

LATE PLEISTOCENE LAST OCCURRENCES OF THE NARROW-NOSED RHINOCEROS *STEPHANORHINUS HEMITOECHUS* (MAMMALIA, PERISSODACTYLA) IN ITALY

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Abstract. Several taxa belonging to the so called megafauna became extinct during the late Quaternary in Eurasia. The extinction chronology of the narrow-nosed rhinoceros, *Stephanorhinus hemitoechus*, in Europe is still uncertain and only estimated around 45 ka. A systematic revision of several rhinoceros findings reveals that this species occurred in Italy at least until 41 ka BP, at the onset of the Heinrich Event 4. Climatic fluctuations during MIS 3 and habitat fragmentation probably created an increase of small *S. hemitoechus* populations in southern Europe which had a tendency to become extinct.

INTRODUCTION

Megafauna extinction was a global event that took place during the end of the Pleistocene (Brook & Bowmann 2002; Barnosky et al. 2004; Elias & Schreve 2007 and references therein). In Eurasia, several species, including *Homo neanderthalensis*, became extinct before the Last Glacial Maximum (Stuart & Lister 2007, 2012, 2014; Elias & Schreve 2007 and references therein) and several "interglacial" large mammal species, e.g. *Palaeoloxodon antiquus*, disappeared from southern Europe during Marine Isotope Stage (MIS) 3 (Stuart 2005; Stuart & Lister 2007). This stage is characterised between 45 and 40 ka by the arrival of *Homo sapiens* in Europe (Benazzi et al. 2011; Hublin 2015 and references therein). Martin (1967) first hypothesized an overkill of large mammals by these new human hunters (*H. sapiens*) and modern humans have been indicated as the primary driver of worldwide megafauna losses (Sandom et al. 2014). However, extinction during the late Quaternary has been also related to climatic fluctuations (Barnosky 1986; Wroe & Field 2006; Lister & Stuart

2008). MIS 3 was indeed characterised by cooling during Heinrich events, the fourth of which (HE4, around cal. 38-40 ka BP; Watts et al. 1996; Long & Stoy 2013) was a brief but drastic cooling episode (Heinrich 1988; Bond et al. 1993; Broecker 1994; Mayewski et al. 1994; Cortijo et al. 1997; Vidal et al. 1997; Paillet & Bard 2002; Geraga et al. 2005). The Campanian Ignimbrite eruption (CIE) from the Phlegraean Fields Caldera, which represents the largest late Quaternary volcanic event (Fedele et al. 2003), also occurred during MIS 3 (around cal. 40 ka BP). In the Monticchio sequences (southern Italy), aridity and cooling, with a decrease of arboreal pollen and an increase of *Artemisia* and Chenopodiaceae (with values comparable to those of the Last Glacial Maximum), were in progress before the CIE, but they seem to display an acceleration after the CIE event (Paterne et al. 1999; Fedele et al. 2003). In the Cretan Basin and southern Aegean sea, the most pronounced stadials, characterised by increase in aridity, occurred at cal. 41 ka BP and cal. 13 ka BP and are related to the HE4 and the Younger Dryas events respectively (Geraga et al. 2005). Nevertheless, extinctions, as in the case of the European spotted hyena (*Crocuta spelaea*), cannot

be explained solely as a function of climate changes (Valera et al. 2010; Stuart & Lister 2014). Other authors have suggested a combination of overkill, climate and environmental changes to explain megafauna extinction (Stuart 1991; Barnosky et al. 2004; Stuart & Lister 2007, 2014; Pushkina & Raia 2008; Nogués-Bravo et al. 2008).

Due to the complex framework of the late Quaternary, it is crucial to calibrate the latest occurrences of megafaunal taxa in order to investigate the causes and patterns of their extinction. The timing of extinction of the narrow-nosed rhinoceros *Stephanorhinus hemitoechus* is still uncertain (Stuart & Lister 2007, 2012) and only approximated to around 45 ka (Stuart & Lister 2012). The oldest record of *S. hemitoechus* is from southern Europe, around 500 ka (Pandolfi et al. 2013), but the species was widely distributed throughout Europe during the late Middle and early Late Pleistocene (Guérin 1980). *Stephanorhinus hemitoechus* also reached the Near East and northern Africa during the last interglacial (Guérin 1980).

According to Guérin (1980) the preferred biotope of the narrow-nosed rhinoceros was the “prairie-parc boisée” or the open forest with a not-preferred type of food. According to Fortelius (1982) *S. hemitoechus* was a medium-size graviportal rhinoceros with tooth crowns higher than in the Early Pleistocene *S. etruscus* (see also Made 2010), reduced cingula and more cementum, possibly indicating a shift to a diet including more abrasive elements (Fortelius 1982). *Stephanorhinus hemitoechus* probably inhabited temperate open habitats rich in low growing vegetation (Fortelius 1982 and reference therein). According to Fortelius et al. (1993) *S. hemitoechus* displays remarkable convergence in many details with *Coelodonta antiquitatis*, despite it was not a true grazer but an intermediate feeder on low growing vegetation in open habitats. Hennesniemi et al. (2011) pointed out that the diet of *S. hemitoechus* was slightly more abrasive than that of browsing rhinoceroses (e.g., *Rhinoceros sondaicus*) but less abrasive than that of the Recent graze-dominated mixed feeder *Rhinoceros unicornis*. Van Asperen & Kahlke (2015) recently suggested that although the species had a preferred optimal diet, it had considerable dietary flexibility and adapted its diet according to what was available in the environment (Van Asperen & Kahlke 2015).

