



Palaeontology, Systematics and Evolution (Vertebrate palaeontology)

## Revision of the rhinoceros remains (Rhinocerotidae, Mammalia) from the late Pliocene of Etouaires (Auvergne, France) and the morphological distinction between the postcranial bones of *Stephanorhinus elatus* and *S. etruscus*



### Révision des restes de rhinocéros (Rhinocerotidae, Mammalia) du Pliocène supérieur d'Étouaires (Auvergne, France) et distinction morphologique des os post-crâniens de *Stephanorhinus elatus* et *S. etruscus*

Manuel Ballatore<sup>a,\*</sup>, Marzia Breda<sup>b</sup>

<sup>a</sup> Via Antico Filatoio 7, 10093 Collegno, TO, Italy

<sup>b</sup> Department of Human Studies, University of Ferrara, Corso Ercole I d'Este 32, 44121 Ferrara, Italy

#### ARTICLE INFO

##### Article history:

Received 31 July 2017

Accepted after revision 29 June 2018

Available online 29 August 2018

Handled by Lorenzo Rook

##### Keywords:

Étouaires

Rhinoceros

Morphology

Postcranial bones

*Stephanorhinus elatus*

*Stephanorhinus etruscus*

##### Mots clés :

Étouaires

Rhinocéros

Morphologie

Os postcrâniens

*Stephanorhinus elatus*

*Stephanorhinus etruscus*

#### ABSTRACT

This work revises the rhinoceros remains from the well-known early Villafranchian locality of Étouaires (Auvergne, France), which have been collected on multiple occasions since the late 18th century. The species *Stephanorhinus elatus* and *S. etruscus* are present, both represented mainly by postcranial elements. To identify them, a detailed preliminary analysis of the morphological differences between the postcranial skeletons of the two species has been undertaken, using the material from Vialette (Haute-Loire, early Villafranchian) and Senèze (Haute-Loire, early late Villafranchian) as comparison for *S. elatus* and *S. etruscus* respectively, plus some specimens of *S. etruscus* from Upper Valdarno (Tuscany, middle Villafranchian). These localities have been chosen because they all yielded only one of the two species. The morphological distinction between the two species is not easy, since the inter-specific variability often overlaps and includes polymorphic characters. However, a few diagnostic characters are described, and intra-specific variability has been investigated as much as possible with the fossil material under investigation.

© 2018 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

#### R É S U M É

Cette étude propose la révision des restes de rhinocéros collectés à de multiples reprises depuis la fin du XVIII<sup>e</sup> siècle sur le célèbre site d'Étouaires (Auvergne, France) datant du Villafranchien inférieur. Les espèces *Stephanorhinus elatus* et *S. etruscus* sont présentes, et toutes deux représentées principalement par des éléments post-crâniens. Afin de les identifier, nous avons mené une étude préliminaire détaillée sur les différences du squelette post-crânien entre ces deux espèces en nous appuyant sur le matériel de Vialette

\* Corresponding author.

E-mail addresses: [manuel.ballatore@libero.it](mailto:manuel.ballatore@libero.it) (M. Ballatore), [brdmrz@unife.it](mailto:brdmrz@unife.it) (M. Breda).

(Haute-Loire, Villafranchien inférieur) et Senèze (Haute-Loire, début du Villafranchien supérieur), respectivement *S. elatus* et *S. etruscus*, et sur certains spécimens de *S. etruscus* du Valdarno supérieur (Toscane, Villafranchien moyen). Nous avons choisi ces localités, car elles ne comportent qu'une seule des deux espèces. La distinction morphologique entre les deux espèces est complexe en raison d'un recoupement fréquent dans la variabilité interspécifique et de caractères polymorphes. Cependant, peu de caractères diagnostiques sont décrits et la variabilité intraspécifique a été étudiée autant que possible au vu du matériel fossile disponible.

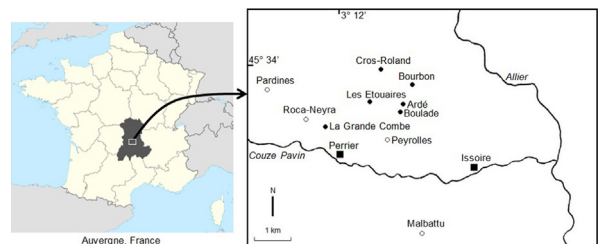
© 2018 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

## 1. Introduction

Several French localities have been famous since the 19th century for their rich Villafranchian faunas (e.g., Rocca-Neyra, Pardines, Saint-Vidal, Coupet, Chiljac, Peyrolles, Blassac; Heintz et al., 1974). Part of them are of particular interest for their abundant rhinoceros remains (Saint-Vallier, Guérin, 2004; Senèze, Delson et al., 2006; Vialette, Lacombat et al., 2008; Étouaires, Ballatore and Breda, 2016). The fossil rhinoceroses from Europe deserve great attention because their remains are relatively abundant in the terrestrial large mammal palaeocommunities and their investigation contributes to ecological and evolutionary research on the Quaternary Period.

Among the Villafranchian French localities, Étouaires deserves particular attention since it brings two rhinoceros species (*Stephanorhinus elatus* and *S. etruscus*), and also, because it represents the type locality of the species *S. elatus*, described as *Rhinoceros elatus* by Croizet and Jobert (1828) mainly from postcranial remains. More than a century later, Guérin (1972) described the remains from Vialette as the new species *Dicerorhinus jeanvireti* although openly declaring that it was the same species described at Étouaires. The generic name *Dicerorhinus* is replaced by the valid name *Stephanorhinus* (as recently discussed by Pandolfi and Tagliacozzo, 2015, after Groves, 1983 and Fortelius et al., 1993), while the specific name “*jeanvireti*”, which has been preferentially used in the literature, is invalid, as shown by Ballatore and Breda (2016). As pointed out by Ballatore and Breda (2016), the original name ‘*elatus*’ could not be considered ‘oblitum’ by Guérin (1972) and the type series described by Croizet and Jobert (1828) can still be recognised in the collections of the ‘Muséum national d’histoire naturelle’ in Paris. [Although not officially submitted to the ICZN, the case was discussed in 2013 with Prof. A. Minelli (University of Padova - former president of the ICZN), who considered the case clear enough not to require a direct involvement of the Commission. As for his suggestion, the case has been explained in an international journal (Ballatore and Breda, 2016), a lectotype has been chosen, and the rules supporting the restoration of the earlier specific name have been quoted.

Ballatore and Breda (2016) described this type series, demonstrated it is a homogeneous batch only pertaining to the species *S. elatus*, and chose a lectotype and paralectotype. However, many other remains from Étouaires, collected in later years, still need a revision because, despite their importance, they have never been studied in detail,



**Fig. 1.** Map of the Perrier Mountain area in the Puy-de-Dôme (Auvergne, France) showing the localities included into the ‘Étouaires’ site (full circles) and the other main ones (empty circles) of Roca-Neyra, Pardines, Peyrolles and Malbattu. Present Municipalities of Issoire and Perrier are indicated with full squares. Adapted from Pastre (2004; Fig. 1).

**Fig. 1.** Carte de la zone de la montagne Perrier dans le Puy-de-Dôme (Auvergne, France) montrant les sites inclus dans les « Étouaires » (cercles pleins) et les autres sites principaux (cercles vides) de Roca-Neyra, Pardines, Peyrolles et Malbattu. Les villes d’Issoire et Perrier sont indiquées par des carrés. Adapté d’après Pastre (2004 ; Fig. 1).

and have only been referred to very superficially in few papers (i.e. Guérin, 1972, 1980, and Heintz et al., 1974).

Thus, the first aim of this work is to revise in full the rhinoceros material from Étouaires, assigning each specimen to either of the two species recorded at the site, *S. elatus* and *S. etruscus*. However, since this material is almost entirely composed of postcranial remains, a detailed morphological analysis of the characters distinguishing the two species has been carried out and this gives us the opportunity to describe in detail the morphological distinction between the two species.

A long series of names has been used for the deposits at Étouaires, the most common being ‘Perrier’ or ‘Perrier-Étouaires’, but here the denomination ‘Étouaires’ is intended sensu Heintz (1970) as a replacement of the ancient denominations. A historical overview is given below.

### 1.1. The locality of Étouaires (Puy-de-Dôme, Auvergne, France)

The locality of Étouaires is a palaeontological site in the Perrier Plateau (Puy-de-Dôme, Auvergne, Fig. 1), a fluvio-volcanic sequence spanning from the late Pliocene to the early Pleistocene, consisting of sedimentary deposits by the Allier river and trachytic pyroclastites by the Mont-Dore stratovolcano (Pastre, 2004, Valli et al., 2006). The area has been known since the late 18th century (Buc’hoz, 1796, Deveze de Chabriet and Bouillet, 1827) and the

first compendium on the geology of the Perrier Plateau, including the description of the fossils remains, is due to Bravard (1828) and Croizet and Jobert (1828). The Perrier Mountain includes different fossiliferous sites (e.g., Ravin des Étouaires, Roca-Neyra, Peyrolles, Boulade, Cros-Roland, Bourbon, Ardé, Ravin de la Grande Combe, Creux de Traverse, Pardines, Neschers) and the so called ‘faune de Perrier’ was problematic, since the earliest collections were made by mixing bones from different outcrops (see Bout, 1960, Depéret et al., 1923, Jung, 1946). Bravard (1828) pointed out that the numerous fossil remains from the Perrier Mountain come from several different outcrops including the ‘ravin des Étouaires’.

After Croizet and Jobert’s (1828) work, many other works on geology and palaeontology of the Perrier were published, but none of them treated the rhinoceroses selectively: Pomel (1846, 1854), Depéret (1884), Boule (1888), Michel-Lévy and Munier-Chalmas (1889, 1892), Stehlin (1904), Biélawski (1905), Depéret et al. (1923), Schaub (1941, 1943, 1949), Piveteau (1958), Jung (1946), Bout and Azzaroli (1952), Bout (1960). In his review of the authors who dealt with the fossil remains from the Perrier Mountain, Bout (1960) associated Croizet and Jobert with Étouaires: “Bravard (1828) pour tous les ravins qui entaillent le plateau sur ses diverses faces, Croizet et Jobert (1828) pour le ravin des Étouaires, Munier-Chalmas et Michel-Lévy (1890) en une coupe synthétique, ont décrit ou figuré les alluvions poncées de Perrier” (Bout, 1960; p. 149). Heintz (1967) confirmed that the fossils described by Croizet and Jobert (1828) constitute the fauna from Étouaires: “La faune de Étouaires a été étudiée pour la première fois par Croizet et Jobert” (Heintz, 1967; p. 540). Finally, Heintz (1970) put order to the locality of Étouaires and suggested to use this name to replace the ancient denominations such as “Perrier, Perrier-Étouaires, niveau inférieur de Perrier, Perrier bas, Ravin des Étouaires, etc.” (Heintz, 1970; p. 19). Moreover, he gave a detailed characterization of the re-labelled site which “désigne un gisement situé au fond d’un ravin qui entaille le flanc E-S-E du plateau ou de la montagne de Perrier, non loin (à peine 1 km) à l’W-N-W de la ferme de Boulade”.

Obviously this modern characterization does not fit the bones collected in the previous century: “les matériaux recueillis à Perrier par les anciens auteurs (Devèze de Chabriol et Bouillet, Croizet, Bravard et d’autres) proviennent en partie du Ravin des Étouaires et en partie des localités ou lieux-dits suivants: Boulade ou Montagne de Boulade, Cros-Roland, Bourbon, Ardé ou cote d’Ardé, Ravin de la Grande Combe, Creux de Traverse, Pardines, mais ne désignant pas le gisement de La Loubières de Pardines, découvert et exploité plus tard, Neschers, qui ne désigne cependant pas la formation fossilifère de Neschers qui contient du Renne. (...) Dans l’état actuel de ces collections, il est généralement impossible de savoir de quelle localité précise provient tel ou tel fossile. Nous avons donc, à la suite de S. Schaub regroupé tous ces matériaux sous l’unique appellation: Étouaires” (Heintz, 1970; p. 19). This last statement deserves a translation: “in the present state of the collections, it is mostly impossible to know from which exact locality each fossil comes from. Thus, as Schaub already did, we group all this material under the unique

name of Étouaires”. This applies well to the rhinoceros, since both Guérin (1972) and Heintz et al. (1974) discussed this taxon giving lists of the material from Étouaires that includes part of the bones described by Croizet and Jobert (1828).

### 1.1.1. Stratigraphy

The stratigraphic question about the Perrier Mountain regards the distinction among some major localities (e.g., Étouaires and Roca-Neyra, Bout, 1960, 1970, Heintz, 1967) from which four distinct local faunas have been recently identified (Étouaires, Roca-Neyra, Pardines and Peyrolles, Nomade et al., 2014). On the contrary, the minor localities grouped within Étouaires (e.g., Grande Combe, Bourbon, Ardé) are considered roughly coeval (Heintz, 1970). Actually, the ‘formation des Étouaires’ has been studied in detail and three sedimentary cycles have been identified: a basal layer of rhyolitic pumice dated at 3.18 Ma underlies cycle I, then another rhyolitic pumice stratum dated at 2.60 Ma underlies cycle II, while cycle III is directly superposed on it; at the top of the sequence, fallout trachytic sands, possibly synchronous with sedimentary cycle III, are dated at 2.47 and 2.35 Ma (Poidevin et al., 1984). Cycles I and II outcrop at the minor localities of la Grande Combe and Sablou do Lossa, cycle III outcrops at the localities of Étouaires s.s., Ardé and Bourbon, and all three cycles are superposed at les Bardelles (Poidevin et al., 1984). However, since no reference links each bone to a specific minor locality, it is impossible to subdivide the fauna. Therefore, the fauna from Étouaires (sensu Heintz, 1970) is not chronologically homogenous but groups different forms ranging from 3.18 to 2.35 Ma. However, since Étouaires is the richest site, most of the fauna can be referred to the most recent part of this range.

The first absolute dating proposed for the site was quite old: 3.2–3.3 Ma (Bout, 1960, 1967) and 3.1–3.4 (Bout, 1975). Later, it was considered much more recent, with Pastre (2004) suggesting a date of 2 Ma. Finally, Nomade et al. (2014) gave a  $^{40}\text{Ar}/^{39}\text{Ar}$  dating at 2.78 Ma, hence placing Étouaires in the early MNQ 16b or early Villafranchian, equivalent to the Triversa FU of the Italian biochronological scale (see correlation in Rook and Martínez-Navarro, 2010).

