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Stephanorhinus hundsheimensis (Rhinocerontidae, Mammalia) teeth from the early Middle Pleistocene of Isernia La Pineta (Molise, Italy) and comparison with coeval British material

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ABSTRACT

The present work examines the abundant dental remains from the renowned anthropic site of Isernia La Pineta (Molise, Italy), early Middle Pleistocene (Middle Galerian). The rhinoceros, *Stephanorhinus hundsheimensis*, is the most represented species after *Bison*, and is represented mainly by skull and dental remains and by strongly fractured long bones (suggesting exploitation of the carcasses by the hominine). The high sample size of the dental remains allowed a detailed analysis of the dental morphology. The frequency analysis of the morphological characters shows a high degree of regional variation within the species with the Isernia population significantly widening the morphological variability of *S. hundsheimensis* (thus limiting the diagnostic power of several characters). In particular, comparing *S. hundsheimensis* from Isernia with coeval British populations, some specimens could be safely assigned to *S. hundsheimensis* that do look strongly anomalous within the British sample but find a match in the wider morphological range of the Isernia specimens. From a biometrical point of view, the Isernia population attains slightly smaller sizes than the coeval British specimens, suggesting a latitudinal size increase gradient.

1. Introduction

A great variety of rhinoceros species is recorded from the European Pleistocene. Rhinocerontidae are among the most typical elements of the Pleistocene mammal faunas and, thanks to their wide geographical distribution and number of forms and to their good preservation rate, are useful biochronological markers. Remains of this taxon are known from the XVII century and were first referred to the genus *Rhinoceros* (at present represented by two Asian species). During the past century, the European fossils rhinoceroses were located in the genus *Dicerorhinus* (at present represented by *D. sumatrensis*), along with the well known extinct Asian genus *Coelodonta*. Nowadays, the species from the European Pleistocene are referred to the genus *Stephanorhinus* (Groves, 1983) in which Fortelius et al. (1993) include Pliocene species. However, the name *Dicerorhinus* is still used by some authors (e.g. Guérin, 2004).

Four *Stephanorhinus* species are recorded from the European Pleistocene: *Stephanorhinus etruscus* (Middle and Late Villafranchian, Early Pleistocene), *Stephanorhinus hundsheimensis* (Late Villafranchian and Galerian, late Early–Middle Pleistocene), *Stephanorhinus hemitoechus* (Middle Galerian and Aurelian, Middle–Late Pleistocene) and *Stephanorhinus kirchbergensis* (Late Galerian and Aurelian, late Middle–Late Pleistocene). These species are morphologically very similar to each other and, due to the scarcity of remains in the different sites, the correct specific attribution is sometimes difficult. In order to find diagnostic characters distinctive among the different species, researchers concentrate on dental material (Guérin, 1980; Fortelius et al., 1993; Lacombat, 2005, 2006a; van der Made, 2010) which is generally more frequent and best preserved than the cranial or postcranial skeletal elements. This paper reports a detailed analysis of the rhinoceros dental material from Isernia La Pineta (Molise, Italy), which has been attributed to *S. hundsheimensis* by Sala (1983) and Sala and Fortelius (1993).

1.1. *Stephanorhinus hundsheimensis* (Toula, 1902)

S. hundsheimensis is a slender and medium sized rhinoceros, with a partially ossified nasal septum. The dentition is reduced to

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the jugal teeth, with the lack of first premolar. The teeth of *S. hundsheimensis* are low-crowned and very similar, in shape and proportions, to those of its possible parent species *S. etruscus* and, as in the latter, probably adapted to a browsing diet. *S. hemitoechus* is distinguishable because of its higher hypsodonty (especially of the molars), while *S. kirchbergensis* because of its larger size and "molten" shape of the molars (Fortelius et al., 1993).

S. hundsheimensis is recorded in the whole of Europe, in the late Early and Middle Pleistocene (Fortelius et al., 1993; Mazza et al., 1993; Lacombat, 2005; Schreiber, 2005; van der Made, 2010). Lacombat (2006b), Fortelius et al. (1993), and Breda and Marchetti (2007) recognize two evolutionary stages: a smaller form from the Early Pleistocene (often misidentified with *S. etruscus*) and a larger one from the early Middle Pleistocene. On the contrary, van der Made (2010) believes that these small forms are actually *S. etruscus*.

The brachyodont dentition and the slender, subcursorially structured limbs suggest that both *S. etruscus* and *S. hundsheimensis* probably inhabited environments with variable forest cover similar to those in which black rhino lives today, i.e. open scrub woodlands and the margins of small woods (Mazza, 1993). Evidence for a variable forest cover has been suggested by the pollen analysis of the sediment adhering to *S. etruscus-hundsheimensis* bones from Leffe, Northern Italy (Ravazzi et al., 2009). The Leffe record documents the occurrence of this rhinoceros in warm-temperate dense mixed forest to conifer forest, to open xerophytic communities and steppe with tree birch and with sparse woodland patches.

The extinction of *S. hundsheimensis* is probably due to ecological competition: the more specialized rhinoceroses *S. hemitoechus*, a grazer, and *S. kirchbergensis*, a stricter browser, probably overcame the generalist *S. hundsheimensis* in both forest and grassland habitats leading to its extinction through bilateral competition (Kahlke and Kaiser, 2011).

1.2. Isernia La Pineta Palaeolithic site

Discovered in 1978 and now dated to 610,000 ± 10,000 years (Coltorti et al., 2005), the archaeological levels of Isernia yielded an extremely rich and well-preserved amount of palaeontological remains and lithic artefacts, evidence of an ancient human settlement along the river side. The mammal fauna from Isernia is particularly abundant and well-documented, although made up of isolated and commonly fragmented specimens (Arobba et al., 2004; Thun Hohenstein et al., 2009). Rhinoceroses are well represented by cranial and postcranial elements, with long bones usually fragmented, but teeth and short bones generally intact. In terms of number of remains, *S. hundsheimensis* is second only to the bison (*Bison schoetensacki*), with the straight tusked elephant (*Palaeoloxodon antiquus*) in third position. Besides these three most represented taxa, Thun Hohenstein et al. (2009) record four species of deer [*Praemegaceros solilhacus*, *Cervus elaphus* cf. *C. e. acoronatus*, *Dama dama* cf. *D. d. clactoniana* (*Dama* cf. *D. roberti*, according to Breda and Lister, 2013), and *Capreolus* sp.], scanty remains of the goat-like thar (*Hemitragus* cf. *H. bonali*), hippopotamus (*Hippopotamus* cf. *H. antiquus*), pig (*Sus scrofa*), bear (*Ursus deningeri*) and large cats (*Panthera leo fossilis* and *Panthera pardus*). The richness of this large mammal fauna, gives reason of the fact that Isernia is the type locality of the homonymous Faunal Unit (Gliozzi et al., 1997). Among the small mammals, Isernia records the earliest presence in Europe of *Arvicola mosbachensis*, the water vole with unrooted molars replacing the rooted *Mimomys savini*, and setting the beginning of the Middle Galerian (beginning of Toringian small Mammal Age). Other rodents of the genera *Microtus* and *Pliomys* and Soricidae are also biochronologiacally consistent with the early Middle Pleistocene (early Toringian).

The palaeoenvironment reconstruction supported by pollen analysis of the sediment from the archaeosurfaces, indicates a steppe-grassland environment, with dominant Graminaceae, but also tree species related to wet and marshy environment such as *Alnus*, *Salix* and *Populus* (Accorsi et al., 1996). Presence of extended grassland and restricted woodland, particularly in the valley bottom and related to the presence of water, is in accordance with the variety of large mammals: bison, rhinoceros and elephant are typical inhabitants of grassland; deer and wild boar of bush; hippopotamus indicates the presence of abundant water bodies and swamp.

2. Materials and methods

In the teeth analysis, a total of 202 specimens have been studied, some of them consisting in associated teeth, thus getting to a total number of 229 studied teeth. The material comes from the Isernia La Pineta levels identified as 3a, 3coll and 3s 10-1 (Thun Hohenstein et al., 2009), and is now stored partially in the Museo del Paleolitico, in Isernia La Pineta, and partially in the Palaeontology and Prehistory Museum "Piero Leonardi" of the University of Ferrara (Department of Biology and Evolution).

Most of the dental material is represented by isolated teeth so the recognition of their place in the tooth row is sometimes difficult. Identification of P2 and M3 is straightforward but distinction between P3 and P4 or M1 and M2 is often problematic because of their close morphology. A size-based distinction is not used in order to avoid data circularity and amplification of the average size difference among dental types. The following morphological distinction for molars are used: in comparison to M^1, M^2 has a more distally elongated metaloph resulting in a wider lingual valley, and in a more trapezoidal shape in occlusal view (distal side shorter than medial one); M_1 differs from M_2 for the presence of a bulge along the syncline (see Fig. 1 for dental nomenclature). The premolars cannot be identified with certainty.