Here, a critical revision of several rhinoceros

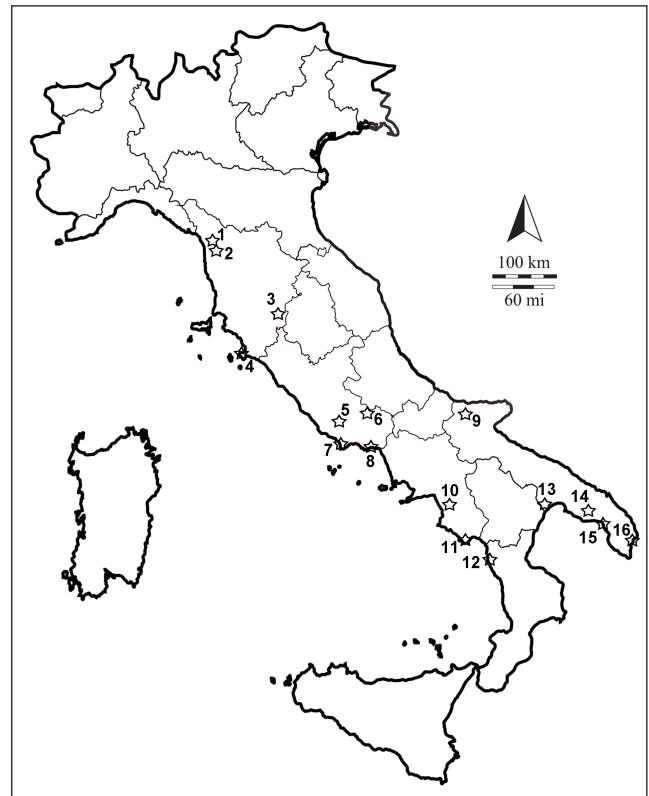


Fig. 1- Location map of the latest Pleistocene Italian localities mentioned in the text. 1, Grotta del Capriolo, Buca del Tasso and Buca della Iena; 2, Grotta Parignana; 3, Grotta di Gosto; 4, Grotta dei Santi; 5, Cava Muracci and Canale delle Acque Alte; 6, Sora-Valle Radice; 7, Grotta del Fossellone; 8, Grotta di S. Agostino and Grotta dei Moscerini; 9, Ingarano; 10, Grotta di Castelcivita; 11, Grotta della Cala; 12, Torre Talao; 13, Riparo l'Oscurusciuto; 14, Avetrana; 15, Grotta del Cavallo; 16, Grotta Romanelli.

findings chronologically related to MIS 4 and MIS 3 allows us to pinpoint the latest occurrences of the narrow-nosed rhinoceros in Italy and possibly explain its extinction.

MATERIAL AND METHODS

Rhinoceros remains included in this study are housed in several Italian institutions and museums. A systematic revision of the studied specimens was carried out in order to confirm the presence of the narrow-nosed rhinoceros in Italian Late Pleistocene localities (Fig. 1; Tab. 1). The specimens were morphologically compared with several Pleistocene remains referred to *Coelodonta antiquitatis* (Blumenbach, 1799), *Stephanorhinus kirchbergensis* (Jäger, 1839) and *S. hemitoechus* (Falconer, 1859) currently housed in different European institutions and museums (HNHM, IGF, MfN, MNCN, MPUR, NHML, NHMW, NMB). Tooth terminology follows that introduced by Guérin (1980) and revised by Antoine (2002). The metric methodology is based on the work of Guérin (1980).

Institutional Abbreviations: DSFTA, Università di Siena, Dipartimento di Scienze Fisiche della Terra e dell'Ambiente, Siena, Italy; DSPFS, Università di Roma “Tor Vergata”, Dipartimento

Site	Taxonomy	Age	References
Sora-Valle Radice	<i>Stephanorhinus hemitoechus</i>	MIS 4	Pandolfi & Tagliacozzo 2015
Ingarano, sandy-clays level	<i>Stephanorhinus hemitoechus</i>	? MIS 4	Pandolfi & Petronio 2011
Grotta del Fossellone, levels 32-33	<i>Stephanorhinus hemitoechus</i>	end MIS 5a-beginning MIS 4	Caloi & Palombo 1994; Pandolfi & Tagliacozzo 2015
Canale delle Acque Alte (level C2)	<i>Stephanorhinus hemitoechus</i>	MIS 4	Farina 2011
Torre Talao	<i>Stephanorhinus hemitoechus</i>	? MIS 4	Pandolfi & Tagliacozzo 2015
Grotta Parignana	<i>Stephanorhinus hemitoechus</i>	? MIS 4-early MIS 3	Caterini 1921; Farina 2012
Avetrana, bed 8	<i>Stephanorhinus hemitoechus</i>	MIS 4-early MIS 3	Pandolfi & Petronio 2011; Pandolfi et al. 2013
Grotta del Capriolo	? <i>Stephanorhinus</i> sp.	early MIS 3	Pitti & Tozzi 1971
Buca del Tasso	<i>Stephanorhinus hemitoechus</i>	early MIS 3	Fabiani 1922
Grotta dei Santi layers 150 and 110	<i>Stephanorhinus hemitoechus</i> , <i>S. cf. hemitoechus</i>	MIS 3	Spagnolo et al. 2016; This work
Grotta Romanelli, level G	<i>Stephanorhinus hemitoechus</i>	>69-40 ka BP	Pandolfi & Petronio 2011; Pandolfi & Tagliacozzo 2013; Pandolfi unpubl. data
Grotta di S. Agostino, level A2	<i>Stephanorhinus</i> sp.	ca. 55-43 ka BP	Tozzi 1970, Caloi & Palombo 1994
Grotta dei Moscerini	Rhinocerotini indet.	early MIS 3	Caloi & Palombo 1994
Grotta di Gosto	<i>Stephanorhinus hemitoechus</i>	> 48 ka U-Th	Tozzi 1974
Grotta del Cavallo, levels I, L	<i>Stephanorhinus cf. hemitoechus</i>	> cal. 45 600–42 900 yrs BP	Boscato & Crezzini 2007
Riparo l'Oscuruscio, levels 3,5	<i>Stephanorhinus cf. hemitoechus</i>	> cal. 43 ka BP	Boscato & Crezzini 2012
Buca della Iena, level D	<i>Stephanorhinus hemitoechus</i>	> cal. 41 ka BP	Pitti & Tozzi 1971
Cava Muracci	<i>Stephanorhinus hemitoechus</i>	cal. 41 ka BP	Gatta et al. 2016; This work
Grotta di Castelcivita level gar	Rhinocerotini indet.	<cal. 43 ka BP	Masini & Abbazzi 1997
Grotta della Cala level 14	<i>Stephanorhinus hemitoechus</i>	? (> cal. 33 ka BP)	Benini et al. 1997

Tab. 1 - Table of the latest records of *S. hemitoechus* in Italy (see text for discussion).

