

Pleistocene Rhinoceroses in Mediterranean Europe and in Massif Central (France)

With 14 figs, 3 tabs

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Abstract

This work presents the palaeontological study of four Plio-Pleistocene species of the genus *Stephanorhinus*, which occurred in twenty sites scattered throughout Mediterranean Europe and the Massif Central. These species are *S. etruscus* (Senèze, Upper Valdarno), *S. hundsheimensis* (Sainzelles, Ceysseguet, Soleilhac, Durfort, Vallonnet cave, Tour de Grimaldi, Cagnes-sur-Mer and Isernia), *S. hemitoechus* (Caune de l'Arago, Mars cave, Orgnac 3, Baume Bonne, Terra Amata, Prince cave, Cavillon cave, Observatoire cave and Barma Grande) and *S. kirchbergensis* (Aldène, Prince Cave and the Grotte des Enfants). The Vallonnet cave, Isernia La Pineta and Caune de l'Arago have provided particularly important contributions to our knowledge of European rhinoceroses. They have yielded remains of a small rather primitive *S. hundsheimensis*, of an advanced *S. hundsheimensis* and of *S. hemitoechus*, respectively. Morphological and biometric characteristics are outlined to illustrate the differences separating these species. Variations in size during the Pleistocene are also described. *S. etruscus* is characterised by a steady decrease in its size throughout time. In contrast, both *S. hundsheimensis* and *S. hemitoechus* demonstrate irregular size modifications: small Early Pleistocene *S. hundsheimensis* representatives are followed by larger Middle Pleistocene ones, whereas *S. hemitoechus* shows marked fluctuations in size, with the earliest and the most recent forms being larger than the intervening ones. Thanks to these fluctuations in size, Pleistocene rhinoceroses may result very helpful biochronological tools.

Key words: Rhinoceros, Pleistocene, Mediterranean Europe, Massif Central, Morphology, Biometry

Introduction

The study illustrates the major morphological and biometrical differences separating the upper P2 and lower M3 as well as the humerus, third metacarpal and astragalus of various Pleistocene species of the genus *Stephanorhinus*. The analysis shows that thanks to their size fluctuations through time the European fossil rhinoceroses are valuable biochronological tools.

This study concerns twenty sites of Mediterranean Europe and of the Massif Central (fig. 1, table 1) spanning the very end of Late Pliocene through to the whole Pleistocene. Four species of the genus *Stephanorhinus* characterize the faunal assemblages of these localities: *S. etruscus* (Senèze [Haute-Loire, France], Upper Valdarno [Toscany, Italy]), *S. hundsheimensis* (Cagnes-sur-Mer [Maritimes-Alps, France], Sainzelles [Haute-Loire, France], Ceysseguet [Haute-Loire, France], Vallonnet cave [Maritimes-Alps, France], Tour de Grimaldi [Liguria, Italy], Durfort [Gard, France], Soleilhac [Haute-Loire, France] and

Isernia la Pineta [Molise, Italy]), *S. hemitoechus* (Caune de l'Arago [Oriental Pyrenees, France], Baume Bonne [Haute-Provence Alps, France], Terra Amata [Maritimes-Alps, France], Orgnac 3 [Ardèche, France], Mars cave [Maritimes-Alps, France], Prince cave [Liguria, Italy], Observatoire cave [Principality of Monaco] and Barma Grande [Liguria, Italy]) and *S. kirchbergensis* (Aldène [Hérault, France], Prince cave [Liguria, Italy], Grotte des Enfants [Liguria, Italy]).

This study examines the rhinoceros material from three major sites: Vallonnet cave, Isernia la Pineta and Caune de l'Arago. The Vallonnet cave is located between the Principality of Monaco and Menton (France) in South-Eastern France. This small cave has yielded a late Early Pleistocene (Epivillafranchian) fauna according to LUMLEY et al. (1963, 1976, 1988), MOUILLÉ (1992, 1997) and MOUILLÉ et al. (2004), which is correlated with the Italian Colle Curti Faunal Unit. The stratigraphy is composed of five units. The first unit is a 1.37 My (ESR dating) stalagmitic floor (YOKOYAMA et al. 1988) The second unit

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Fig. 1: Location map of the sites.

is a marine deposit with foraminifers and with remains of *Monachus monachus*. The third unit, which is magnetically referred to the Jaramillo subzone (LUMLEY 1988) and thus dated from 1.07 My to 0.99 My, is a layer of clayey sand containing archaeological materials (fauna and lithic tools). The palynological analysis of this deposit indicates a vertical transition from cold and dry climatic conditions at the base to warmer ones at the top (RENAULT-MISKOVSKY & GIRARD 1988). The fourth unit is a 0.91 My (ESR dating) stalagmitic floor (YOKOYAMA et al. 1988). The last unit is a deposit of fallen rocks. This cave has yielded remains of a small-sized *S. hundsheimensis* (LACOMBAT 2003, 2005).

Isernia la Pineta is located in Italy, in the Molise Province, between Rome and Naples. This open-air site presents five lithological units (CREMASCHI 1983, COLTORTI 1983). The main archeological unit (t3a) includes volcanic elements dated around 600,000 years (COLTORTI et al. 2000, 2005); it covers a clayey deposit and travertine. This layer has yielded a Middle Galerian fauna (SALA 1983, 1986, 1990, 1996, SALA & FORTELIUS 1993) and numerous flint tools and residual cores (PERETTO 1994). Palynological analyses (ACCORSI 1985, LEBRETON 2001) indicate a long, dry season followed by a short, wet one. An evolved *Stephanorhinus hundsheimensis* characterizes this locality (SALA & FORTELIUS 1993, LACOMBAT 2003, 2005).

The Caune de l'Arago is located near Perpignan, in Southern France. The top of the stratigraphical sequence dates to the first half of the Middle Pleistocene, from 700,000 to 100,000 years (LUMLEY et al. 1984). The rhinoceros material was mostly found in the level G (0.45 My, MIS 14, Late Galerian, correlated with the Italian Fontana Ranuccio Faunal Unit) associated with numerous human remains and lithic tools. The palynological study

(RENAULT-MISKOVSKY 1980) of this layer shows the transition from a cold and dry steppe to a warmer and damper forest. The presence of *Stephanorhinus hemitoechus* is ascertained (LACOMBAT 2003, 2005), while that of *S. kirchbergensis* (GUERIN 1980, 1981) is not retained.