Morphological analysis considered the characters analysed in previous studies on this taxon by Guérin (1980), Fortelius et al. (1993) and Lacombat (2005). Fig. 2 summarizes the characters examined and the different possible states for each. For the median fossette (character d) a new state is introduced, here called

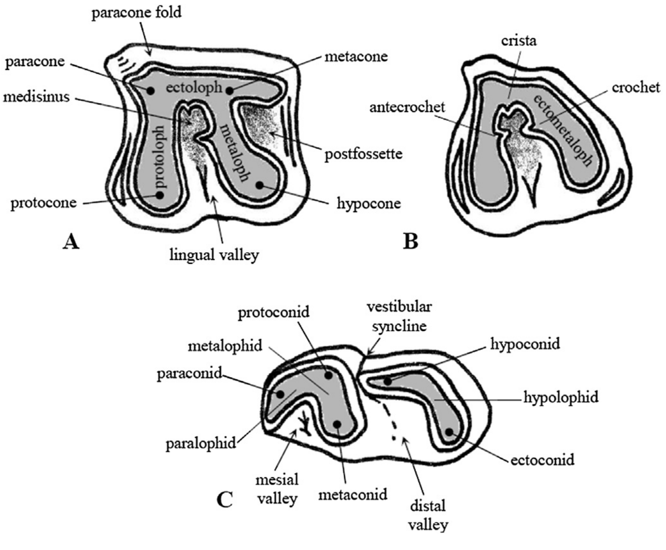

Fig. 1. Nomenclature of rhinoceros teeth (drawings by M. Ballatore). (A–B: upper tooth (A, sketched premolar/molar in occlusal view; B, M^3 in occlusal view). C: lower tooth (premolar/molar in occlusal view).

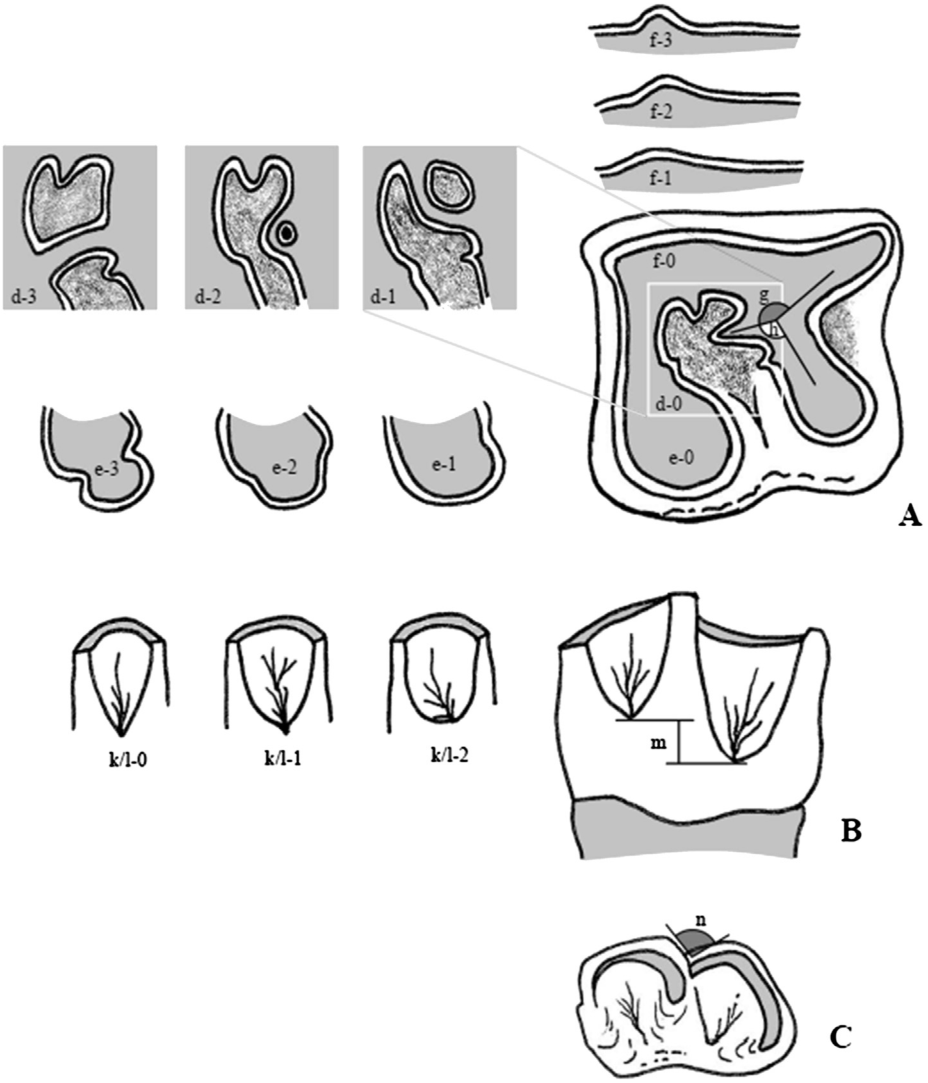

Fig. 2. Sketches of the dental characters with their different states (drawings by M. Ballatore – see Tab. 1 for the letters' legend). A: upper tooth in occlusal view (characters d, e, f, in states 0, 1, 2, 3, and angles g, h). B: lower tooth in lingual view (characters k, l, in states 0, 1, 2, and character m). C: lower tooth in occlusal view (angle n).

"secondary mediofossette closed", deriving from the fusion of two crochets (Fig. 2A, d2). This method, via the attribution of a state to each character, facilitates comparison among numerous samples and allows calculating the frequency of incidence of the single states, but is a simplification that implies lost of information in morphological description. For example, only presence/absence and quantity information about secondary folds of medisinus is detected, but shape information is lost (typically these folds are short and thin, but some elongated and massive ones have been observed, some are bifid, and, when more than one is present, generally only one is predominant in size).

The metrical analysis follows the method used by Lacombat (2005) who summarizes and integrates previous works (Guérin, 1980; Fortelius et al., 1993) (Fig. 3). Metrical data are investigated using common descriptive statistics, and results are compared with those recorded by Lacombat (2005) for a different sample from Isernia La Pineta (now stored in the Museo Nazionale di Santa Maria delle Monache - Soprintendenza per i Beni Archeologici del Molise, Isernia) and temporarily unavailable. Biometrical comparison among dental types is graphically represented in scatter plot diagrams.

In order to evaluate which features of the dental morphology can be used as species diagnostic, or if intra-specific variability is present, the morphologies scored on the population from Isernia are compared against the dental characterizations of other Pleistocene species (*S. hundsheimensis* included) as reassumed by Lacombat (2006a), the most updated and comprehensive study on the teeth of the genus *Stephanorhinus* (van der Made, 2010 is precise and updated; but *S. hundsheimensis* is only marginally considered).

Moreover the teeth of the population of *S. hundsheimensis* from Isernia have been morphologically and biometrically compared with coeval British *S. hundsheimensis* specimens stored at the Natural History Museum in London (NHM) and Norwich Castle Museum in Norwich (NCM) and described by Breda et al. (2010), plus additional unpublished data. In particular, the British localities considered are the two hominid localities of the Cromer Forest-bed Formation (CF-bF), Pakefield (Suffolk; Parfitt et al., 2005) and Happisburgh (Norfolk; Parfitt et al., 2010), the type Cromerian West Runton Freshwater Bed (Norfolk; Stuart and Lister, 2010), the Calcareous Member of the cave infill at Westbury-sub-Mendip (Somerset; Andrews et al., 1999), and the hominid locality of Boxgrove (West Sussex; Roberts and Parfitt, 1999).

3. Results – morphological data

The frequency analysis of morphological characters is summarized in Table 1. The sample size for characters related to the cingula is smaller than for characters observable on the occlusal surface, because detecting information on cingula is often not possible in fragmentary teeth and in teeth inserted in tooth rows.

Table 1
Dental characters examined in the present study with the different possible states for each of them (most of the morphologies are sketched in Fig. 2).

Upper teeth

a) Crochet: 0 (absent), 1 (single), 2 (double), 3 (multiple)
b) Crista: *idem*
c) Antecrochet: *idem*
d) Median fossettes: 0 (medisinus open), 1 (mediofossette close), 2 (secondary mediofossette close), 3 (medisinus close)
e) Protocone constriction: 0 (absent), 1 (very light), 2 (light), 3 (strong)
f) Paracone fold: 0 (absent), 1 (very light), 2 (light), 3 (strong)
g) Angle between crochet/ectoloph: 0 (acute), 1 (right), 2 (obtuse), 3 (flat)
h) Angle between crochet/metaloph: *idem*

Lower teeth

k) Mesial valley: 0 (V-shaped), 1 (broad V-shaped), 2 (U-shaped)
l) Distal valley: *idem*
m) Difference in height between the bottoms of the valleys: 0 (null), 1 (small), 2 (high)
n) Opening of the vestibular syncline: 0 (acute angle), 1 (right angle), 2 (obtuse angle)

Cingula

no – absent
00 – horizontal and continuous
01 – horizontal and discontinuous
10 – oblique and continuous
11 – oblique and discontinuous

3.1. Upper teeth

P^2 (n. 19):

The crochet is mainly single but can be double and in one case is absent.

The crista is always present, mainly double but also single or multiple.

The antecrochet is always absent, although Lacombat (2006a) reports it can be observed on the P^2 of *S. hundsheimensis*.