di Storia, Patrimonio culturale, Formazione e Società, Rome, Italy; DSTR, Dipartimento di Scienze della Terra, Sapienza, Università di Roma, Rome, Italy; HNHM, Hungarian Natural History Museum, Budapest, Hungary; IGF, Museo di Storia Naturale, sezione di Geologia e Paleontologia, Firenze, Italy; MfN, Museum für Naturkunde, Berlin, Germany; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNPELP, Museo Nazionale Preistorico Etnografico Luigi Pigorini, Rome, Italy; MPUR, Museo Paleontologico, Sapienza Università di Roma, Rome, Italy; MSNP, Museo di Storia Naturale, Certosa di Calci, Pisa, Italy; NHMUK, Natural History Museum, London, United Kingdom; NHMW, Naturhistorisches Museum, Wien, Austria; NMB, Naturhistorisches Museum, Basel, Switzerland; MCPPM, Museo Civico di Paleontologia e Paleontologia di Maglie, Lecce, Italy.

THE LATEST RECORDS OF *STEPHANORHINUS HEMITOECHUS* IN ITALY

Fossil rhinoceros records during MIS 4 and MIS 3 are relatively scarce in Italy (Fig. 1; Tab. 1) and mainly represent juvenile individuals.

Sora-Valle Radice (Frosinone)

The fossiliferous deposit of Sora-Valle Radice (Frosinone) which has yielded many *S. hemitoechus* remains (Biddittu et al. 1967; Pandolfi & Tagliacozzo 2015) has been referred to a cold phase of the Late Pleistocene, probably MIS 4. Remains collected from the karst cavities include sixty-nine specimens belonging to at least four individuals (one young and three adults). The material is housed at the MNPELP in Rome and was recently described and illustrated by Pandolfi & Tagliacozzo (2015). This record is the only one with abundant postcranial elements in southern Europe, including Italy. It enabled a careful analysis of the most important morphometric features in the postcranial skeleton of the species (Pandolfi & Tagliacozzo 2015). Unfortunately, rhinoceros remains sampled for ¹⁴C dating contained insufficient collagen (Stuart & Lister 2007).

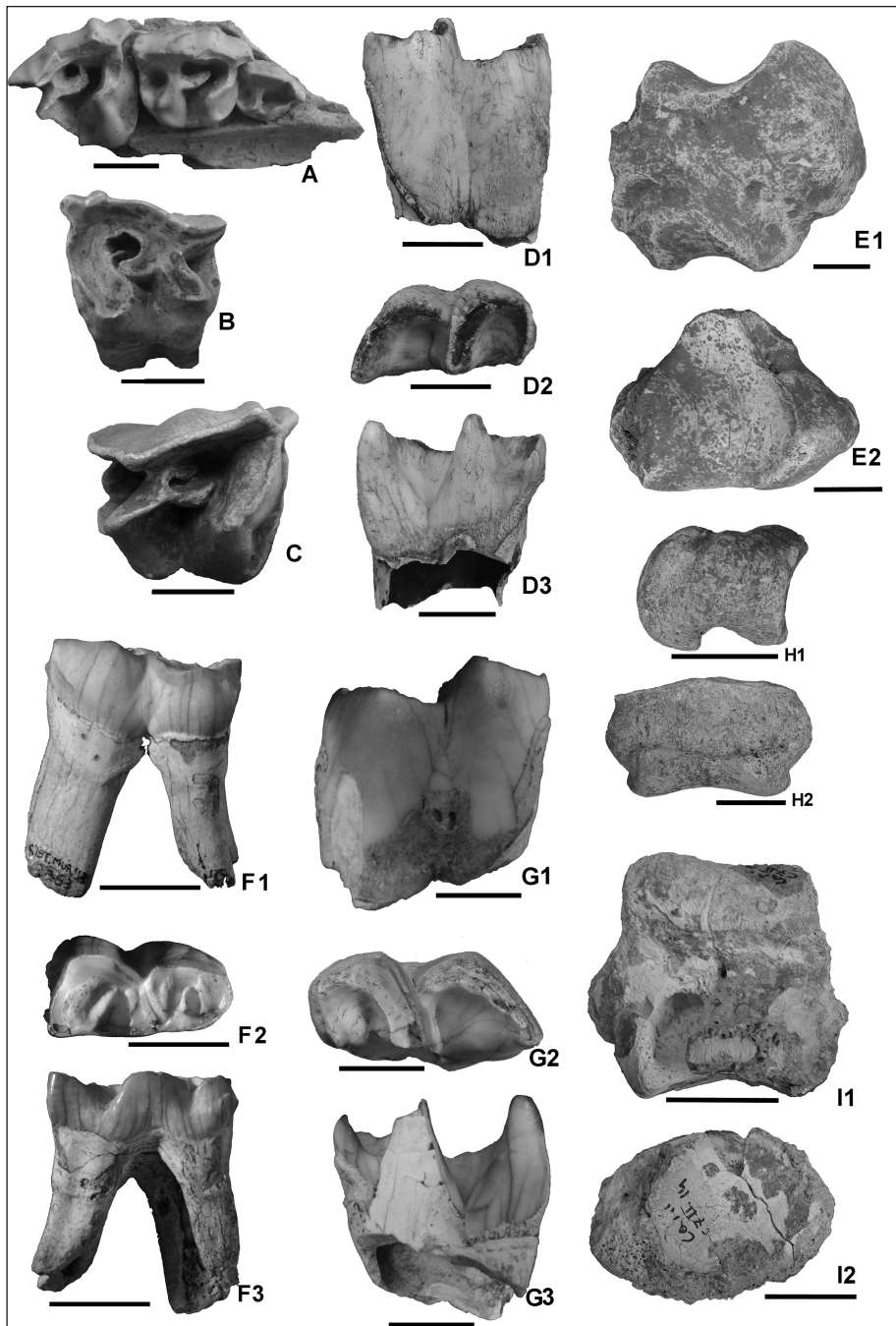


Fig. 2 - Remains of *Stephanorhinus hemitoechus* from the latest Pleistocene of Italy. A: DP1-DP3 from Torre Talao (MNPELP/P365), occlusal view; B: M1 from Grotta Parignana (NMB66), occlusal view; C: M2 from Grotta Parignana (NMB66), occlusal (2) and lingual (3) views; D: m1 or m2 from Grotta dei Santi (DSFTA G6/150/1) in labial (1), occlusal (2) and lingual (3) views; E: Scaphoid from Grotta di Gosto (DSFTA n60) in medial (1) and proximal (2) views; F: dp3 from Cava Muracci (DSPFS es. 363) in labial (1), occlusal (2) and lingual (3) views; G: m1 or m2 from Cava Muracci (DSPFS es. 365) in labial (1), occlusal (2) and lingual (3) views; H: Second central phalanx from Grotta di Castelcivita (DSFTA ctc84gar/g14II) in lateral (1) and dorsal (2) views; I: pyramidal from Grotta della Cala (DSFTA C7II14) in posteromedial (1) and distal (2) views. Scale bar = 2 cm.

