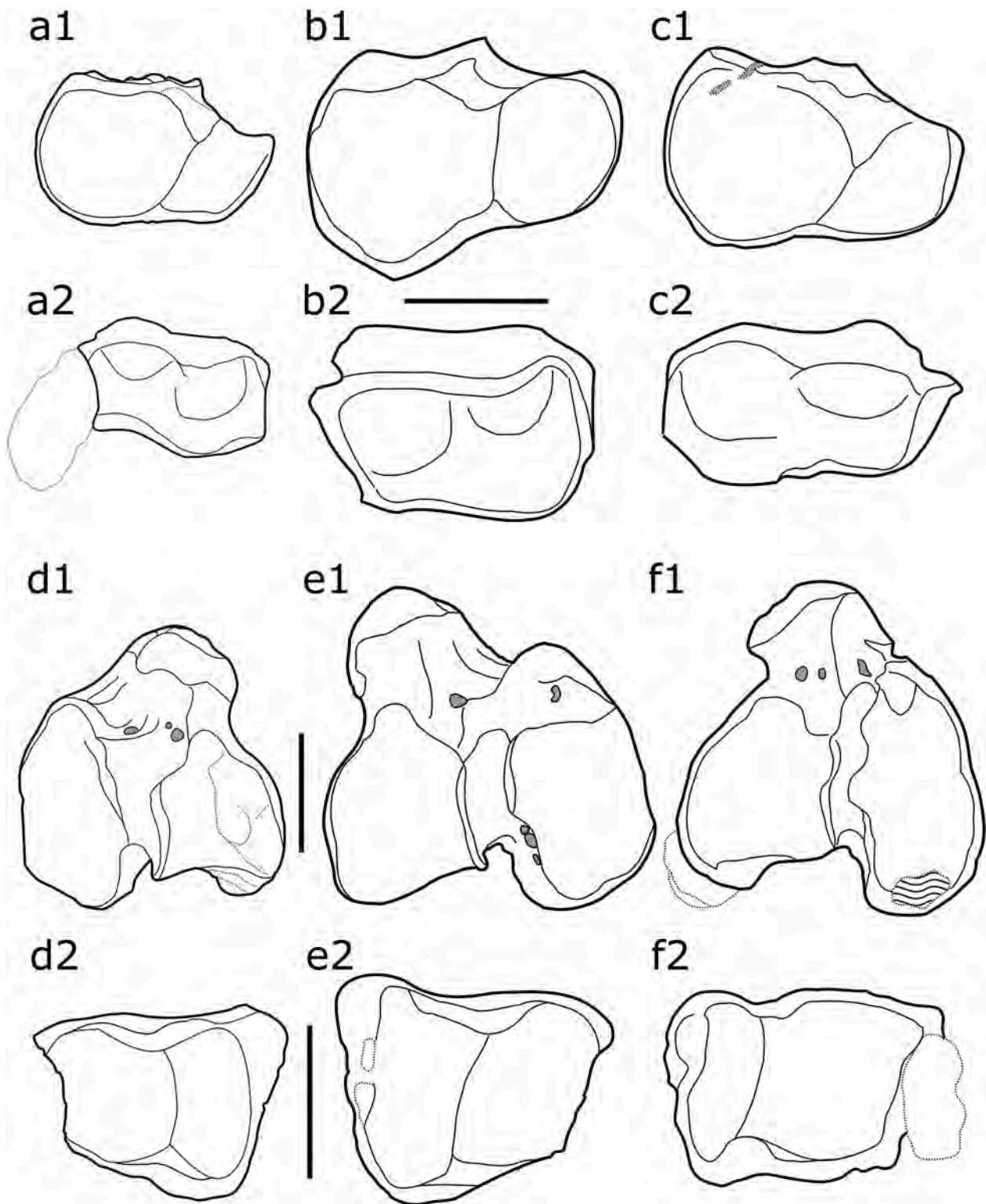


Fig. 5. Comparative drawing of the zeugopodials. Radius (a) *Stephanorhinus etruscus* IGF8212V; (b), *Stephanorhinus jeanvireti* from Roatto (Campanino et al., 1994); (c), *Stephanorhinus hundsheimensis* from Untermassfeld (Kahlke, 2001), in proximal view (1) and distal view (2). Tibia (d) *Stephanorhinus etruscus* IGF8212V; (e), *Stephanorhinus jeanvireti* from Vialette, NMB nc; (f) *Stephanorhinus hundsheimensis* from Hundsheim, NHMW 2013/0282/0001, in proximal view (1) and distal view (2).

with the particularly slender femur of IGF8212V, that of *S. hundsheimensis* is more massive and stockier. IGF8212V shows a more developed greater trochanter (opposite to the observation reported by Fortelius et al., 1993) and a slenderer third trochanter. Furthermore, in the studied specimen the greater trochanter connects the articular head

while in *S. hundsheimensis* they are separated. The femurs of IGF8212V are smaller than those of *S. jeanvireti* and *S. hundsheimensis* while they fall inside the range given by Guérin (1980) for *S. etruscus*.

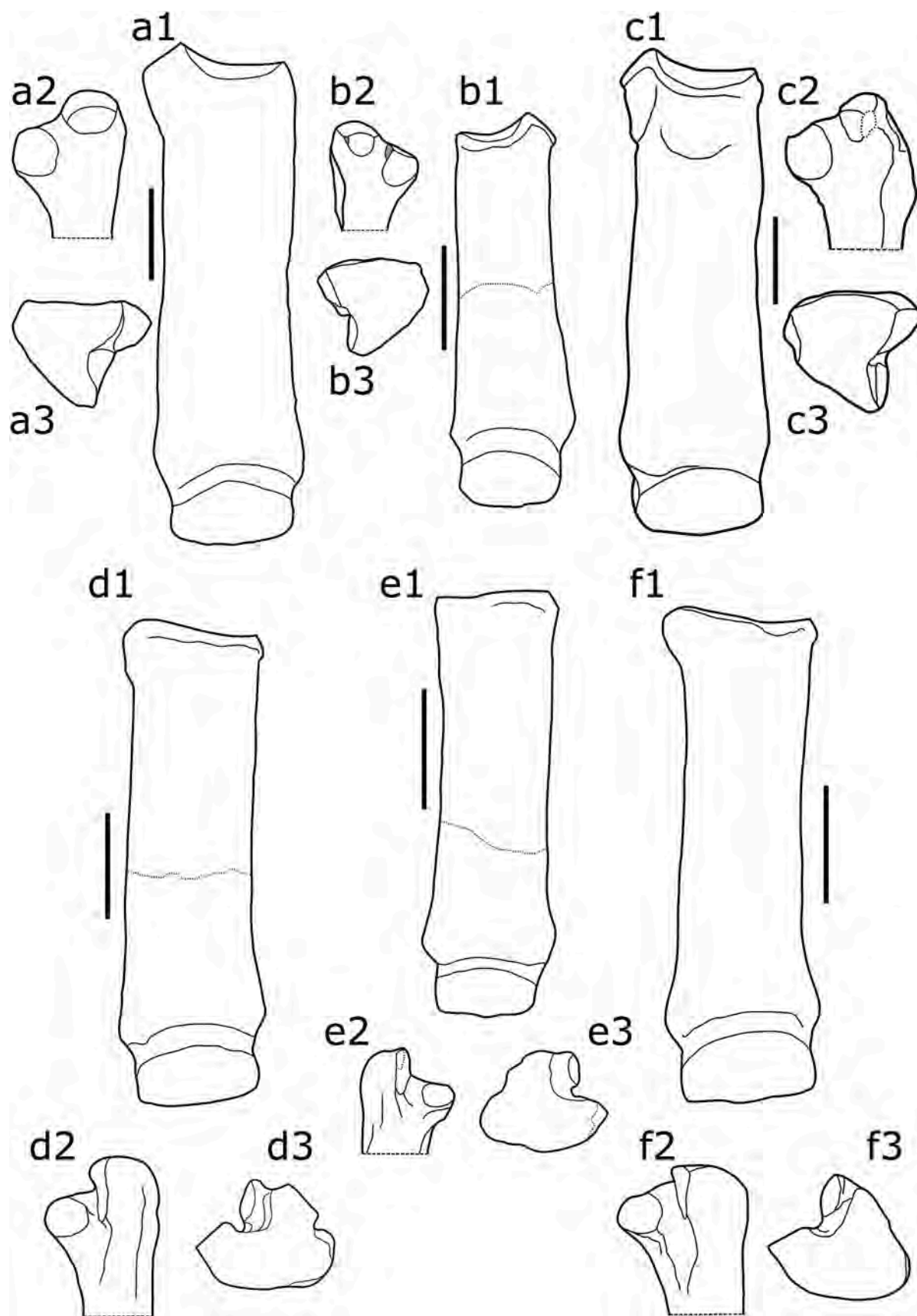


Fig. 6. Comparative drawing of third metapodials: third metacarpal (a) *Stephanorhinus jeanvireti* from Milia (Guérin and Tsoukala, 2013); (b) *Stephanorhinus etruscus* IGF8212V; (c) *Stephanorhinus hundsheimensis* from Untermassfeld (Kahlke, 2001), in anterior view (1), lateral view (2), proximal view (3); third metatarsal (d) *Stephanorhinus jeanvireti* from Milia (Guérin and Tsoukala, 2013); (e) *Stephanorhinus etruscus* IGF8212V; (f) *Stephanorhinus hundsheimensis* from Untermassfeld (Kahlke, 2001), in anterior view (1), lateral view (2), proximal view (3).