In some cases (6/19), the protocone is not joined to the paracone but it is free in the lingual wall (Fig. 4A). Lacombat (2006a) does not record this feature. However, protocone and paracone are usually joined to form the protoloph in *S. hundsheimensis*, as in the other Middle Pleistocene *Stephanorhinus* species. Moreover, protocone and paracone are always joined in the specimens from the CF-bF and from other British early Middle Pleistocene localities (Breda et al., 2010), with the sole exception of an aberrant individual from Boxgrove (Breda et al., 2010 - see below).

In the Isernia sample, the medisinus is typically open but a closed mediofossette can be observed (a single tooth shows a secondary mediofossette closed).

The protocone constriction is always absent.

The paracone fold is very weak.

The angle between crochet and ectoloph cannot be detected while the one between crochet and metaloph is generally right-angled.

The vestibular cingulum is always absent, while the lingual one is always present (mainly horizontal and continuous, but sometimes variable). Mesial and distal cingula are present too, even if the presence of distal cingulum is not reported in literature (Lacombat, 2006a).

P^3 (n. 19):

The crochet is always present, single or double (rarely multiple).

The crista is variable, mainly single or double but also multiple or absent.

As in P^2, the antecrochet is absent in this sample, although Lacombat (2006a) reports it as rarely present in this species.

The medisinus is usually open but a closed mediofossette can rarely be observed.

The protocone constriction is always absent.

The paracone fold is weak (strong in a single case).

The angle between crochet and ectoloph can't be detected while the angle between crochet and metaloph is generally right-angled.

The vestibular cingulum is always absent, while the lingual one is always present (mainly horizontal and continuous, but sometimes variable). The mesial cingulum has been detected on a reduced sample (4 teeth) but it is always present and oblique.

P^4 (n. 18):

The crochet is always present, single or double (rarely multiple); a particular morphology is found in one specimen with double crochet (I-1 3a 47.48 – Fig. 4B) where an isolated pillar in the medisinus is in contact with the lingual crochet.

The crista is variable, generally single but also double, sometimes multiple or absent.

As for P^2 and P^3, the antecrochet is absent in the sample.

In the Isernia sample, the medisinus is typically open but a closed mediofossette can sometimes be observed (a single tooth shows a secondary mediofossette closed).

The protocone constriction, absent from the other premolars (as in any *Stephanorhinus* species, according to Lacombat, 2006a), is generally absent also on most P^4 from Isernia, being present, but weak, in some cases (8/13).

The paracone fold is weak (strong in a single case).

The angle between crochet and ectoloph is mainly flat and rarely obtuse while the angle between crochet and metaloph is generally obtuse and sometimes right-angled.

The vestibular cingulum is always absent, while the lingual one is always present and horizontal (mainly continuous but sometimes discontinuous).

M^1 (n. 15):

The crochet is always present and single.

The crista is variable, generally single but also absent and double.

The antecrochet is generally absent, as in the other *Stephanorhinus* species (Lacombat, 2006a), but it can also be present (single).

The medisinus is typically open but a closed mediofossette can sometimes be observed, and a closed medisinus too. These different morphologies are characteristic of *S. hundsheimensis* because the medisinus is always open in all other Pleistocene species (Lacombat, 2006a).

The protocone constriction is very variable, from absent to strong, and so unusual with respect to the usual state in *S. hundsheimensis* where, according to Lacombat (2006a), should be always absent.

The paracone fold is variable, but generally marked.

The angle between crochet and ectoloph is obtuse and rarely flat, while the angle between crochet and metaloph, mainly obtuse, can also be right-angled.

The vestibular cingulum is typically absent, but present in rare cases (2/10), while the lingual cingulum is always present (mainly

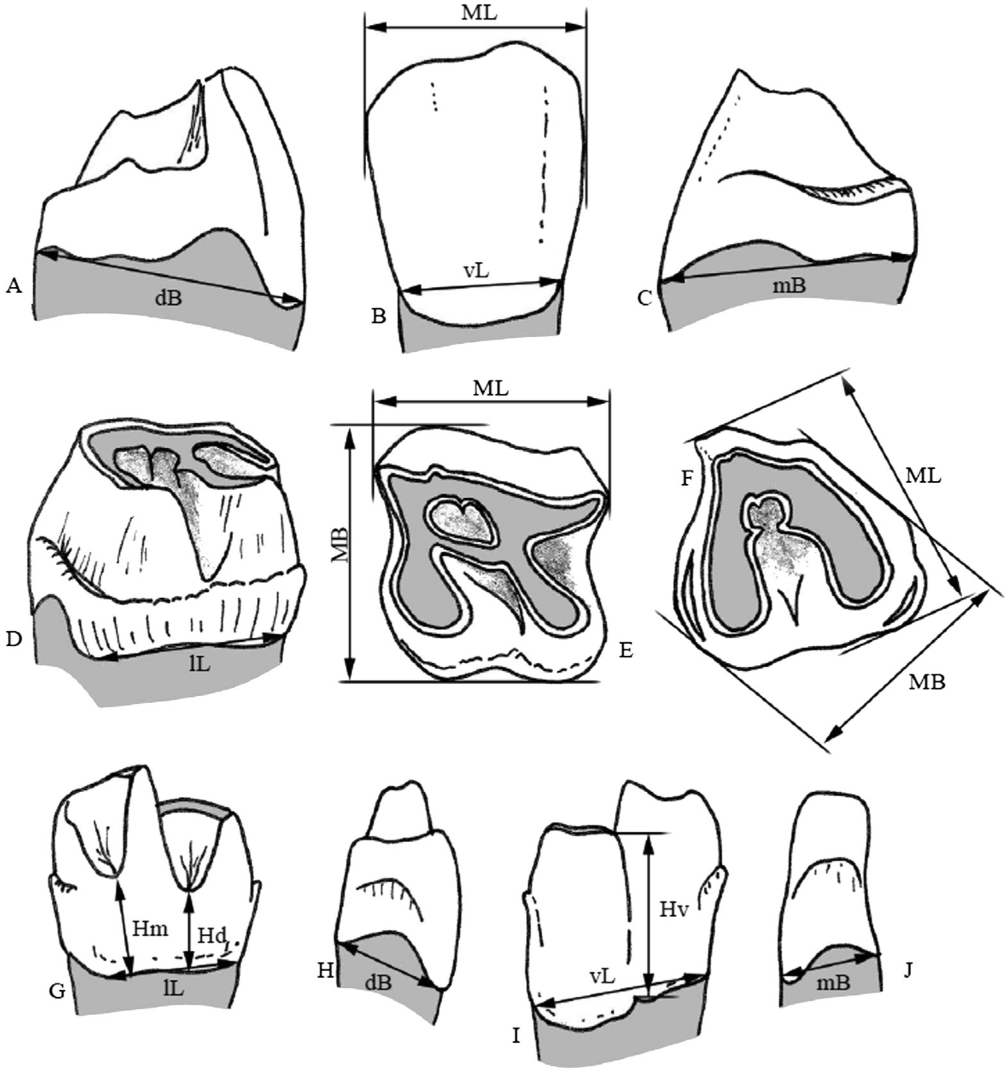

Fig. 3. Dental measurements taken in this study (drawings by M. Ballatore): vestibular length at the crown base (vL), lingual length at the crown base (lL), mesial breadth at the crown base (mB), distal breadth at the crown base (dB), maximum length (ML), maximum breadth (MB), height at the vestibular syncline (Hv), height of the bottom of the mesial valley from the crown base (Hm), height of the bottom of the distal valley from the crown base (Hd). A–F: upper teeth (A, distal view; B, vestibular view; C, mesial view; D, lingual view; E, occlusal view; F, occlusal view M^3). G–J: lower teeth (G, lingual view; H, distal view; I, vestibular view; J, mesial view).

horizontal and discontinuous, but sometimes oblique and continuous). The distal cingulum has been detected on a small sample (4 teeth) but it is always present, continuous and oblique.

M^2 (n. 32):

The crochet is always present and single (rarely double); often the crochet shows a particular morphology, been arched, convex on the lingual side and directed towards the crista (always present in these cases) but without reaching it (e.g. specimen I-1 3coll 78.114 – Fig. 4C).

The crista is variable from absent to multiple but mainly single.

The antecrochet is equivalently absent or single.

The medisinus is always open.

The protocone constriction is variable (generally weakly marked).

The paracone fold is always present and generally strong.

The angle between crochet and ectoloph is flat or obtuse while the angle between crochet and metaloph is generally obtuse.

The vestibular cingulum is generally absent but rarely present, (Fig. 4D–E) while the lingual cingulum is always present (mainly horizontal and discontinuous - Fig. 4D). Mesial and distal cingula are always present, continuous and oblique.

M^3 (n. 32):

The crochet is always present and single (rarely double).

The crista is variable from absent to multiple but mainly single.

The antecrochet is mainly single but can be absent.

The medisinus is often closed but it can also be open; sometimes there is a mediofossette closed or a secondary mediofossette closed.

The protocone constriction is generally absent but it can be present (however weak).

The paracone fold is always present, weak or strong.

The angle between crochet and ectometaloph is always open (right-angled or obtuse).

The vestibular cingulum is always absent while the lingual one is mainly present (horizontal and discontinuous) but sometimes absent. The mesial cingulum is always present (oblique).