Ingarano (Foggia)

Juvenile remains of *S. hemitoechus* from Ingarano Cave deposits (= Ferrovia Quarry) (Foggia), generally attributed to MIS 4, were collected from sandy-clay sediments that are in unclear stratigraphic relationship with the cave succession and also contains, among other taxa, *C. antiquitatis* and *Hippopotamus amphibius*, indicating that more than one climatic phase is represented (Stuart 2005). The rhinoceros remains probably belong to single individual and include fragments of the skull with the maxillae, one tibia, one astragalus and two metatarsals. The specimens are currently housed at MPUR

and were included in the study of Pandolfi & Petronio (2011).

Grotta del Fossellone (Latina)

A few juvenile *Stephanorhinus* remains (two fragmentary lower teeth and one upper deciduous tooth, MNPELP/P1136/1-2-3) have been collected from the levels 32-33 of Grotta del Fossellone (Latina), chronologically related to the end of MIS 5a and the beginning of MIS 4 (Caloi & Palombo 1994; Petronio et al. 2011; Pandolfi & Tagliacozzo 2015). The specimens were referred to *S. hemitoechus* by Pandolfi & Tagliacozzo (2015).

Canale delle Acque Alte (= Canale Mussolini = Gnif Gnaf; Latina)

A fragmentary scapula has been collected from level C2 of Canale delle Acque Alte, chronologically assigned to MIS 4 (Farina 2011). The specimen was figured by Farina (2011; Pl. 4 fig. 1) and referred to *S. hemitoechus*. The morphology and morphometry of the figured specimen are in agreement with this taxonomic attribution.

Torre Talao (Cosenza)

A juvenile fragmentary maxilla of *S. hemitoechus* (MNPELP/P365; Fig. 2A) has been recovered from the Late Pleistocene (MIS 4?) deposits at Torre Talao, Cosenza (Pandolfi & Tagliacozzo 2015). The specimen differs from *Coelodonta*, which displays hypsodont teeth, a wavy ectoloph profile and closed medifossette.

Grotta Parignana (Pisa)

Rhinoceros remains collected at Grotta Parignana (= Buca delle Fate) were described and illustrated by Caterini (1921). Unfortunately, these remains were collected without a scientific method and lack stratigraphic data. The mammal fauna has been subdivided into two different assemblages (referred to MIS 5 and MIS 3) by Farina (2012) basing on palaeoecological considerations. The mammal assemblage, with dominant *Marmota marmota* and presence of *Chionomys nivalis*, *Cricetus cricetus* and *Microtus*, suggests an age referable to the last Glacial (see Kotsakis et al. 2003 for the occurrences of these taxa), probably MIS 4 or the first half of MIS 3. At Grotta Parignana, *S. hemitoechus* seems to be the only large mammal (Caterini 1921; Farina 2012: tab. 1). The species is represented by juvenile and subadult individuals (Caterini 1921). A complete list of specimens was recently reported by Farina (2014: p. 26). The material is currently housed at MSNP, with several casts also housed at NMB (Fig. 2B, C). Among other characters, the upper deciduous row, DP1-DP4 (Caterini 1921: pl. II, figs 6-7; Farina 2012: pl. 3, figs 3-3a), and the upper molars (Caterini 1921: pl. II, figs 8-9; Farina 2012: pl. 3, fig. 4) differ from the hypsodont teeth of *Coelodonta* by having less wavy ectoloph profiles and by lacking the medifossette on DP4 and upper molars. The specimens also differ from *S. kirchbergensis*, which displays shallow vestibular folds, smooth enamel and generally larger size.

Avetrana (Taranto)

Rhinoceros remains from Avetrana karst filling (Taranto) have been previously reported from beds 3 and 6 (Petronio et al. 2008; Pandolfi et al. 2013). In addition, a proximal epiphysis of a third metacarpal, a third cuneiform and a fragment of a third metatarsal have been collected from bed 8 of Avetrana, which was recently referred to MIS 4 or MIS 3 (Pandolfi et al. 2013; Berté & Pandolfi 2014). U/Th dating on *Bos primigenius* teeth collected from bed 8 gave an improbable age around 18 and 14 ka (C. Petronio pers. comm. 2015).

The rhinoceros specimens are housed at DSTR. The fragment of third metatarsal (DSTR A8-81) is poorly preserved and it has been previously reported as belonging to *Bos primigenius*. The third cuneiform (DSTR no number) belongs to a juvenile individual and the articular surfaces are poorly preserved. The anterior face of the bone is rather rectangular in shape and its morphology resembles the third cuneiforms of *S. hemitoechus*. On the third metacarpal (DSTR no number), the proximal articular surface for the magnum is subtriangular in proximal view and its anterior border is rather sinuous. This surface is separated from that for the uncinata, which is subtrapezoidal in shape, by a strong saliency. In lateral view, the anterior articular surface for the fourth metacarpal is rather elliptical, whereas the posterior one is larger and rounded. The morphology of the specimen is similar to third metacarpals of *S. hemitoechus* collected from several Italian localities (e.g., Sora-Valle Radice; Pandolfi & Tagliacozzo 2015).

Grotta del Capriolo (Lucca)

At Grotta del Capriolo (Lucca; early MIS 3) fragments of a deciduous tooth were referred to *Rhinoceros* sp. by Pitti & Tozzi (1971). The specimen was not figured and its location is currently unknown. However, a determination at the specific level seems to be impossible.