Material and method

This research is based on over 6,000 remains stored in the following institutions: National Museum of Natural History of Paris (Senèze, Durfort, Soleilhac, Mars cave and Upper Valdarno), Museum of Regional Prehistory of Menton (Vallonnet cave and Tour de Grimaldi), Museo d'Isernia (Isernia la Pineta), European Centre of Prehistoric Research of Tautavel (Caune de l'Arago and Orgnac 3), Museum of Natural History of Nice (Cagnes-sur-Mer), Museum Crozatier of Puy-en-Velay (Sainzelles, Ceysaguet and Soleilhac), Museum of Prehistoric Anthropology of Monaco (Aldène, Prince cave, Cavillon cave, Observatoire cave and Grotte des Enfants), Museum Terra Amata of Nice (Terra Amata) and Museum of Natural History of Florence (Upper Valdarno).

The different species were distinguished here using a selection of morphological traits. Although *Stephanorhinus* rhinoceroses have very uniform dental morphologies, the various species can be discriminated by calculating the frequencies of the different dental features illustrated by GUÉRIN (1980) and FORTELIUS et al. (1993). The presence/absence and state of the internal folds and of the different cingula of the upper and lower teeth are explained in LACOMBAT (2003, 2005, 2006) and shown in figs 2 and 3.

Only the distal part of the humerus is diagnostic:

Site (Location)	Age		References	
Senèze (Haute-Loire, France)	~2.09 My MIS 85 to 76 Late Pliocene Late Middle Villafranchian Costa S. Giacomo F. U.		ROGER et al. (2000) GLIOZZI et al. (1997)	
Upper Valdarno (Toscany, Italy)	~ 1.8 My Late Middle Villafranchian Tasso F. U.		GLIOZZI et al. (1997)	
Cagnes-sur-Mer (Maritimes-Alps, France)	Early Pleistocene		IRR (1975) LACOMBAT (2002, 2005)	
Sainzelles (Haute-Loire, France)	1.6 - 1.3 My / 1.4 - 1.3 My MIS?	Early Pleis- tocene Epivilla- franchian Pirro F. U.	MÉON et al. (1979) THOUVENY & BONIFAY (1984)	
Ceyssaguet (Haute-Loire, France)	1.2 My		BONIFAY (1986)	
Tour de Grimaldi (Liguria, Italy)	~ 1.0 My MIS 30 Early Pleistocene Epivillafranchian Colle Curti F.U.		MOULLÉ (1996) LACOMBAT & MOULLÉ (2005)	
Durfort (Gard, France)	~ 0.8 My ? late Early /early Middle Pleistocene Early Galerian Slivia F. U.		BRUGAL (1994)	
Soleilhac (Haute-Loire, France)	~ 0.7-0.6 My ? early Middle Pleistocene Middle Galerian Isernia F. U.		LACOMBAT et al. (2003) LACOMBAT (2004-2005)	
Baume Bonne (rhinoceros level) (Haute-Provence Alps, France)	> 0.4 My MIS 12 Middle Pleistocene Late Galerian? Fontana Ranuccio F. U. ?		LUMLEY and collaborators (in LACOMBAT 2005: 11-12)	
Terra Amata (Maritime-Alps, France)	0.38 My MIS 11	Middle Pleistocene Early Aurelian Torre in Pietra F. U.	FALGUÈRES (1986)	
Aldène (rhinoceros level) (Hérault, France)	? ~ 0.35 MIS 10		BONIFAY & BUSSIÈRE (1989, 1994)	
Orgnac 3 (Ardèche, France)	0.34 My MIS 9		FALGUÈRES et al. (1988)	
Mars Cave (Maritimes-Alps, France)	? MIS 6 End of late Middle Pleistocene Late Aurelian Vitinia F. U.		LUMLEY (1969)	
Grotte des Enfants (rhinoceros level) Prince cave (rhinoceros level) Cavillon Cave Barma Grande (Liguria, Italy)	Grimaldi's caves	MIS 5-3	Late Pleistocene	MOULLÉ (in LACOMBAT 2005: 12-14)
		MIS 4-3		
		MIS 4		
		MIS 4		
Observatoire cave (Principality of Monaco)	MIS 3 Late Pleistocene		MOULLÉ (in LACOMBAT 2005: 13)	

Table 1: Datations and references of the sites studied.