### 1.1.2. Faunal list

The faunal list reported by Heintz et al. (1974) consists of the following species: *Zygodon borsoni* (= *Mammuth borsoni*), *Anancus arvernensis*, *Tapirus arvernensis*, *Dicerorhinus etruscus* (= *Stephanorhinus etruscus*), *D. jeanvireti* (= *S. elatus*, Ballatore and Breda, 2016), *Cervus cusanus* (= *Procacpeolus cusanus*), *Croizetoceros ramosus*, *Cervus pardinensis*, *Cervus perrieri*, *Arvernoceros ardei*, *Sus arvernensis*, *Pliotragus ardeus*, *Gazella borbonica*, *Leptobos elatus*, *Nyctereutes megamastoides*, *Canis aff. etruscus*, *Baranogale antiqua*, *Enhydriactis ardea*, *Aonyx bravardi* (= *Lutra bravardi*), *Ursus etruscus*, *Hyena perrieri* (= *Pliocrocota perrieri*), *Euryboas lunensis* (= *Chasmaporthetes lunensis*), *Felis issiodorensis* (= *Lynx issiodorensis*), *Acinonyx pardinensis*, *Megantereon* (= *Megantereon cultridens*), *Galemys* sp., *Talpid* indet.

**Table 1**

Comparison of the lists given by Guérin (1972) and Heintz et al. (1974) of the rhinoceroses *Stephanorhinus elatus* and *S. etruscus* from Étouaires. Some points need a brief discussion: McII “AC 2933” in Guérin (1972) corresponds to ‘AC 2333’ in Heintz et al. (1974); McIII ‘2339’ in both Guérin (1972) and Heintz et al. (1974) corresponds to specimen labelled as ‘2332’ in the MNHN collection; Guérin (1972) lists correctly six tarsal bones (still present in the MNHN collection), while Heintz et al. (1974) count only five tarsal bones; MNHN.F.PET 243, corresponding to the label ‘AC 2331’ *pro parte*, is wrongly considered as metatarsal by Guérin (1972) and Heintz et al. (1974).

**Tableau 1**

Comparaison des listes proposées par Guérin (1972) et Heintz et al. (1974) sur les rhinocéros *Stephanorhinus elatus* et *S. etruscus* d'Étouaires. Certains points demandent une brève discussion : McII « AC 2933 » de Guérin (1972) correspond au « AC 2333 » de Heintz et al. (1974) ; McIII « 2339 » de Guérin (1972) et Heintz et al. (1974) correspondent au spécimen du MNHN étiqueté « 2332 » ; Guérin (1972) liste correctement six os du tarse (toujours présents dans les collections du MNHN), alors qu'Heintz et al. (1974) en comptent seulement cinq ; MNHN.F.PET 243 correspond à l'étiquetage « AC 2331 » *pro parte* et est considéré à tort comme un métatarse par Guérin (1972) et Heintz et al. (1974).

Guérin, 1972 (p. 137)	Heintz et al., 1974 (p. 173)	Actual catalogue
<b><i>S. elatus</i></b>	<b><i>S. elatus</i></b>	
1 radius (Paris)	1 radius (2317) (Paris)	Radius MNHN.F 2317 (previous AC 2317)
1 McII (AC 2933) (Paris)	2 metacarpal bones (Ac 2333 and 2339) (Paris)	McII MNHN.F PET 242 (previous AC 2333)
1 McIII (AC 2339) (Paris)		McIII MNHN.F PET 244 (previous AC 2332)
1 femur (Paris)	1 right femur (Paris)	Femur MNHN.F PET 2003 (no previous number)
1 fragment of femur (Clermont-Ferrand)		(Clermont-Ferrand: material not analysed)
1 astragalus and 2 calcanei (AC 2327) (Paris)	5 tarsal bones (Ac 2327) (Paris)	Astragalus MNHN.F PET 240 (previous AC 2327)
2 cuboids (Paris)		Calcanei MNHN.F PET 239 and 252
1 cuneiform III (Paris)		Cuboids MNHN.F PET 258 and 261
		Cuneiform III MNHN.F PET 259
1 fragmentary MtII, 2 MtIII, 1 MtIV (Paris)– <i>one of them is actually a metacarpal bone</i>	5 metatarsal bones (Ac 2331) (Paris)– <i>one of them is actually a metacarpal bone</i>	MtII MNHN.F PET 247
		MtIII MNHN.F PET 245
		MtIV MNHN.F PET 248
		MtV MNHN.F PET 249
		McIII MNHN.F.PET 243 (previous AC 2331 p.p.)
<b><i>S. etruscus</i></b>	<b><i>S. etruscus</i></b>	
	2 right humeri (Paris)	Humeri MNHN.F PET 2002 and 2004
	1 atlas (Paris)	Not present in MNHN
Unnumbered femurs stored in Basel	3 femurs (Prr 155, 323, 340) (Basel)	Femurs NMB Prr. 155 and 323
		(Prr. 340 not present in NMB)
	1 calcaneus of a young individual (P.86) (Lyon)	Calcaneus MHNL P.86
	“tibia juvenile incomplete” and “moitié proximale de radius” (D. 17 and D. 8-10) (Clermont-Ferrand)	(Clermont-Ferrand: material not analysed)

As far as the palaeoenvironmental reconstruction is concerned, Guérin (1980) reported a temperate forest vegetation with Mediterranean influences.

### 1.2. The rhinoceroses from Étouaires

The rhinoceros remains from Étouaires were initially described by Croizet and Jobert (1828). Later additional specimens have been collected but never studied in detail. Guérin (1972) described the rhinoceros remains from Vialette (Table 1) and added a brief note to some roughly coeval rhinoceros-bearing localities, including Étouaires where he recognized the two species *S. etruscus* and *S. elatus* (*D. etruscus* and *D. jeanvireti* in Guérin, 1972). After that, Heintz et al. (1974) revised the faunal lists of the most important French Villafranchian sites and provided detailed comments for the different taxa represented. In this work (Table 1), they gave precious information on the rhinoceroses from Étouaires, including direct mention of several specimens. Finally, Guérin (1980) published an extensive monograph on the European fossil rhinoceroses, including the specimens from Étouaires but not properly describing the rhinoceroses from this locality. In fact, his work discusses each anatomical element in a detailed comparison among different species from several localities, but does not provide proper information on any of the

specimens, failing to mention the catalogue numbers of the material analysed or even to tell how many specimens from each locality are included in the mean values of the measurements.

## 2. Materials and methods

The revision includes the main collections of fossil rhinoceroses from Étouaires, housed in the ‘Muséum national d’histoire naturelle’ in Paris (MNHN), the ‘Naturhistorisches Museum Basel’ (NMB), the ‘Université Claude-Bernard Lyon-1’ (UCBL, Collections de géologie, Laboratoire de géologie de Lyon Terre Planètes Environnement), the ‘Musée des Confluences’ (formerly the ‘Musée d’histoire naturelle de Lyon’, MHNL) and the Natural History Museum of London (NHM). Three additional specimens stored at Clermont-Ferrand (one fragment of femur, Guérin, 1972; portions of tibia and radius Heintz et al., 1974), have not been analysed in this research.

The material from Étouaires has been collected from different outcrops and in different periods. Unfortunately, it has not been possible to reconstruct precisely the history of the collections, started in the early 19th century, but the main information available is here summarised:



- the first publication on the rhinoceros from Étouaires is the monograph by Croizet and Jobert (1828), based on a first batch of fossils collected in the Perrier Mountain, but including also remains from Malbattu (Issoire). This collection was offered to the 'Muséum national d'histoire naturelle' in Paris in 1830 (Grellet, 1863). Most of this material is still preserved in Paris (Ballatore and Breda, 2016; Tab. 1);
- Croizet carried on a second collection (Croizet, 1853, 1855) that was sold to the British Museum (Natural History collections) of London in 1848 (Bello et al., 2013, Dugas, 1979), now at the Natural History Museum;
- Heintz (1970) gives a note on the locality of Étouaires (under the names 'Les Étouaires' and 'Perrier') stating that the material there collected is "disséminées dans divers musées d'Europe" (p. 19) and, among these, the Museum of Basel houses the only homogeneous collection, derived from an excavation carried out in the thirties (Heintz, 1970);
- Guérin (1972) lists the museums storing the rhinoceros remains from Étouaires: Paris, Basel, Lyon, and Clermont-Ferrand (London is not included). He also provides a list of the specimens belonging to *S. elatus* (although he does not give complete catalogue references), but avoids any information about the specimens of *S. etruscus* (he only mentions "des fémurs conservés au musée de Bâle"; Guérin, 1972; p. 137);
- Heintz et al. (1974) give the most recent list of the rhinoceroses from Étouaires, distinguishing the two species *S. elatus* and *S. etruscus*;
- Pandolfi et al. (2017) recently revise the biogeography and chronology of the species *S. etruscus* and briefly list some specimens from Étouaires (they use the denomination "Perrier-Les Étouaires") housed in Basel NMB.

The lists by Guérin (1972) and Heintz et al. (1974) have been compared here (Table 1), to check for the material preserved in the different museums, and they have been found matching, with just few incongruences discussed in the table's caption. As a matter of fact, some specimens listed in previous works (Croizet and Jobert, 1828, Guérin, 1972, Heintz et al., 1974) have not been found, and went probably lost. A total of 39 specimens constitutes the whole amount of Étouaires' rhinoceros, including the 8 specimens chosen as lectotype and paralectotype of the species *S. elatus* by Ballatore and Breda (2016) and described in detail in that work.

The present study relies on a detailed analysis of the morphological differences between the postcranial skeleton of *S. elatus* and *S. etruscus*, to identify the rhinoceros remains from Étouaires, which includes mainly postcranial elements. For the species *S. elatus* we use the type material from Étouaires (Ballatore and Breda, 2016) housed in the MNHN, and the material from Vialette (Haute-Loire, early Villafranchian) (Guérin, 1972) housed in the NMB, UCBL and MNHN. For the species *S. etruscus* we use the specimens from the locality of Senèze (Haute-Loire, early late Villafranchian) (latest attribution by Lacombat, 2005) stored in the NMB, UCBL and MNHN and a few bones from the type locality of Upper Valdarno (Tuscany, middle Vil-

lafranchian) (latest attribution by Mazza, 1988) stored in the NMB and MNHN, so when we refer to this locality we just intend these few bones and not the whole population. The rhinoceros remains from Vialette, Senèze and Upper Valdarno, can all be attributed to a single species, respectively *S. elatus* the first and *S. etruscus* the other two, so that, thanks to the monospecificity attested in these localities (Guérin, 1972, 1980; Lacombat, 2005; Mazza, 1988; Pandolfi et al., 2017), they can be used as a reference to investigate the morphological differences between the two species.

A biometrical comparison was carried out on the measurements taken per the biometric method by Ballatore (Bachelor thesis and PhD thesis; Ballatore, 2012, 2016a), which sums up those used in previous works (Fortelius et al., 1993, Guérin, 1980, Lacombat, 2005, Mazza, 1988, Van der Made, 2010). The metrical comparison is based on original measurements directly taken by one of us (M. Ballatore) on the bones from the monospecific localities chosen as reference. Although other measurements are available in the literature (e.g., Fortelius et al., 1993; Mazza, 1988; Pandolfi et al., 2017) we choose to use only original measurements to have full consistency in the measuring techniques. In fact, despite the great effort of some authors (e.g., Fortelius et al., 1993; Mazza, 1988; Pandolfi and Petronio, 2011) in providing description and illustrations of their measuring techniques, the very precise way to take specific measures on a bone is significantly variable and, when measures taken from different authors are plotted in a graph, the lack of accuracy is a permanent bias. On the other hand, using only original measures reduces the sample size and does not allow a wide generalization at the species level.

Metrical data are provided as on-line supplementary files and morphological characters are discussed in the section 'Results and discussion', including a description of the characters distinguishing *S. elatus* and *S. etruscus* from each other.

### 3. Results and discussion

#### 3.1. Skull

Cranial remains from Étouaires are poorly preserved and have not been mentioned in previous works (Guérin, 1972, 1980, Heintz et al., 1974).

A nasal horn base, housed in Paris (MNHN), without catalogue number and just labelled as "Perrier", does not have any characteristic morphology or recognizable measuring points, thus a specific identification is not possible.

An isolated upper premolar (broken in its labial side) is housed in Lyon, UCBL FSL 211584 (the label reports erroneously the species *Mastodon arvernensis*, but the catalogue number is clearly written on the enamel). It misses completely the labial wall as well as part of the distal portion. We can exclude it is a P<sup>2</sup>, but it is not possible to assess whether it is a P<sup>3</sup> or a P<sup>4</sup>.

Since standard measurements are not possible, we consider the morphological characters. The specimen has a single crista and a multiple crochet (the antecrochet is absent) but we observed a similar pattern both in *S. elatus*

from Vialette and *S. etruscus* from Senèze. On the contrary, the absence of the lingual cingulum associated with an evident mesial cingulum, as shown by the specimen from Étouaires, has been observed on two individuals of *S. elatus* from Vialette out of five (the other three individuals have both lingual and mesial cingula), but never on *S. etruscus* from Senèze (6/6 individuals have lingual and mesial cingula). This supports the attribution to *S. elatus*.

Although the measures are incomplete, the maximum breadth should have most likely reached the mean value of the P<sup>3</sup> of *S. elatus* (see [on-line metric table](#)), while the maximum length should have been much shorter (therefore closer to *S. etruscus*). However, this could be explained by the quite advanced wear, because the tooth row becomes shorter with age and the single tooth's length is reduced as well.

Neither lower jaws nor isolated lower teeth are present and, given their stoutness and usual frequency in the rhinoceros fossil record (e.g., British early middle Pleistocene, [Breda et al., 2010](#); Palaeolithic site at Isernia La Pineta, [Ballatore and Breda, 2013](#)), this is a quite unusual circumstance, unlikely due to taphonomic reasons but, possibly, to collection bias.

### 3.2. Vertebrae

#### 3.2.1. Atlas

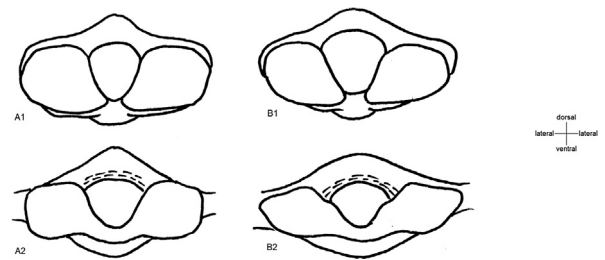
A single atlas is present, UCBL FSL 211580, with a well-preserved body but lacking part of the wings. [Guérin \(1972, 1980\)](#) does not provide any morphological character distinguishing *S. elatus* and *S. etruscus*.

