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Equids from the late Middle Pleistocene to Early Holocene of the Apulia Peninsula (southern Italy): reassessment of their taxonomy and biochronology

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ABSTRACT
The Apulian Peninsula represents a key-region for the study of climatic changes and paleoenvironmental dynamics during the Quaternary. Both large and small-sized horses are well documented in this region during the Pleistocene and are frequently found associated. The caballoid horses from Middle to Late Pleistocene of Europe show a large intraspecific ecomorphological variation, emphasizing a strong link between skeletal adaptations and specific aspects of the palaeoenvironment. This large variability led to an extended debate concerning the taxonomy of equids and their evolutionary history. In the Italian Peninsula, fossils from the Middle to the Late Pleistocene have been historically referred to several species (or even subspecies), emphasizing the uncertainty of the taxonomic attribution. Here, a large craniodental sample of Equidae fossils from late Middle Pleistocene to the Early Holocene localities of the Apulia Peninsula are described for the first time. The comparison of the protocone index allowed us to determine the first occurrences of *Equus mosbachensis* von Reichenau, 1903 in the Apulian Peninsula, from a few localities chronologically referred to late Middle Pleistocene. Most of the material from the late Middle to the end of the Late Pleistocene is instead attributed to *Equus ferus* Boddaert, 1785. The results of this work thus add novel information on the biochronology of Italian fossil equids and their evolutionary history through the Middle and Late Pleistocene.

KEY WORDS
Caballoid horse,
Aurelian,
Mediterranean,
body-size,
biometry.

RÉSUMÉ

Les équidés du Pléistocène moyen à l'Holocène inférieur de la péninsule des Pouilles (sud de l'Italie) : réévaluation taxonomique et briochronologique.

La péninsule des Pouilles représente une région clé pour l'étude des changements climatiques et des dynamiques paléoenvironnementales au cours du Quaternaire. Les chevaux de grande et de petite tailles sont bien documentés dans cette région au cours du Pléistocène et sont fréquemment associés. Les chevaux caballoïdes du Pléistocène moyen à supérieur d'Europe montrent une grande variation écomorphologique intraspécifique, soulignant un lien fort entre les adaptations squelettiques et des aspects spécifiques du paléoenvironnement. Cette grande variabilité a conduit à un débat prolongé concernant la taxonomie des restes d'équidés et leur histoire évolutive. Dans la péninsule italienne, les fossiles du Pléistocène moyen à supérieur ont été historiquement associés à plusieurs espèces (ou même sous-espèces), soulignant l'incertitude de l'attribution taxonomique. Ici, un grand échantillon craniodental de fossiles d'Equidae provenant de localités de la fin du Pléistocène moyen à l'Holocène inférieur de la péninsule des Pouilles est décrit pour la première fois. La comparaison de l'indice du protocône nous a permis de déterminer les premières occurrences d'*Equus mosbachensis* von Reichenau, 1903 dans la péninsule des Pouilles, à partir de quelques localités chronologiquement référencées au Pléistocène moyen supérieur. La plupart du matériel de la fin du Pléistocène moyen à la fin du Pléistocène supérieur est plutôt attribué à *Equus ferus* Boddaert, 1785. Les résultats de ce travail apportent donc de nouvelles informations sur la biochronologie des équidés fossiles italiens et sur leur histoire évolutive au cours du Pléistocène moyen et supérieur.

MOTS CLÉS
Cheval caballoïde,
Aurélien,
Méditerranée,
taille du corps,
biométrie.

INTRODUCTION

The Italian Peninsula is considered a crossroads in the Mediterranean area, representing a key area for the study of climatic changes and paleoenvironmental dynamics during the Quaternary. The Apulian region, or Apulian Peninsula (AP; southern Italy), is a "peninsula within a peninsula" due to its isolated position which extends mostly along the latitudinal axis (Fig. 1). The AP maintained this conformation through most of the Pleistocene Epoch and is rich in localities with mammal fossil remains frequently associated to lithic artefacts referred to both the Middle (Middle to Late Pleistocene) and the Upper Palaeolithic (Late Pleistocene to Early Holocene) (Berto *et al.* 2017; Spinapolice 2018; Sardella *et al.* 2018, 2019; Zanchetta *et al.* 2018). The abundance of Middle Pleistocene and Early Holocene sites makes this region a key-territory to study the evolution of the mammal fauna and of the climatic changes that took place during the Quaternary in the Mediterranean area (e.g., Mecozzi & Bartolini Lucenti 2018; Iannucci *et al.* 2020; Iurino *et al.* 2020).