Buca del Tasso (Lucca)

At Buca del Tasso (Lucca), generally referred to the first half of MIS 3, two lower rhinoceros teeth (p4? and m3) were collected and ascribed to *Rhinoceros mercki* by Fabiani (1921, 1922). The dimensions given by Fabiani (1921, 1922) are close to the minimal values reported by Guérin (1980) for *S. kirchbergensis* (= *D. mercki*) and the mean values of

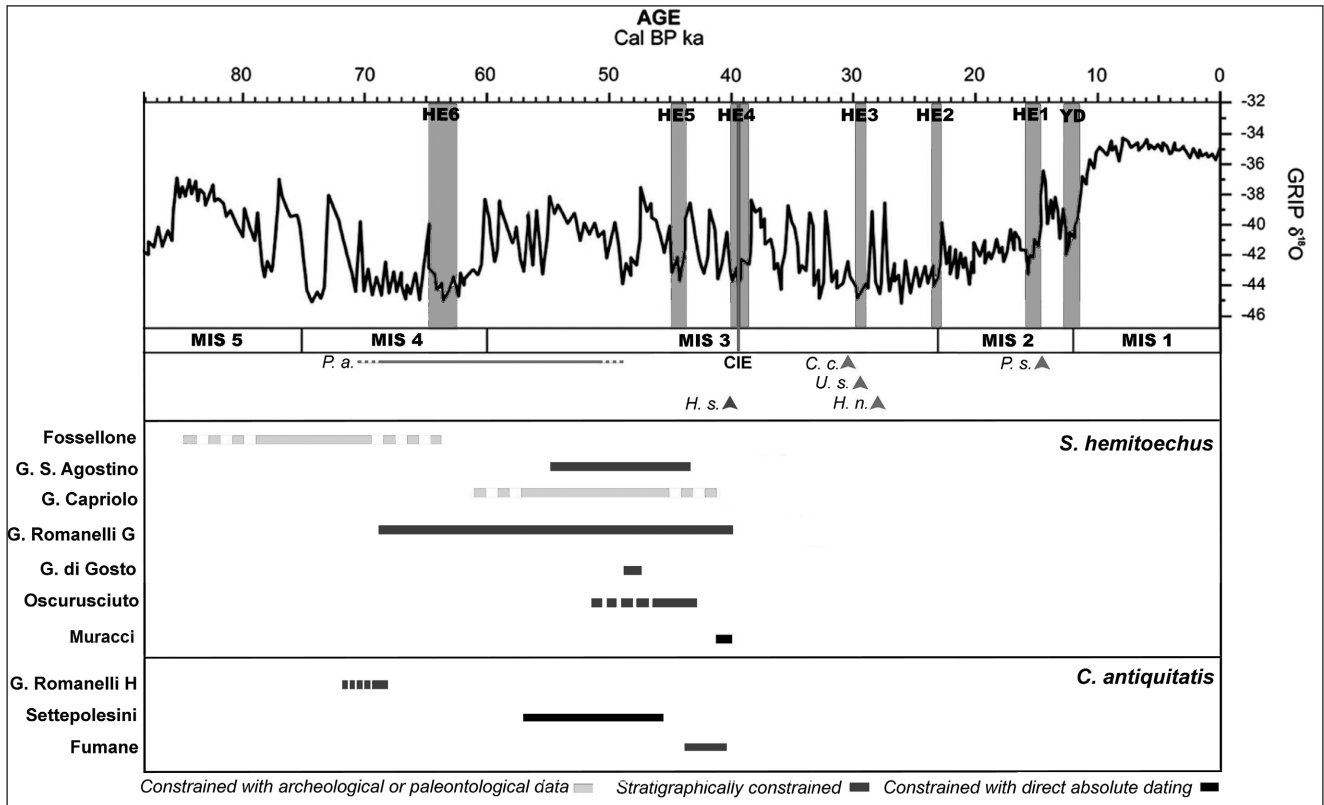


Fig. 3 - Chronological distribution of *Stephanorhinus hemitoechus* and *Coelodonta antiquitatis* in Italy; only selected localities are reported (see text and Tab. 1). The main cold episodes (HE) during MIS 3 and the Campanian Ignimbrite eruption (CIE) are shown (Fedele et al. 2003; Long & Stoy 2013). The chronological extinction of selected megafaunal taxa in Europe and the occurrence of *H. sapiens* are also reported (Palombo & Ferretti 2005; Stuart 2005; Stuart & Lister 2007, 2012, 2014; Lister & Stuart 2008; Benazzi et al. 2011; Hublin 2015). *P. a.* = *Palaeoloxodon antiquus*; *C. c.* = *Crocota crocuta*; *P. s.* = *Panthera spelaea*; *U. s.* = *Ursus spelaeus*; *H. n.* = *Homo neanderthalensis*; *H. s.* = *Homo sapiens*.

S. hemitoechus. The m3 figured by Fabiani (1921: pl. I, fig. 6) clearly belongs to *Stephanorhinus* rather than *Coelodonta* and the morphology of the lingual valleys (V shaped) and of the vestibular groove (open and deep) suggest an attribution to *S. hemitoechus*.

Grotta dei Santi (Grosseto)

Two unpublished teeth of rhinoceros have been collected at Grotta dei Santi (Monte Argentario; Grosseto). The Mousterian levels are still under investigation, but layers 110 and 150, where the specimens were recovered, can be assigned to the first half of MIS 3 (Spagnolo et al. 2016). The (first or second) lower molar, DSFTA G6/150/1, collected from this locality displays a rounded trigonid, V-shaped lingual valleys, deep vestibular groove and mesial and vestibular cingula (Fig. 2D). The specimen morphologically resembles the lower molars of *S. hemitoechus*. The second upper deciduous tooth (DSFTA F6/110/t5A) displays a well-developed mesial cingulum, two medifossettes, a shallow paracone fold and a well-developed parastyle. The tooth

is morphologically closer to *Stephanorhinus* rather than *Coelodonta*, but an attribution to *S. hemitoechus* is doubtful.