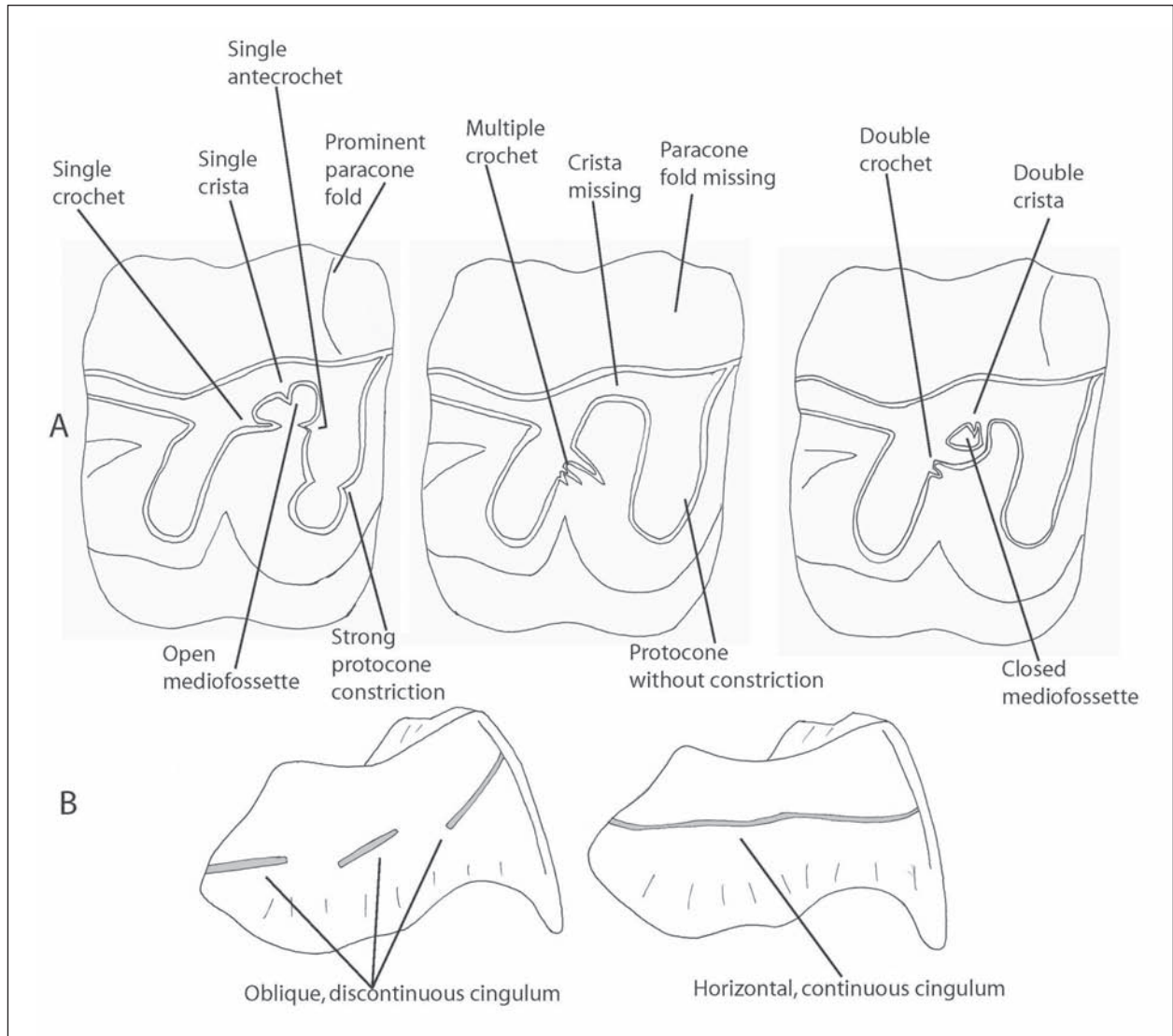


Fig. 2: Morphological features of the upper teeth. A – occlusal view; B – mesial view.

particularly important are the shape of the trochlea, the development of the lateral tuberosity, and the height and the development of the lips of the trochlea (GUÉRIN 1980, FORTELIUS et al. 1993). The most indicative features in the third metacarpal are the breadth of the proximal articular surface and the arrangement and shape of the proximal articular facets (GUÉRIN 1980, FORTELIUS et al. 1993), while in the astragalus, significant morphological differences can be noticed in the development of the trochlea, in the position of the medial tuberosity as well as in the proximo-distal height of the bone (GUÉRIN 1980, FORTELIUS et al. 1993).

The biometrical procedure adopted in this work is a compendium of several published methods. The measurement points of the upper and lower teeth are those indicated by GUÉRIN (1980), MAZZA (1988), FORTELIUS et al. (1993) and LACOMBAT (2003, 2005, 2006).

Comparisons are made using SIMPSON's (1941) ratio diagrams and the present day African black rhinoceros,

Diceros bicornis (studied collections from the Laboratory of Compared Anatomy of the National Museum of Natural History of Paris and the Museum of Prehistoric Anthropology of Monaco) as reference, which prevents from the uncertainties that stem from using a fossil reference (imperfect knowledge of sexual dimorphism, sized sample dependence, etc.).

Results

Upper P2 (figs. 4, 5, table 2)

The states of the morphological variables in the upper teeth are exposed in table 2 and fig. 4. *S. hundsheimensis* shows a larger P2 than *S. etruscus* (fig. 5). The lingual length, in particular, gives the upper P2 of *S. etruscus* a more triangular shape than that of *S. hundsheimensis*. This archaic character of *S. hundsheimensis* discriminates

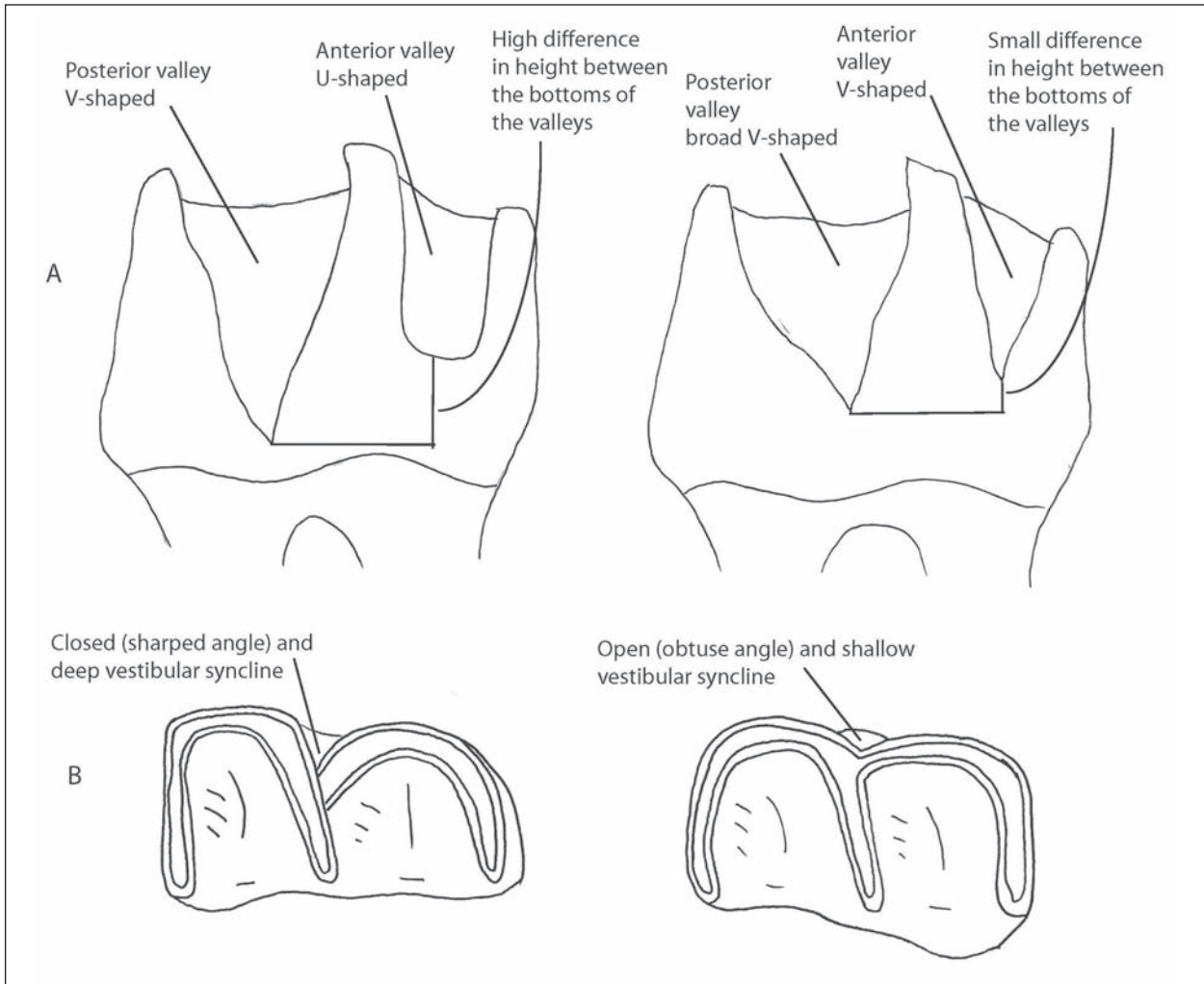


Fig. 3: Morphological features of the lower teeth. A – lingual view; B – occlusal view.