In many of these fossil localities of the AP caballoid horses are well represented and frequently associated with fossil remains of *Equus hydruntinus* Regàlia, 1907 (European ass) (e.g., Grotta Paglicci, Boschin & Boscato 2016; Melpignano, Rustioni 1998; Tana delle Iene, Conti *et al.* 2010).

The fossil record often only faunal lists are reported for unheated in archeological sites of the AP. With the exception of the material from Tana delle Iene (Conti *et al.* 2010) and Grotta del Cavallo (Sarti *et al.* 1998, 2002) horse fossil materials usually are not formally studied and described. Moreover, due to the probable exploitation of the carcasses by human populations (Sarti e*t al.* 1998; Boscato *et al.* 2006), equid fossil remains are often highly fragmented. Consequently, fossil material from many archeological localities of the AP is rarely studied from a paleontological perspective. Nevertheless, the isolated and fragmentary craniodental remains can represent an important source of information for the study of the evolution of equids in the AP through the Middle Pleistocene and Early Holocene.

Several preliminary studies were conducted on the material from Cardamone (Rustioni 1998), Cava Spagnulo (Mecozzi *et al.* 2018), Grotta del Cavallo (Sarti *et al.* 1998, 2002), Grotta Paglicci (Boscato 1994), Melpignano (Rustioni 1998) and Tana delle Iene (Conti *et al.* 2010) where the material were referred to *Equus ferus*. The material from San Sidero was attributed to the large-sized *Equus chosaricus* by Eisenmann (1991b) and *Equus ferus by* De Giuli (1983) and Rustioni (1998). The taxonomic attribution of other material from the AP was mainly based on the chronology of deposits and therefore frequently ascribed to *Equus ferus* (Table 1).

Equids were considered an important and a very common component of European large vertebrate fauna during the Middle and Late Pleistocene, but their taxonomy remains controversial (Eisenmann 1991b; Forstén 1991; van Asperen 2012; Boulbes & van Asperen 2019). The lack of clear diagnostic morphological characters has led the proliferation of species and subspecies mainly due to the notable size variation observed in the Middle Pleistocene *Equus* (van Asperen 2012; Boulbes & van Asperen 2019).

For Pleistocene equid taxa, a useful character for taxonomic determination is the protocone index (length of protocone × 100/length of tooth). Caloi & Palombo (1987) effectively utilized this index for differentiating late Early to early Middle Pleistocene *Equus* material from different Italian localities. Caloi (1997) used the index for differentiating late Pliocene to early Middle Pleistocene *Equus* samples from European sites. The protocone index, calculated on the upper teeth has allowed the comparison of teeth of various sizes to establish relative protocone length (Caloi & Palombo 1987; Caloi 1997). Recently, the validity of the protocone index for taxonomic determination in stenonid group was corroborated by Boulbes & van Asperen (2019), who nevertheless rejected the use of the length of protocone for paleoenvironmental inferences. Moreover, this approach was also followed by Hadjouis (1998) for the study of *E. ferus* from the Middle Pleistocene site of Maisons-AIfort (Val-de-Marne, France) and Langlois (2005) for that of *Equus mosbachensis micoquii* Langlois, 2005 from the Middle Pleistocene site of La Micoque (Les Eyzies-de-Tayac, France). Likewise, the postflexid index was also tested for taxonomical purpose, but the analysis of the fossil Equidae sample highlighted its poor reliability (Boulbes 2010). The postflexid index, calculated on lower teeth [(length of postflexid × 100)/length of teeth], allows the comparison of teeth of various sizes to establish relative postflexid length (Caloi & Palombo 1987; Caloi 1997; Boulbes 2010).

In this scenario, we perform a comparison of protocone and postflexid indices in order to investigate the biometric variability and taxonomy through the Middle to Late Pleistocene equids from AP. In this work, we present for the first time the craniodental material of fossil *Equus* from late Middle to Late Pleistocene selected sites of the AP: Grotta di Capelvenere, Grotta delle Tre Porte, Grotta Mario Bernardini, Grotta Uluzzo C, Castellaneta, Grotta dei Giganti, Grotta Santa Croce, Grotta Laceduzza, Grotta Zinzulusa, Fondo Focone and Santa Maria d'Agnano. In addition, the revision of the material from Cardamone, Melpignano and San Sidero is carried out. The results allow us to assemble a preliminary evolutionary framework for the horses during the Middle Pleistocene to Early Holocene.