Grotta Romanelli (level G) (Lecce)

Several *Stephanorhinus* remains have been recovered from the Terre Rosse deposits (level G) of Grotta Romanelli (Lecce), chronologically U/Th dated between >69 and 40 ka (Fornaca Rinaldi & Radmilli 1968; Pandolfi & Tagliacozzo 2013). The dating methodology, however, should be revised and the Terre Rosse deposits could be an older age. Rhinoceros bones collected from Terre Rosse have been recently investigated for ^{14}C dating but they did not contain collagen (M. Mannino pers. comm. 2015). The rhinoceros remains from Grotta Romanelli were assigned to *Rhinoceros mercki* by Blanc (1920) and *S. kirchbergensis* by Bologna et al. (1994). Pandolfi & Petronio (2011) reassigned the specimens housed at the MCPPM to *S. hemitoechus*. Several specimens of rhinoceros collected during the 1960s and 1970s from the level G of the Cave and

currently housed at MNPELP can be also referred to the latter species. The material includes isolated teeth and several postcranial remains (Pandolfi & Tagliacozzo unpubl. data). The teeth display rough enamel, the upper teeth have a marked paracone fold and the lower teeth display V-shaped lingual valleys. The postcranial remains show morphological similarities with *S. hemitoechus* rather than *S. kirchbergensis* or *C. antiquitatis*. The dimensions of the remains are close to the minimal values of *S. hemitoechus* as well as other specimens collected from the Salentinian area (Pandolfi & Petronio 2011).

Grotta di Sant'Agostino (Gaeta)

Rhinoceros remains (18 tooth fragments), probably belonging to *Stephanorhinus*, were collected from level A2 of Grotta di S. Agostino (Gaeta), which was assigned to a time span between 55 and 43 ka (Tozzi 1970; Caloi & Palombo 1994).

Grotta dei Moscerini (Gaeta)

An indeterminate rhinoceros is reported from the middle levels of the long stratigraphic sequence of Grotta dei Moscerini (Gaeta), which are tentatively correlated with level A2 (55–43 ka) of Grotta San Agostino by Caloi & Palombo (1994). The location of the specimen is currently unknown.

Grotta di Gosto (Siena)

At Grotta di Gosto (Siena), U/Th dated around 48 ka (± 4 ka) (however this date needs to be revisited), Tozzi (1974) reported scanty and indeterminate fragments classified as *Rhinoceros* sp. Among the specimens, a relatively well-preserved scaphoid (Fig. 2E) temporarily housed at DSFTA was figured by Tozzi (1974: fig. 13). The specimen differs from *C. antiquitatis* which displays, as suggested by Guérin (1980: fig. 91) and Pandolfi & Tagliacozzo (2015) and observed on several specimens housed at HHM, MfN, NHMUK and NHMW, a larger and rounded proximal articular surface in proximal view, and a regularly convex anterior border of the bone in medial view. The morphology of the studied scaphoid suggests an attribution to *S. hemitoechus* (cf. Pandolfi & Tagliacozzo 2015).

Grotta del Cavallo (Lecce)

Scanty *Stephanorhinus* remains from Grotta del Cavallo (Lecce) (Sarti et al. 2002; Arobba et al. 2004; Boscato & Crezzini 2007) were collected from levels

I and L, which are stratigraphically lower than the Mousterian level F II dated cal. 45 600–42 900 yrs BP (Fabbri et al. 2016). The tooth fragments display rough enamel and are less hypsodont than those referable to *C. antiquitatis*. An attribution to *S. hemitoechus* seems probable but well-preserved material needs to be recovered for a better determination.

Riparo l'Oscurusciuto (Taranto)

Several fragments of rhinoceros teeth (cf. *Stephanorhinus* in Boscato & Crezzini 2012) have been reported from levels 3 and 5 of the Middle Palaeolithic site of Riparo l'Oscurusciuto (Taranto). These levels underlie level 1, ^{14}C dated around cal. 42 975 yrs BP (Boscato & Crezzini 2012). The morphology of the tooth fragments, less hypsodont and with a rough but less thick enamel than in *Colodonta*, suggests the presence of the genus *Stephanorhinus*, in particular *S. hemitoechus* (*S. kirchbergensis* is characterised by smooth enamel).

Buca della Iena (Lucca)

Rhinoceros material is recorded from level D of Buca della Iena (Lucca; Pitti & Tozzi 1971). This level is older than level C dated, around cal. 41 ka BP (Caloi & Palombo 1994). The remains collected from Buca della Iena include several bone and tooth fragments, two third upper molars, a fourth upper premolar (erroneously identified as a second upper molar by Pitti & Tozzi 1971) and a complete tibia attributed to *Rhinoceros* sp. by Pitti & Tozzi (1971). Unfortunately, the tibia was not figured by Pitti & Tozzi (1971) but the maximal length (370 mm) enables us to exclude an attribution to *S. kirchbergensis* (maximal length between 404 mm and 457 mm; Guérin 1980: tab. 144). The upper teeth from Buca della Iena (Pitti & Tozzi 1971: fig. 6) cannot be attributed to *C. antiquitatis* which, among other characters, displays hypsodont teeth, wavy ectoloph profile, squared shape of M3, and closed medifossette. The base of the protocone on M3s from Buca della Iena is not enlarged as in *S. kirchbergensis* whereas the ectoloph profile on P4 is rather flattened than on P4s of *S. kirchbergensis* at the same stage of wear. Accordingly, the specimens from Buca della Iena are ascribed to *S. hemitoechus*.

Cava Muracci (Cisterna di Latina)

A few remains attributable to *S. hemitoechus* have been collected from Cava Muracci at Cister-

na di Latina (Latina) (Gatta & Rolfo 2015; Gatta et al. 2016). The remains include three lower teeth (DSPFS es 363, 365, 645) and a fragment of juvenile femur (DSPFS es 842). Four calibrated ^{14}C dating have returned for the quarry a Late Pleistocene chronology between cal. 44 054 yrs BP and cal. 34 810 yrs BP (Gatta et al. 2016), with particular interest to this study for the dating to cal. 42 054-40 804 yrs BP [36 885 \pm 350 yrs BP (LTL15760A)], performed on a sample of *S. hemitoechus* (Gatta et al. 2016; Tab. 2). The lower teeth (Fig. 2F, G) display rough enamel, V-shaped lingual valleys and a rounded trigonid. The femur is relatively slender with respect to juvenile femura of *C. antiquitatis*.