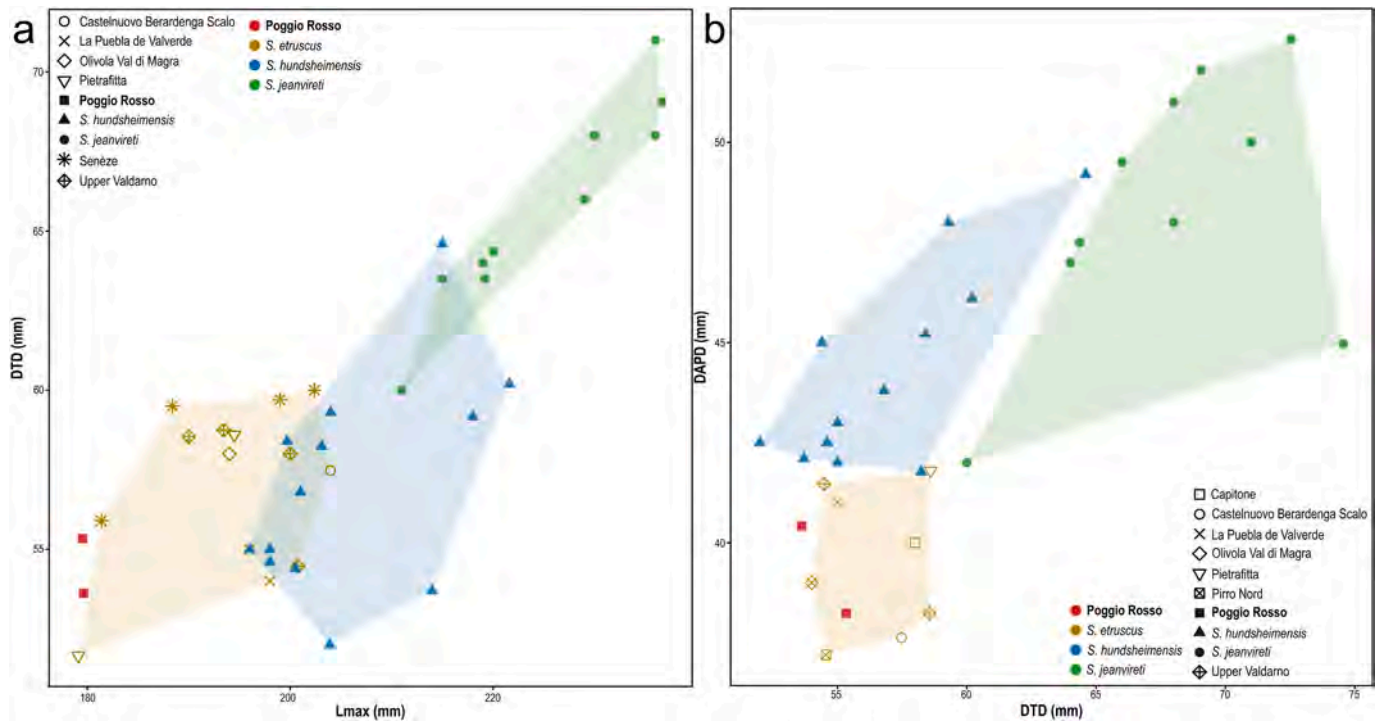


Fig. 7. Bivariate plots of the third metacarpal (MCIII) in *Stephanorhinus etruscus*, *Stephanorhinus hundsheimensis*, *Stephanorhinus jeanvireti* and IGF8212V from Poggio Rosso. (a) Maximal length (L) plotted against distal transverse diameter (DTD). (b) Distal transverse diameter (DTD) plotted against distal anteroposterior diameter (DAPD). Convex hulls summarize the sampled morphospace.

2.10. Tibia

The tibia of IGF8212V and those of *S. etruscus*, *S. hundsheimensis* and *S. jeanvireti* are very similar regarding overall morphology (Fig. 5d–f), by showing similar proportions in the diaphysis, two well pronounced tibial spines and a prominent medial malleolus. In proximal view, the proximal epiphysis of IGF8212V resembles other specimens from Upper Valdarno attributed to *S. etruscus*. The popliteal incisure of IGF8212V is narrow and proportionally very similar to *S. jeanvireti*. IGF8212V differs from *S. hundsheimensis* in having a proportionally stubbier tibial tuberosity and shallower tibial groove. *Stephanorhinus jeanvireti* shows a stronger tibial tuberosity (more verging outward) and a deeper digital fossa in comparison with IGF8212V. Fortelius et al. (1993) described the tibia of *S. hundsheimensis* as “having much wider epiphyses and diaphyses more compressed dorso-plantarly” compared to *S. etruscus*; however, such differences cannot be detected while comparing IGF8212V with *S. hundsheimensis* from Hundsheim and Untermassfeld. Chitoglou et al. (2025) suggested that some distal tibial characters, such as the shape of the medial articular surface and the development of the medial malleolus, may instead retain some diagnostic value. The rhinoceros from Hundsheim shows indeed a wider medial articular surface and a more rectangular distal epiphysis in distal view compared to *S. etruscus* and Poggio Rosso (Fig. 5d–f). Dimensionally, the tibia of IGF8212V is much smaller than those of *S. hundsheimensis* and *S. jeanvireti*, while the length and the dimensions of the epiphyses are for the most part lower than the minimum values given by Guérin (1980) for *S. etruscus*.

2.11. Astragalus

The astragali of IGF8212V (Fig. 9a–c) show a very similar morphology to *S. etruscus* while they differ from *S. jeanvireti* in having a slightly oblique trochlea with a more sinuous distal border and a medial lip of the trochlea closer to the anterior border of the distal articular surface. In dorsal view the medial tuberosity is rounded both in

IGF8212V and in *S. jeanvireti*, but in this latter species it's slightly more developed. The astragali of IGF8212V and *S. hundsheimensis* look very much alike as also observed by Fortelius et al. (1993). In the astragalus of *S. hundsheimensis* from Untermassfeld the proximal articular surface for the calcaneus is broader medio-laterally and more compressed proximo-distally. Similarly to the specimen from Apollonia-1, the studied specimens differ from the astragalus of *S. hundsheimensis* from Hundsheim in the more subtle inclination of the axis of the trochlea in anterior view. The arrangement of the calcaneal facets on the plantar face of IGF8212V is broadly consistent with the condition described for *S. etruscus*. The presence of three articular surfaces for the calcaneus, the strongly concave proximal-lateral facet, the deep and narrow sinus tarsi, and the elongated lateral-distal facet are particularly close to the morphology reported by Mazza (1988) for Upper Valdarno *S. etruscus*. The proximal-lateral facet of IGF8212V is trapezoidal and ends distally in a small triangular convex extension, a condition also recalling the Viallette rhinoceros referred to *S. jeanvireti* by Guérin (1972), although in that taxon the facet is more externally expanded and higher. The medio-distal facet of IGF8212V is bell-shaped and mostly flat, differing from the trapezoidal condition described for *S. hundsheimensis* by Lacombat (2005). The lateral-distal facet is transversely elongated and reaches the medio-distal facet, as in the condition described for *S. etruscus*, although it is somewhat more distinct than in the latter and approaches the more marked condition reported for *S. hundsheimensis*. IGF8212V astragali (Fig. 9a–c) are much smaller than those of *S. jeanvireti*, while they are dimensionally very similar to the minimal values reported for *S. hundsheimensis* (Vallonnet). The heights (Hmax, Hm, Hl) of IGF8212V are lower than those of *S. hundsheimensis*, suggesting that the astragalus of the studied specimen is more compressed proximo-distally than those of *S. hundsheimensis* (Fig. 10). The measurements of IGF8212V fall within the range of values given by Guérin (1980) for *S. etruscus*.