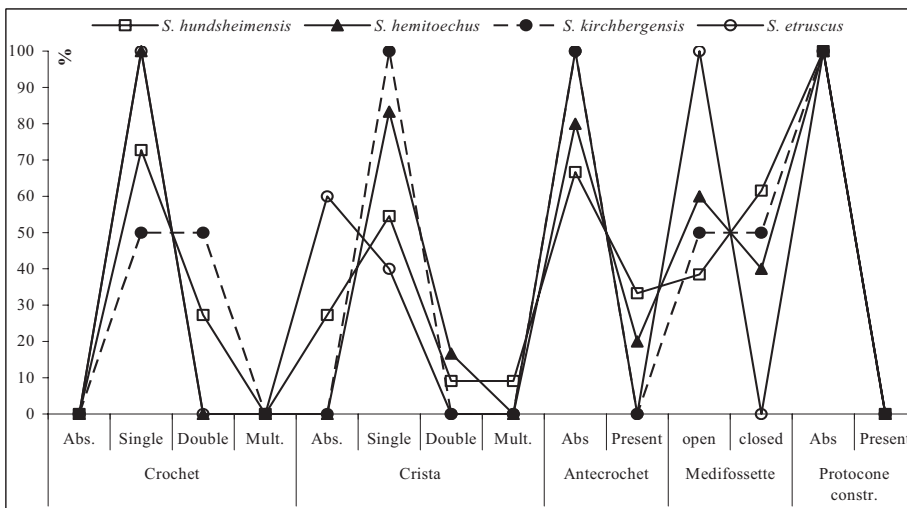


Fig. 4: Percentage distributions of qualitative character states of the upper P2.

it easily from *S. etruscus*. The polynomial curve of tendency of *S. hundsheimensis* is slightly concave, whereas that of *S. etruscus* is distinctly convex approaching that of the reference specimen (fig. 5). The upper P2s of the early Middle Pleistocene *S. hundsheimensis* (i.e. Isernia)

have broader mesial breadths (measurement n°7), and are therefore more asymmetrical, than the P2s borne by the Early Pleistocene representatives (i.e. Vallonnet cave). *S. hemitoechus* possesses the smallest upper P2. The sizes of the cheek teeth of *S. kirchbergensis* were obtained

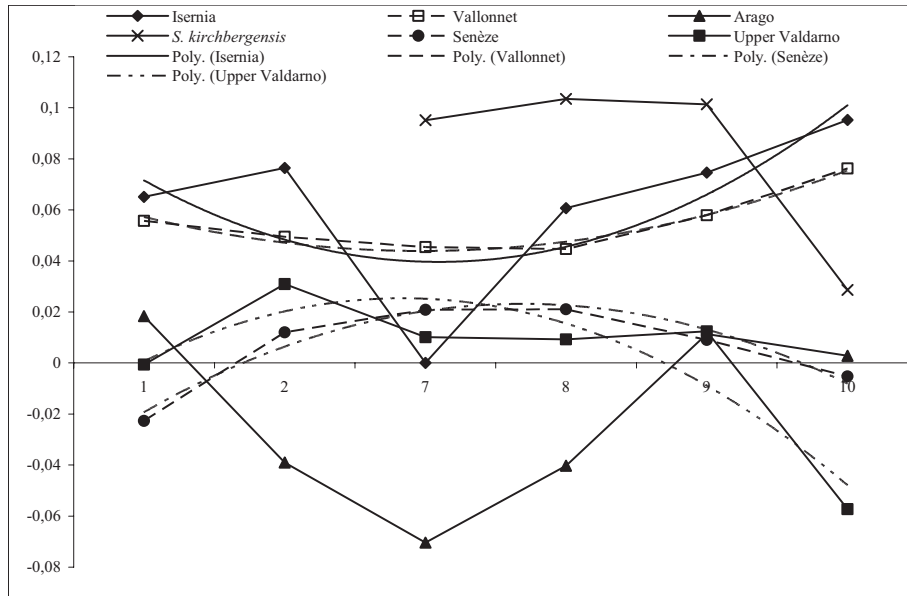


Fig. 5: Ratio diagram of the upper P2. The referential is the present-day *Diceros bicornis*. Data of *S. kirchbergensis* taken from FORTELIUS et al. (1993). Measure 1: Maximal length; Measure 2: Maximal breadth; Measure 7: Mesial breadth, taken at the collar; Measure 8: Distal breadth, taken at the collar; Measure 9: Vestibular length, taken at the collar; Measure 10: lingual length, taken at the collar.

P ²	<i>S. etruscus</i>	<i>S. hundsheimensis</i>	<i>S. hemitoechus</i>	<i>S. kirchbergensis</i>
Crochet	Always single	Single (72.7%) or double (27.3%)	Always single	Single (50%) or double (50%)
Crista	Presence observed in 40%	Potentially absent (27.3%) Potentially multiple when present (9.1%) Single 54.6%)	Always present Single (83.3%) Double (6.7%)	Always present and single
Antecrochet	Absent	Potentially present (33.3%)	Potentially present (20%)	Absent
Mediofossette	Always Open	Open (38.5%) Closed (61.5%)	Open (60 %) Closed (40%)	Open (50%) Closed (50%)
Angle C/M	Sharp	Obtuse to right	Variable	Obtuse to rightt
Protocone constriction	Absent	Absent	Absent	Absent
Mesial Cingulum	Continuous and Horizontal	Continuous and Horizontal	Continuous and Horizontal	Continuous and Horizontal
Distal Cingulum	Absent	Absent	Absent	Absent
Lingual Cingulum	Continuous and Horizontal	Continuous and Horizontal	Continuous and Horizontal	Continuous and Horizontal
Vestibular Cingulum	Absent	Absent	Absent	Potentially present
Paracone fold	Absent	Slightly marked	Marked	slightly marked

Table 2: Morphological features of the upper P2 of each Pleistocene species of the genus *Stephanorhinus*.

from FORTELIUS et al. (1993). *S. kirchbergensis* is the largest of the Pleistocene species and shows outstanding dental proportions. The drop in the size of the premolars, especially of the P2, is therefore an advanced character in *Stephanorhinus* (MADE 2000). Another important trend is the drop in the hypsodonty of P2, archaic representatives having more hypsodont P2s than advanced forms. In fact, the index of hypsodonty (Hy) is higher in the upper P2 of *S. hundsheimensis* from Vallonnet cave (Early Pleistocene; Hy = 125.9 to 130.0) than in that from Isernia (early Middle Pleistocene; Hy = 100.5 to 104.2). The same occurs in

S. hemitoechus from Arago cave (Middle Pleistocene; Hy = 142.4) compared with that from Mars cave and Prince cave (Late Pleistocene; Hy = 114.5 to 125.5). The hypsodonty index of the P2 can thus be assumed to represent an evolutionary character.