Grotta di Castelcivita (Salerno)

Masini & Abbazzi (1997) reported the presence of rhinoceros from the Mustertian level gar of Castelcivita (the underlying level cgr, yielded two dates: cal. 43 295 \pm 942 and 46 322 \pm 1 401 yrs BP) on the basis of a second central phalanx only (DSFTA ctc84gar/g14II; Fig. 2H). Although Masini & Abbazzi (1997) admitted that it is not possible to ascribe the specimen to a species they referred it to *S. cf. hemitoechus*. This record appears very doubtful and an attribution to *Coelodonta* cannot be discounted. The faunal assemblage also includes *Ursus spelaeus*, *Megaloceros cf. giganteus*, *Bison priscus* and *Chionomys nivalis*, which are indicative of relatively cold conditions. The rhinoceros specimen should be assigned to *Rhinocerotini* indet.

Grotta della Cala (Salerno)

Benini et al. (1997) reported the presence of a rhinoceros (*S. cf. hemitoechus*) from the Uluzzian level 14 of Grotta della Cala (Salerno) on the basis of a pyramidal (DSFTA C7II14; Benini et al. 1997: fig. 12; Boscato & Crezzini 2007). The age of level 14, cal. 33 567 \pm 381 yrs BP, has been considered problematic and unreliable as it is too recent for the Uluzzian techno-complex (Benini et al. 1997: p. 65). The maximal height (H) of the bone (43.4 mm) is less than in *S. hemitoechus* (range 48-63 mm in Guérin et al. 1980: tab. 134; range 47-59.59 mm in Pandolfi & Tagliacozzo 2015), the antero-posterior diameter (DAP) (47.7 mm in Benini et al. 1997; 48.5 mm measured by LP) is slightly larger (35.5-46 mm in Guérin et al. 1980; 34.4-46.46 mm in Pandolfi & Tagliacozzo 2015) and the transverse diameter (DT) (51 mm) falls in the range of *S. hemitoechus* (47-60

mm in Guérin 1980; 44.9-61.49 mm in Pandolfi & Tagliacozzo 2015). Nevertheless the H is probably underestimated because the specimen lacks part of the proximal articular surface on the lateral side, whereas the value of DAP can be influenced by carbonate concretions that covered the bone. In posteromedial view (Fig. 2I), the dorsal profile of the proximal articular surface is less concave than in *C. antiquitatis*, in particular on its anterior half, and the anterior face appears lower than the posterior one as well as in *S. hemitoechus*. The specimen was sampled for ^{14}C dating but it contained insufficient collagen, like that from Castelcivita (Stuart & Lister 2007; A.J. Stuart pers. comm Nov. 2015). The faunal assemblage collected from level 14 of Grotta della Cala is characterised by a high number of identified remains of fallow deer (43.8%) followed by red deer (16.7%), roe deer (9.8%) and wild boar (13.2%). This assemblage is suggestive of relatively warm conditions.

CONSIDERATIONS OF THE EXTINCTION OF *STEPHANORHINUS HEMITOECHUS*

The available data indicate that the last occurrence of *S. hemitoechus* in the Italian Peninsula was during the first half of MIS 3, around cal. 41 ka BP, at the onset of HE4 (Fig. 3).

In the United Kingdom, *S. hemitoechus* is reported from Wood Quarry (Nottinghamshire) dated around 66.8 ka (Pike et al. 2005). However, this species was listed in the faunal assemblage on the basis of a reminiscence rather than actual specimens (Pike et al. 2005). According to Stuart (1991) *S. hemitoechus* retreated to southern Europe during the Last Cold Stages and was absent in northern Europe.

In France and Monaco, the genus *Stephanorhinus* occurs in several localities chronologically ranging from MIS 4 to the first half of MIS 3 (Prince Cave, Cavillon Cave, Observatoire Cave and Enfants Cave) but radiometric ages are not available (Lacombat 2005).

In Spain, *S. hemitoechus* is recorded at La Ventana (Madrid). This record appears uncertain (Sánchez et al. 2003: 164) and, according to Sánchez et al. (2003), the two fragments of teeth were probably collected from the lower levels of the cave. *Stephanorhinus hemitoechus* occurs at Can Rubau (Gerona).

In this locality, lithic industries have been tentatively referred to the Mousterian culture (Cerdeño 1990; Álvarez-Lao & García 2010; Maroto in Álvarez-Lao & García 2011) and the site has been chronologically referred to a time span between 120 and 42.5 ka (Álvarez-Lao & García 2010). The occurrence of *S. hemitoechus* at Abric Romani (Barcelona) is uncertain. According to Sánchez (1990) an indeterminate rhinoceros is represented by a fragment of an upper molar. Later, Russell et al. (2012) reported the presence of *S. hemitoechus* from levels H and Ja of Abric Romani, respectively dated around 44.5 ka and 47.1 ka (Bischoff et al. 1988, 1994; Russell et al. 2012). Stuart & Lister (2007) reported a radiocarbon age of about 42–45 ka for *S. hemitoechus* collected at Cueva del Castillo (Santander).

S. hemitoechus seems to survive in Portugal until the end of MIS 3 (Cardoso 1995, 1996). A human tooth from Gruta da Figueira Brava, which also yielded remains of *S. hemitoechus*, was dated around 24 ka (Antunes & Cardoso 2000), whereas a molar plate of elephant was dated around 30–31 ka (Stuart 2005). The south-western part of Europe probably represents the last refugium of the narrow-nosed rhinoceros, but further investigations are needed to better calibrate the occurrences and extinction of the species in that area.

Most probably, the dietary flexibility of *S. hemitoechus* (see Van Asperen & Kahlke 2015) enabled the species to survive during cold steppe phases, which may therefore not directly related to its extinction.

In Africa, biotic stressors such as predation and more competitors (in particular elephants), may be affecting the reproductive physiology of the black rhino negatively (Birkett 2002; Brett & Adcock 2002; Okita-Ouma et al. 2009; Freeman et al. 2014). In Europe, despite differences in climatic conditions and cycles, megaherbivore guilds and competition among them, a possible effect on rhinoceros populations inferred from predation and competition with elephants and other rhinoceros species cannot be excluded a priori.