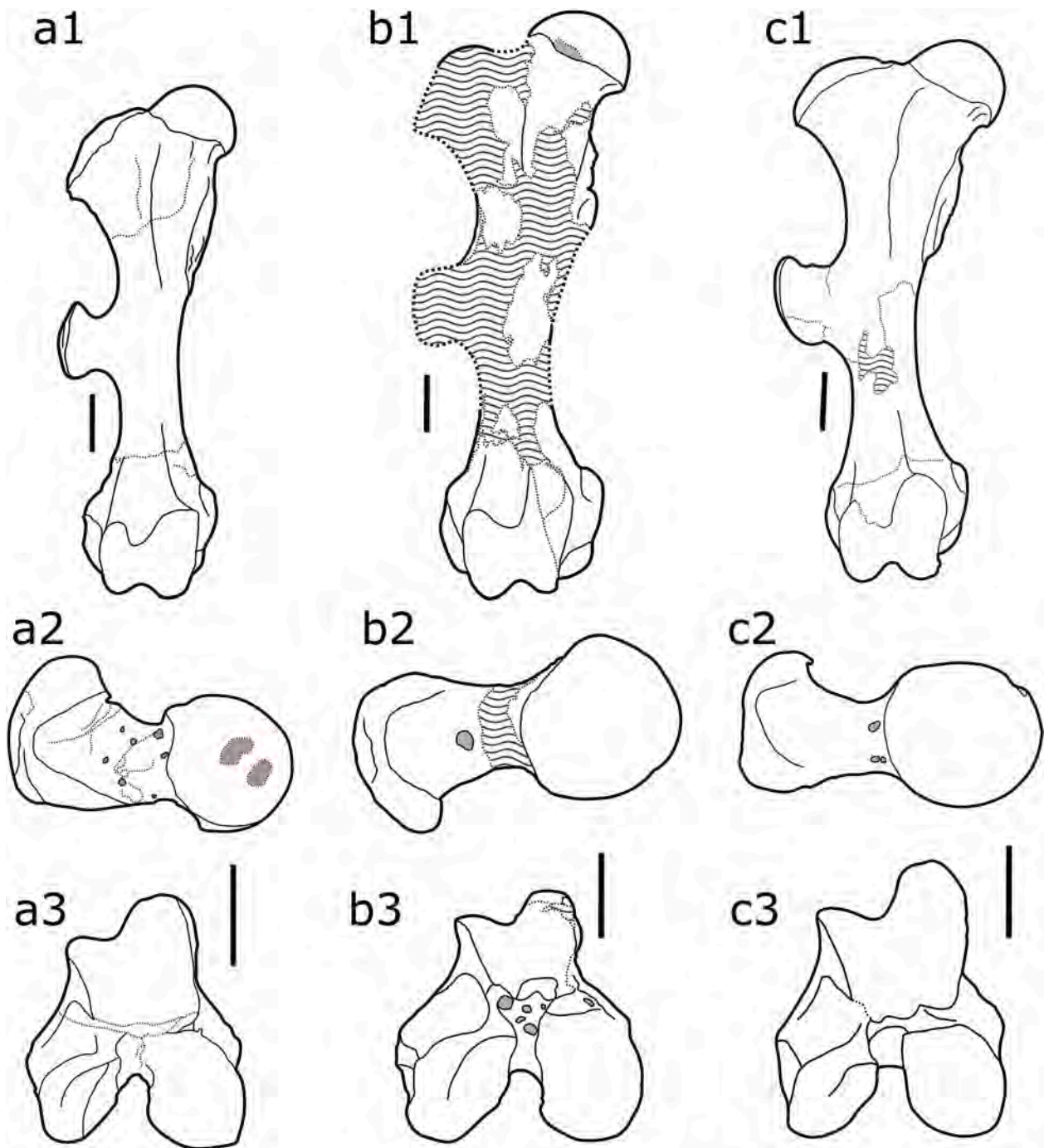


Fig. 8. Comparative drawing of the femur: (a) *Stephanorhinus etruscus* IGF8212V; (b) *Stephanorhinus jeanvireti* from Vialette, NMB nc; (c) *Stephanorhinus hundsheimensis* from Soleihac, NMB SL76, in anterior (1), proximal (2) and distal (3) views.

2.12. Calcaneus

The calcaneus from Poggio Rosso (Fig. 9d–f) is morphologically very similar to the individuals from Upper Valdarno, Capitone and Senèze attributed to *S. etruscus*. The articular surface on the *sustentaculum tali* is elliptical, transversely elongated and clearly developed, and the *sustentaculum tali* itself is medially well developed, slightly curved anteriorly and almost orthogonal to the body of the calcaneus in posterior view. Compared to *S. jeanvireti*, the calcaneus of IGF8212V is stockier (low ratio between the maximal length and the transverse diameter). The calcanei of *S. jeanvireti* from Vialette and Colţeşti have a slender body and a more developed *sustentaculum tali* but a less prominent beak.

The calcaneus from Milia attributed to *S. jeanvireti* is morphologically more similar to IGF8212V than those from Vialette and Colţeşti being stockier and with a more prominent beak. The calcanei from Poggio Rosso and *S. hundsheimensis* look very much alike. Although the classical differences proposed by Fortelius et al. (1993), such as a stockier calcaneus and a more extended summital tuberosity in *S. hundsheimensis*, are not evident in the comparison between IGF8212V and the Hundsheim and Untermassfeld material. Chitoglou et al. (2025) identified additional calcaneal features that may help separate *S. etruscus* from *S. hundsheimensis*. The Greek specimens attributed to *S. etruscus* share with Poggio Rosso the shape and size of the tuber calcanei and the rounded end of the *sustentaculum tali*, suggesting that these features may

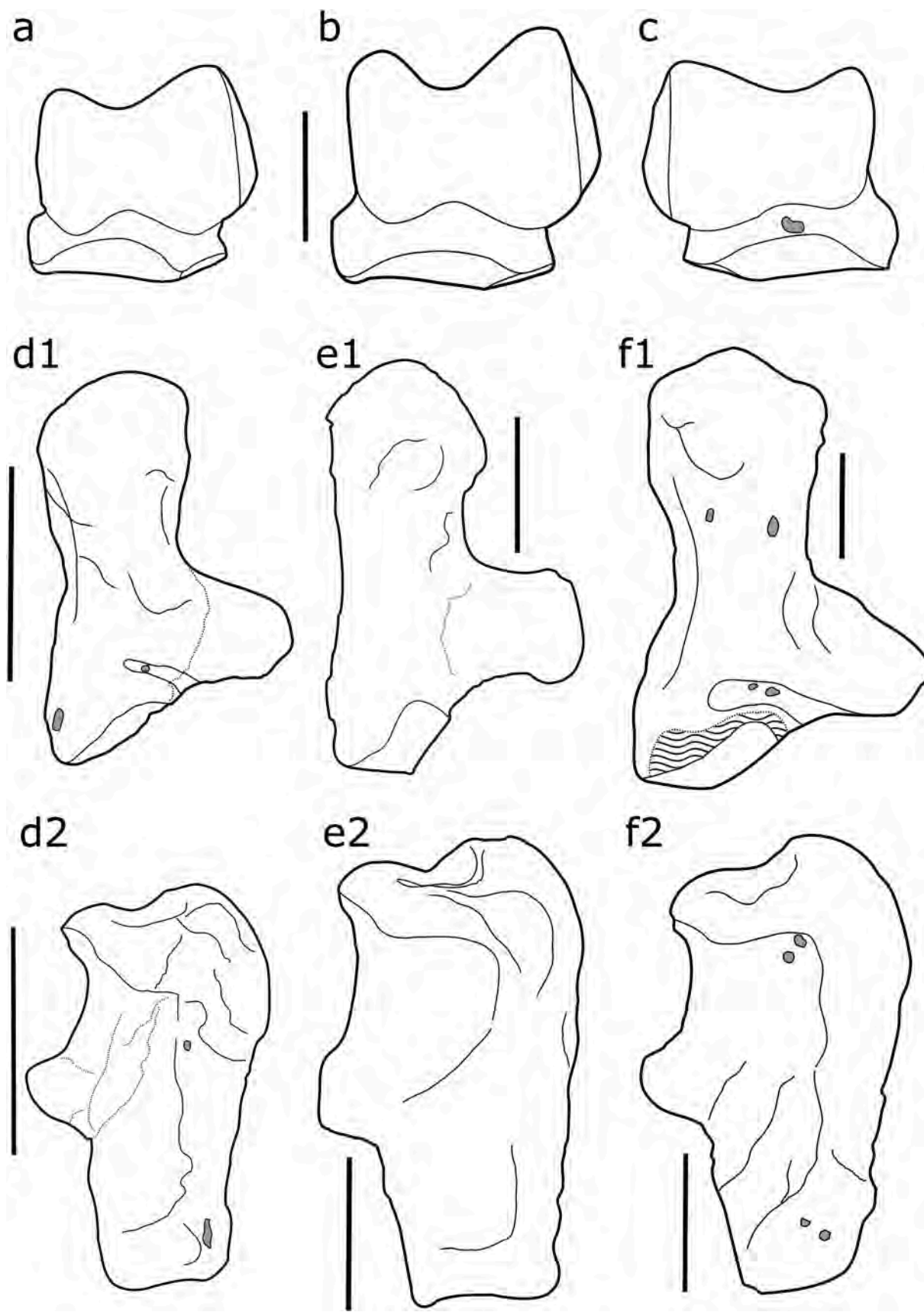


Fig. 9. Comparative drawing of astragalus and calcaneus. Astragalus, (a) *Stephanorhinus etruscus* IGF8212V, (b) *Stephanorhinus jeanvireti* from Pradalbino (Pandolfi et al., 2013), (c) *Stephanorhinus hundsheimensis* from Untermassfeld (Kahlke, 2001), in anterior view. Calcaneus (d) *Stephanorhinus etruscus* IGF8212V, (e) *Stephanorhinus jeanvireti* from Colțești (Pandolfi et al., 2019), (f) *Stephanorhinus hundsheimensis* from Untermassfeld (Kahlke, 2001), in plantar view (1) and lateral (2) views.