However, atlas FSL 211580 clearly resembles *S. etruscus* from Senèze in the cranial and caudal articular surfaces, being different from the single *S. elatus* specimen from Vialette ([Fig. 2](#)). The cranial articular surfaces in the *S. elatus* individual are shaped as two kidneys, being more dorso-ventrally symmetrical. On the contrary, in *S. etruscus* from Senèze (6/6 individuals) and FSL 211580 from Étouaires, they look like two commas, because the ventral portion gradually reduces its breadth while the dorsal part is laterally stretched. In a similar way, the caudal articular surfaces of the single *S. elatus* specimen from Vialette are uniform from the top to the bottom while those of FSL 211580 from Étouaires and *S. etruscus* from Senèze (4/4 individuals) are laterally stretched in the dorsal part and a distinct rung is evident on the medial edge (hemming the vertebral foramen).

Compared with the samples from Senèze (see [on-line metric table](#)), it shows a general larger size, exceeding the range of *S. etruscus* in the articular breadth and falling in the higher part of the range in the dorso-ventral height. Unfortunately, only one atlas of *S. elatus* is known from Vialette, and its measures are comparable with *S. etruscus*, so the size by itself does not allow a specific identification.

Therefore, on morphological grounds, FSL 211580 is attributed to *S. etruscus*.

This bone was not mentioned by either [Guérin \(1972, 1980\)](#) or [Heintz et al. \(1974\)](#).



**Fig. 2.** Atlas, articular surfaces in 1) cranial view and 2) caudal view. A: *Stephanorhinus elatus*, B: *S. etruscus*. In *S. elatus* (Vialette, one specimen) the cranial articular surfaces are in shape of “kidneys”, being more dorso-ventrally symmetrical, while in *S. etruscus* (Senèze, 6/6; Étouaires, one specimen) they are in shape of “commas”, because the ventral portion gradually reduces its breadth while the dorsal part is laterally stretched. The caudal articular surfaces are uniform from the top to the bottom in *S. elatus* (Vialette, one specimen), while they are laterally stretched in the dorsal part and a distinct rung is evident in the medial edge in *S. etruscus* (Senèze, 4/4; Étouaires, one specimen).

**Fig. 2.** Atlas, surfaces articulaires en vue 1) crâniale et 2) caudale. A : *Stephanorhinus elatus*, B : *S. etruscus*. Chez *S. elatus* (Vialette, un spécimen), les surfaces articulaires en vue crâniale ont une forme de rein et sont plus symétriques dorso-ventralement, alors que chez *S. etruscus* (Senèze, 6/6; Étouaires, un spécimen) elles sont en forme de virgule, en raison d'une diminution progressive de la largeur de la portion ventrale et d'un étirement latéral de la partie dorsale. En vue caudale, les surfaces articulaires sont uniformes de haut en bas chez *S. elatus* (Vialette, 1 spécimen), tandis que chez *S. etruscus* (Senèze, 4/4; Étouaires, un spécimen), elles sont étirées latéralement sur la partie dorsale et présentent un barreau distinct évident sur le bord médian.

#### 3.2.2. Axis

A single axis fragment, NMB Prr. 326, consisting of the cranio-ventral part of the body, is present.

Unfortunately, no axis is available for *S. elatus* at Vialette, and no descriptions are available in the literature ([Guérin, 1972, 1980](#); [Guérin and Tsoukala, 2013](#)).

The morphology of the dentis, short and stocky, mirrors that of the *S. etruscus* samples from Senèze and the cranial articular breadth falls in the upper part of the range of this population (see [on-line metric table](#)). Because of the metrical and morphological conformity to *S. etruscus* but, given the lack of *S. elatus* bone for comparison, we attribute the specimen to *S. cf. etruscus*.

This bone was not mentioned by either [Guérin \(1972, 1980\)](#) or [Heintz et al. \(1974\)](#).

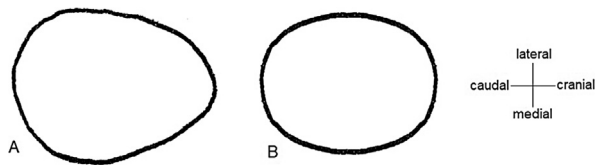
### 3.3. Forelimb

#### 3.3.1. Scapula

A single specimen is stored in London, NHM OR 34732. It consists of the neck and glenoid portion, with the broken coracoid process.

The two species are not clearly distinct, and very few specimens are available for *S. elatus*. [Guérin \(1980\)](#) records a difference in the outline of the articular (glenoid) surface: this would be a symmetrical ellipse in *S. etruscus* while in *S. elatus* it would be caudally enlarged. However, from our observation, *S. etruscus* is polymorphic in this character, with some specimens from Senèze (3/9) having the caudal enlargement as well ([Fig. 3](#)).

Concerning this character, the specimen from Étouaires NHM OR 34732 has an asymmetrical shape, with a



**Fig. 3.** Scapula, glenoid surface (distal view). A: asymmetrical (caudal enlargement), B: symmetrical (ellipse). The outline of the glenoid surface is asymmetrical in *Stephanorhinus elatus* (Violette, 2/2 A) while it is polymorphic in *S. etruscus* (Senèze, 3/9 A and 6/9 B).

**Fig. 3.** Scapula, surface glénoïde (vue distale). A : asymétrique (élargissement caudal), B : symétrique (ellipse). Les contours de la surface glénoïde sont asymétriques chez *Stephanorhinus elatus* (Violette, 2/2 A), mais polymorphes chez *S. etruscus* (Senèze, 3/9 A and 6/9 B).

caudal enlargement, thus the morphology shared by *S. elatus* and some *S. etruscus* specimens. The specimen at issue has a distinct concavity on the cranial side of the neck that we recorded in the specimens of *S. etruscus* from Senèze, but unfortunately the presence of this concavity cannot be checked in the specimens of *S. elatus* from Violette, because of their broken condition. Finally, in NHM OR 34732 the coracoid apophysis is clear and distinct, completely separated from the coracoid process. Even if coracoid apophysis and coracoid process are usually joined in *S. etruscus*, they are isolated in one out of five specimens from Senèze (MNHN 1923-4), and this character seems to be variable in *S. elatus* as well (only two individuals show the character: joined morphology in the NMB specimen without number and separated morphology in MHNH V277).

The measurements of the bone mostly fall in the range of *S. etruscus* from Senèze, but the scanty remains of *S. elatus* make the comparison unreliable (see [on-line metric table in supplementary material and sm1](#)).

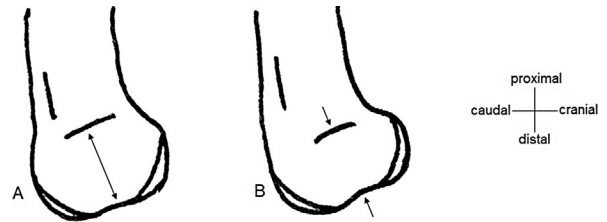
As a matter of fact, specimen NHM OR 34732 cannot be ascribed with confidence to a species and is thus assigned to *Stephanorhinus* sp.

This bone was not mentioned before (Guérin, 1972, 1980, Heintz et al., 1974).

### 3.3.2. Humerus

At the MNHN two humeri are present, PET 2002 and PET 2004. The former, although badly preserved and missing diagnostic morphological characters, has been attributed to *S. elatus* by Ballatore and Breda (2016) because it articulates perfectly with the associated radius MNHN 2317 (it was already considered part of an associated leg by Croizet and Jobert, 1828 who collected the material). The latter, MNHN PET 2004, is an almost complete right humerus. It is fragmented but well restored and just missing part of the proximal epiphysis (only the articular head is present). Two specimens are stored in Basel: an indeterminable fragment, NMB Prr. 57, and an almost complete right bone, NMB Prr. 429, just missing part of the proximal epiphysis (only the articular head is present).

From a morphological point of view, Guérin (1980) reports that the diaphysis and distal epiphysis of this bone do not have any significant difference between *S. elatus* and *S. etruscus*. However, the coracobrachialis insertion (medial protuberance of the diaphysis: Guérin's "tubérosité symétrique de la tubérosité deltoïdienne") is much more



**Fig. 4.** Humerus, distal epiphysis (lateral view). A: *Stephanorhinus elatus*, B: *S. etruscus*. In *S. elatus* (Violette, 5/5), the cranio-caudally oriented transversal crest on the lateral side of the distal epiphysis is distant from the distal trochlea, while in *S. etruscus* (Senèze, 6/6; Upper Valdarno, one specimen) it is closer to it; consequently, the shape of the lateral epicondyle is much more compressed in *S. etruscus*.

**Fig. 4.** Humérus, épiphyse distale (vue latérale). A : *Stephanorhinus elatus*, B : *S. etruscus*. Chez *S. elatus* (Violette, 5/5) la crête transversale orientée crânio-caudalement sur le côté latéral de l'épiphyse distale est distante de la trochlée distale, alors que chez *S. etruscus* (Senèze, 6/6; Valdarno supérieur, un spécimen) elle est plus proche ; en conséquence, la forme de l'épicondyle latéral est bien plus compressée chez *S. etruscus*.

protruding in the *S. elatus* specimens from Violette (evident in 3 specimens out of 4) than in the *S. etruscus* from Senèze (absent in all 7 specimens) and in the single analysed specimen from Upper Valdarno (V.A. 1080). It is absent in the humeri MNHN PET 2002 and 2004, similarly to *S. etruscus* from Senèze and Upper Valdarno, while it is protruding in NMB Prr. 429, matching the morphology of the *S. elatus* from Violette. Comparing the strength of the diaphysis at the minimum (near the connection with the distal epiphysis), it appears rather slender in PET 2004 and in the *S. etruscus* specimens from Senèze and Upper Valdarno, compared to the more robust specimens PET 2002, NMB Prr. 429 and the *S. elatus* specimens from Violette. In addition, on the lateral side of the distal epiphysis, the cranio-caudally oriented transverse crest (Fig. 4) is high in the *S. elatus* specimens from Violette (5/5 individuals) while it is in a lower position, giving a more compressed shape to the lateral side of the epicondyle, in the *S. etruscus* specimens from Senèze (6/6 individuals) and Upper Valdarno (V.A. 1080). In MNHN PET 2004 the crest is not as high as in *S. elatus*, and the lateral epicondyle is more compressed as in *S. etruscus*. In NMB Prr. 429 the lateral epicondyle does not appear as compressed as in the specimens from Senèze but resembles those of Violette. (The character is not detectable on MNHN PET 2002 because it is eroded).

Biometric values of MNHN PET 2004 fall in the upper range of *S. etruscus*, while NMB Prr. 429 fits in the range of *S. elatus* (see Fig. Sm1).

We assign here MNHN PET 2004 to *S. etruscus*, we confirm the attribution of PET 2002 to *S. elatus* (Ballatore and Breda, 2016) and assign also NMB Prr. 429 to this latter species.

Heintz et al. (1974) assign two right humeri from Violette at the MNHN to *D. etruscus*. Although they do not provide catalogue numbers, they probably refer to MNHN PET 2002 and 2004 as these are the only humeri present in Paris. However, we can confirm the attribution to *S. etruscus* only for MNHN PET 2004, while MNHN PET 2002 belongs to *S. elatus*.

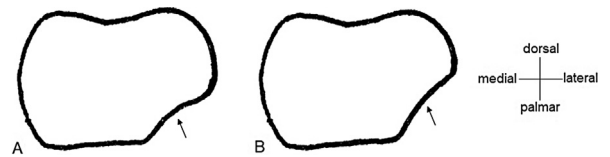
Guérin (1972, 1980) and Heintz et al. (1974) do not mention NMB Prr. 429 since they do not quote any humerus from Étouaires stored in Basel. According to Pandolfi et al. (2017, p. 768), this bone “resembles *S. jeanvireti* in having a well-developed and marked lateral tuberosity and a less concave dorsal border of the trochlea”. The authors do not give reasons why these characters should be diagnostic of this species. In fact, the deltoid tuberosity (the “lateral tuberosity”) is well developed in both species according to Guérin (1980) and our observations, and the proximal outline of the trochlea (the “dorsal border” – on which Guérin did not comment) is slightly concave in our sample both of *S. elatus* (Vialeite and Étouaires) and *S. etruscus* (Senèze and Upper Valdarno). Nevertheless, we agree with Pandolfi et al. (2017) about the specific identification of this specimen.

### 3.3.3. Radius

Two radii are present in Paris: MNHN 2317 is a complete bone and the lectotype of the species *S. elatus* (Ballatore and Breda, 2016); MNHN PET 241 roughly consists of the proximal half, with the medial part of the proximal epiphysis and a portion of the diaphysis; the palmar articular facets for the ulna are completely obliterated. Other two radii are present in Basel: NMB Prr. 52 and NMB Prr. 109, both well restored but missing the distal epiphysis. Additional two radii are stored in Lyon: UCBL FSL 211575 is represented by nearly the proximal half of the bone and UCBL FSL 211576 consists of the proximal epiphysis only.

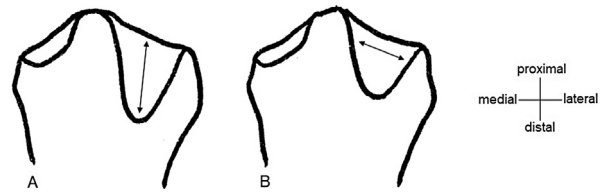
Guérin (1980) describes three morphological characters apparently discriminating between the radii of *S. etruscus* and *S. elatus*, but two of them are not valid. The medial outline of the proximal epiphysis in dorsal view is suggested to be straight in *S. etruscus* and convex in *S. elatus*, but from our observations (individuals from Senèze, Upper Valdarno, Vialeite and the lectotype from Étouaires), it is slightly convex in both *S. etruscus* and *S. elatus*. The second character given by Guérin (1980) concerns the dorsal outline of the proximal articular surface that, in proximal view, should be less concave in *S. etruscus* and with a stronger concavity in *S. elatus*. However, this outline is moderately concave in both *S. elatus* from Vialeite (4/4 individuals) and the lectotype from Étouaires, and in *S. etruscus* from Senèze (3/4 individuals – it is weak in the fourth individual) and Upper Valdarno (2/3 individuals – it is weak in the third one). The third morphological distinction described by Guérin (1980) regards the palmar edge of the lateral half of the proximal articular surface (proximal view, Fig. 5) which would be more oblique in *S. etruscus* than in *S. elatus*. Our observations suggest that *S. etruscus* has a strongly oblique edge (4/4 individuals from Senèze and 4/4 individuals from Upper Valdarno), while *S. elatus* shows both strongly oblique (2/4 individuals from Vialeite and the lectotype from Étouaires) and mildly oblique morphologies (the 2 left individuals from Vialeite).