Lower M3 (fig. 6, 7; table 3)

The morphological differences separating the M3 of the various *Stephanorhinus* species are shown in table 3 and fig. 6. *S. kirchbergensis* differs markedly from other spe-

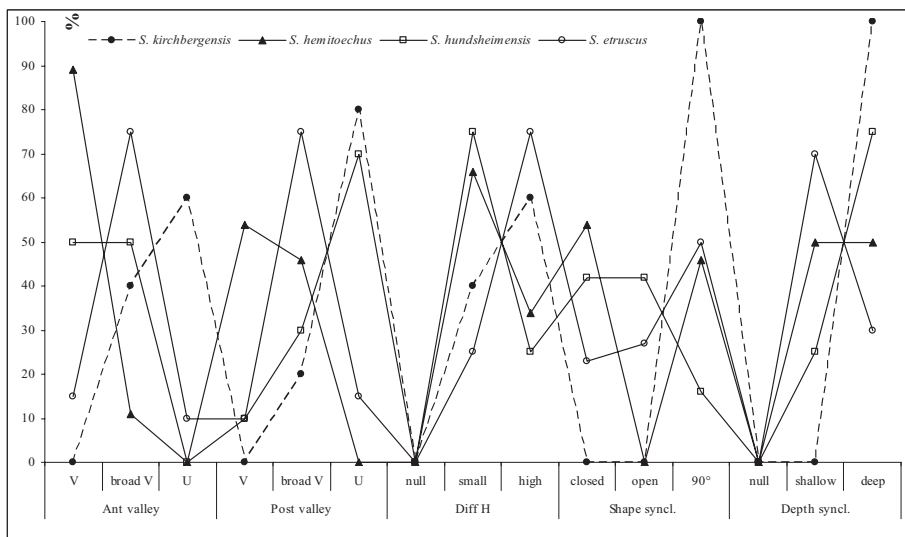


Fig. 6: Percentage distributions of qualitative character states of the lower M3.

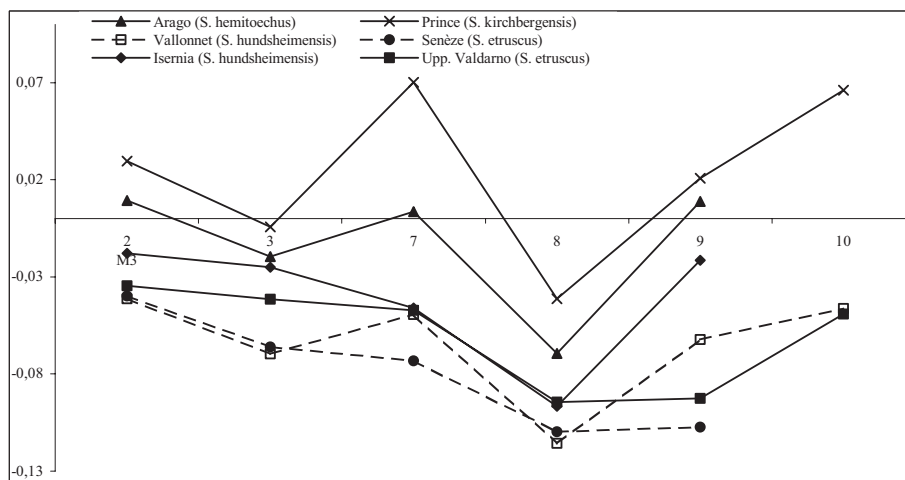


Fig. 7: Ratio diagram of the lower M3. The referential is the present-day *Diceros bicornis*. Measure 2: Distal breadth, taken at the collar; Measure 3: Mesial breadth, taken at the collar; Measure 7: Maximal length; Measure 8: Maximal breadth; Measure 9: Vestibular length, taken at the collar; Measure 10: lingual length, taken at the collar.

M ₃	<i>S. etruscus</i>	<i>S. hundsheimensis</i>	<i>S. hemitoechus</i>	<i>S. kirchbergensis</i>
Anterior Valley	Broad V-shaped (75%) U-shaped (10%) V-shaped (15%)	V-shaped (50%) Broad V-shaped (50%)	Broad V-shaped (89%) V-shaped (11%)	U-shaped (60%) Broad V-shaped (40%)
Posterior Valley	Broad V-shaped (75%) U-shaped (15%) V-shaped (10%)	Broad V-shaped (30%) U-shaped (70%)	V-shaped (54%) Broad V-shaped (46%)	U-shaped (80%) Broad V-shaped (20%)
Difference in height	Average	Small, rarely high	Normally small	High
Mesial Cingulum	Absent	Normally present	Potentially present	Potentially present
Distal Cingulum	Absent	Normally present	Potentially present	Normally present
Lingual Cingulum	Absent	Absent	Absent	Absent
Vestibular Cingulum	Present	Absent	Rare	Normally present
Vestibular Syncline	90°	Variable	Closed to 90°	90°
Depth of the syncline	High	High	Small to high	High

Table 3: Morphological features of the lower M3 of each Pleistocene species of the genus *Stephanorhinus*.

cies in its larger size and in specific proportions (fig. 7). *S. hemitoechus* has the smallest lower M3. The curve of *S. hemitoechus* is close to that of *S. kirchbergensis*, as the

curve of *S. hundsheimensis* approaches that of *S. etruscus*. The M3s of the two latter species show differences in a few specific lengths (measurements n° 7, 9 and 10).