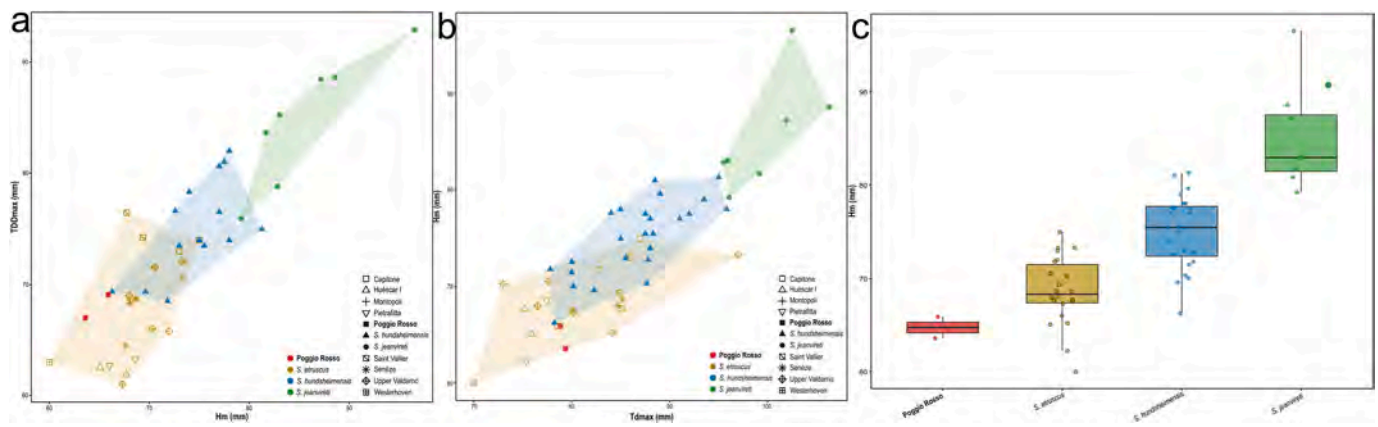


Fig. 10. Morphometric comparison of the astragalus in *Stephanorhinus etruscus*, *Stephanorhinus hundsheimensis*, *Stephanorhinus jeanvireti* and IGF8212V from Poggio Rosso. (a) Medial height (Hm) plotted against distal maximal diameter (TDDmax). (b) Medial height (Hm) plotted against maximal transverse diameter (TDmax). (c) Boxplot of medial height (Hm) by taxonomic group, with the two Poggio Rosso values shown as individual points. Convex hulls summarize the sampled morphospace.

be more informative than general robustness alone. In IGF8212V, no distinct tibial or fibular facets can be recognized. A similar condition is observed in several specimens referred to *S. etruscus*, including the material from Apollonia (see Chitoglou et al., 2025), and from the Upper Valdarno (e.g., NMB VA612, IGF731 and IGF2238V). In these specimens, as in Poggio Rosso, the articular surface present on the *sustentaculum tali* is separated from the latero-distal astragalar facet by a distinct groove. This arrangement differs from the condition observed in some specimens referred to *S. jeanvireti*, such as those from Vialette, Milia and Colțești, where tibial and fibular facets are present and the astragalar articular surfaces tend to be connected. By contrast, *S. hundsheimensis* shows a more variable condition. In the Untermassfeld material, the tibial and fibular facets are not recognizable, and the general arrangement resembles that of Poggio Rosso, although this condition may be influenced by ontogenetic stage (see Antoine, 2002). In specimens from Voigtstedt and Hundsheim, a tibial facet is present, but the remaining morphology of the calcaneus is broadly comparable to that observed in IGF8212V. The calcaneus from Poggio Rosso (Table S1) is dimensionally much smaller than *S. jeanvireti* but also smaller than *S. hundsheimensis*. The measurements of IGF8212V fall within the range of values given by Guérin (1980) for *S. etruscus*.

2.13. MTIII

The MTIII from IGF8212V (Fig. 6d–f) resembles those of Capitone, Upper Valdarno, Pietrafitta and Senèze, all attributed to *S. etruscus*. The Pietrafitta individual, in anterior view, shows a more concave dorsal profile of the proximal epiphysis. The MTIII of *S. jeanvireti* are proportionally very similar to IGF8212V. In anterior view, the MTIII of *S. jeanvireti* differs from the studied specimen in having a more concave dorsal profile of the proximal epiphysis. Mazza (1988) reports that on the lateral face of the proximal epiphysis the posterior articular facet is lower than the anterior one, while in *S. etruscus* is the opposite. Such difference cannot be observed when comparing the studied specimen with *S. jeanvireti* from Colțești, Montopoli, Vialette and Milia, as also in IGF8212V where the posterior articular facet is lower than the anterior one. In dorsal view the MTIII of *S. hundsheimensis* shows a more concave dorsal profile of the proximal epiphysis while in lateral view the dorsal articular facet for the MTIV is more laterally placed than in *S. etruscus* (also visible in dorsal view). Fortelius et al. (1993) report that, in dorsal view, the diaphysis of *S. etruscus* is parallel flanked while in *S. hundsheimensis* the diaphysis widens gradually distally. Such difference could not be seen in the specimen from Poggio Rosso, as its diaphysis also widens distal wards similarly to the individuals from Untermassfeld and Hundsheim. However, this feature is an

ontogenetically-variable feature on central metapodials of several rhinocerotids (see Antoine, 2002). IGF8212V MTIII (Fig. 11) are much smaller than those of *S. jeanvireti* but also smaller than *S. hundsheimensis*. The MTIII of *S. etruscus* shows a wide morphometrical variability in particular in its maximum length; IGF8212V, is smaller than the minimum value given by Guérin (1980) for *S. etruscus*, however is dimensionally very similar to other individuals, all attributed to *S. etruscus*, from Poggio Rosso, Westerhoven, Wissel and Pietrafitta (Fig. 11).

3. Discussion

3.1. Taxonomic attribution of Poggio Rosso skeleton

The overall morphology of the Poggio Rosso specimen clearly supports its attribution to *Stephanorhinus etruscus* (Table 2). The skull shares with Upper Valdarno rhinoceros a slightly flat dorsal profile, a small and rounded orbital cavity, and a slender, sinuous zygomatic arch. These characters agree with the general cranial morphology described for *S. etruscus* by Guérin (1980), Mazza (1988), Fortelius et al. (1993) and Lacombat (2005). The anterior margin of the orbit lies above M2, a condition that differs from some traditional diagnoses placing the orbit more posteriorly in *S. etruscus*, but which has been shown to vary within the species and cannot be considered diagnostic on its own (Pandolfi, 2023). The preserved upper molars are unworn and relatively low-crowned, and their morphology is compatible with *S. etruscus*, whereas the fragmentary mandible is less informative because the ascending branch displays a morphology broadly comparable to both *S. etruscus* and *S. hundsheimensis*. Nevertheless, no cranial, mandibular or dental character supports attribution to *S. hundsheimensis* or *S. jeanvireti*. The scapula shows an elliptical glenoid cavity and a short, rounded supraglenoid tubercle, resembling the condition observed in *S. etruscus* rather than the more transversely developed tubercle with a stronger coracoid process observed in *S. hundsheimensis* and *S. jeanvireti*. The humerus, especially its distal epiphysis, closely resembles specimens from Capitone, Upper Valdarno and Senèze referred to *S. etruscus*, and shows an oblique distal trochlea with a straight and oblique medial border of the medial lip, as also observed in Greek material attributed to *S. etruscus*. The radius is less diagnostic, because its general proportions and articular morphology overlap among Early Pleistocene *Stephanorhinus* species. The femur and tibia are also compatible with *S. etruscus*. The femur is relatively slender and small, with a large triangular greater trochanter, a well-developed lesser trochanter, a strongly projected third trochanter, and a distal trochlea in which the medial lip is more developed than the lateral one. Some of these characters have been used in the literature to separate *S. etruscus*, *S. hundsheimensis* and *S. jeanvireti*, but