Moreover, the lateral ulnar facet (palmar view, Fig. 6), is elongated downward in *S. elatus* from Vialeite (4/4 individuals) and in the lectotype from Étouaires, while it is more medio-laterally enlarged in *S. etruscus* from Senèze (5/5 individuals) and from Upper Valdarno (3/3 individuals).



**Fig. 5.** Radius, proximal articular surface (proximal view). A: palmar edge of the lateral half mildly oblique, B: strongly oblique. The palmar edge can be either mildly or strongly oblique in *Stephanorhinus elatus* (Vialeite, 2/4 A and 2/4 B; Étouaires, 1/1 B) while it is always strongly oblique in *S. etruscus* (Senèze, 4/4 B; Upper Valdarno, 4/4 B).

**Fig. 5.** Radius, surface articulaire proximale (vue proximale). Bord palmaire A : peu oblique, B : très oblique sur sa moitié latérale. Le côté palmaire peut être peu ou très oblique chez *Stephanorhinus elatus* (Vialeite 2/4 A and 2/4 B; Étouaires, 1/1 B), alors qu'il est toujours très oblique chez *S. etruscus* (Senèze, 4/4 B; Valdarno supérieur, 4/4 B).



**Fig. 6.** Radius, proximal epiphysis in (palmar view). A: *Stephanorhinus elatus*, B: *S. etruscus*. In *S. elatus* (Vialeite, 6/6; Étouaires, one specimen) the lateral ulnar facet is elongated downward, while in *S. etruscus* (Senèze, 5/5; Upper Valdarno, 3/3) it is more medio-laterally enlarged.

**Fig. 6.** Radius, épiphyse proximale (vue palmaire). A : *Stephanorhinus elatus*, B : *S. etruscus*. Chez *S. elatus* (Vialeite, 6/6 ; Étouaires, un spécimen) la facette ulnaire latérale est allongée vers le bas, tandis que chez *S. etruscus* (Senèze 5/5 ; Valdarno supérieur, 3/3) elle est plutôt étendue médio-latéralement.

From a morphological point of view, MNHN PET 241 is incomplete in the dorsal outline of the proximal articular surface. The two bones stored in Basel, NMB Prr. 52 and 109, are very similar to each other in their general morphology. The lateral ulnar facet is elongated downward in NMB Prr. 109 (*S. elatus* character – not visible in NMB Prr. 52). The proximal articular surface shows an evident but not deep concavity in the dorsal outline (*S. elatus* and *S. etruscus* character) and the palmar edge of the lateral surface is mildly oblique so that the lateral facet itself is not too small (*S. elatus* characters). What differentiates the two specimens is the more accentuated curvature of the diaphysis in NMB Prr. 109 (even if the diaphysis itself is not complete); moreover, this specimen shows a robust and distinct bulge in the dorso-lateral part of the proximal epiphysis, just below the proximal articular surface edge. These elements can be interpreted as related to a sturdier individual, in fact the same variability has been observed in both the species.

Concerning the two radii stored in Lyon, the lateral ulnar facet is enlarged in UCBL FSL 211575 (*S. etruscus* character – not visible in UCBL FSL 211576). In both the specimens, the proximal articular surface shows an evident but rather shallow concavity in the dorsal outline (more *S. etruscus*-like) and the palmar edge of the lateral surface is very oblique so that the lateral facet itself is noticeably reduced (*S. etruscus* characters). The general shape of the proximal articular surface is dorso-palmarly compressed in both the considered specimens (again *S. etruscus* character).



From a metrical point of view (see [on-line metric table and Fig. Sm1](#)), MNHN PET 241 shows a depth of the diaphysis comparable to those of *S. elatus* from Vialette, but the breadth of the diaphysis falls in the overlapping range of the two species, while the proximal depth is in the range of *S. etruscus* (being too small with respect to *S. elatus*); the broken proximal epiphysis does not allow other matches. The measures of NMB Prr. 52 and Prr. 109 fall in the overlapping range of *S. elatus* and *S. etruscus*, even if the diaphysis is a little bit slenderer than in the specimens from Vialette. The biometric value of specimens UCBL FSL 211575 and 211576 are comparable with the metrics of *S. etruscus* from Senèze.

We attribute both NMB Prr. 52 and Prr. 109 to *S. elatus* while UCBL FSL 211575 and 211576 are attributed to *S. etruscus*. Instead, MNHN PET 241 cannot be specifically identified and it is thus assigned to *Stephanorhinus* sp.

An additional proximal half of a radius (D.8–10), stored at the Museum of Clermont-Ferrand and not analysed in this work, is attributed to *D. etruscus* (Heintz et al., 1974). Instead, no mention of any of the bones analysed here is given by Guérin (1972, 1980) and by Heintz et al. (1974), but Pandolfi et al. (2017, p. 768) tell that Prr. 52 and Prr. 109 “differ from *S. jeanvireti* from Vialette which has, in proximal view, a more marked concavity on the anterior border and a proportionally narrower medial articular surface”. Although they give a picture of the dorsal view of the bone only, they probably mean that the dorsal outline of the proximal articular surface of the bones is not marked, as mentioned above, but this character is consistent with both *S. etruscus* and *S. elatus*.

### 3.3.4. Carpus

A single carpal bone, the left magnum NMB Prr. 56, is present, rather well preserved but lacking the proximal prominence.

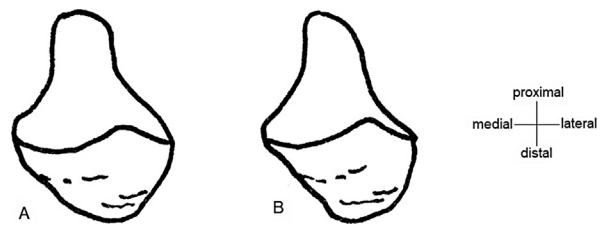
Guérin (1980) suggests that the only morphological character distinguishing this element of *S. elatus* from *S. etruscus* is the anterior enlargement of the distal articular facet for the McIII. Actually, this facet shows a similar morphology with a weak lateral concavity in the two species (3/3 individuals for *S. etruscus* from Senèze and 4/4 individuals of *S. elatus* from Vialette). However, the dorsal wall is more proximo-distally elongated in some *S. etruscus* specimens from Senèze (3/4 individuals) while it is medio-laterally enlarged in the *S. elatus* specimens from Vialette (6/6 specimens) (Fig. 7). In this character the specimen from Étouaires resembles the morphology of *S. etruscus* because of its proximo-distal elongation.

Magnum NMB Prr. 56 is smaller than the specimens from Vialette and metrically closer to those from Senèze, even if slightly deeper (see [on-line metric table](#)). It is here attributed to *S. etruscus*.

No mention of carpal bones is found in previous works (Guérin, 1972, 1980; Heintz et al., 1974) but Pandolfi et al. (2017, p. 768) report this bone and note its dimensions are smaller than *S. elatus*.

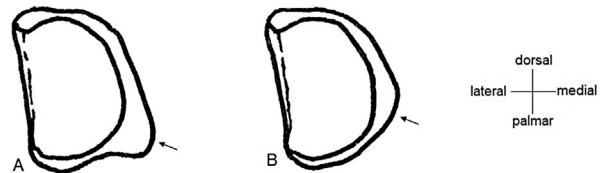
### 3.3.5. Metacarpal bones

Associated McII MNHN PET 242 and McIII MNHN PET 244 belong to the lectotype of the species *S. elatus* (Ballatore



**Fig. 7.** Magnum, dorsal view. A: *Stephanorhinus elatus*, B: *S. etruscus*. In *S. elatus* (Vialette, 6/6) the dorsal wall is more medio-laterally enlarged than in *S. etruscus* (Senèze, 4/4).

**Fig. 7.** Magnum, vue dorsale. A : *Stephanorhinus elatus*, B : *S. etruscus*. Chez *S. elatus* (Vialette, 6/6) le mur dorsal est plus étendu médio-latéralement que chez *S. etruscus* (Senèze 4/4).



**Fig. 8.** McII, proximal epiphysis (proximal view). A: medial tubercle strongly stretched, B: medial tubercle reduced. The medial tubercle is strongly stretched in plantar direction in *Stephanorhinus elatus* (Vialette, 4/4 A; Étouaires, 1/1 A), while it can be also reduced in *S. etruscus* (Senèze, 3/7 A and 4/7 B).

**Fig. 8.** McII, épiphyse proximale (vue proximale). A : tubercule médial très étiré, B : tubercule médial réduit. Le tubercule médial est très étiré en direction plantaire chez *Stephanorhinus elatus* (Vialette, 4/4 A ; Étouaires, 1/1 A), alors qu'il peut être très réduit chez *S. etruscus* (Senèze, 3/7 A et 4/7 B).

and Breda, 2016). Two additional McIII are present: a nearly complete left McIII stored in Paris, MNHN PET 243, damaged in the proximal epiphysis, and a right McIII, NMB Prr. 55, fragmented and lacking the distal epiphysis. A single fragmented left McIV, MNHN PET 251, consists of the proximal half of the bone.

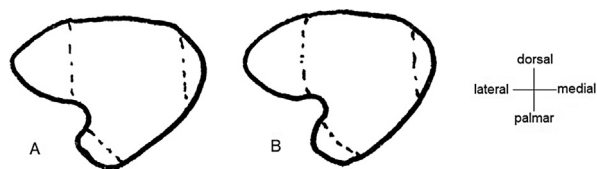
#### - McII

On the proximal epiphysis of McII PET 242, in proximal view, the medial tubercle is strongly stretched in the plantar direction (Ballatore and Breda, 2016), as it is in the specimens from Vialette (4/4 individuals) while in *S. etruscus* from Senèze it is mainly reduced (4/7 individuals) (Fig. 8).

#### - McIII

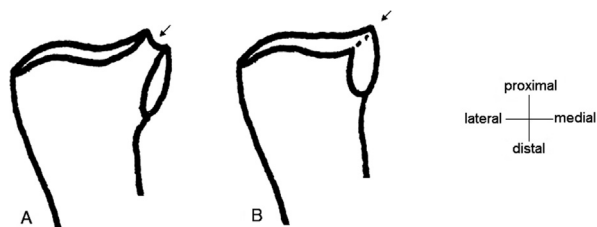
Morphological remarks are possible only for the specimen belonging to the lectotype and described by Ballatore and Breda (2016), the other specimens being too badly preserved. On the proximal articular surface that articulates with the magnum of McIII PET 244, in lateral position, the marked groove, sometimes present in the *S. etruscus* specimens from Senèze (3/7 individuals), is missing, as in *S. elatus* from Vialette (5/5 individuals) (Ballatore and Breda, 2016) (Fig. 9).

The metric values of MNHN PET 243 and NMB Prr. 55 fit better the range of *S. etruscus* specimens from Senèze (see [on-line metric table and Fig. Sm1](#)), so they are tentatively attributed to *S. cf. etruscus* on metric grounds. Pandolfi et al. (2017), to the contrary, state that Prr. 55 has a proximal transverse diameter wider than *S. etruscus* but, since they



**Fig. 9.** McIII, proximal epiphysis (proximal view). A: presence of a lateral marked groove, B: absence. The lateral marked groove is absent in *Stephanorhinus elatus* (Viallette, 5/5 B; Étouaires, 1/1 B), while it can be present in *S. etruscus* (Senèze, 3/7 A and 4/7 B).

**Fig. 9.** McIII, épiphyse proximale (vue proximale). A : présence d'un sillon latéral marqué, B : absence. Un sillon latéral marqué est absent chez *Stephanorhinus elatus* (Viallette, 5/5 B ; Étouaires, 1/1 B), alors qu'il peut être présent chez *S. etruscus* (Senèze, 3/7 A et 4/7 B).



**Fig. 10.** McIV, proximal epiphysis (palmar view). A: palmar facet for the McIII separated from the proximal articular surface, B: palmar facet joined to proximal surface. In *Stephanorhinus etruscus*, the palmar facet for the McIII is always joined to the proximal articular surface (Senèze, 6/6 B; Étouaires, 1/1 B), while in *S. elatus* they can be separated (Viallette, 3/4 A and 1/4 B).

**Fig. 10.** McIV, épiphyse proximale (vue palmaire). A : facette palmaire du McIII séparée de la surface articulaire proximale, B : facette palmaire en contact avec la surface proximale. Chez *Stephanorhinus etruscus*, la facette palmaire du McIII est toujours en contact avec la surface articulaire proximale (Senèze, 6/6 B ; Étouaires, 1/1 B), alors que chez *S. elatus* elles peuvent être séparées (Viallette, 3/4 A et 1/4 B).

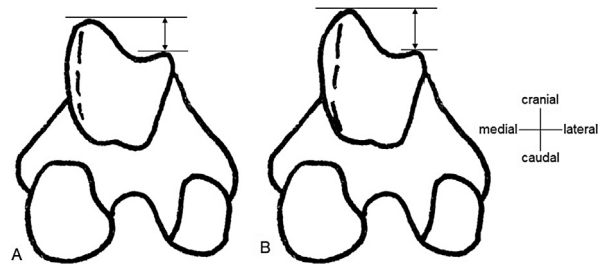
do not include the specimen in the supplementary material, we cannot evaluate the discrepancy.

MNHN PET 243 is damaged and no morphological features are detectable; it has been previously interpreted as a metatarsal and assigned to *S. elatus* (see Tab. 1). In fact, Guérin (1972) listed two MtIII belonging to *D. jeanvireti* but only one is present (MNHN PET 245), and later Heintz et al. (1974) reported that “5 métatarsiens (dont Ac 2331)” are attributed to *D. jeanvireti* (MNHN PET 243 corresponds to A.C. 2331 of the old cataloguing system). NMB Prr. 55 is not mentioned in previous works (Guérin, 1972, 1980, Heintz et al., 1974).