3.2. Lower teeth

P_2 (n. 9):

The distal valley is variable in shape.

The opening of the vestibular syncline is wide (obtuse or right-angled).

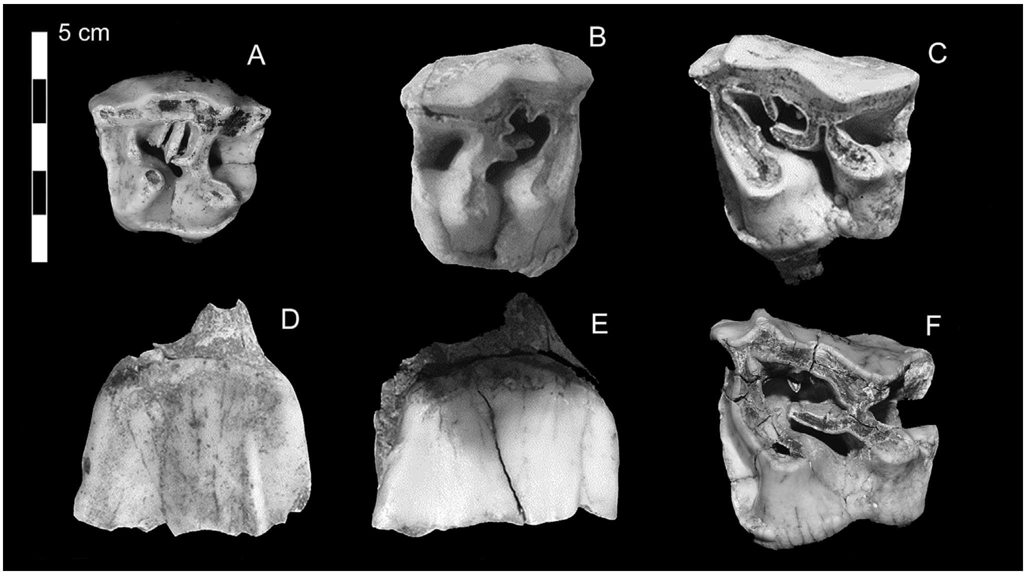

Fig. 4. *Stephanorhinus hundsheimensis* teeth from Isernia La Pineta. A, specimen I-1 3coll 91-2 (P^2, occlusal view – note the free protocone); B, specimen I-1 3a 47-48 (P^4, occlusal view – note the double crochet); C, specimen I-1 3coll 78-114 (M^2, occlusal view – note the arched crochet); D, specimen I-1 3coll 78-22 (M^2, vestibular view – note the vestibular cingulum); E, specimen I-1 3coll 146-140 (M^2, vestibular view – note the vestibular cingulum), F, specimen I-1 3 q.91-45 (M^2, occlusal view – note the swollen bases of protocone and hypocone).

The vestibular cingulum is equivalently absent or present (horizontal and discontinuous); the lingual cingulum is generally absent (rarely present). The mesial and distal cingula are always present on the lower teeth from Isernia, even if Lacombat (2006a) reports that the mesial cingulum is absent in all the Pleistocene species of the genus *Stephanorhinus*.

P_3 (n. 13):

Both the distal and mesial valleys show a V-shape outline, sometimes broad V-shape.

The opening of the vestibular syncline is at a right angle.

The vestibular cingulum is absent or present while the lingual cingulum is always absent. As in P_2, the mesial and distal cingula are always present (oblique and generally continuous).

P_4 (n. 13):

The distal valley is variable in shape while the mesial valley is always V-shaped.

The opening of the vestibular syncline is at a right angle.

The vestibular cingulum is generally absent but rarely present (horizontal and discontinuous) while the lingual cingulum is always absent.

As in P_2 and P_3, the mesial and distal cingula are always present.

M_1 (n. 16):

Both the distal and mesial valleys show a V-shape outline, sometimes broad V-shape.

The opening of the vestibular syncline is wide (right or obtuse angle).

The vestibular cingulum is generally absent but present in one case (horizontal and discontinuous), the lingual cingulum is always absent as well. As in the premolars, the mesial and distal cingula are always present (oblique and generally continuous).

M_2 (n. 23):

The distal valley is variable in shape while the mesial valley is always V-shaped.

The opening of the vestibular syncline is mainly right angle.

The vestibular cingulum is generally absent but sometimes present (horizontal and discontinuous) while the lingual cingulum is always absent. As in the premolars and M_1, the mesial and distal cingula are always present.

M_3 (n. 12):

Both the distal and mesial valleys are variable with predominant U-shape outline.

The opening of the vestibular syncline is always right-angled.

The vestibular cingulum is always absent while the lingual one is generally absent but present in one case. As in the other lower teeth, the mesial and distal cingula are always present (oblique and generally continuous).

4. Results – metrical data

The results of the metrical analysis are shown in Table 2, compared to the same statistics calculated on a different batch of material from Isernia La Pineta analyzed by Lacombat (2005).

Table 2

Frequency (in percentage) of the state of the morphological characters of *Stephanorhinus hundsheimensis* teeth from Isernia La Pineta. Characters a-n are detailed in Table 1 and represented in Fig. 2 with their alternative states. The different cingula are indicated as: cV, vestibular; cL, lingual; cM, mesial; cD, distal; the state for each cingulum is detailed in Table 1.

		P^2	P^3	P^4	M^1	M^2	M^3
cV	*N*	12	15	14	9	23	19
	No	1.00	1.00	1.00	0.80	0.79	1.00
	0 0	0.00	0.00	0.00	0.10	0.04	0.00
	0 1	0.00	0.00	0.00	0.10	0.17	0.00
	1 0	0.00	0.00	0.00	0.00	0.00	0.00
	1 1	0.00	0.00	0.00	0.00	0.00	0.00

Table 2 (*continued*)

		P^2	P^3	P^4	M^1	M^2	M^3
cL	*N*	11	14	14	8	20	17
	No	0.00	0.00	0.00	0.00	0.00	0.35
	0 0	0.55	0.64	0.60	0.10	0.05	0.06
	0 1	0.27	0.29	0.40	0.60	0.85	0.59
	1 0	0.18	0.07	0.00	0.30	0.05	0.00
	1 1	0.00	0.00	0.00	0.00	0.05	0.00
cM	*N*	12	4	–	–	9	13
	No	0.00	0.00			0.00	0.00
	0 0	0.33	0.00			0.00	0.00
	0 1	0.25	0.00			0.00	0.00
	1 0	0.42	0.75			0.89	0.85
	1 1	0.00	0.25			0.11	0.15
cD	*N*	4	–	–	3	5	–
	No	0.00			0.00	0.00	
	0 0	0.00			0.00	0.00	
	0 1	0.00			0.00	0.00	
	1 0	0.75			1.00	1.00	
	1 1	0.25			0.00	0.00	

		P_2	P_3	P_4	M_1	M_2	M_3
cV	*N*	9	11	10	12	15	4
	No	0.56	0.55	0.80	0.92	0.73	1.00
	0 0	0.00	0.00	0.00	0.00	0.00	0.00
	0 1	0.44	0.36	0.20	0.08	0.27	0.00
	1 0	0.00	0.00	0.00	0.00	0.00	0.00
	1 1	0.00	0.09	0.00	0.00	0.00	0.00
cL	*N*	7	10	10	10	12	4
	No	0.86	1.00	1.00	1.00	1.00	0.75
	0 0	0.00	0.00	0.00	0.00	0.00	0.00
	0 1	0.14	0.00	0.00	0.00	0.00	0.25
	1 0	0.00	0.00	0.00	0.00	0.00	0.00
	1 1	0.00	0.00	0.00	0.00	0.00	0.00
cM	*N*	6	7	6	5	10	3
	No	0.00	0.00	0.00	0.00	0.00	0.00
	0 0	0.00	0.00	0.00	0.00	0.00	0.00
	0 1	0.00	0.00	0.00	0.00	0.00	0.00
	1 0	1.00	1.00	1.00	1.00	1.00	1.00
	1 1	0.00	0.00	0.00	0.00	0.00	0.00
cD	*N*	4	5	7	3	11	5
	No	0.00	0.00	0.00	0.00	0.00	0.00
	0 0	0.00	0.00	0.00	0.00	0.00	0.00
	0 1	0.00	0.00	0.00	0.00	0.00	0.00
	1 0	0.75	1.00	1.00	0.67	0.55	0.80
	1 1	0.25	0.00	0.00	0.33	0.45	0.20