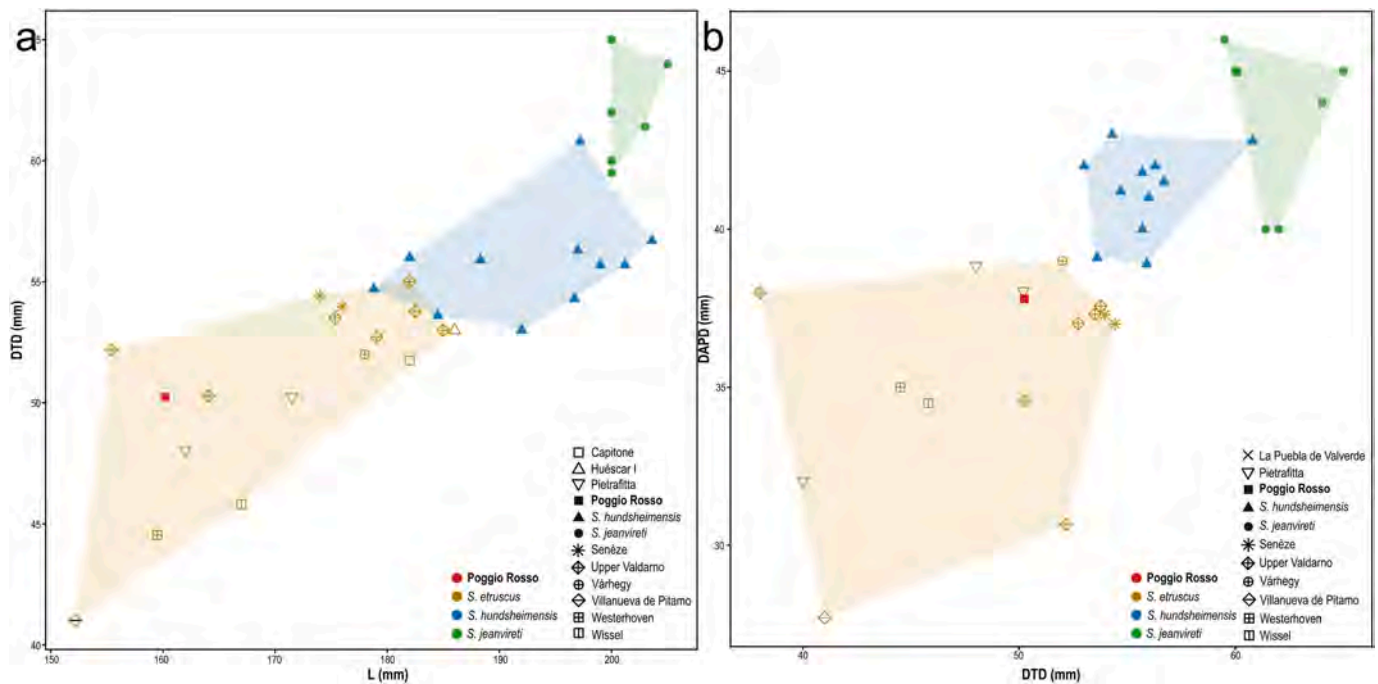


Fig. 11. Bivariate plots of the third metatarsal (MTIII) in *Stephanorhinus etruscus*, *Stephanorhinus hundsheimensis*, *Stephanorhinus jeanvireti* and IGF8212V from Poggio Rosso. (a) Maximal length (L) plotted against distal transverse diameter (DTD). (b) Distal transverse diameter (DTD) plotted against distal anteroposterior diameter (DAPD). Convex hulls summarize the sampled morphospace.

the condition observed in IGF8212V indicates that they should be used cautiously, because they partly overlap among taxa. The tibia does not show the combination of wider epiphyses and a markedly dorso-plantarily compressed diaphysis traditionally reported for *S. hundsheimensis*. Its distal articular morphology, with two well-defined oblique surfaces for the talus and a prominent medial malleolus, is broadly consistent with the condition observed in *S. etruscus*, although tibial characters alone remain weakly diagnostic. The MCIII and MTIII are morphologically close to *S. etruscus* specimens from Upper Valdarno, Pietrafitta, Capitone and Senèze. Its proximal articular surface for the magnum is triangular, transversely concave and anteroposteriorly convex; the articular surface for the uncinate is smaller and sub-triangular; and the two lateral articular surfaces for MCIV are separated by a distinct groove. These features are broadly compatible with *S. etruscus*, even if some characters, such as the breadth of the distal articular surface and the arrangement of the proximal facets, overlap with *S. hundsheimensis*. In the MTIII, the diaphysis widens distally, a condition previously reported as more typical of *S. hundsheimensis* than of *S. etruscus*, but affected by ontogeny within Rhinocerotidae (Antoine, 2002). However, the overall morphology and dimensions of the Poggio Rosso MTIII are close to small *S. etruscus* specimens from the Upper Valdarno and Pietrafitta. The astragalus of IGF8212V shows three calcaneal facets on the plantar face: a strongly concave, trapezoidal proximo-lateral facet with a small triangular convex distal extension; a bell-shaped, mostly flat medio-distal facet; and a transversely elongated latero-distal facet reaching the medio-distal one. The proximo-lateral and medio-distal facets are separated by a deep and narrow *sinus tarsi*. This arrangement is broadly consistent with the condition described for *S. etruscus*, especially in the Upper Valdarno material described by Mazza (1988), although some aspects partly overlap with *S. hundsheimensis* and *S. jeanvireti*. In particular, the shape and distal extension of the proximo-lateral facet recall, in part, the condition described in *S. jeanvireti*, whereas the more marked latero-distal facet partly approaches the morphology reported for *S. hundsheimensis*. Therefore, the astragalus supports an attribution to *S. etruscus*, but also highlights the partial overlap of tarsal characters among Early

Pleistocene *Stephanorhinus* species. The calcaneus also supports a closer resemblance to *S. etruscus*. The *sustentaculum tali* is medially well developed, slightly curved anteriorly and almost orthogonal to the calcaneal body in posterior view. The articular surface on the *sustentaculum tali* is elliptical and transversely elongated, whereas the distal articular surface for the cuboid is crescent-shaped and strongly concave. No distinct tibial or fibular facets can be recognized on the calcaneus of IGF8212V. In addition, the articular surface on the *sustentaculum tali* is separated from the latero-distal astragalus facet by a distinct groove. This condition resembles that observed in several specimens referred to *S. etruscus*, including material from the Upper Valdarno, and differs from the condition observed in some *S. jeanvireti* calcanei, in which tibial and fibular facets are present, and the astragalus articular surfaces tend to be connected. However, *S. hundsheimensis* shows a more variable condition, with specimens from Untermassfeld resembling Poggio Rosso and specimens from Voigtstedt and Hundsheim showing at least a tibial facet. The calcaneus is therefore informative, but not diagnostic alone.

The attribution of IGF8212V to *S. etruscus* is therefore based on several cranial, dental and postcranial traits. This is particularly relevant because some isolated elements of IGF8212V, if considered alone, could be interpreted as displaying characters previously reported for *S. hundsheimensis* or *S. jeanvireti*. However, these characters do not form a coherent diagnostic association supporting attribution to either of these taxa. Instead, the associated skeleton shows that several features traditionally considered taxonomically informative may occur within the morphological variability of *S. etruscus*. Accordingly, IGF8212V represents an important control case for evaluating the taxonomic reliability of isolated postcranial characters in Early Pleistocene rhinoceroses.

3.2. Stability of diagnostic characters in Early Pleistocene rhinoceroses

The exceptional preservation of the articulated skeleton from Poggio Rosso allows us to explore in detail a set of cranial and postcranial characters that in the literature are often treated separately and sometimes considered diagnostic at the species level. Recent studies on Early

Table 2

Main cranial and postcranial characters traditionally used to distinguish *Stephanorhinus etruscus*, *Stephanorhinus hundsheimensis* and *Stephanorhinus jeanvireti*, and their condition in IGF8212V from Poggio Rosso.