#### - McIV

From a morphological point of view, the palmar facet for the McIII is joined to the proximal articular surface for the unciform, as is always the case in *S. etruscus* from Senèze (6/6 individuals), while in *S. elatus* from Viallette it can be joined (3/4 individuals) or sometimes separated and medially protruding (1/4 individuals), Fig. 10.

The measures of MNHN PET 251 match those of *S. etruscus* from Senèze, not only in the absolute values, but in the proportion of the proximal breadth and depth, which are similar to each other, while in *S. elatus* from Viallette the proximal breadth is bigger. We attribute this specimen to *S. etruscus*.



**Fig. 11.** Femur, lips of the trochlea (distal epiphysis, distal view). A: *Stephanorhinus elatus*, B: *S. etruscus*. The top of the medial lip is much higher than the top of the lateral lip in *S. etruscus* (Senèze, 4/4; Upper Valdarno, 2/2) while this difference is lower in *S. elatus* (Viallette, 2/2).

**Fig. 11.** Fémur, lèvres de la trochlée (épiphyse distale, vue distale). A : *Stephanorhinus elatus*, B : *S. etruscus*. Le sommet de la lèvre médiale est plus haut que celui de la lèvre latérale chez *S. etruscus* (Senèze, 4/4 ; Valdarno supérieur, 2/2), tandis que cette différence est moins marquée chez *S. elatus* (Viallette, 2/2).

Possibly this bone had been considered by Guérin (1980) who reports at least one McIV from “Perrier-Étouaires” stored at the MNHN among the material of *D. etruscus etruscus*.

### 3.4. Hindlimb

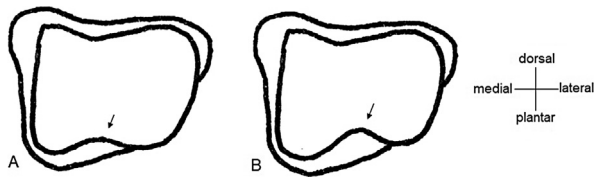
#### 3.4.1. Femur

One femur is present in Paris: MNHN PET 2003, a complete but badly preserved bone, that is the paralectotype of the species *S. elatus* (Ballatore and Breda, 2016). Two specimens are stored in Basel: NMB Prr. 155, almost complete, and NMB Prr. 323, missing the proximal epiphysis.

Guérin (1980) suggests that the femurs of the two species are not distinguishable by specific characters and we mostly confirm this observation (e.g., the lesser trochanter and the third trochanter are similar in their shape, position and extension; the trochlear lips, in cranial view, are slightly divergent in the shape of a narrow “V”). The only difference that we detected between the femora of *S. elatus* from Viallette and *S. etruscus* from Senèze and Upper Valdarno lies in the lips of the distal trochlea. In distal view, the top of the medial lip is much higher than the top of the lateral lip in *S. etruscus* (4/4 individuals from Senèze and 2/2 from Upper Valdarno), while this difference is lower in *S. elatus* (2/2 individuals from Viallette) (Fig. 11). Unfortunately, the lips are broken in the specimens from Étouaires. The diaphysis of both NMB Prr. 155 and Prr. 323 preserves a partial third trochanter but *S. elatus* and *S. etruscus* are similar in this character (Guérin, 1980).

From a metrical point of view, the two bones fit in the range of *S. etruscus* from Senèze (even if they are closer to the highest values), but are smaller than *S. elatus* from Viallette (see on-line metric table and Fig. Sm1). In NMB Prr. 155 also the articular head fits biometrically with *S. etruscus* from Senèze, while it is quite smaller than *S. elatus* from Viallette. Both are thus attributed to *S. cf. etruscus* on metric ground.

These bones were attributed to *D. etruscus* by Guérin (1972) and Heintz et al. (1974). Pandolfi et al. (2017) apparently ascribe Prr. 323 (plus one unnumbered “Prr nn”



**Fig. 12.** Tibia, distal articular surface (distal view). A: plantar outline slightly concave, B: deeply concave. In *Stephanorhinus elatus* the plantar outline of the distal articular surface is slightly concave (Vialeite, 4/4 A; Étouaires, 1/1 A), while in *S. etruscus* it can be deeply concave (Senèze, 3/5 A and 2/5 B; Upper Valdarno, 3/4 A and 1/4 B; Étouaires, 1/1 B).

**Fig. 12.** Tibia, surface articulaire distale (vue distale). A : contour plantaire légèrement concave, B : très concave. Chez *Stephanorhinus elatus*, le contour plantaire de la surface articulaire distale est légèrement concave (Vialeite, 4/4 A ; Étouaires, 1/1 A), tandis qu'il peut être très concave chez *S. etruscus* (Senèze, 3/5 A et 2/5 B ; Valdarno supérieur, 3/4 A et 1/4 B ; Étouaires, 1/1 B).

specimen) to this species too, because of the “wider and shorter medial articular condyle” in respect to *S. elatus*.

Other fragments of diaphysis cannot be identified because too incomplete, hence they are not included in Table 2 (NMB Prr. 324, NMB Prr. 430, UCBL FSL 211704, MNHN PET 237, MNHN PET 257+236, plus one unnumbered left specimen). Some of them possibly correspond to the fragments quoted by Guérin (1972; “des fémurs conservés au musée de Bâle”) and one (NMB Prr. 430) could correspond to the femur listed as Prr. 340 by Heintz et al. (1974).

### 3.4.2. Tibia

Two tibiae are available: NMB Prr. 321 is mostly well-preserved but damaged in the proximal epiphysis; MNHN PET 238 is fragmented and lacks the proximal epiphysis in full.

Guérin (1980) states that the diaphysis and distal epiphysis have similar morphology in the two considered species, but we note the following two differences. In the distal articular surface, the plantar outline is just slightly concave in *S. elatus* (4/4 individuals from Vialeite) and in some *S. etruscus* specimens (3/5 individuals from Senèze and 3/4 from Upper Valdarno), while the concavity is deeper in the remaining specimens (2 from Senèze and 1 from Upper Valdarno) (Fig. 12). Moreover, along the distal portion of the diaphysis a medial groove is little marked in *S. etruscus* from Senèze (5/5 individuals) and Upper Valdarno (2/2 individuals), while it is more marked in *S. elatus* from Vialeite (4/5 individuals, it is little marked in the one left).

The concavity of the plantar outline in the distal articular surface is deep in NMB Prr. 321 (*S. etruscus* character) and less so in MNHN PET 238 (both *S. etruscus* and *S. elatus* character). The medial groove on the distal portion of the diaphysis is little marked in NMB Prr. 321 (*S. etruscus* character), it is apparently more developed in MNHN PET 238 (*S. elatus* character) but we cannot be sure because that portion of the diaphysis is badly preserved.

Concerning size, NMB Prr. 321 falls in the range of *S. etruscus* while MNHN PET 238 is closer to the lower values of *S. elatus* from Vialeite (see on-line metric table and Fig. Sm1).

Prr. 321 is here attributed to *S. etruscus* and Prr. 238 to *S. cf. elatus*.

These specimens are not listed by previous authors (Guérin, 1972, Heintz et al., 1974) but, according to Heintz et al. (1974), one *S. etruscus* tibia should be stored at Clermont-Ferrand, reported as “tibia juvenile incomplete”. Pandolfi et al. (2017) note Prr. 321 is different from *S. elatus* in the “narrower distal lateral facet and a wider and sub-quadrangular distal medial facet”.

### 3.4.3. Tarsus

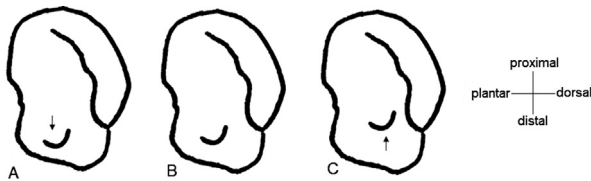
A single astragalus, MNHN PET 240, is present at Étouaires. It is associated with calcaneus MNHN PET 239, and both specimens are described as paralectotype of the species *S. elatus* by Ballatore and Breda (2016). Another five calcanei are available: MNHN PET 252 is complete; NMB Prr. 327 is broken in the beak; NMB Prr. 53 and NMB Prr. 54 are both damaged in the distal extremity and in the sustentaculum talii; MHNL P.86 is damaged, incomplete and belongs to a juvenile because of the incomplete ossification of the tuber. Two cuboids are stored in Paris: MNHN PET 261 and MNHN PET 258. The former is well preserved, except for the broken tip of the proximal articular surface; the latter is complete, but many surfaces are altered. Finally, a cuneiform III, MNHN PET 259, is complete and well preserved.

#### - Astragalus

The astragali of *S. elatus* from Vialeite and *S. etruscus* from Senèze are morphologically very similar to each other. Guérin (1980) describes a broad and asymmetrical trochlea with an oblique axis in both the species, with a mildly marked depression in the neck just behind the trochlea. We can confirm this description based on the observation of 6/6 individuals of *S. etruscus* from Senèze and 7/7 from Upper Valdarno (one has a marked depression), and on 5/6 individuals of *S. elatus* from Vialeite (a single specimen shows a marked depression). The same characters (asymmetrical trochlea with oblique axis and a mildly marked depression behind the trochlea) are present on the specimen from Étouaires.

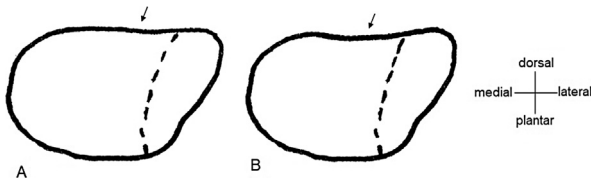
According to Guérin (1980), a possible specific distinction is the position of the medial tubercle shifted near the distal edge in *S. elatus* and quite far from it in *S. etruscus*. Actually, the position of the tubercle is variable: we consider a low position, when it is near the distal edge, and a high position, when it is far from it, plus an intermediate position in between. It varies from high to intermediate in *S. etruscus* (3/5 individuals from Senèze in high position, the remaining two in an intermediate position together with 6 individuals from Upper Valdarno), and from intermediate to low in *S. elatus* (2/5 individuals from Vialeite in low position, the remaining three individuals from Vialeite plus the specimen from Étouaires in an intermediate position) (Fig. 13).

Guérin (1980) suggests also some differences in distal view. The dorsal outline would be convex in *S. elatus* and straight or concave in *S. etruscus*. Actually, from our observations it is straight in *S. etruscus* (6/6 individuals from Senèze and 6/6 from Upper Valdarno) and in most *S. elatus* (4/5 individuals from Vialeite), but concave in one specimen from Vialeite and in the specimen from Étouaires)



**Fig. 13.** Astragalus, position of the medial tubercle (medial view). A: low, B: intermediate, C: high. The position of the medial tubercle is variable in the two species, from low to intermediate in *Stephanorhinus elatus* (Viallette, 2/5 A and 3/5 B; Étouaires, 1/1 B) and from intermediate to high in *S. etruscus* (Senèze, 2/5 B and 3/5 C; Upper Valdarno, 6/6 B).

**Fig. 13.** Astragale, position du tubercule médial (vue médiale). A : bas, B : intermédiaire, C : haut. La position du tubercule médial est variable chez les deux espèces, elle va de bas à intermédiaire chez *Stephanorhinus elatus* (Viallette, 2/5 A et 3/5 B ; Étouaires, 1/1 B) et d'intermédiaire à haut chez *S. etruscus* (Senèze, 2/5 B et 3/5 C ; Valdarno supérieur, 6/6 B).



**Fig. 14.** Astragalus, dorsal outline of the distal articular surface (distal view). A: straight, B: concave. In *S. etruscus*, the dorsal outline is straight (Senèze, 6/6 A; Upper Valdarno, 6/6 A) while in *S. elatus* it is straight or concave (Viallette, 4/5 A and 1/5 B; Étouaires, 1/1 B).

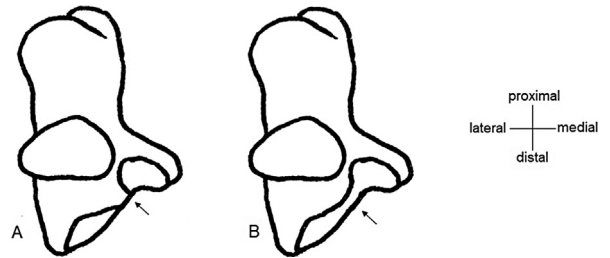
**Fig. 14.** Astragale, contour dorsal de la surface articulaire distale (vue distale). A : droit, B : concave. Chez *S. etruscus*, le contour dorsal est droit (Senèze, 6/6 A ; Valdarno supérieur, 6/6 A), alors que chez *S. elatus*, il est droit ou concave (Viallette, 4/5 A et 1/5 B ; Étouaires, 1/1 B).

(Fig. 14). Guérin (1980) also suggests that the two articular surfaces for the navicular and cuboid, in *S. elatus*, are split by a small notch, and the dorsal outline of the cuboid surface is shifted forward, while in *S. etruscus* it is aligned with the navicular surface and the notch can be absent. From our observations, the notch is absent in most specimens of the two species (4/6 individuals from Senèze, 4/6 from Upper Valdarno and 4/5 individuals from Viallette, as well as in the specimen from Étouaires). The cuboid articular surface is actually shifted forward in the majority of the specimens of *S. elatus* (3/5 individuals from Viallette and the specimen from Étouaires), but it can be shifted also in *S. etruscus* (2/9 individuals from Senèze). Thus, we believe that none of the features observed by Guérin (1980) in distal view have diagnostic value being both too variable.

The size of the bone is instead very different between the two species, *S. elatus* being larger than *S. etruscus* (Guérin, 1980) (see table 2 in Ballatore and Breda, 2016 for details on Étouaires).

#### - Calcaneus

Intra-specific morphological variation is high in the calcaneus as well. The mesio-distal facet for the astragalus and the facet on the sustentaculum tali are always joined in *S. etruscus* from Senèze (5/5 individuals) and Upper Valdarno (3/3 individuals) while they are mostly disjoined in *S. elatus* from Viallette (3/4 individuals) (Fig. 15). These facets are joined in specimens NMB Prr. 327 (*S. etruscus*-like) and disjoined in NMB Prr. 53, MNHN PET 252 and MNHL P.86 (*S. elatus*-like).



**Fig. 15.** Calcaneus, dorsal view. A: medio-distal facet for the astragalus and facet on the sustentaculum tali disjoined, B: joined. In *Stephanorhinus etruscus* the facets are joined (Senèze, 5/5 B; Upper Valdarno, 3/3 B; Étouaires, 1/1 B), while in *S. elatus* they can be disjoined (Viallette, 1/4 A and 3/4 B; Étouaires, 3/3 B).