		P^2	P^3	P^4	M^1	M^2	M^3
a	*N*	19	18	18	14	32	32
	0	0.05	0.00	0.00	0.00	0.00	0.00
	1	0.79	0.44	0.44	1.00	0.88	0.88
	2	0.16	0.44	0.44	0.00	0.12	0.12
	3	0.00	0.12	0.12	0.00	0.00	0.00
b	*N*	19	19	18	14	30	31
	0	0.00	0.11	0.11	0.21	0.07	0.13
	1	0.16	0.58	0.44	0.65	0.53	0.65
	2	0.74	0.26	0.34	0.14	0.33	0.19
	3	0.10	0.05	0.11	0.00	0.07	0.03
c	*N*	13	19	18	13	30	32
	0	1.00	1.00	1.00	0.70	0.57	0.16
	1	0.00	0.00	0.00	0.30	0.43	0.84
	2	0.00	0.00	0.00	0.00	0.00	0.00
	3	0.00	0.00	0.00	0.00	0.00	0.00
d	*N*	19	18	18	15	32	32
	0	0.79	0.95	0.84	0.81	1.00	0.37
	1	0.16	0.05	0.11	0.06	0.00	0.03
	2	0.05	0.00	0.05	0.00	0.00	0.06
	3	0.00	0.00	0.00	0.13	0.00	0.54
e	*N*	15	14	14	10	28	27
	0	1.00	1.00	0.42	0.20	0.29	0.56
	1	0.00	0.00	0.36	0.00	0.04	0.22
	2	0.00	0.00	0.22	0.40	0.46	0.22
	3	0.00	0.00	0.00	0.40	0.21	0.00

(*continued on next page*)

Table 2 (*continued*)

		P^2	P^3	P^4	M^1	M^2	M^3
f	*N*	14	15	14	10	24	25
	0	0.07	0.00	0.00	0.00	0.00	0.00
	1	0.86	0.33	0.14	0.09	0.04	0.00
	2	0.07	0.61	0.78	0.20	0.29	0.60
	3	0.00	0.06	0.08	0.61	0.67	0.40
g	*N*	–	–	11	12	24	–
	0			0.00	0.00	0.00	
	1			0.00	0.00	0.04	
	2			0.18	0.88	0.46	
	3			0.82	0.12	0.50	
h	*N*	17	16	16	14	26	31
	0	0.06	0.12	0.00	0.00	0.00	0.00
	1	0.94	0.88	0.38	0.14	0.11	0.42
	2	0.00	0.00	0.62	0.86	0.89	0.58
	3	0.00	0.00	0.00	0.00	0.00	0.00
		P_2	P_3	P_4	M_1	M_2	M_3
k	*N*	–	9	8	7	16	12
	0		0.78	1.00	0.86	0.88	0.25
	1		0.22	0.00	0.14	0.12	0.33
	2		0.00	0.00	0.00	0.00	0.42
l	*N*	5	10	11	14	23	12
	0	0.40	0.70	0.37	0.79	0.31	0.16
	1	0.40	0.30	0.27	0.21	0.56	0.42
	2	0.20	0.00	0.36	0.00	0.13	0.42
m	*N*	4	10	10	12	17	11
	0	0.00	0.00	0.40	0.00	0.00	0.00
	1	0.50	0.80	0.40	0.67	0.53	0.64
	2	0.50	0.20	0.20	0.33	0.47	0.36
n	*N*	5	13	13	16	21	9
	0	0.00	0.00	0.00	0.00	0.00	0.00
	1	0.40	0.92	0.92	0.56	0.81	1.00
	2	0.60	0.08	0.08	0.44	0.19	0.00

Table 3

Statistical summary of the metrical data of *Stephanorhinus hundsheimensis* teeth from Isernia La Pineta. Where possible, specimens analysed in this research (on the left) are compared with a different batch of specimens (on the right) analysed by Lacombat (2005). The measures acronyms refers to Fig. 3.

Upper teeth		vL	lL	ML	ML Lacombat 2005	mB	mB Lacombat 2005	dB	dB Lacombat 2005	MB	MB Lacombat 2005
P^2	*N*	11	11	9	17	10	2	6	2	9	11
	x_m	29.09	22.64	34.00	34.41	30.50	32.27	37.67	39.70	39.44	40.61
	s	1.97	1.80	1.22	2.72	3.81	3.63	1.51	0.28	1.42	2.50
	CV	0.07	0.08	0.04	0.08	0.12	0.11	0.04	0.01	0.04	0.06
	ES x_m	0.59	0.54	0.41	0.66	1.20	2.57	0.61	0.20	0.47	0.75
	Max	31	26	36	40	38	35	39	40	41	45
	Min	26	20	32	30	25	30	35	40	37	36
P^3	*N*	15	10	16	11	11	2	9	2	16	8
	x_m	35.13	30.10	40.38	41.00	47.27	49.60	44.67	49.93	50.81	52.62
	s	2.17	1.97	1.63	2.72	3.50	1.59	3.67	2.11	2.34	2.04
	CV	0.06	0.07	0.04	0.07	0.07	0.03	0.08	0.04	0.05	0.04
	ES x_m	0.56	0.62	0.41	0.82	1.05	1.13	1.22	1.49	0.59	0.72
	Max	39	34	43	45	53	51	50	51	55	55
	Min	31	28	37	35	42	48	40	48	47	50
P^4	*N*	16	16	15	14	14	5	15		15	10
	x_m	37.56	33.13	43.87	43.41	53.36	53.32	49.93		55.33	56.10
	s	1.09	1.86	1.68	3.14	2.17	2.17	3.01		2.26	1.66
	CV	0.03	0.06	0.04	0.07	0.04	0.04	0.06		0.04	0.03
	ES x_m	0.27	0.46	0.43	0.84	0.58	0.97	0.78		0.58	0.53
	Max	40	35	47	50	57	56	55		60	58
	Min	36	30	40	40	50	50	45		53	53
M^1	*N*	5	3	6	15	4		7		5	8
	x_m	38.80	32.67	49.33	48.62	53.00		47.57		56.40	59.93
	s	4.60	1.15	2.34	7.68	2.58		5.47		3.29	1.84
	CV	0.12	0.04	0.05	0.16	0.05		0.12		0.06	0.03
	ES x_m	2.06	0.67	0.95	1.98	1.29		2.07		1.47	0.65
	Max	44	35	52	53	57		56		60	62
	Min	32	32	46	22	50		38		51	57

Table 3 (*continued*)

Upper teeth		vL	lL	ML	ML Lacombat 2005	mB	mB Lacombat 2005	dB	dB Lacombat 2005	MB	MB Lacombat 2005
M^2	*N*	18	18	18	6	15		12		18	8
	x_m	42.72	36.78	53.50	54.64	57.40		50.17		60.00	62.50
	s	3.03	3.98	2.01	1.31	3.64		3.74		3.60	2.11
	CV	0.07	0.11	0.04	0.02	0.06		0.07		0.06	0.03
	ES x_m	0.71	0.94	0.47	0.53	0.94		1.08		0.85	0.75
	Max	47	46	57	56	65		57		68	67
	Min	37	31	50	53	51		45		53	61
M^3	*N*	18	22	21	10	13		–		21	9
	x_m	46.56	43.27	54.19	50.32	51.77		–		47.81	56.14
	s	4.00	3.13	2.56	3.54	2.39		–		2.62	2.78
	CV	0.09	0.07	0.05	0.07	0.05		–		0.05	0.05
	ES x_m	0.94	0.67	0.56	1.12	0.66		–		0.57	0.93
	Max	55	54	58	55	55		–		52	60
	Min	41	40	50	46	47		–		42	52

Lower teeth		vL	lL	mB	mB Lacombat 2005	dB	dB Lacombat 2005	Hv	Hv Lacombat 2005	Hm	Hm Lacombat 2005	Hd	Hd Lacombat 2005
P_2	*N*	9	8	8		8		7		–		6	
	x_m	28.89	25.88	14.63		17.38		22.14		–		13.50	
	s	3.98	1.36	1.85		2.62		3.13		–		1.52	
	CV	0.14	0.05	0.13		0.15		0.14		–		0.11	
	ES x_m	1.33	0.48	0.65		0.92		1.18		–		0.62	
	Max	39	27	18		20		27		–		15	
	Min	26	24	13		12		17		–		11	
P_3	*N*	10	11	11		11		10		7		9	
	x_m	33.90	31.36	21.55		23.00		24.10		17.57		13.11	
	s	2.64	2.91	3.93		2.53		5.45		1.13		1.54	
	CV	0.08	0.09	0.18		0.11		2.23		0.06		0.12	
	ES x_m	0.84	0.88	1.19		0.76		1.72		0.43		0.51	
	Max	39	36	26		27		32		19		15	
	Min	31	27	12		18		13		16		10	
P_4	*N*	14	9	8		11	4	9		8		9	
	x_m	36.29	35.22	23.88		26.55	32.97	27.00		15.00		12.44	
	s	3.02	3.11	3.64		1.97	5.41	6.02		2.62		1.67	
	CV	0.08	0.09	0.15		0.07	0.16	0.22		0.17		0.13	
	ES x_m	0.81	1.04	1.29		0.59	3.12	2.01		0.93		0.56	
	Max	41	41	28		29	39	32		18		15	
	Min	31	31	18		23	28	12		10		10	
M_1	*N*	11	14	11	3	10	4	7		6		8	
	x_m	42.91	40.36	29.00	30.34	29.00	33.11	29.00		15.67		10.50	
	s	3.14	3.77	2.53	1.07	2.91	3.82	4.93		6.35		1.77	
	CV	0.07	0.09	0.09	0.04	0.10	0.12	0.17		0.41		0.17	
	ES x_m	0.95	1.01	0.76	0.62	0.92	1.91	1.86		2.59		0.63	
	Max	49	46	32	31	33	38	33		28		15	
	Min	39	35	23	29	22	29	21		10		7	
M_2	*N*	23	17	17	3	15	4	14	3	10	3	10	3
	x_m	41.65	41.76	28.24	30.98	27.83	33.08	27.43	27.16	15.00	12.57	9.00	10.40
	s	3.11	3.65	3.05	0.94	2.92	3.68	4.40	3.21	4.59	1.35	2.00	4.73
	CV	0.07	0.09	0.11	0.03	0.10	0.11	0.16	0.12	0.31	0.11	0.22	0.17
	ES x_m	0.65	0.89	0.74	0.54	0.76	1.84	1.18	1.86	1.45	0.78	0.63	1.00
	Max	48	47	34	32	32	39	33	31	26	14	13	12
	Min	37	36	24	30	21	31	18	25	10	11	6	9
M_3	*N*	10	10	10		11		6		5		7	
	x_m	41.50	43.10	26.00		27.55		23.33		10.40		7.57	
	s	3.21	4.01	3.43		1.81		4.84		3.36		2.76	
	CV	0.08	0.09	0.13		0.07		0.21		0.32		0.36	
	ES x_m	1.01	1.27	1.09		0.55		1.98		1.50		1.04	
	Max	47	47	31		31		30		16		13	
	Min	37	35	21		25		17		7		5	