Anatomical element	Character proposed in literature	Condition observed in IGF8212V	Agreement with proposed character	Interpretation
Skull	Anterior border of the orbit placed above M3 in <i>S. etruscus</i> ; orbit position used to distinguish <i>S. etruscus</i> from other <i>Stephanorhinus</i> species.	The anterior border of the orbit extends above M2.	Not in agreement with a strict use of the traditional orbit-position character for <i>S. etruscus</i> .	Variable character; not reliable alone. The condition observed in IGF8212V overlaps with that reported in other <i>S. etruscus</i> individuals and some <i>S. hundsheimensis</i> specimens.
Skull	Zygomatic arch thicker and straighter in <i>S. hundsheimensis</i> than in <i>S. etruscus</i> ; dorsal cranial profile and orbital shape used in comparative diagnosis.	Skull overall close to Upper Valdarno <i>S. etruscus</i> , with slightly flat dorsal profile and slender, sinuous zygomatic arch; zygomatic arch similar in thickness and curvature to the Hundsheim skull.	Partly supports <i>S. etruscus</i> , but shows overlap with <i>S. hundsheimensis</i> .	Cranial evidence supports <i>S. etruscus</i> as a whole, but single cranial characters such as zygomatic thickness and orbit position should be used cautiously.
Mandible	Mandibular proportions, ascending branch morphology, condylar region and mandibular angle used in comparisons among <i>S. etruscus</i> , <i>S. hundsheimensis</i> and <i>S. jeanvireti</i> .	Ascending branch broadly comparable to <i>S. etruscus</i> and <i>S. hundsheimensis</i> ; condylar neck less developed than in some <i>S. etruscus</i> ; smaller than <i>S. jeanvireti</i> and with a different mandibular-angle morphology.	Largely non-discriminant between <i>S. etruscus</i> and <i>S. hundsheimensis</i> ; differs mainly from <i>S. jeanvireti</i> by size and proportions.	Weak diagnostic value. Cannot alone separate <i>S. etruscus</i> from <i>S. hundsheimensis</i> .
Scapula	Supraglenoid tubercle more transversely developed and coracoid process more pronounced in <i>S. hundsheimensis</i> and <i>S. jeanvireti</i> than in <i>S. etruscus</i> .	Glenoid cavity elliptical; supraglenoid tubercle anteriorly developed but transversely short and rounded; coracoid process reduced.	Supports the condition expected for <i>S. etruscus</i> .	One of the clearer postcranial characters supporting attribution to <i>S. etruscus</i> , although scapular characters should still be combined with other elements.
Humerus	Shape of the greater tubercle, distal trochlea, lesser tubercle and distal epiphysis used to separate <i>S. etruscus</i> , <i>S. hundsheimensis</i> and <i>S. jeanvireti</i> .	Distal epiphysis close to <i>S. etruscus</i> from Capitone, Upper Valdarno, Senèze and Apollonia; distal trochlea oblique; greater tubercle convexity partly recalls <i>S. jeanvireti</i> ; some proximal features partly overlap with <i>S. hundsheimensis</i> .	Mostly supports <i>S. etruscus</i> , but it is not in agreement or weakens a strict use of some proximal humeral characters.	Informative only in combination with other elements. The humerus shows the mosaic expression of characters emphasized in the manuscript.
Radius	Proximal articular morphology, development of the radial styloid process and distal proportions considered useful in comparative diagnosis.	General proportions and proximal morphology broadly similar to <i>S. etruscus</i> , <i>S. hundsheimensis</i> and <i>S. jeanvireti</i> ; dimensions close to or slightly below the lower range of <i>S. etruscus</i> .	No clear in agreement, but poorly useful for discrimination at species-level.	Low diagnostic value. The radius confirms the small size of IGF8212V but does not provide strong species-level separation.
Ulna	Breadth of olecranon, development of the anconeus process and humeral articular surface used in Stefanelli et al. to compare <i>S. etruscus</i> and <i>S. hundsheimensis</i> .	Olecranon broken proximally but prominent and posteriorly elongated; sigmoid notch broad and divided distally; distal articular surface rectangular.	Partly observable, but not sufficiently distinctive for a secure taxonomic assessment.	Weak diagnostic value in IGF8212V. Should not be used as an isolated diagnostic element.
MCIII	Broader distal articular surface and different proximal facet arrangement reported in <i>S. hundsheimensis</i> compared with <i>S. etruscus</i> ; proximal facet morphology emphasized by Stefanelli et al.	Distal breadth does not clearly differ from the Hundsheim specimen; proximal articular morphology close to <i>S. etruscus</i> , but some facet relationships overlap with <i>S. hundsheimensis</i> .	Partly contradicts a strict separation between <i>S. etruscus</i> and <i>S. hundsheimensis</i> based on MCIII.	Weak diagnostic value when isolated. Supports the broader conclusion that MCIII characters overlap among Early Pleistocene <i>Stephanorhinus</i> .
Femur	Lesser trochanter development and distal trochlea orientation used to distinguish <i>S. etruscus</i> from <i>S. jeanvireti</i> ; greater trochanter development used in comparisons with <i>S. hundsheimensis</i> .	Femur slender and small; overall close to <i>S. etruscus</i> , but lesser trochanter and distal trochlea differences from <i>S. jeanvireti</i> are not consistently observed; greater trochanter more proximally developed than in <i>S. hundsheimensis</i> .	Mostly compatible with <i>S. etruscus</i> , but partly contradicts some proposed differences from <i>S. jeanvireti</i> and <i>S. hundsheimensis</i> .	Weak to moderate diagnostic value. Femoral morphology mainly supports <i>S. etruscus</i> in the context of the whole skeleton, but isolated femora may be misleading.
Tibia	Wider epiphyses and dorsoplantarly compressed diaphysis in <i>S. hundsheimensis</i> ; popliteal incisure and distal morphology used in comparisons with <i>S. jeanvireti</i> and <i>S. etruscus</i> .	Differences from Hundsheim and Untermaassfeld are not always evident; popliteal incisure similar to <i>S. jeanvireti</i> ; distal epiphysis closer to <i>S. etruscus</i> than to typical <i>S. hundsheimensis</i> .	Partly contradicts a strict use of general robustness and popliteal-incisure morphology.	Weak to moderate diagnostic value. Some distal tibial characters may be informative, but general robustness and proportions overlap among species.
Astragalus	Trochlear inclination, proximal-lateral calcaneal facet, medio-distal calcaneal facet, latero-distal calcaneal facet and their connections used as diagnostic or comparative features.	Proximo-lateral facet concave and trapezoidal, with a small triangular convex distal extension. Medio-distal facet bell-shaped and mostly flat, with a slightly convex distal margin. Latero-distal facet transversely elongated and reaching the medio-distal facet. The first two facets are separated by a deep and narrow sinus tarsi.	Mostly supports <i>S. etruscus</i> , especially the morphology observed in Upper Valdarno specimens, but shows partial overlap with <i>S. jeanvireti</i> and <i>S. hundsheimensis</i> .	Moderate diagnostic value only when associated with the complete skeleton. The astragalus supports <i>S. etruscus</i> but confirms overlap in tarsal morphology.
Calcaneus	Shape and development of the sustentaculum tali, astragalar facets, and presence/absence of tibial and	Sustentaculum tali medially well developed, slightly curved anteriorly and almost orthogonal to the calcaneal body in posterior view. Tibial and	Supports <i>S. etruscus</i> relative to several <i>S. jeanvireti</i> calcanei; partly overlaps with <i>S. hundsheimensis</i> , which is variable.	Useful character complex, but not diagnostic alone. The absence of tibial/fibular facets and separated astragalar facets match several

(continued on next page)

Table 2 (continued)

Anatomical element	Character proposed in literature	Condition observed in IGF8212V	Agreement with proposed character	Interpretation
	fibular facets used in comparative diagnosis.	fibular facets absent. The articular surface on the sustentaculum tali is separated from the latero-distal astragalar facet by a distinct groove.		<i>S. etruscus</i> specimens from Apollonia and Upper Valdarno.
MTIII	Parallel-flanked diaphysis in <i>S. etruscus</i> versus distally widening diaphysis in <i>S. hundsheimensis</i> ; relative position of proximal lateral articular facets used in species-level distinction.	Diaphysis widens distally, resembling the condition reported for <i>S. hundsheimensis</i> , but this character is affected by ontogeny. Dimensions and overall morphology are close to small <i>S. etruscus</i> specimens from Pietrafitta.	Contradicts a strict use of MTIII diaphyseal profile and proximal facet position as diagnostic for <i>S. hundsheimensis</i> .	Overlap with <i>S. hundsheimensis</i> in some characters, but overall compatible with <i>S. etruscus</i> . MTIII strongly supports the conclusion that isolated metapodial characters may be misleading.

and Middle Pleistocene European rhinoceroses support the view that several postcranial characters traditionally used to distinguish *S. etruscus* from *S. hundsheimensis* are more variable than previously assumed. For instance, Chitoglou et al. (2025) revised Early Pleistocene rhinoceros remains from Greece and highlighted the limited diagnostic value of some isolated and/or fragmented postcranial elements. Their study documents *S. etruscus* and *Stephanorhinus* cf. *S. hundsheimensis* in partly overlapping chronological and geographical contexts but also shows that some appendicular elements display combinations of characters that are difficult to assign unambiguously at species level. This agrees with the observations from IGF8212V that preserves an overall *S. etruscus* morphology, but individual bones may show features classically reported as typical for *S. hundsheimensis* or *S. jeanvireti*. Accordingly, a detailed morphological comparison of IGF8212V with *S. etruscus*, *S. hundsheimensis*, and *S. jeanvireti* challenges several previously proposed diagnostic differences between these three taxa. The condition observed in IGF8212V is summarized in Table 2 in relation to the main characters proposed in the literature and recently discussed by Stefanelli et al. (2025). The table shows that several characters traditionally considered useful at species level are not consistently observable in the Poggio Rosso skeleton. Some of them support the attribution to *S. etruscus*, whereas others overlap with conditions reported for *S. hundsheimensis* or *S. jeanvireti*. Accordingly, this pattern reveals that individual postcranial characters may have limited diagnostic value when they are considered outside an associated cranial and dental remain.