**Fig. 15.** Calcaneus, vue dorsale. A : facette médio-distale de l'astragale et facette du talon sustentaculaire séparées, B : en contact. Chez *Stephanorhinus etruscus* les facettes sont en contact (Senèze, 5/5 B ; Valdarno supérieur, 3/3 B ; Étouaires, 1/1 B), tandis que chez *S. elatus* elles peuvent être séparées (Viallette, 1/4 A et 3/4 B ; Étouaires, 3/3 B).

By a metrical point of view (see on-line metric table and Fig. Sm1), NMB Prr. 53, MNHN PET 252 and MNHL P.86 (even if not complete and rather young) match the specimens of *S. elatus* from Viallette.

These three specimens are thus attributed to *S. elatus*.

On the contrary, specimen NMB Prr. 327 is smaller and falls in the size range of *S. etruscus* from Senèze, so it is attributed to this species. Finally, NMB Prr. 54 is metrically closer to *S. etruscus* (although its measures are not complete) and thus attributed to *Stephanorhinus* sp.

Calcaneus MNHN PET 252 has been attributed to *S. elatus* already by Guérin (1972), while MNHL P.86 had been assigned to *S. etruscus* by Heintz et al. (1974). The other bones are not listed in previous works (Guérin, 1972, 1980, Heintz et al., 1974) but Pandolfi et al. (2017) comment on Prr. 327, Prr. 53 and Prr. 54 that are slenderer than *S. elatus*, thus suggesting they belong to *S. etruscus*.

#### - Cuboid

According to Guérin (1980) the two species here considered do not differ in any evident morphological character, but their size is clearly distinct. From personal observations, the distal articular surface is wider than long in *S. elatus* from Viallette (7/7 individuals), while *S. etruscus* shows this morphology only rarely (2/7 individuals from Senèze) and has otherwise a longer than wide distal articular facet (5/7 individuals from Senèze and 1/1 individual from Upper Valdarno) (Fig. 16).

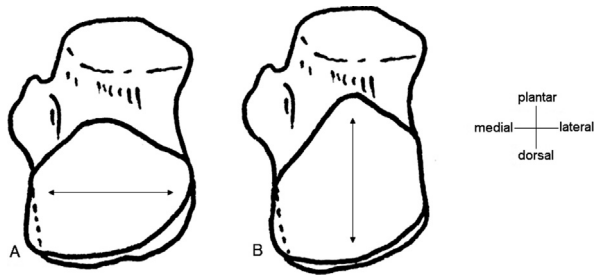
The two specimens from Étouaires share the enlarged distal articular surface with *S. elatus*. The two bones are metrically quite similar to each other, being larger than *S. etruscus* from Senèze and fitting well with *S. elatus* from Viallette (see on-line metric table).

We agree with Guérin (1972) and Heintz et al. (1974) in assigning both the cuboids to *S. elatus*.

#### - Cuneiform III

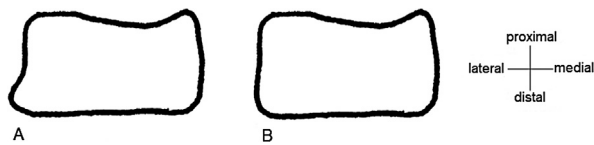
Guérin (1980) reports that the dorsal wall is elongated in its latero-distal angle (acute angle) in both *S. etruscus* and *S. elatus*. However, we observed a variable morphology in both species with a nearly perpendicular angle, and thus a sub-rectangular shape of the dorsal wall, in 2/5 individuals from Viallette, 3/5 individuals from Senèze and the





**Fig. 16.** Cuboid, distal articular surface (distal view). A: wider than long, B: longer than wide. In *Stephanorhinus elatus*, the distal articular surface is wider than long (Vialeite, 7/7 A; Étouaires, 2/2 A), while in *S. etruscus* it can be longer than wide (Senèze, 2/7 A and 5/7 B; Upper Valdarno, 1/1 B).

**Fig. 16.** Cuboïde, surface articulaire distale (vue distale). A : plus large que longue, B : plus longue que large. Chez *Stephanorhinus elatus*, la surface articulaire distale est plus large que longue (Vialeite, 7/7 A ; Étouaires, 2/2 A), alors que chez *S. etruscus* elle peut être plus longue que large (Senèze, 2/7 A et 5/7 B ; Valdarno supérieur, 1/1 B).



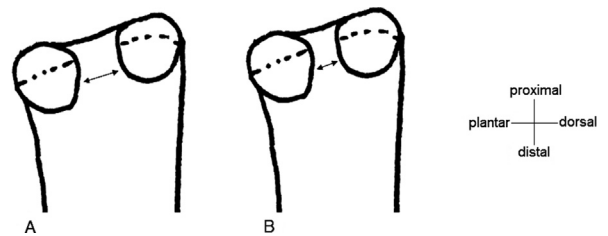
**Fig. 17.** Cuneiform III, dorsal wall (dorsal view). A: elongated in its latero-distal angle (acute angle), B: sub-rectangular (nearly perpendicular angle). The character is variable in both species: *Stephanorhinus elatus* (Vialeite, 3/5 A and 2/5 B) and *S. etruscus* (Senèze, 2/5 A and 3/5 B; Upper Valdarno 1/1 B; Étouaires, 1/1 B).

**Fig. 17.** Cunéiforme III, mur dorsal (vue dorsale). A : allongée dans son angle latéro-distal (angle aigu), B : sub-rectangulaire (angle presque perpendiculaire). Ce caractère est variable chez les deux espèces *Stephanorhinus elatus* (Vialeite, 3/5 A et 2/5 B) et *S. etruscus* (Senèze, 2/5 A et 3/5 B ; Valdarno supérieur, 1/1 B ; Étouaires, 1/1 B).

single individual from Upper Valdarno (Fig. 17). According to Guérin (1980), no particular morphologies distinguish the articular facets of the two species either. However, the postero-proximal facet for the cuboid bends upward on its lateral side in one out of five specimens of *S. etruscus* from Senèze, while it is vertical and close to the corpus of the bone in the remaining individuals from Senèze, in the individual from Upper Valdarno and in the *S. elatus* specimens from Vialeite (3/3 individuals). We also notice that the proximal articular surface shows a deep depression in its lateral side in most of the specimens of *S. etruscus* from Senèze (4/5 individuals – not in the specimen from Upper Valdarno), while the same is rare in the *S. elatus* specimens from Vialeite (1/4 individuals).

In the specimen from Étouaires, MNHN PET 259, the dorsal wall is sub-rectangular and not very elongated in its latero-distal angle (observed in both *S. elatus* and *S. etruscus*), the postero-proximal facet for the cuboid bends upward on its lateral side (*S. etruscus*-like) and the proximal articular surface shows a deep depression in its lateral side (*S. etruscus*-like).

The measurements are comparable to those of *S. etruscus* from Senèze being smaller than *S. elatus* from Vialeite (see on-line metric table) and the specimen is thus attributed to the former species, although it was listed as *D. jeanvireti* by Guérin (1972).



**Fig. 18.** MtII, proximal epiphysis (lateral view). A: *Stephanorhinus elatus*, B: *S. etruscus*. The distance between the dorsal and plantar facets for the MtIII and the cuneiform III, is large in *S. elatus* (Vialeite, 2/2; Étouaires 1/1) while it is smaller in *S. etruscus* (Senèze, 5/5).

**Fig. 18.** MtII, épiphyse proximale (vue latérale). A : *Stephanorhinus elatus*, B : *S. etruscus*. La distance entre les facettes dorsale et plantaire de MtIII et du cunéiforme III est importante chez *S. elatus* (Vialeite, 2/2 ; Étouaires 1/1), alors qu'elle est plus faible chez *S. etruscus* (Senèze, 5/5).

#### 3.4.4. Metatarsal bones

A single right MtII is present, MNHN PET 247, lacking the distal portion. A single left MtIII, MNHN PET 245, has been described as part of the paralectotype of the species *S. elatus* (Ballatore and Breda, 2016). Two right MtIV are present: MNHN PET 248, a complete but fragmentary bone composed of two perfectly fitting pieces, and MNHN PET 249, a badly preserved proximal fragment.

##### - MtII

From a morphological point of view, we notice that, in lateral view, the distance between the dorsal and plantar facets for the MtIII and the cuneiform III is large in *S. elatus* from Vialeite (2/2 individuals), while it is smaller in *S. etruscus* from Senèze (5/5 individuals), it is not observable in the single specimen from Upper Valdarno because it is broken (Fig. 18). This difference possibly corresponds to the statement by Guérin (1980), that the two facets are “largement séparées” in *S. elatus* and “bien séparées” in *S. etruscus*.

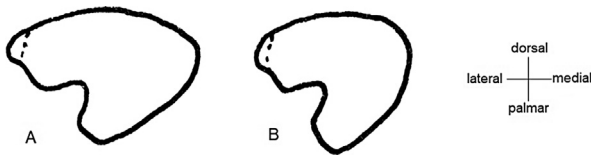
The specimen from Étouaires, MNHN PET 247, shows a large distance between the lateral facets (*S. elatus* character). The metric values of MNHN PET 247 fall in the range of *S. elatus* from Vialeite (see on-line metric table), thus supporting the attribution to this species.

##### - MtIII

From a morphological point of view, a diagnostic difference between the two species considered here lies in the proximal articular surface for the cuneiform III. This is medio-laterally enlarged in the specimens from Vialeite (3/4 individuals) and in the paralectotype of *S. elatus* from Étouaires (Ballatore and Breda, 2016), while it is isodiametric in the *S. etruscus* from Senèze (3/3 individuals) (Fig. 19).

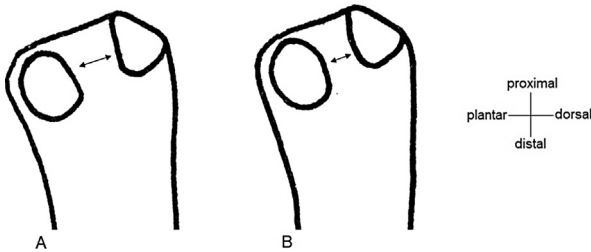
##### - MtIV

The distance between the medial facets for the MtIII is large in *S. elatus* from Vialeite (3/4 individuals), while it is smaller in *S. etruscus* (8/8 individuals) (Fig. 20). Guérin (1980) does not provide notes on this character but states that in *S. elatus* the dorsal facet “a un développement inférieur ou équivalent” to the plantar facet, while in *S. etruscus* the plantar facet is “très variable mais reste en principe plus petite que l'antérieure (= the dorsal one)”. However, our observations show that the interspecific variability in this



**Fig. 19.** MtIII, proximal epiphysis (proximal view). A: proximal articular surface for the cuneiform III medio-laterally enlarged, B: isodiametric. In *Stephanorhinus etruscus*, it is always isodiametric (Senèze, 3/3 B), while in *S. elatus* it is variable (Viallette, 3/4 A and 1/4 B; Étouaires, 1/1 A).

**Fig. 19.** MtIII, épiphyse proximale (vue proximale). A : surface articulaire proximale du cunéiforme III élargi médio-latéralement, B : isodiamétrique. Chez *Stephanorhinus etruscus* elle est toujours isodiamétrique (Senèze, 3/3 B), tandis que chez *S. elatus* elle est variable (Viallette, 3/4 A et 1/4 B ; Étouaires, 1/1 A).



**Fig. 20.** MtIV, proximal epiphysis (medial view). A: large distance between the medial facets for the MtIII, B: small distance. In *Stephanorhinus etruscus* the distance is small (Senèze, 8/8 B), while in *S. elatus* it is prevalently large but can be small (Viallette, 3/4 A and 1/4 B; Étouaires, 1/1 A). The relative size of the facets is variable in the two species (see the text).

**Fig. 20.** MtIV, épiphyse proximale (vue médiale). A : distance importante entre les facettes médiales de MtIII, B : faible distance. Chez *Stephanorhinus etruscus* cette distance est faible (Senèze, 8/8 B), alors qu'elle est majoritairement importante chez *S. elatus*, même si elle peut être petite (Viallette, 3/4 A et 1/4 B ; Étouaires, 1/1 A). La taille relative des facettes est variable chez les deux espèces (voir texte).

feature is high in the two species considered: *S. elatus* has a dorsal facet smaller than the plantar one in 1 individual but equal to it in the remaining 2 individuals; *S. etruscus* has a plantar facet smaller than the dorsal in 2/6 individuals and they are equal in 3/6 cases, but a single individual has a dorsal facet smaller than the plantar.

Specimen MNHN PET 248 shows a large distance between the medial facets (*S. elatus* character) and the dorsal facet is smaller than the plantar one (*S. elatus*-like). The great length of the specimen brings to exclude with confidence an attribution to *S. etruscus* (see [on-line metric table and Fig. Sm1](#)), thus MNHN PET 248 is attributed to *S. elatus*.

MNHN PET 249 is too damaged for a confident morphological description, but it is smaller than the other one and falls within the range of *S. etruscus* from Senèze (see [on-line metric table and Fig. Sm1](#)). It is thus attributed to *S. cf. etruscus*.

Guérin (1972) ascribed four metatarsal bones stored in Paris to *D. jeanvireti*, including one MtII (corresponding to MNHN PET 247), two MtIII (namely MNHN PET 245 plus the McIII discussed above) and one of the two MtIV (MNHN PET 248 and 249). Later Heintz et al. (1974) reported five metatarsal bones, counting the four discussed metatarsals

plus, again, the wrongly identified McIII of Guérin. We consider one of the two MtIV as *S. cf. etruscus*.

#### 4. Conclusion

The detailed comparison of the postcranial remains of *Stephanorhinus elatus* from Viallette and *S. etruscus* from Senèze and Upper Valdarno, all localities yielding only one of the two species considered, allows the identification of morphological characters distinguishing them. This, in turn, allowed the identification of the specimens from Étouaires, confirming the coexistence of the two species, as claimed by previous authors (Guérin, 1972, 1980, Heintz et al., 1974).

From a morphological point of view, the distinction between *S. elatus* and *S. etruscus* is difficult, since both species share common characters and the interspecific variability often overlaps and includes polymorphic characters.