For the upper teeth, the averages of the two samples are similar, except for the maximum breadth (MB) in M^3, probably due to a different orientation of the calliper. For the lower teeth, the comparison is not very significant because Lacombat (2005) gives a reduced number of measures for most teeth (none for P_2, P_3 and M_3, only dB for P_4, only mB and dB for M_1), but the measures he gives for M_2 (the only tooth seriously considered), match well with this data. Precision of the average is good, with errors in the order of 1 mm; the coefficient of variation indicates a limited dispersion, generally slightly larger than 10% for upper teeth and until 30% for lower teeth. Molars show a wider dimensional variability with respect to premolars.

Metrical differences among dental types are illustrated in Fig. 5. A general size increase is found along the upper tooth row, from P^2 to M^2, with overlaps between P^3 and P^4 and between M^1 and M^2. M^3 has roughly the same length as M^2 while its width cannot be

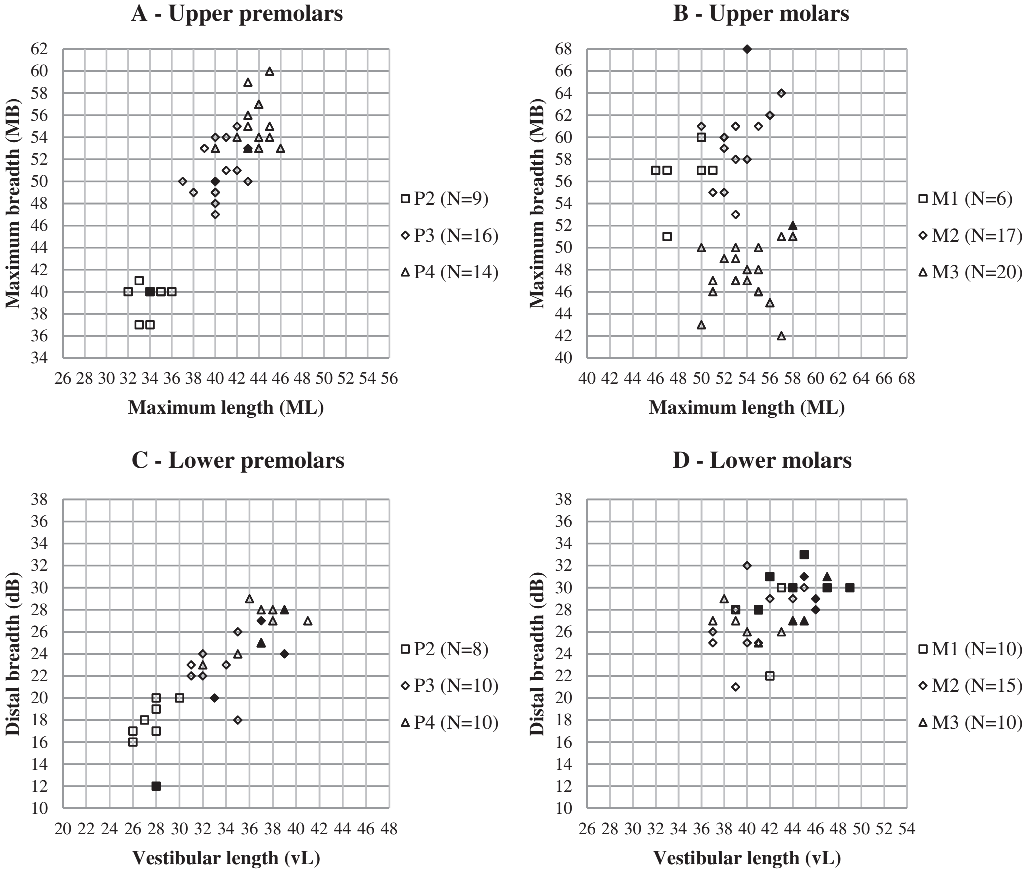

Fig. 5. Scatter plot diagrams of the metrical data of *Stephanorhinus hundsheimensis* teeth from Isernia La Pineta. Open symbols refer to isolated tooth whose position in the tooth row cannot be completely certain. Closed symbols are teeth in tooth row (therefore their position is certain). A, upper premolars; B, upper molars; C, lower premolars; D, lower molars.

compared, because its general outline is completely different. Similarly, in lower teeth, the premolar size gradually increases (with partial overlap between P_3 and P_4), but there is full superposition in the size ranges of the molars.

5. Discussion – morphological comparison with coeval British populations

The teeth of *S. hundsheimensis* from Isernia, have been morphologically compared with coeval *S. hundsheimensis* population from Britain described by Breda et al. (2010) plus an unpublished specimen from Happisburgh. While the lower teeth from both the collections appear morphologically quite variable and will not be discussed in detail, several features of the upper teeth deserve attention.

Breda et al. (2010, p. 140) record as the upper teeth of Cromerian British specimens differ in some characters from *S. hundsheimensis* as described by Lacombat (2006a) for Continental Europe. The analysis of the Isernia sample widens the morphological variability of this species, matching good part of the British morphologies. In particular:

- the protocone constriction, apparently rare in *S. hundsheimensis* (Lacombat, 2006a), is actually always present (and sometimes strong) in all the upper molars from British localities (Breda et al., 2010, feature a) and in most of the Isernia specimens. In the population from Isernia it can be present also on P^4;
- the paracone fold is described as thin and slightly prominent in the upper premolars of *S. hundsheimensis* (Lacombat, 2006a), while it can actually be medium or strong in the British upper P^3 and P^4 (Breda et al., 2010, feature b) and in the Isernia P^4;
- the crochet, apparently always single or double in *S. hundsheimensis* (Lacombat, 2006a), can actually be triple or multiple in the upper premolars from British localities (Breda et al., 2010, feature c) and from Isernia.

The authors agree with Breda et al. (2010), in considering these as minor differences that do not shadow the identity of the species but simply enlarge its known morphological variability.

However, a specimen from Boxgrove (NHM M82482-97 – associated right P^2–M^3 and left P^2–P^4 plus fragments of M^1 and M^3), morphologically different from other British Cromerian specimens, had been considered unlikely belonging to *S. hundsheimensis* and first provisionally marked as *Stephanorhinus* sp. A by Parfitt (1998), then as “hitherto unrecognised rhinoceros with affinities to *Rhinoceros megarhinus* de Christol” by Schreve et al. (1999), and at last as *Stephanorhinus* cf. *megarhinus* by Breda et al. (2010, Fig. 6). This startling identification had been made “while bearing in mind the stratigraphically unexpected presence of a ‘Pliocene’ species in early Middle Pleistocene deposits” (Breda et al., 2010, p. 143), but comforted by the fact that this species had been recorded in Late Pleistocene deposits from the Rhone Valley (Meryrargues; Bonifay, 1961; Guérin, 1980) and Rhine Valley (Gross Rohrheim and other localities from the Upper Rhine Valley; von Koenigswald, 1988, 1991).