1. Position of the orbit: Fortelius et al. (1993) suggested that the anterior rim of the orbit in *S. etruscus* lies above M3. However, IGF8212V displays an orbit extending well above M2. This character is affected by age and sexual maturity in rhinoceroses, as noted by Pandolfi (2022).
2. Zygomatic arch: Mazza (1988) and Fortelius et al. (1993) reported that *S. hundsheimensis* displays a thicker and straighter zygomatic arch compared to *S. etruscus*. However, the skulls of Poggio Rosso and Hundsheim show a similar zygomatic arch thickness. This character seems to be affected by feeding behaviour of the animal and may also depend on ontogeny, as observed in extant Asian species (Groves, 1967, 1982; Antoine, 2002; Pandolfi, 2022; Pandolfi et al., 2025).
3. Humerus morphology: Guérin (1972, 1980) reported a straight greater tubercle convexity in *S. jeanvireti* and a sinuous one in *S. etruscus*. In contrast, IGF8212V shows a straight greater tubercle convexity, similarly to *S. jeanvireti*.
4. Scapular morphology: Stefanelli et al. (2025) considered the morphology of the glenoid cavity, the development of the supraglenoid tubercle and the coracoid process as relevant comparative characters. In IGF8212V, the glenoid cavity is elliptical, the supraglenoid tubercle is anteriorly developed but transversely short and rounded, and the coracoid process is reduced. This combination supports attribution to *S. etruscus*,

although the glenoid outline alone partly overlaps with *S. hundsheimensis*.

5. Metacarpal morphology: Fortelius et al. (1993) suggested a broader distal articular surface of the MCIII in *S. hundsheimensis* compared to *S. etruscus*. This difference is not observed between IGF8212V and the Hundsheim specimen. Chitoglou et al. (2025) noted that the morphology of the proximal articular surface of the MCIII may overlap between *S. etruscus* and *S. hundsheimensis*.
6. Femur morphology: Guérin (1980) noted a lesser developed lesser trochanter and a more oblique axis of the trochlea in distal view in *S. etruscus* compared to *S. jeanvireti*. These differences are not observed between IGF8212V and *S. jeanvireti* specimens from Montopoli and Viallette. In addition, Fortelius et al. (1993) reported that the greater trochanter is more developed in *S. hundsheimensis* compared to *S. etruscus*. However, IGF8212V shows a more proximally developed greater trochanter than in *S. hundsheimensis*.
7. Tibia morphology: Fortelius et al. (1993) noted wider epiphyses and more compressed dorsoplantar diaphysis in *S. hundsheimensis* compared to *S. etruscus*. These differences are not detected comparing IGF8212V with *S. hundsheimensis* from Hundsheim and Untermassfeld. In addition, Mazza (1988) suggested a proportionally narrower popliteal incisure of the tibia in *S. jeanvireti* than in *S. etruscus*. However, the popliteal incisure of IGF8212V is proportionally very similar to *S. jeanvireti*.
8. Astragalar morphology: The astragalus of IGF8212V supports attribution to *S. etruscus* in the general arrangement of the calcaneal facets and in the presence of a deep and narrow sinus tarsi. However, the trapezoidal proximo-lateral facet with a small triangular distal extension recalls, in part, the condition described in *S. jeanvireti*, whereas the more marked latero-distal facet partly approaches the condition reported for *S. hundsheimensis*.
9. Calcaneal morphology: Fortelius et al. (1993) reported a stockier calcaneus with a more extended summital tuberosity in *S. hundsheimensis* compared to *S. etruscus*. These differences are not observed between IGF8212V and specimens from Hundsheim and Untermassfeld.
10. Metatarsal morphology: Fortelius et al. (1993) reported a parallel flanked diaphysis of the MTIII, in dorsal view, in *S. etruscus* and a gradually widens distal in *S. hundsheimensis*. This difference is not observed in IGF8212V. Mazza (1988) noted that the posterior articular facet on the lateral face of the proximal epiphysis is lower than the anterior one in *S. hundsheimensis*, while it is the opposite in *S. etruscus*. However, in IGF8212V the posterior articular facet is lower than the anterior one. Chitoglou et al. (2025) observed that the shape of the metatarsal facets, may overlap between *S. etruscus* and *S. hundsheimensis* and are not always enough for a certain taxonomic assignment when the material is isolated or fragmented.

3.3. Morphometric variability in fossil rhinoceroses and body mass estimation

Morphometric analysis of the postcranial elements from Poggio Rosso confirms that the studied individual was relatively small. Despite being an adult (stage 7 in Pandolfi et al., 2024), most postcranial measurements fall close to, or slightly below, the lower dimensional range reported by Guérin (1980) for *S. etruscus*. This pattern is particularly evident in the long bones and metapodials, while the astragalus and calcaneus remain broadly within the known dimensional variability of the species. Following the results obtained by Faggi and Pandolfi (2022), suggesting that *S. etruscus* males exhibited slightly larger forelimbs and hindlimbs than females, it is plausible to refer the studied skeleton to an adult female. In the bivariate plots, Poggio Rosso occupies the lower portion of the *S. etruscus* morphospace, but it does not fall outside it. In the MCIII plots (Fig. 7), IGF8212V shows low values for both length (L) and distal transverse diameter (DTD) and also occupies the lower part of the *S. etruscus* range in the dimension of the distal epiphysis (DTD-DAPD plot). The specimen is therefore smaller than most comparative *S. etruscus* material, but remains within the morphometric range of the species, particularly when compared with small-sized individuals from Pietrafitta, Olivola Val di Magra and some Upper Valdarno specimens. By contrast, *S. jeanvireti* is displaced toward higher values, especially in metapodial length and transverse diameter, whereas *S. hundsheimensis* generally occupies an intermediate to larger morphospace, with partial overlap with the upper range of *S. etruscus*. The bivariate plots based on astragalus measurements (Fig. 10) show that the two Poggio Rosso values lie at the lower end of the *S. etruscus* distribution, below most *S. hundsheimensis* and clearly below *S. jeanvireti*. Similarly, the Hm boxplot indicates that Poggio Rosso is smaller than the central distribution of *S. etruscus*, but its values remain close to the lower values of the species range. In the MTIII plots (Fig. 11), Poggio Rosso falls within the lower part of the *S. etruscus* distribution for length and distal transverse diameter, whereas *S. hundsheimensis* and especially *S. jeanvireti* show larger and more robust metatarsals. Overall, these plots indicate that the small size of IGF8212V represents the lower end of a broad intraspecific morphometric range. The comparison among *S. etruscus* localities further shows that the species is characterized by marked morphometric variability. Some considered samples of *S. etruscus* include relatively large individuals, such as those from Saint Vallier, La Puebla de Valverde and Les Etouaires, whereas others include smaller specimens, such as those from Olivola Val di Magra, Pietrafitta, Westerhoven and parts of the Upper Valdarno sample. However, these locality-level differences do not form a simple chronological sequence. The Poggio Rosso remains (ca. 1.8 Ma) are comparable in size to those from Pietrafitta (ca. 1.6 Ma, Italy) and Westerhoven (latest Early Pleistocene, Netherlands). Looking at the available European sample, it is evident that while some Early Pleistocene localities are characterized by large-sized individuals (Villaroya: Cerdeño and Alberdi, 2016; Guérin, 1980; de Villalta Comella, 1952; St. Vallier: Guérin, 2004; Perrier-Etouaires Guérin 1972,1980, 2007; Heintz et al., 1974; Nomade et al., 2014; La Puebla de Valverde: Guérin and Heintz, 1971; Nomade et al., 2014) and other localities show small-sized individuals (Venta Micena: Santafé-Llopis and Casanovas-Cladellas, 1987; Cerdeño, 1993; Huéscar I: Cerdeño, 1993; van der Made, 2010, Villanueva de Pitamo: Aguirre, 1989), many of them do not fit neatly into these groups (Sénèze: Guérin, 1980, Cúllar de Baza: Ruiz Bustos, 1976; Cerdeño, 1989; Cerdeño, 1993). As a matter of the fact, *S. etruscus* from Sénèze (2.2 Ma, Alpes-de-Haute-Provence, France, Guérin, 2024) exhibits a wide range of morphometric variability, including both large-sized individuals, close to *S. jeanvireti* (Chitoglou et al., 2025), and individuals similar in size to IGF8212V. For instance, the length of MCIII at Sénèze varies from 181.4 to 219.2 mm ($n = 5$; CV = 7.30%), whereas it ranges from 194 to ca. 197 mm ($n = 2$; CV = 1.09%) at Olivola Val di Magra and from 190 to 200.8 mm in the Upper Valdarno sample ($n = 4$; CV = 2.65%).