It must be kept in mind that, in particular for *S. elatus* from Viallette, the limited number of remains for some postcranial elements restricts at the population level the significance of the results. So, the results of this analysis should be tested on a larger number of populations to account for the intraspecific variability, but still considering only monospecific populations to avoid data circularity.

However, the morphological differences here considered having a discriminant value between the two species, in the populations considered, and provided that we analysed only a limited portion of the Upper Valdarno collection, are listed below by anatomical element:

- Atlas (Fig. 2)
  - the cranial articular surfaces are kidney-shaped in *S. elatus* from Viallette and comma-shaped in *S. etruscus* from Senèze and Étouaires;
  - the caudal articular surfaces are uniform from the top to the bottom in *S. elatus* from Viallette and laterally stretched in the dorsal part in *S. etruscus* from Senèze and Étouaires.
- Humerus (Fig. 4)
  - the coracobrachialis insertion is present and protruding – or rarely absent – in *S. elatus* from Viallette and Étouaires, and systematically absent in *S. etruscus* from Étouaires, Senèze and Upper Valdarno;
  - the strength of the diaphysis at the minimum is robust in *S. elatus* from Viallette and Étouaires, while is slender in *S. etruscus* from Étouaires, Senèze and Upper Valdarno;
  - on the lateral side of the distal epiphysis, the cranio-caudally oriented transversal crest is high in *S. elatus* from Viallette, while it is in a lower position in *S. etruscus* from Étouaires, Senèze and Upper Valdarno. In MNHN PET 2004 the crest is not as high as in *S. elatus*, and the lateral epicondyle is more compressed than in *S. etruscus*.
- Magnum (Fig. 7)
  - The dorsal wall is more proximo-distally elongated in *S. etruscus* from Étouaires and Senèze, while is medio-laterally enlarged in *S. elatus* from Viallette.
- Femur (Fig. 11)

**Table 2**List of specimens of *Stephanorhinus elatus* and *S. etruscus* from Étouaires according to the attribution discussed in this work.**Tableau 2**Liste des spécimens de *Stephanorhinus elatus* et *S. etruscus* d'Étouaires selon l'attribution discutée dans cet article.

Element	Side	Museum	Catalogue number	Species	Pandolfi et al., 2017
Nasals	\	MNHN	(no number)	<i>Stephanorhinus</i> sp.	
Upper P3/4	L	UCBL	FSL 211584	<i>S. elatus</i>	
Atlas	\	UCBL	FSL 211580	<i>S. etruscus</i>	
Axis	\	NMB	Prr. 326	<i>S. cf. etruscus</i>	
Scapula	R	NHM	OR 34732	<i>Stephanorhinus</i> sp.	
Humerus	R	MNHN	PET 2002	<i>S. elatus</i> *	
Humerus	R	MNHN	PET 2004	<i>S. etruscus</i>	
Humerus	R	NMB	Prr. 429	<i>S. elatus</i>	<i>S. elatus</i>
Radius	R	MNHN	2317	<i>S. elatus</i> *	
Radius	L	MNHN	PET 241	<i>Stephanorhinus</i> sp.	
Radius	R	UCBL	FSL 211575	<i>S. etruscus</i>	
Radius	R	UCBL	FSL 211576	<i>S. etruscus</i>	
Radius	L	NMB	Prr. 52	<i>S. elatus</i>	<i>S. etruscus</i>
Radius	R	NMB	Prr. 109	<i>S. elatus</i>	<i>S. etruscus</i>
Magnum	L	NMB	Prr. 56	<i>S. etruscus</i>	<i>S. etruscus</i>
McII	R	MNHN	PET 242	<i>S. elatus</i> *	
McIII	L	MNHN	PET 243	<i>S. cf. etruscus</i>	
McIII	R	MNHN	PET 244	<i>S. elatus</i> *	
McIII	R	NMB	Prr. 55	<i>S. cf. etruscus</i>	<i>S. elatus</i>
McIV	L	MNHN	PET 251	<i>S. etruscus</i>	
Femur	R	MNHN	PET 2003	<i>S. elatus</i> *	
Femur	L	NMB	Prr. 155	<i>S. cf. etruscus</i>	
Femur	R	NMB	Prr. 323	<i>S. cf. etruscus</i>	<i>S. etruscus</i>
Tibia	R	MNHN	PET 238	<i>S. elatus</i>	
Tibia	L	NMB	Prr. 321	<i>S. etruscus</i>	<i>S. etruscus</i>
Astragalus	L	MNHN	PET 240	<i>S. elatus</i> *	
Calcaneus	L	MNHN	PET 239	<i>S. elatus</i> *	
Calcaneus	L	MNHN	PET 252	<i>S. elatus</i>	
Calcaneus	L	NMB	Prr. 53	<i>S. elatus</i>	<i>S. etruscus</i>
Calcaneus	L	NMB	Prr. 54	<i>Stephanorhinus</i> sp.	<i>S. etruscus</i>
Calcaneus	L	NMB	Prr. 327	<i>S. etruscus</i>	<i>S. etruscus</i>
Calcaneus	R	MHNL	P.86	<i>S. elatus</i>	
Cuboid	R	MNHN	PET 258	<i>S. elatus</i>	
Cuboid	R	MNHN	PET 261	<i>S. elatus</i>	
CuneiformIII	R	MNHN	PET 259	<i>S. etruscus</i>	
MtII	R	MNHN	PET 247	<i>S. elatus</i>	
MtIII	L	MNHN	PET 245	<i>S. elatus</i> *	
MtIV	R	MNHN	PET 248	<i>S. elatus</i>	
MtIV	R	MNHN	PET 249	<i>S. cf. etruscus</i>	

The supposed attribution by Pandolfi et al. (2017), for some remains stored in Basel, is given in the last column. MNHN: Muséum national d'histoire naturelle, Paris, NMB: Naturhistorisches Museum Basel, UCBL: Université Claude-Bernard Lyon-1, Collections de géologie, Laboratoire de géologie de Lyon Terre Planètes Environnement, MHNL: Musée d'histoire naturelle de Lyon, NHM: The Natural History Museum, London.

Le symbole (\*) identifie le lectotype et le paralectotype de *S. elatus* décrits par Ballatore et Breda (2016). L'attribution proposée par Pandolfi et al. (2017), pour certains fossiles stockés à Bâle, est donnée dans la dernière colonne. MNHN: Muséum national d'histoire naturelle de Paris, NMB: Naturhistorisches Museum Basel, UCBL: Université Claude-Bernard Lyon-1, Collections de géologie, laboratoire de géologie de Lyon Terre Planètes Environnement, MHNL: Musée d'histoire naturelle de Lyon, NHM: The Natural History Museum, Londres.

The top of the medial lip of the trochlea is higher than the top of the lateral lip in *S. etruscus*, while this difference is lower in *S. elatus*.

- MtII (Fig. 18)

the distance between the dorsal and plantar facets for the MtIII and the cuneiform III is large in *S. elatus* from Vialette and small in *S. etruscus* from Senèze.

In other cases, some characters are shared by the two species with a different frequency, or one species shows a single morphology while the other is polymorphic. Interestingly, the two species are polymorphic in different characters and there is not one of them that is more polymorphic than the other, neither any pattern among the characters or anatomical elements can be identified:

- upper premolar: the lingual cingulum is always present in *S. etruscus*, while can be present or absent in *S. elatus*;
- scapula (Fig. 3): the glenoid surface is asymmetrical in *S. elatus*, while *S. etruscus* is polymorphic;
- radius (Fig. 5): the palmar edge of the lateral half of the proximal articular surface is strongly oblique in *S. etruscus*, while *S. elatus* is polymorphic;
- tibia (Fig. 12): the plantar outline of the distal articular surface is slightly concave in *S. elatus*, while *S. etruscus* is polymorphic;
- metapodial bones: concerning the characters on these elements, *S. etruscus* is polymorphic in McII (Fig. 8) and McIII (Fig. 9), while *S. elatus* is polymorphic in McIV (Fig. 10), MtIII (Fig. 19) and MtIV (Fig. 20);

- tarsus: *S. etruscus* is polymorphic in the cuboid (Fig. 16), while *S. elatus* is polymorphic in the astragalus (Fig. 14) and calcaneus (Fig. 15);
- both species are polymorphic in two characters in the astragalus (Fig. 13) and cuneiform III (Fig. 17).

From a metrical point of view the range of the two species was already set by Guérin (1980); however, the partial superposition of some dimension is significant, and our graph (Fig. S1) shows at a glance the sometimes small difference in size between the two species.

We must remember that Vialette is dated at 3.1 Ma (Biquand et al., 1981, Thouveny and Bonifay, 1984) and Senèze at 2.2 Ma (Nomade et al., 2014), thus the locality of Étouaires, ranging from 3.18 to 2.35 Ma, is intermediate in age between them. Although the scantiness of the remains partly hampers the results of the biometric investigation, the following considerations can be drawn: *S. elatus* from Étouaires falls in the lower part of the restricted size-range of Vialette (based on few individuals, two complete skeletons and scanty isolated bones) and broadens its lower edge. In particular, *S. elatus* from Étouaires is slightly smaller than its coeval/older conspecific from Vialette in the proximal elements of the legs (humerus, radius, femur, tibia), but not so much in the distal elements (tarsals and metapodial bones). *S. etruscus* from Étouaires, on the contrary, plots in the upper part of the range of the conspecific rhino from Senèze (scapula, humerus, radius, femur, carpal and tarsal bones, metapodial bones) and only the atlas exceeds the range.

Concerning the locality of Étouaires, the identification of both *S. elatus* and *S. etruscus* confirms the coexistence of the two species, as claimed by previous authors (Guérin, 1972, 1980, Heintz et al., 1974) and recently supported by Pandolfi et al. (2017). A comprehensive list of the rhinoceroses remains and their attribution to the species *S. elatus* and *S. etruscus* is given in Table 2.

Considering the presence of the two species at Étouaires from a chronological point of view, we must remember that Mazza (1988), in a careful revision of the species *S. etruscus*, prudently states: “the occurrence of *D. etruscus* at time older than that of the sites St. Vallier-Puebla de Valverde may even be possible, but still deserves careful verification”. The quoted sites are coeval with Senèze, while Étouaires is older. However, the earliest occurrence of the species, from the locality of Las Higuieruelas, in Spain, dated at ca. 3.3 Ma by Mazo (1995) has been recently confirmed by Pandolfi et al. (2017), thus, although the fauna from Étouaires is not precisely dated (see Section 1.1), the presence of *S. etruscus* here does not represent the first appearance of the species. On the contrary, the locality of Étouaires represents the last occurrence of *S. elatus*.

Does the presence of two distinct species at Étouaires, mean that the two species really coexisted at the same time in the same place? Ecological niche partitioning could be advocated to explain this fact, and the different sizes of the two species could support such an idea. As a matter of fact, two species of rhinoceros can live in the same area without competing for food. Examples are the present-day white rhinoceros, *Ceratotherium simum*, and black rhinoceros, *Diceros bicornis*, from African savannahs, or the late

middle Pleistocene *S. hemitoechus* and *S. kirchbergensis* from several European localities (Mazza, 1993, Van Asperen and Kahlke, 2015, Van der Made and Grube, 2010). However, while modern African rhinoceroses and the two quoted middle Pleistocene species show consistent morphological differences in dentition and gait that support a niche partitioning, the dental material of *S. elatus* and *S. etruscus* is very similar (Ballatore et al., 2017).

In order to evaluate the difference in the diets of the two species, several methods of investigation have been attempted. A carbon isotope analysis gave no results because the samples had undergone recrystallization and the biogenic signal had been lost (Ballatore, 2016b). Szabó et al. (2017), however, obtained some results from carbon isotopes and concluded that there is no significant difference between the diets of *S. elatus* and *S. etruscus*. A multi-approach analysis, based on morpho-biometry, mesowear and DMTA (Dental Microwear Texture Analysis), suggests that *S. elatus* and *S. etruscus* had the same diet, thus niche partitioning is difficult to support (Ballatore et al., 2017).

Therefore, the apparent coexistence of the two species at Étouaires needs an explanation. The answer could be found in the chronological difference of the various levels labelled as “Étouaires” (see Section 1.1). Since no detailed information is available on the stratigraphic origin of the specimens from old excavations, only the retrieval of new material in stratigraphic context could solve the question of whether the two species really coexisted in the same place at the same time.

## Funding

This work was supported by the University of Ferrara (grant ‘Giovani Ricercatori’ supported by the 5 × 1000 tax from individual income tax return 2011; grant IUSS-Ferrara 1391; and the Athenaeum Research Funds FAR 2012 and 2013) and by the SYNTHESYS Project (<http://www.synthesys.info/>), which is financed by European Community Research Infrastructure Action under the FP7 “Capacities” Program (FR-TAF-3273, GB-TAF-5189; 2015).

## Acknowledgments

We are very grateful to the curators of the collections who allowed M. Ballatore to study the material: Christine Argot (‘Muséum national d’histoire naturelle’, Paris), Loïc Costeur and Martin Schneider (‘Naturhistorisches Museum Basel’), Emmanuel Robert (‘Collections de géologie’ of the ‘Laboratoire de géologie de Lyon–Terre Planètes Environnement, Université Claude-Bernard Lyon-1’), Didier Berthet (‘Musée des Confluences’, Lyon), Adrian Lister and Pip Brewer (The Natural History Museum, London). We also thank the librarians who provided help in retrieving old literature: Emilia Cianci (Biblioteca Malaroda, Department of Earth Sciences, University of Turin) and Marie-Astrid Angel (MNHN).

All the scratches of the bones are drawings by M. Ballatore. We thank Elisa Zenoni for the graphic preparation of



the figures and Manon Hullot and Quentin Vanturin for the translations into French.

We acknowledge the anonymous referees whose advices led to the improvement of the manuscript.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.crpv.2018.06.003>.