Humerus

The articular trochlea is more oblique in *S. etruscus* than in *S. hundsheimensis* (fig. 8). The two lips of the trochlea differ in height and are separated by a wide and deep trough in *S. etruscus*. In distal view, the medial epicondyle is as aligned with the medial lip. The wide and massive lateral epicondyle protrudes laterally more than the lateral lip. It is separated from the trochlea by a thick, flat plane. In *S. hundsheimensis* the proximal outline of the medial lip of the trochlea is oblique and plunges straight to the trough. The distal outline, instead, is less oblique. The lateral lip of the trochlea is short, rounded, with flat to slightly rounded proximal and distal outlines. The trochlear trough is larger and shallower in *S. hundsheimensis* than in *S. etruscus*. The lateral epicondyle is slightly developed and rounded. Its size is similar to that of the medial epicondyle. The distal part of the humerus of *S. hemitoechus* is larger and flatter than in *S. etruscus* and *S. hundsheimensis*. The medial lip of the trochlea is wide and its proximal outline points obliquely towards the wide and shallow trochlear trough. The lateral lip of the trochlea is rounded and narrow. The

lateral epicondyle is massive, rounded and larger than the medial one. The latter is enlarged in its distal part. The lateral tuberosity is prominent in this species. The bivariate diagram (fig. 9) shows that the distal part of the humerus of *S. hemitoechus* is more robust than those of *S. etruscus* and *S. hundsheimensis*. *S. etruscus* clusters with the smaller population of *S. hundsheimensis*.

Metacarpal III

The dorsal side of the proximal epiphysis of the third metacarpal is convex in *S. etruscus* and in *S. hundsheimensis* (fig. 10) and concave in *S. hemitoechus*. In *S. hemitoechus* the transversal diameter the proximal epiphysis is longer than in *S. hundsheimensis* and shorter than in *S. etruscus*. The proximal articular area is sub-triangular with rounded angles in *S. etruscus*; it is trapezoidal-shaped in *S. hundsheimensis*. On the lateral face, the dorsal articular facet is higher than the palmar articular facet in both species. They are both semi-elliptic in *S. etruscus* and *S. hemitoechus*; the dorsal one is trapezoidal, the palmar one is circular in *S. hundsheimensis*. These two facets can be fused in *S. hemitoechus* where the palmar facet is more

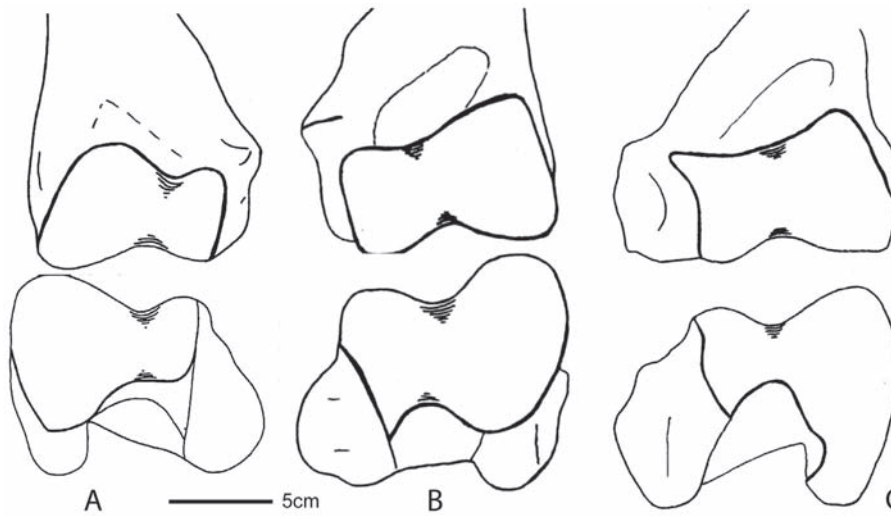


Fig. 8: Distal epiphyses of: A – left humerus of *S. etruscus* (Senèze, 1923-8); B – right humerus of *S. hundsheimensis* (Soleilhac, 2003-4-264-SOL); C – right humerus of *S. hemitoechus* (Arago, E16-2596). Dorsal and distal view.

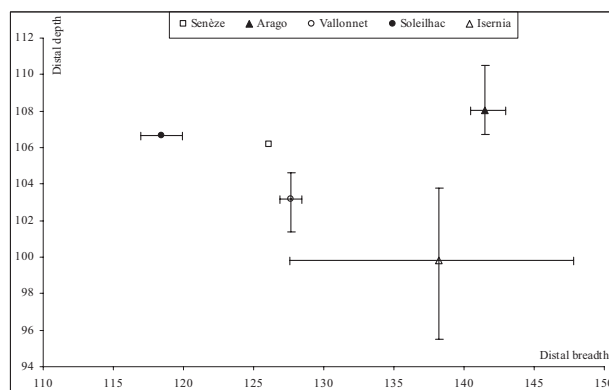


Fig. 9: Bivariate diagram of distal breadth / distal length of humerus.

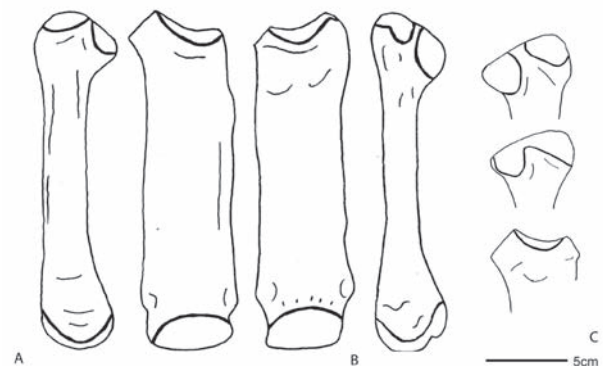


Fig. 10: Right third metacarpals of: A – *S. etruscus* (Senèze, 1923-8); B – *S. hundsheimensis* (Vallonnet, C8-1768); C – *S. hemitoechus* (Arago, D17-3018 & D20-1906). Dorsal and palmar view.

developed than the dorsal one. The section of the diaphysis is elongated and narrow in *S. etruscus*, and oval-shaped in *S. hundsheimensis*. The bivariate diagram (fig. 11) shows a very robust third metacarpal in *S. hemitoechus* compared with *S. etruscus* and *S. hundsheimensis*.

Astragalus

The dorsal side of the astragalus of *S. etruscus* shows a narrow, shallow, slightly oblique and asymmetrical trochlea (fig. 12). The trochlea is wider and deeper in *S. hundsheimensis* and *S. hemitoechus*. The lateral lip of the trochlea is less developed distally than the medial lip in *S. etruscus* and *S. hundsheimensis* while it is slightly more developed in *S. hemitoechus*. The distal extension of the trochlea is separated from the distal articular surface by a broad central depression located under the trochlear trough in *S. etruscus*; this depression is less marked and more elongated in *S. hundsheimensis* and in *S. hemitoechus*. The medial lip of the astragalus is rounded and more prominent than the narrow lateral lip in *S. etruscus* and *S. hundsheimensis* while the medial lip of the astragalus of *S. hemitoechus* is smaller and less rounded than the lateral lip. In medial view a large tuberosity in the distal part of the bone can be located either on the bone's axis, as in *S. etruscus*, shifted towards the dorsal margin, as in *S. hundsheimensis*, or towards the plantar margin, as in *S. hemitoechus*. The medial height of the astragalus is statistically significant (fig. 13).