The radius-, tibia- and humerus-length-based body mass estimates

obtained for IGF8212V range from 904 to 954 kg, with a mean value of 930 kg and a median value of 927 kg (Supplementary File 3). The standard deviation is 18.6 kg, and the coefficient of variation is 2%, indicating low dispersion among the estimates (Table 1). This suggests that the radius- and tibia-based estimates are internally consistent and provide a reliable approximation of the body mass of the Poggio Rosso individual. Furthermore, when compared with locality-level body-mass ranges, the mean estimate for Poggio Rosso falls within the observed ranges of Olivola Val di Magra, Pietrafitta, and the Upper Valdarno samples. Notably, the median value of IGF8212V is virtually close to that of Olivola Val di Magra (1009 kg), one of the best-represented locality samples in the dataset (Table 1). The Poggio Rosso mean value is also included within the ranges of Pietrafitta and the Upper Valdarno. These comparisons indicate that IGF8212V represents a small-sized adult individual, but its estimated body mass remains compatible with the documented intraspecific variability of *S. etruscus*. A Kruskal–Wallis test performed on the three best-represented *S. etruscus* locality samples, namely Pietrafitta, Olivola Val di Magra and Upper Valdarno, revealed no significant differences in estimated body mass among localities ($\chi^2 = 1.23$, $df = 2$, $p = 0.53$). Pairwise Dunn post-hoc comparisons with Bonferroni correction confirmed the absence of significant differences between Pietrafitta and Olivola Val di Magra ($p_{\text{adj}} = 0.513$), Pietrafitta and Upper Valdarno ($p_{\text{adj}} = 0.965$), and Olivola Val di Magra and Upper Valdarno ($p_{\text{adj}} = 0.513$). These results indicate broad overlap in estimated body mass among the best-represented *S. etruscus* locality samples and do not support a robust locality-level separation based on body mass. Finally, a broader comparison including Olivola Val di Magra, Pietrafitta, Upper Valdarno, Saint Vallier, La Puebla de Valverde and Les Etouaires is here performed. Among these six localities, mean body-mass estimates range from 1014 kg at Olivola Val di Magra to 1140 kg at Saint Vallier, with broadly overlapping ranges. A Kruskal–Wallis test revealed no significant differences in estimated body mass among these localities ($\chi^2 = 7.39$, $df = 5$, $p = 0.193$). Pairwise Dunn post-hoc comparisons with Bonferroni correction also showed no significant differences between any locality pair. Although Olivola Val di Magra tends to show the lowest mean value and Saint Vallier the highest, this difference is not statistically significant after correction for multiple comparisons. These results indicate broad locality-level overlap in estimated body mass and do not support a robust separation among the considered European *S. etruscus* samples. The small size of IGF8212V may also have been influenced by local ecological conditions. The Poggio Rosso deposits belong to the lacustrine-palustrine and alluvial succession of the Upper Valdarno Basin, which records variable environmental settings during the Early Pleistocene. However, the available evidence does not allow us to directly link the body size of IGF8212V to a specific climatic or vegetational phase. Body size in rhinoceroses may reflect several interacting factors, including sex, ontogenetic stage, population structure, resource availability and geographic variability. Therefore, an ecophenotypic component cannot be excluded, but it cannot be tested from the Poggio Rosso individual alone.

4. Implications for the latest Early Pleistocene “small *Stephanorhinus*”

The Rhinocerotidae family exhibits sexual dimorphism in both extant and extinct species (Groves, 1982), and a recent study by Faggi and Pandolfi (2022) documented a subtle but measurable sexual dimorphism in the limbs of *S. etruscus*. Additionally, ontogenetic patterns reveal complex morphological and morphometric changes throughout the lifespan of rhinoceroses (Guérin, 1980; Groves, 1982; Pandolfi, 2022; Pandolfi et al., 2024). Accordingly, the differences among *S. etruscus* specimens reported in literature may be explained, at least in part, by sexual dimorphism, ontogeny, and geographic variability, rather than a size reduction trend or presence of different morphotypes. A comparable pattern has recently been documented in *S. hemitoechus*, for which size-based subspecific distinctions have been

rejected and body-size variation appears to reflect complex regional and ecological dynamics rather than a simple chronological pattern (Pandolfi et al., 2025; Uzunidis and Pandolfi, 2026). The morphometric distribution of IGF8212V may be therefore considered in light of the long-standing debate concerning the so-called “small *Stephanorhinus*” recorded in several latest Early Pleistocene European localities. Mazza et al. (1993) interpreted the small rhinoceros from Pietrafitta as close to *S. hundsheimensis* and possibly representing an intermediate stage between *S. etruscus* and *S. hundsheimensis*. However, this interpretation was critically reconsidered by van der Made (2010, 2015), who noted that the ratio diagrams used by Mazza et al. (1993) lack a clear legend, may be affected by small sample size, and may have been interpreted using an ambiguous comparative standard. Following this criticism, the Pietrafitta material can be interpreted as closer to *S. etruscus* than to *S. hundsheimensis*, as also suggested by Pandolfi and Petronio (2011), Pandolfi et al. (2017) and Cirilli et al. (2020), not only in size but also in proportions. Furthermore, van der Made (2015) emphasized that morphometric ranges among *S. etruscus*, the “small *Stephanorhinus*”, and *S. hundsheimensis* may overlap, and that different skeletal elements may fall outside the range of one or another taxon depending on sample composition. This point was later highlighted by Chitoglou et al. (2025), who discussed the limited diagnostic value of several isolated or fragmented postcranial elements. A comparable methodological problem is raised by the Contrada Monticelli rhinoceros assemblage. Mazza and Varola (1999) revised the rhinoceros material from this locality and referred the cranial, mandibular and postcranial remains to *S. hundsheimensis*, although they also noted the occurrence of a small-sized femur with *etruscus*-like affinities, interpreted as probably reworked. Stefanelli et al. (2025) later assigned the postcranial sample to *S. hundsheimensis* as the most parsimonious interpretation, but also recognized that the marked morphological and biometric variability could reflect alternative scenarios, including the possible presence of both *S. etruscus* and *S. hundsheimensis*, hybridisation, or different morphotypes within the same species. However, the morphology of some elements suggests that the taxonomic composition of the Contrada Monticelli rhinoceros assemblage may be more complex than a single highly variable population of *S. hundsheimensis*. For instance, the humerus MSTB-CM 30603 differs from the other humeri from Contrada Monticelli in having a more laterally developed lateral epicondyle, a more posteriorly pointed medial epicondyle and a slightly oblique trochlear tilt. These features recall, at least in part, the morphology observed in *S. kirchbergensis* from Taubach and are consistent with the more bulging epicondylar region reported for *S. kirchbergensis* compared with *S. hundsheimensis*. In addition, some cranial and mandibular features of the Contrada Monticelli material, although previously referred to *S. hundsheimensis* by Mazza and Varola (1999), may be compatible with the morphology of *S. kirchbergensis*. Therefore, although a formal reassessment of the Contrada Monticelli assemblage is beyond the scope of the present contribution, this sample may represent, at least in part, a taxonomically mixed assemblage rather than a single highly variable population of *S. hundsheimensis*. In this context, the Poggio Rosso skeleton provides direct evidence that isolated postcranial remains can lead to misleading taxonomic identification when characters are shared among closely related species or when size is used as the main criterion. It therefore shows that some characters previously regarded as taxonomically informative may occur in combination within *S. etruscus*. The reduced dimensions of IGF8212V, similar to the specimens from Pietrafitta, also indicate that small postcranial size can occur in an associated adult skeleton attributable to *S. etruscus*. Consequently, isolated small postcranial remains should not be assigned to a transitional form or to *S. hundsheimensis* on the basis of size, proportions or single postcranial characters alone, without supporting cranial, dental, or associated postcranial evidence, including anatomical arguments.

5. Conclusion

Complete fossil rhinoceros skeletons are rare in the Pleistocene record of western Europe, yet they are pivotal for assessing morphological and morphometric variability within extinct taxa. The well-preserved Upper Valdarno specimen studied here (IGF8212V) provides a detailed description of the postcranial anatomy of a single *Stephanorhinus etruscus* individual. In doing so, it supplies new comparative data that improve taxonomic identifications and cross-checks against other Plio-Pleistocene species. Comparative analysis of IGF8212V with cranial and postcranial material of *S. etruscus*, *S. hundsheimensis*, and *S. jeanvireti* from multiple western European localities questions several previously reported diagnostic distinctions among these taxa. In particular, the available postcranial and body-mass data do not support a simple unidirectional size-reduction trend in western European *S. etruscus*. The broad morphometric ranges observed in the Upper Valdarno and at Senèze are indeed more plausibly explained by intraspecific factors, most notably sexual dimorphism and/or ontogenetic variation, than by simple taxonomic or temporal differentiation. More broadly, IGF8212V demonstrates that the taxonomic identification of isolated postcranial remains of Early Pleistocene rhinoceroses should be approached with caution. Several characters traditionally considered diagnostic are shown here to overlap among *S. etruscus*, *S. hundsheimensis* and *S. jeanvireti*, or to vary within the morphology of a single associated *S. etruscus* skeleton. The Poggio Rosso specimen therefore provides an important reference for future revisions of Quaternary rhinoceros assemblages and for reassessing the taxonomic significance of small-sized *Stephanorhinus* remains in Europe.

CRedit authorship contribution statement

Luca Pandolfi: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Andrea Faggi:** Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Saverio Bartolini-Lucenti:** Writing – review & editing, Visualization. **Lorenzo Rook:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition, Data curation.

Declaration of competing interest

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

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Appendix A. Supplementary data

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