However, the features that set M82482-97 from Boxgrove apart from other British coeval specimens and from the described morphological range of *S. hundsheimensis* (cfr. Lacombat, 2006a),

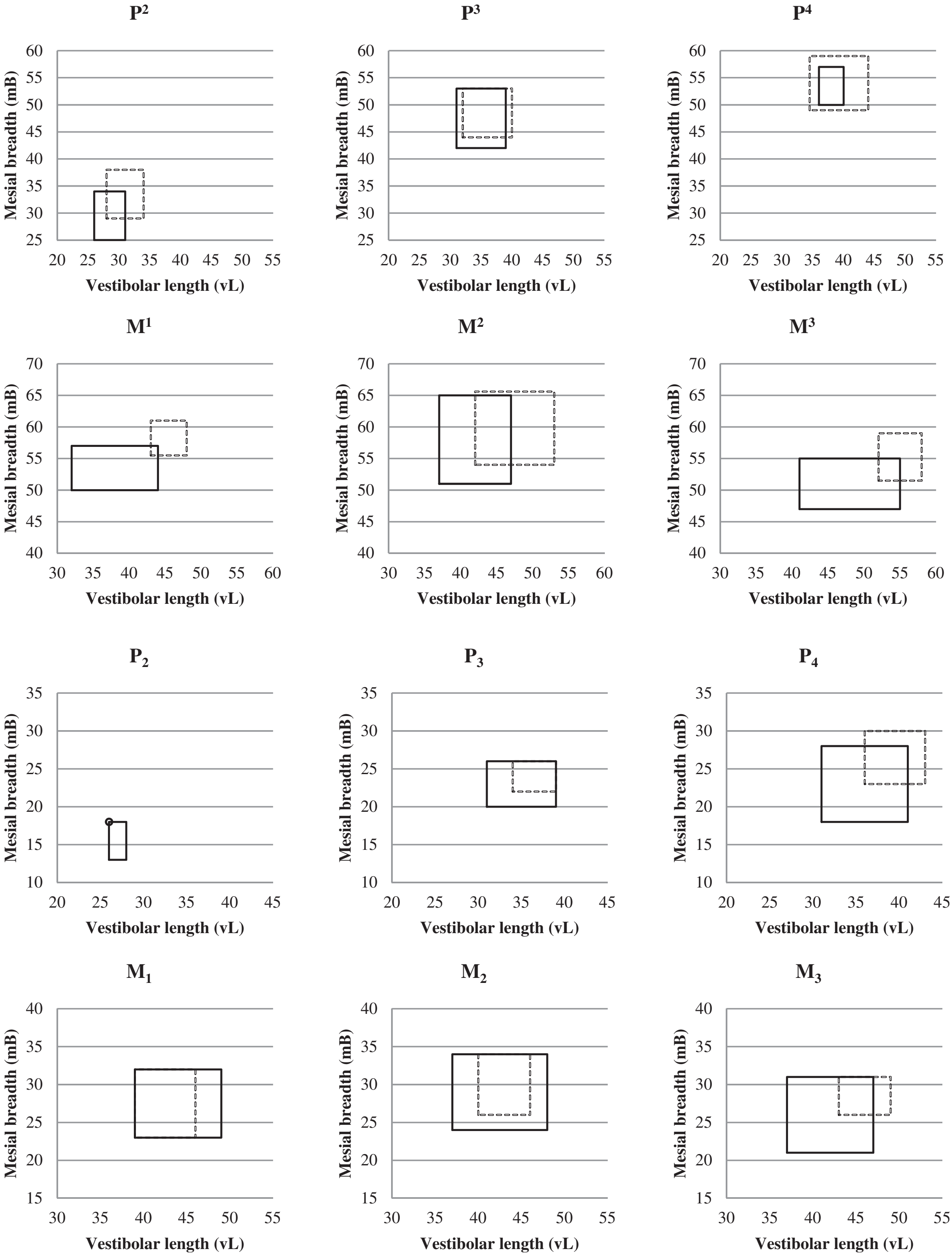

Fig. 6. Metrical comparison of the size ranges of *Stephanorhinus hundsheimensis* teeth from Isernia La Pineta (solid line, data from the present analysis) and from the British early Middle Pleistocene (blank line, data from Breda et al. 2010, plus unpublished data for NCM 1982.358.1 from Happisburgh).

approaching *S. megarhinus*, find a match in some individuals from Isernia (Breda et al., 2010 lettering within brackets):

- protocone of P^2 isolated from the paracone (Breda et al., 2010, feature d) is present in 6/19 Isernia P^2s (Fig. 4A);
- protocone constriction on P^3 and/or P^4 (Breda et al., 2010, feature e) is recorded in 8/13 P^4s from Isernia;
- particularly low crown and low lingual cingulum of premolars (Breda et al., 2010, feature f); both low and higher cingula are present in Isernia;
- protocones of M^1 and M^2 swollen at their bases and tapering toward the occlusal surface, giving a larger medial valley (Breda et al., 2010, feature g); in Isernia the protocones can be more or less swollen (Fig. 4F);

- lingual walls of molar hypocone concave, contributing, with the protocone, to wide lingual valley. M^1 hypocone also bulges at its base (Breda et al., 2010, feature h); in Isernia also the hypocones can be more or less swollen (Fig. 4F).

Therefore the morphologically wider Isernia dental sample encompasses the morphological variability of specimen M82482-97 from Boxgrove that couldn't fit in the more restricted variability of the other early Middle Pleistocene British specimens and in the variability range of Lacombat (2006a) used as species reference by Breda et al. (2010) being the most updated and comprehensive study on the teeth of *S. hundsheimensis*.

This suggests that M82482-97 can be ascribed to *S. hundsheimensis* as expected from the biochronological constrain. However, a detailed study of the morphological variation of the skulls from Isernia would be necessary to verify if, in the same way as for the teeth, it encompasses the morphology of skull M82542, tentatively attributed to *S.* cf. *megarhinus* by Breda et al. (2010, p. 144, Fig. 7d–f).

Two other "morphotypes" from the Cromer Forest-bed Formation have been recorded as anomalous for *S. hundsheimensis* by Breda et al. (2010). Part of the morphological features that sets them apart from other British specimens (cfr. Breda et al., 2010, features k, l, n, o) and from *S. hundsheimensis* (as described by Lacombat, 2006a), are more or less matched in the wider variability of the Isernia specimens. However, some are distinctive:

- the associated left and right P^3 from West Runton (NHM M19462) are distinguished by the complete absence of a lingual cingulum (Breda et al., 2010, feature j, pag. 144–145, Fig. 8). Although a smooth and very oblique ridge extends from the lingual valley along the hypocone wall to reach the distal cingulum, it cannot be in any way considered a proper cingulum. Contrary to Lacombat (2006a), who states that *S. hundsheimensis* premolars always have a strong and continuous lingual cingulum, the Isernia sample shows some discontinuous and weaker cingula, but never their complete absence;
- specimen CRM 1984.2.1-2 from West Runton (left P^2–P^4 plus right P^2–M^1), together with specimen NCM 1986.14.1-7 from Pakefield (left P^2–P^3 and M^1–M^3 plus right M^1–M^3) are distinguished by the "U" shaped morphology of the lingual valley in P^2 and P^3 (Breda et al., 2010, feature m, pag. 145–146, Fig. 9). The same morphology is present (again in both P^2 and P^3) also in specimen NCM 1982.358.1 from the Cromerian levels of Happisburgh (Norfolk – Breda, unpublished data). This morphology, unique in the British sample, has never been described for *S. hundsheimensis* from the Continent and is not present in any Isernia specimen as well. Specimen CRM 1984.2.1-2 and NCM 1982.358.1 share also the smallest P^2s and P^3s of the British sample (Breda et al., 2010, Fig. 3), in NCM 1982.358.1 also the P^4 being extremely small.

Whether such characters are intra-specific variants, or reflect separate taxonomic status, is difficult to say and a larger sample would be needed to investigate individual variability.

6. Discussion – metrical comparison with coeval British populations

The teeth of *S. hundsheimensis* from Isernia, have been metrically compared with coeval *S. hundsheimensis* populations from Britain described by Breda et al. (2010) plus an unpublished specimen from Happisburgh (Fig. 6). On average, the population from Isernia has slightly smaller teeth than the British specimens.

For the upper premolars, the difference is mostly evident in P^2 where the Isernia's range is all shifted toward lower values. For P^3, the upper ranges of the two batches are very close but Isernia specimens have a smaller lower range, and for P^4 the lower range is close but the English specimens have a higher upper range.

For the upper molars, the difference is mostly visible in M^1 (with basically no superposition of the ranges) and M^3 (with just a reduced superposition) and much less in M^2 (where there is a shift in the vestibular length – with English range on higher values – but a good correspondence of the mesial breadth – with upper range equal, but Isernia reaching lower values).

For the lower premolars, only one P_2 is present in the British sample, which is at the very upper limit of the Isernia breadth range but at the lower limit of the length range, for P^3 the British range fits just within the upper limit of the Isernia range, while for the P^4 there is a proper shift between the two ranges, with the British sample on higher values.

For the lower molars, the situation is more confused, with a proper size shift only in the M_3 length (the British breadth falls within the upper portion of the Isernia range), while for M_2 the British batch fits within the Isernia range (even if in the upper portion of the breadth), and for M_1 the British and Isernia ranges superpose nearly perfectly with the Isernia range actually attaining a higher upper limit for the vestibular length.

Although with the exception of M_1, the general pattern might suggest that the British specimens attained a slightly larger size than the coeval Isernia population. An increase in the size of *S. hundsheimensis* from Southern Europe (Italy and France) to Central Europe (Germany) is suggested by Lacombat (2009) basing on the variability size index used by archaeozoologists (Eisenmann and David, 2002; Eisenmann and Mashkour, 2005). A direct comparison with Lacombat's (2009) data is not possible, since the variability size index is calculated on postcranial bones and the row data are not given in his paper. The question is interesting and will be addressed in further studies but, at present, it is not known whether the British rhinoceros were larger than or equal to the coeval German populations.