Discussion

Stephanorhinus hundsheimensis shows two size variants. One is small and characterises the Early Pleistocene sites of Pirro Nord, Pietrafitta (MAZZA et al. 1993), Fuente Nueva

3 and Barranco León 5 (MARTINEZ-NAVARRO et al. 2003), Ceysaguet, Sainzelles, Vallonnet and Tour de Grimaldi (LACOMBAT 2003, 2005). The other one is larger and occurs in sites dated from the Early-Middle Pleistocene boundary through to the early Middle Pleistocene, such as Durfort, Soleilhac, Isernia (LACOMBAT 2003, 2005). This size growth parallels the climatic degradation of this period shown by the inflection in the $\delta^{18}\text{O}$ curve (SHACKLETON 1995) as well as by the ample fluctuations in the $\delta^{18}\text{O}$ values (fig. 14). *S. etruscus* contrasts Cope's rule (GUÉRIN 1980): the populations of this species first fragmented giving rise to isolated demes and then finally became extinct (SALA et al. 1992).

The trend in *S. hemitoechus* is more complex. Three variants have been identified. The first is a large-sized animal, which lived in the Middle Pleistocene, approximately at the time of MIS 14 (G level in the Caune de l'Arago). The second is small-sized and is distributed from MIS 11 (Terra Amata) to the end of the Middle Pleistocene (MIS 7). The third *S. hemitoechus* variant ranges from the late Middle Pleistocene (MIS 6, Mars cave) through to the Late Pleistocene (Prince cave, Cavillon cave and Observatoire cave). Its size is equivalent to, or even larger than, the first Middle Pleistocene variant. These size fluctuations are related to the palaeoecological and palaeoclimatical changes and the climatic instability of this period.

Although imperfectly represented in Southern Europe, *S. kirchbergensis* shows a decrease in size between MIS 10 (Aldène) and MIS 4 and 3 (Prince cave and the Grotte des Enfants). Larger specimens lived in northern Europe (MADE 2000), in strict accordance with Bergman's rule. The size fluctuations observed in *Stephanorhinus* (fig. 14) can be used to set the sites containing their remains in biochronological order (for all the detailed data see LACOMBAT 2003, 2005, 2006).

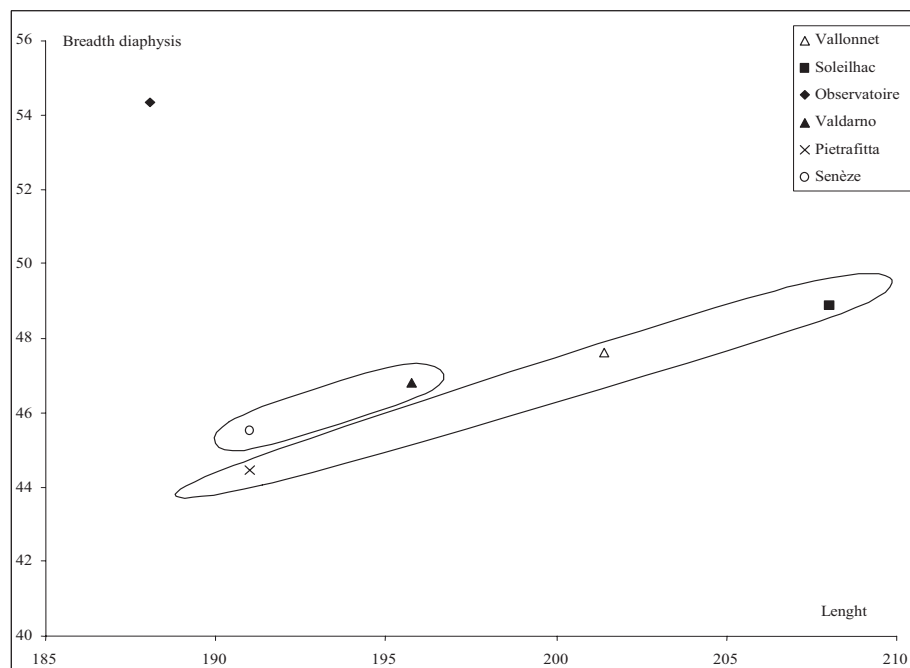


Fig. 11: Bivariate diagram of length / breadth of the diaphysis of the third metacarpal. Data for the Upper Valdarno specimens from MAZZA (1988) and for the Pietrafitta specimens from MAZZA et al. (1993).

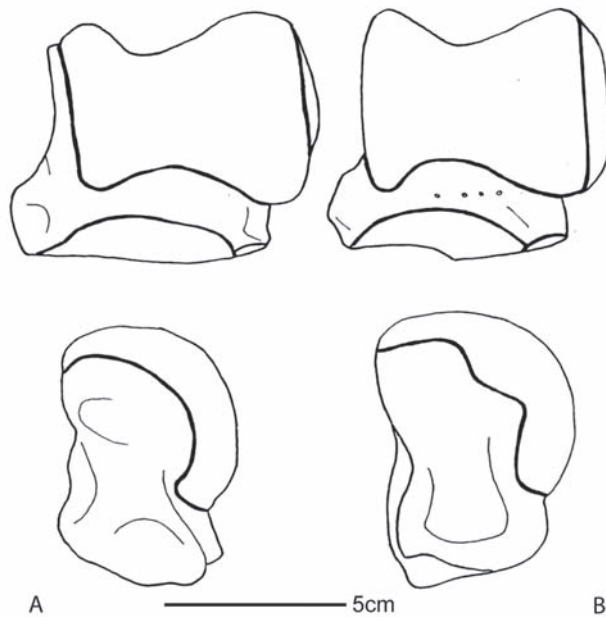


Fig. 12: Left astragalus of: A – *S. hundsheimensis* (Isernia, 4629); B – *S. hemitoechus* (Arago, A12–64). Dorsal and plantar view.

here have important palaeoecological and stratigraphic implications. If similar trends will be observed in a larger sample from a wider area, these can be interpreted as evolutionary modifications. *S. hundsheimensis* shows two distinct variants: a small-sized, Early Pleistocene one and a larger early Middle Pleistocene one. *S. hemitoechus* grows progressively smaller until the time of the MIS 11. It then turns larger from MIS 7 to the Late Pleistocene. In the same interval, southern European *S. kirchbergensis* populations became smaller, while northern European ones show different trends that still need to be studied. Climatic and environmental conditions certainly play a role in these fluctuations, especially in *S. hemitoechus*. It is still unclear whether these changes in the *Stephanorhinus* populations are true evolutionary trends or simply a response to climatic oscillations. Whatever the case, these fluctuations in size can be used to define a reference biochronological scheme for the Pleistocene provided that they are considered within their faunal contexts and not in isolation.