## References

- Ballatore, M., 2012. Plio-Pleistocene rhinoceroses of the genus *Stephanorhinus* and the revision of the material from Dusino and Roatto (Villafranca d'Asti, Piedmont) and Isernia La Pineta (Isernia, Molise). Bachelor thesis, University of Ferrara, Italy, 150 p.
- Ballatore, M., 2016a. Palaeoecological investigations on Plio-Pleistocene European Rhinoceroses (Genus *Stephanorhinus*): powder X-ray diffraction, carbone isotope geochemistry, tooth wear analyses and biometry. PhD thesis, University of Ferrara, Italy, 192 p.
- Ballatore, M., 2016b. Palaeoecological investigations on Plio-Pleistocene European rhinoceroses (Genus *Stephanorhinus*): powder X-ray diffraction, carbon isotope geochemistry, tooth wear analyses and biometry. Pliinius, <http://dx.doi.org/10.19276/plinius.2016.01001>.
- Ballatore, M., Breda, M., 2013. *Stephanorhinus hundsheimensis* (Rhinocerotidae, Mammalia) teeth from the early Middle Pleistocene of Isernia La Pineta (Molise, Italy) and comparison with coeval British material. *Quat. Int.* 302, 169–183.
- Ballatore, M., Breda, M., 2016. *Stephanorhinus elatus* (Rhinocerotidae, Mammalia): proposal for the conservation of the earlier specific name and designation of a lectotype. *Geodiversitas* 38 (4), 579–594.
- Ballatore, M., Merceron, G., Breda, M., 2017. Inferences on the diet of fossil European rhinoceroses. Palaeoecological inferences from the dental material of Pliocene to Early Pleistocene rhinoceroses. ed. LAP Lambert Academic Publishing, Saarbrücken, Germany.
- Bello, S.M., Delbarre, G., Parfitt, A.S., Curren, A.P., Kruszynski, R., Stringer, C.B., 2013. Lost and found: the remarkable curatorial history of one of the earliest discoveries of Paleolithic portable art. *Antiquity* 87, 237–244.
- Biélawski, J.B.M., 1905. Gisement et faune de la Roca-Neyra à Perrier. *Soc. Amis Univ. Clermont*.
- Biquand, D., Cassignol, C., Chambaudet, A., Couthures, J., 1981. Nouvelles données chronostratigraphiques concernant les dépôts lacustres de Viallette (Haute-Loire). *Bull. Assoc. fr. Ét. Quat.* 18 (2), 83–87.
- Boule, M., 1888. Constitution géologique des environs du Puy. *Bull. Soc. géol. France* 3, 17–89.
- Bout, P., 1960. Le Villafranchien du Velay et du Bassin hydrographique moyen et supérieur de l'Allier. ed. Jeanne d'Arc, Le Puy.
- Bout, P., 1967. Observations sur le Villafranchien d'Auvergne et du Velay (compte rendu de l'excursion de l'AFEQ du 19 au 22 mai 1966). *Bull. Assoc. fr. Ét. Quat.* 4 (1), 3–64.
- Bout, P., 1970. Absolute ages of some volcanic formations in the Auvergne and Velay areas and chronology of the European Pleistocene. *Palaeogeogr. Plalaeoclimatol. Palaeoecol.* 8, 95–106.
- Bout, P., 1975. The contribution of the volcanic Massif Central of France to European Quaternary chronology. ed. Moutonédit, La Hague, Paris.
- Bout, P., Azzaroli, A., 1952. Stratigraphie et faune du Creux de Peyrolles près Perrier (Puy-de-Dôme). Ed. Masson.
- Bravard, A., 1828. Monographie de la Montagne de Perrier, près d'Issoire (Puy-de-Dôme) et de deux espèces fossiles du genre *Felis*, découvertes dans l'une de ses couches d'alluvion : avec une carte et deux planches. Ed. Dufour.
- Breda, M., Collinge, S.E., Parfitt, S.A., Lister, A.M., 2010. Metric analysis of ungulate mammals in the early Middle Pleistocene of Britain, in relation to taxonomy and biostratigraphy: I: Rhinocerotidae and Bovidae. *Quat. Int.* 228 (1), 136–156.
- Buc'hoz, P.-J., 1796. Histoire naturelle de la ci-devant province d'Auvergne, divisée actuellement en deux départemens, le Cantal et le Puy-de-Dôme. Extrait de la grande collection d'Histoire Naturelle Buc'hoz, médecin. Paris.
- Croizet, J.B., Jobert, A., 1828. Recherches sur les ossements fossiles du département du Puy-de-Dôme. Ed. A. Delahays, Paris.
- Croizet, J.-B., 1853. Observations générales sur la géologie et la paléontologie. Hubler, Bayle & Dubos, Clermont-Ferrand.
- Croizet, J.-B., 1855. *Compte rendu des découvertes de Neschers*. Paper presented at the Congrès Scientifique de France, 22<sup>e</sup> Session. Le Puy (France), September 1855.
- Daugas, J.-P., 1979. Les gisements préhistoriques de la grotte du Cheix Saint-Diéry et de Neschers (Puy-de-Dôme). In: de Sonneville-Bordes, D. (Ed.), *La Fin des temps glaciaires en Europe: chronostratigraphie et écologie des cultures du Paléolithique final 2*. CNRS, Paris, pp. 537–543.
- Delson, E., Faure, M., Guérin, C., Aprile, L., Argant, J., Blackwell, B.A.B., Debard, E., Harcourt-Smith, W., Martin-Suarez, E., Monguillon, A., Parienti, F., Pastre, J.-F., Sen, S., Skinner, A.R., Swisher III, C.C., Valli, A.M.F., 2006. Franco-American renewed research at the Late Villafranchian locality of Senèze (Haute-Loire, France). *Cour. Forsch. -Inst. Senckenberg* 256, 275–290.
- Depéret, C., 1884. Ruminants pliocènes et quaternaires d'Auvergne.
- Depéret, C., Mayet, L., Roman, F., 1923. *Les éléphants pliocènes*. Ed. A. Rey, Lyon.
- Devezé de Chabriol, J.S., Bouillet, J.B., 1827. Essai géologique et minéralogique sur les environs d'Issoire, département du Puy-de-Dôme, et principalement sur la Montagne de Boulade, avec la description et les figures lithographiées des ossements fossiles qui y ont été recueillis, 104 p.
- Fortelius, M., Mazza, P., Sala, B., 1993. *Stephanorhinus* (Mammalia: Rhinocerotidae) of western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). *Palaeontographia Italica* 80, 63–155.
- Grellet, F., 1863. L'Éloge biographique de l'Abbé Croizet, Paper presented at the Meeting of l'Academie des Sciences, Belles-Lettres et Arts de Clermont-Ferrand, Clermont-Ferrand (France), 4 June 1863. Available at: <http://www.anales.org/archives/cofrhigeo/croizet.html>.
- Groves, C.P., 1983. Phylogeny of the living species of rhinoceros. *Zeitschr. f. zoo. Systematik u. Evolutionsforsch.* 21, 293–313.
- Guérin, C., 1972. Une nouvelle espèce de rhinocéros à Viallette et dans d'autres gisements du Villafranchien inférieur européen : *Dicerorhinus jeanvireti* n. sp. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 49, 53–150.
- Guérin, C., 1980. Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe Occidentale. Comparaison avec les espèces actuelles. *Doc. Lab. Géol. Fac. Sciences de Lyon* 79, t. II-III.
- Guérin, C., 2004. Les rhinocéros (Mammalia, Perissodactyla) du gisement Villafranchien moyen de Saint-Vallier (Drôme). *Geobios* 37, S259–S278.
- Guérin, C., Tsoukala, E., 2013. The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). *Geodiversitas* 35 (2), 447–489.
- Heintz, E., 1967. Données préliminaires sur les cervidés villafranchiens de France et d'Espagne. Colloques internationaux du CNRS, Problèmes actuels de Paléontologie (évolution des vertébrés), Paris 1966. Éditions du CNRS 163, Paris, 1966, pp. 540–551.
- Heintz, E., 1970. Les Cervidés villafranchiens de France et d'Espagne. *Bull. Museum national d'Histoire naturelle*, Paris 22, 1–303.
- Heintz, E., Guérin, C., Martin, P., Prat, F., 1974. Principaux gisements villafranchiens de France : listes fauniques et biostratigraphie. *Mem. BRGM* 78 (1), 169–182.
- Jung, J., 1946. Géologie de l'Auvergne et de ses confins bourbonnais et limousins. *Mém. Expl. Carte géol. dét. France*, 372 p.
- Lacombat, F., 2005. Les Rhinocéros fossiles des sites préhistoriques de l'Europe méditerranéenne et du Massif Central, Paléontologie et implications biochronologiques. *British Archaeological Research, International Series* 1419, 1–175.
- Lacombat, F., Abbazzi, L., Ferret, M.P., Martínez-Navarro, B., Moullé, P.-E., Palombo, M.-R., Rook, L., Turner, A., Valli, A.M.F., 2008. New data on the Early Villafranchian fauna from Viallette (Haute-Loire, France) based on the collection of the Crozatier Museum (Le Puy-en-Velay, Haute-Loire, France). *Quat. Int.* 179, 64–71.
- Mazo, A.V., 1995. *Stephanorhinus etruscus* (Perissodactyla, Mammalia) en el Villafranchiense Inferior de Las Higuieruelas. *Alcolea de Calatrava* (Ciudad Real). *Estudios Geol.* 51, 285–290.
- Mazza, P., 1988. The Tuscan Early Pleistocene rhinoceros *Dicerorhinus etruscus*. *Palaeontographia Italica*, Pisa 75, 1–87.
- Mazza, P., 1993. Ethological inferences on Pleistocene rhinoceroses of Europe. *Atti dell'Accademia Nazionale dei Lincei - Rendiconti dell'Accademia dei Lincei, Scienze Fisiche e Naturali*. Roma 9 (4), 127–137.
- Michel-Lévy, A., Munier-Chalmas, 1892. *Compte rendu de l'excursion du 19 septembre à Pardines, Perrier et Issoire*, in : Réun, Extr. De la S. G. F. à Clermont-Ferrand et au mont-Dore. *Bull. Soc. géol. France*, 929 p.
- Michel-Lévy, A., Munier-Chalmas, 1889. Etude sur les environs d'Issoire. *Bull. Soc. géol. France* 17, 269 p.

- Nomade, S., Pastre, J.-F., Guillou, H., Faure, M., Guérin, C., Delson, E., Debard, E., Voinchet, P., Messenger, E., 2014.  $^{40}\text{Ar}/^{39}\text{Ar}$  constraints on some French landmark Late Pliocene to Early Pleistocene large mammalian paleofaunas: Paleoenvironmental and paleoecological implications. *Quat. Geochronol.* 21, 2–15.
- Pandolfi, L., Cerdeño, E., Codrea, V., Kotsakis, T., 2017. Biogeography and chronology of the Eurasian extinct rhinoceros *Stephanorhinus etruscus* (Mammalia, Rhinocerotidae). *C. R. Palevol* 16, 762–773.
- Pandolfi, L., Petronio, C., 2011. *Stephanorhinus etruscus* (Falconer, 1868) from Pirro Nord (Apricena, Foggia, Southern Italy) with notes on the other late Early Pleistocene rhinoceros remains of Italy. *Rivista Italiana di Paleontologia e Stratigrafia* 117 (1), 173–187.
- Pandolfi, L., Tagliacozzo, A., 2015. *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from the Late Pleistocene of Valle Radice (Sora, Central Italy) and re-evaluation of the morphometric variability of the species in Europe. *Geobios* 48, 169–191.
- Pastre, J.-F., 2004. The Perrier Plateau: a Plio-Pleistocene long fluvial record in the river Allier Basin, Massif Central, France. *Quaternaire* 15 (1), 87–101, <http://dx.doi.org/10.3406/quate.2004.1757>.
- Piveteau, J., 1958. *Traité de Paléontologie*, t. VI, vol. 2. Masson & C<sup>ie</sup>, Paris, 962 p.
- Poidevin, J.-L., Cantagruel, J., GUERPA, 1984. Un site unique du Plio-Pléistocène en Europe : le plateau de Perrier (Puy-de-Dôme). Confrontation des données volcanologiques, stratigraphiques et paléontologiques. *Revue de sciences naturelles d'Auvergne, Clermont-Ferrand* 50, 87–95.
- Pomel, A., 1846. Quelques nouvelles considérations sur la paléontologie de l'Auvergne. *Bull. Soc. geol. France*, ser. 2 III, 198–231.
- Pomel, A., 1854. Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire, et surtout dans la vallée de son affluent principal l'Allier. J.-B. Baillière, Paris.
- Rook, L., Martínez-Navarro, B., 2010. Villafranchian: the long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quat. Int.* 219, 134–144.
- Schaub, S., 1941. Eines neues Hyaenidengenues von der Montagne de Perrier. *Eclog. Geol. Helv.* 34, 279–286.
- Schaub, S., 1943. Die Oberpliocäne Säugetierfauna von Senèze (H.te-Loire) und ihre verbreitungsgeschichtliche Stellung. *Eclog. Geol. Helv.* 36 (2), 270–289.
- Schaub, S., 1949. Révision de quelques Carnassiers villafranchiens du Niveau des Étouaires (montagne de Perrier, Puy-de-Dôme). *Société Paleontol. Suisse*, <http://dx.doi.org/10.5169/seals-161185>.
- Stehlin, H.G., 1904. Une faune à Hipparion à Perrier. *Bull. Soc. geol. France* 4, 432–444.
- Szabó, P., Kocsis, L., Vennemann, T., Pandolfi, L., Kovács, J., Martinetto, E., Demény, A., 2017. Pliocene-Early Pleistocene climatic trends in the Italian Peninsula based on stable oxygen and carbon isotope compositions of rhinoceros and gomphothere tooth enamel. *Quat. Sci. Rev.* 157, 52–65.
- Thouveny, N., Bonifay, E., 1984. New chronological data on European Plio-Pleistocene faunas and hominid occupation sites. *Nature* 308 (5957), 355–358.
- Valli, A.M., Caron, J.-B., Debard, E., Guérin, C., Pastre, J.-F., Argant, J., 2006. Le gisement paléontologique villafranchien terminal de Peyrolles (Issoire, Puy-de-Dôme, France): résultats de nouvelles prospections. *Geodiversitas* 28 (2), 297–317.
- Van Asperen, E.N., Kahlke, R.-D., 2015. Dietary variation and overlap in Central and Northwest European *Stephanorhinus kirchbergensis* and *S. hemitoechus* (Rhinocerotidae, Mammalia) influenced by habitat diversity. *Quat. Sci. Rev.*, <http://dx.doi.org/10.1016/j.quascirev.2014.10.001>.
- Van der Made, J., 2010. The rhinos from the Middle Pleistocene of Neumark-Nord (Saxony-Anhalt). *Veröffentlichungen des Landesamtes für Denkmalpflege und Archäologie* 62, 433–527.
- Van der Made, J., Grube, R., 2010. The rhinoceroses from Neumark-Nord and their nutrition, in: *Elefantenreich—Eine Fossilwelt in Europa*. Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt, Halle (Saale), Germany.