As pointed out in the previous section, some British individuals (NHM M82482-97 from Boxgrove, NHM M 19462 and CRM 1984.2.1-2 from West Runton, NCM 1986.14.1-7 from Pakefield, NCM 1982.358.1 from Happisburgh) show peculiar morphologies that distinguish them from other British specimens and from the described morphological variability of *S. hundsheimensis* as detailed by Lacombat (2006a). Although the closer morphological match with the population from Isernia La Pineta outlined in the present analysis would allow their tentative attribution to the species *S. hundsheimensis*, they still need a discussion from a biometrical point of view. In Fig. 7, these specimens have been plotted individually against the size ranges of the population from Isernia and from the remaining British Cromerian specimens. Although the molars fit well in the size ranges of other British specimens (Fig. 7B), the premolars are rather small, fitting better in the smaller Isernia size ranges (Fig. 7A). In particular:

- for P^2, NCM 1986.14.1-7 from Pakefield is the only specimen of the above discussed, fitting in the British range, the others being much smaller but within the range of Isernia La Pineta;
- for P^3, the considered specimens are partly distributed in the overlap area between the British and Isernia ranges, with the small CRM 1984.2.1-2 from West Runton and NCM 1982.358.1 from Happisburgh fitting only in the Isernia range;
- for P^4, most of the discussed specimens fit well in the superposition between British and Isernia ranges, but for specimen NCM 1982.358.1 from Happisburgh which is much smaller, plotting beyond the lower boundary of both the British and Isernia ranges.

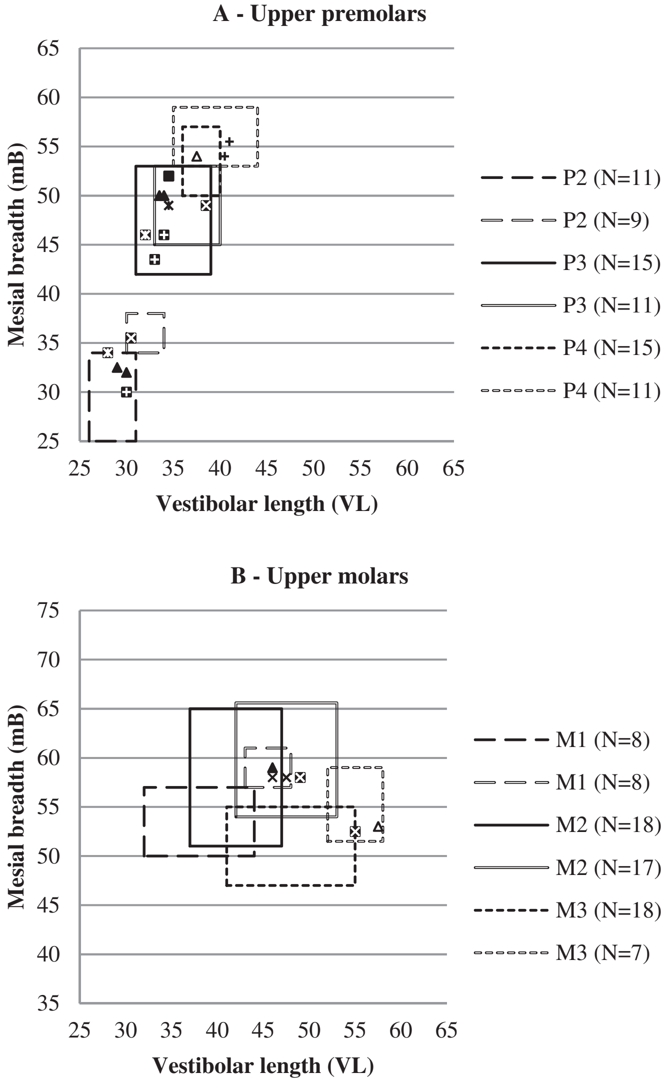

Fig. 7. Metrical comparison of the size ranges of *Stephanorhinus hundsheimensis* upper teeth from Isernia La Pineta (solid line, data from the present analysis) and from the British early Middle Pleistocene (blank line, data from Breda et al. 2010). The specimens discussed in the text (chapters 5 and 6), as morphologically different from other specimens from Britain, are here excluded from the ranges and plotted individually: Δ NHM M82482-97 (Boxgrove), □ NHM M19462 (West Runton), + CRM 1984.2.1-2 (West Runton), × NCM 1986.14.1-7 (Pakefield), * NCM 1982.358.1 (Happisburgh); P^2, P^3, M^2 and M^3 are plotted as solid symbols, while P^4 and M^1 are plotted as blank symbols).

If these specimens might pertain to a different species from *S. hundsheimensis*, as tentatively suggested by Breda et al. (2010), the shift in the upper premolars size range from larger values on the British specimens to smaller values on the Isernia population, would be much more pronounced.

7. Conclusion

The frequency analysis of morphological characters allows a precise characterization of the *S. hundsheimensis* population from Isernia La Pineta (early Middle Pleistocene, Southern Italy). In the upper teeth:

- the crista is too variable and not diagnostically significant;
- the crochet is variable as well: although Lacombat (2006a) reports that it can only be single or double in *S. hundsheimensis* premolars, it is triple in four individuals (two P^3 and two P^4) from Isernia. Multiple crochets (triple or more) are relatively frequent also in *S. hundsheimensis* from the British CF-bF and Boxgrove (Breda et al., 2010). As far as the molars are concerned, the crochet is usually single but can be also double in M^1 and M^2 from Isernia, whereas it is always single in the British specimens;
- with the exception of M^3, the antecrochet is rare in any *Stephanorhinus* species, being present only in some *S. hemitoechus* (P^2, P^3 and M^2 only) and *S. hundsheimensis* populations (Lacombat, 2006a). However, from Lacombat's (2006a) graphs of percentage distribution of the characters, the antecrochet can be present in small samples of both premolars and molars of *S. hundsheimensis*, while in both the Isernia population and the British batch considered, it is present only on molars (in Isernia 4/14 M^1 and 13/30 M^2);
- the median fossettes in the molars are exclusive of some *S. hundsheimensis* populations, among which Isernia. However, in M^2 the medisinus is always open;
- the protocone constriction is variable in the different *Stephanorhinus* species and not diagnostic for the molars. However, according to Lacombat (2006a) it should always be missing in *S. hundsheimensis* premolars, while it is present in some P^4 from Isernia and in P^3–P^4 of the above discussed specimen NHM M82482-97 from Boxgrove.

As far as cingula are concerned, *S. hundsheimensis* from Isernia La Pineta has the same distribution reported by Lacombat (2006a) for this species, but with some peculiarities referring to the upper teeth:

- the vestibular cingulum, that after Lacombat (2006a) should always be absent in *S. hundsheimensis* as well as in other Pleistocene *Stephanorhinus* species, is absent in most of the Isernia specimens, but present in some upper molars (2/10 M^1, 5/23 M^2; Fig. 4D and 4E). The vestibular cingulum is always absent in the British Cromerian sample (Breda, pers. observation);
- according to Lacombat (2006a), the lingual cingulum is always present on *S. hundsheimensis* upper premolars. The Isernia population and the specimens from Britain match this description, the only exception being the above discussed associated P^3 from West Runton (NHM M19462). Lacombat (2006a) reports that the lingual cingulum is sometimes present on *S. hundsheimensis* M^1 and M^2. In the Isernia sample, it is always present in M^1 and M^2 and, sometimes, also in M^3.

For the lower teeth there are no characters with diagnostic relevance, and variability among species is extremely high. The features of the population from Isernia well agree with the characterization given by Lacombat (2006a). The only difference is the presence of mesial and distal cingula on all the lower teeth, P_2s included. According to Lacombat (2006a), they should not be present in *S. hundsheimensis* P_2s.

In conclusion, the large sample of upper teeth from Isernia widens the morphological intra-specific variability recorded by Lacombat (2006a) for the species *S. hundsheimensis* outlining a more detailed description of the possible morphologies shown by this species. This is not surprising considering that *S. hundsheimensis* was a generalist species widespread in the whole of Europe, from the Mediterranean areas, to Central Europe and British Isles, therefore adapted to quite different environments.

The comparison between the Isernia population and the British Cromerian specimens suggests a more reduced morphological variability for the latter. A possible explanation is that Britain, being an island, suffered alternated periods of isolation from the continent, and thus a bottle-neck effect, resulting in a reduced gene pool. This highlights the necessity of a review of the British sample, in a strict comparison with continental material and an acknowledgement of the timing of reinvasion of the British Isles from continental stocks following any major Glacial oscillation.

From a biometrical point of view, this research suggests a slightly larger size of the British Cromerian specimens when compared to the coeval population from Isernia. This is in good agreement with the observation by Lacombat (2009) that the *S. hundsheimensis* populations from southern Europe (Italy and France) are smaller in size than coeval populations from central Germany.

This observation is interesting in that it conforms to the ecogeographic principle known as Bergman's rule, which, with the due exceptions, is mostly valid for large mammals (e.g. Ashton et al., 2000). Whether the latitudinal size cline is due to the varying temperature (and so to the surface to volume ratio and heat loss) or to the distribution of food available for individual animal (and so to the net primary production of plants and population density, as demonstrated for deer by Langvatn and Ibon, 1986; Wolverton et al., 2009), is another interesting aspect of the problem which will be investigated in future studies.

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