Pleistocene European competitors for *S. hemitoechus* could be the straight-tusked elephant *Palaeoloxodon antiquus*, the woolly mammoth *Mammuthus primigenius* and the woolly rhinoceros *Coelodonta antiquitatis*. *Palaeoloxodon antiquus* seems to become extinct in Europe around 40–50 ka (Stuart 2005); in Iberia it survives as late as 33–34 ka, but in Italy

the evidence for late survival beyond MIS 5a is weak (Palombo & Ferretti 2005; Stuart 2005). This species, however, is widely distributed throughout the Peninsula during the Middle Pleistocene and is usually associated with *S. hemitoechus* (Petronio et al. 2011 and references therein; Marra et al. 2014). The cold Late Pleistocene stages allowed the diffusion of the cold fauna through all of Europe, in particular of *Mammuthus* and *Coelodonta*, which also spread to southern Italy (Petronio et al. 2011; Marra et al. 2014). The grazer *Coelodonta* was, of course, more specialized and much more adapted to feed on the low growing vegetation than *S. hemitoechus* (Guérin 1980; Fortelius 1982). In Italy, *C. antiquitatis* has been recorded in a very few MIS 4 and MIS 3 localities and most of them (Opicina, Fadalto nel Polesine, Tiber terraces, Monte Circeo, Ingarano) lack detailed chronological data (Pandolfi & Tagliacozzo 2013; Pandolfi & Marra 2015). The species was chronologically dated at Settepolesini di Bondeno (northern Italy; Gallini & Sala 2001) with a median date >49 ka (95% range 45 199–56 986 yrs BP; Stuart & Lister 2012) and Riparo di Fumane (northern Italy; Cremaschi et al. 2005), where levels containing rhinoceros remains were dated between cal. 43 600 and 40 400 yrs BP (Higham et al. 2009). Accordingly, *C. antiquitatis* and *S. hemitoechus* co-occurred in Italy between approximately 69 ka and 41 ka (Fig. 3) but their coexistence is documented only in the problematic sandy level of Ingarano (MIS 4?). *Mammuthus primigenius* is documented during MIS 4 and MIS 3 in Italy (Riparo Tagliente, Buca della Iena, Canale delle Acque Alte level C2: Caloi & Palombo 1994; Palombo & Ferretti 2005) and the species is radiometrically dated to around 33–34 ka at Settepolesini di Bondeno (Ferrara) and around 20–19 ka at Arene Candide (Cassoli & Tagliacozzo 1994; Gallini & Sala 2001; Palombo & Ferretti 2005). However, the species is also recorded earlier than MIS 4, e.g., Bucine, Po valley, Torrente Conca (Caloi & Palombo 1994; Palombo & Ferretti 2005), suggesting a co-occurrence with *S. hemitoechus* at least from early MIS 4 to the first half of MIS 3. The presence of both *S. hemitoechus* and *M. primigenius* is only documented at Buca della Iena and Canale delle Acque Alte (layer C2).

Concerning predation, rhinoceros remains are abundant in several late Pleistocene hyena dens of central Europe (Diedrich 2013). According to Stuart & Lister (2014) remains of adult rhinocero-

ses were collected by hyenas whereas juvenile individuals of rhinoceros were occasionally predated. Of course, juvenile individuals of both *Coelodonta* and *Stephanorhinus* represented a potential prey for large Pleistocene carnivores (*Panthera leo* and *Crocodylus crocuta*) and also for human hunters (*Homo neanderthalensis*). Nevertheless, evidence of an extensive hunting of *Stephanorhinus* species is not demonstrated and traces of anthropogenic action are not evident on studied material from several MIS 4 and MIS 3 Italian localities mentioned above. In addition, an important role as accumulating agents of bones, including remains of rhinos, was played by scavengers (e.g., hyenas) which scavenge, carry and gnaw several parts of rhino skeletons regardless of the way they died (e.g., Diedrich 2013, 2014, 2015).

Several studies have highlighted that variation in rainfall regime drives the dynamics of African savannah ecosystems and influence resource availability, distribution, nutritional status and reproductive capacity of large mammals, including rhinoceroses (Goddard 1970; Thomposn 1971; Coe et al. 1976; Sinclair 1979; Hamilton & Blaxter 1980; East 1984; Hall-Martin 1986; Owen-Smith 1990; Foose et al. 1993; Hillman-Smith & Groves 1994; Kretzschmar et al. 2004; Hrabar & Toit 2005; Okita-Ouma et al. 2009; Berkeley & Linklater 2010).

In recent rhinoceroses, reduction in numbers of rhinoceros individuals took place with a decline in birth rates, increase in mortality rate and emigration and increases in the number of small populations (Hanski et al. 1996; McCullough 1996; Hanski and Simberloff 1997; Ouma 2004). Of course small populations are vulnerable to random fluctuations in size and eventual extinction. Small populations have a greater tendency to become extinct than large populations for several reasons including loss of genetic variability, inbreeding, genetic drift, demographic fluctuations and environmental variations or natural catastrophes (Gilpin & Soulé 1986; Menges 1992; Loeschcke et al. 1994; Lacy & Lindenmayer 1995; Avise & Harmrick 1996; Morales et al. 1997; Woodruff 2001).

CONCLUSIONS

Dating the extinction of the Eurasian megafauna and understanding the causes that led to their extinction is a subject of debate among researchers.

Several large mammals disappeared diachronously in different areas and were probably affected by different selective pressures. The available data suggest that, in Italy, the steppe rhinoceros was present at least until cal. 41 ka BP.

Studies on extant rhinoceros populations have shown that a decrease in numbers of individuals is related to environmental variation and fragmentation of habitats. Environmental variation influenced several aspects of extant rhinoceros ecology and reproduction whereas habitat fragmentation created an increase in small populations that have a tendency to become extinct. The climatic fluctuations occurring during the Late Pleistocene, in particular during MIS 4 and early MIS 3, and the contraction of the geographic range of the species probably led to an increase in, and isolation of, several small populations. These factors, also associated with the presence of possible ecological competitors (i.e., *M. primigenius* and *C. antiquitatis*), probably drove the species towards extinction. Further investigations on the paleoecology of the extinct rhinoceroses would help to better understand their biology and the causes of their extinction.

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