Conclusion

The palaeontological study of the upper and lower teeth and of the postcranial material of *Stephanorhinus* reveals morphological and biometrical differences that can be used to discriminate the different species of Mediterranean Europe and of the Massif Central. The size fluctuations detected in the *Stephanorhinus* specimens analysed

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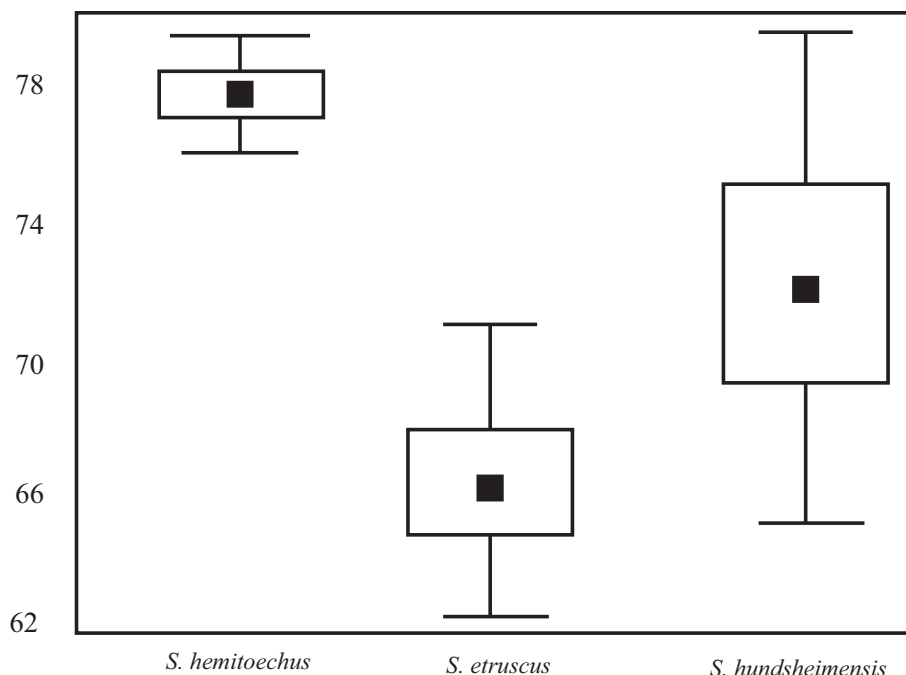


Fig. 13: Graphical representation of the medial height (in mm) of the astragalus.

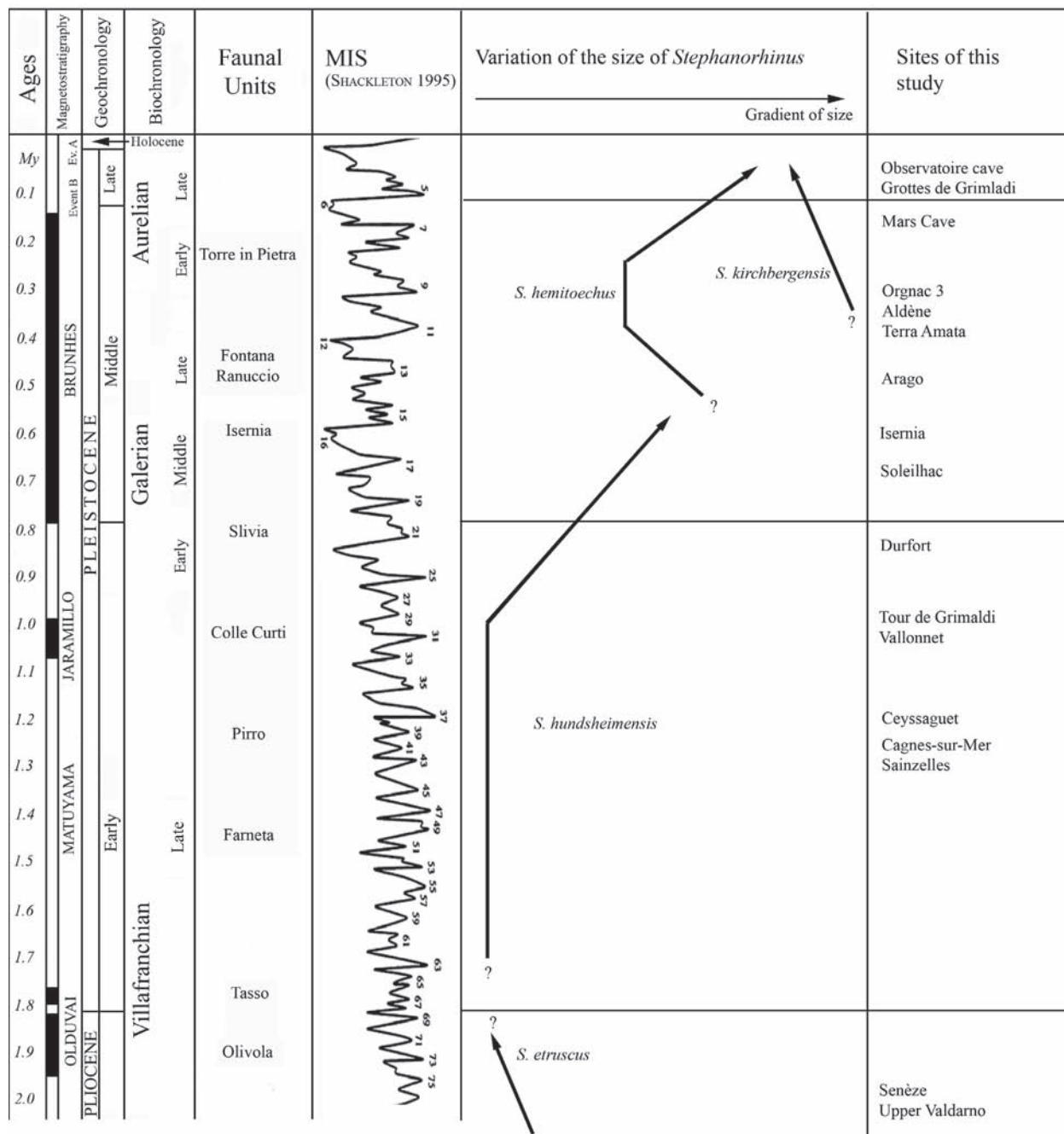


Fig. 14: Size variations of the genus *Stephanorhinus* of Mediterranean Europe and the Massif Central.

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