TAXONOMY OF MIDDLE-LATE PLEISTOCENE HORSES

After decades of debate, the systematics of caballoid horses has been recently redefined. In 2003, the International Commission on Zoological Nomenclature proposed to use *Equus ferus* Boddaert, 1785 a wild horse, to distinguish it from the domestic species *Equus caballus* Linnaeus, 1758 (Gentry *et al.* 2004). Although many studies focused on caballoid horses and their biostratigraphic importance, the taxonomic status of the Middle and Late Pleistocene fossils is still a controversial topic (Forstén 1991; van Asperen 2012; Boulbes & van Asperen 2019). The main issue concerns the interpretation of the morphological changes and biometric variations as intra-specific variability or ecomorphotypes (Azzaroli 1983; Forstén 1988; Cramer 2002; van Asperen 2012; Boulbes & van Asperen 2019). The diffusion of the first caballoid horses into Europe occurred in the early Middle Pleistocene and led to the development of several ecomorphotypes through the Middle and Late Pleistocene, including: *E. ferus mosbachensis* von Reichenau, 1903*, E. ferus germanicus* Nehring, 1804*, Equus ferus gallicus* Prat, 1968*, E. ferus gmelini* Antonuis, 1912. These subspecies of *E. ferus* are mainly distinguished by their overall size and differences in skeletal proportions. According to van Asperen (2013), this inter- and intraspecific variability cannot be explained by sexual dimorphism and/or age variability in adult skeletal elements. Indeed, the author found no differences in size related to age and sex variation in the extant specimens, assuming these factors have a very limited effect on studies of fossil samples.

Fig. 1. — Location of the considered Apulian sites: **1**, Grotta Santa Croce; **2**, SMA-esterno; **3**, Grotta Laceduzza; **4**, Castellaneta; **5**, Cardamone; **6**, Grotta Mario Bernardini - Grotta Uluzzo C - Grotta di Capelvenere; **7**, San Sidero – Melpignano; **8**, Grotta Zinzulusa; **9**, Fondo Focone; **10**, Grotta dei Giganti Grotta delle Tre Porte.

Based on the European fossil record, *Equus mosbachensis* von Reichenau, 1903 is the first occurring caballine *sensu lato* from the early Middle Pleistocene from the Germany localites of Mauer (MIS 17/15; 609 ± 40 ka; Wagner *et al.* 2011) and Süssenborn (MIS 16, 640-620 ka, Kahlke 2014) (Eisenmann *et al.* 1985; Langlois 2005; Boulbes & van Asperen 2019). This taxon has been instituted by von Reichenau (1915) based on the material from the fossiliferous sites of Mosbach (about 0.5 Ma) (Germany). Although the Mosbach horse (*E. mosbachensis*) shared several features with the wild horse (*E. ferus*), it possesses some "archaic" morphological features (presence of the tendon insertion of the anterior brachialis muscle on the inner edge of the diaphysis of the radius, strong supraarticular tuberosities on metapodials) (Bonifay 1980; Eisenmann 1991a; Guadelli & Prat 1995; Hadjouis 1998; Langlois 2005; Boulbes & van Asperen 2019). The affinity of the morphological features between *E. ferus* and *E. mosbachensis* suggests a close phyletic relationship between them, supported by the lack of clear craniodental diagnostic characters. This homogeneous overall morphology led some authors (van Asperen 2012) to refer the European Middle Pleistocene sample to a singles species, *E. ferus* ssp., where the slight morphological and biometric variability is considered to reflect the adaptive responses to local climatic and palaeoenvironmental conditions. These differences could otherwise be considered to be due to normal population variability. However, there is a substantial consensus considering *Equus mosbachensis* as a distinct taxon because of its large-sized and robust build (Eisenmann *et al.* 1985;

Table 1. — *Equus* Linnaeus, 1758 fossil material from the late Middle to Early Holocene of the Apulian Peninsula. Date abbreviations: **Biochr.**, biochronology; **Chrono-cult.**, chrono-cultural;

Species reported in previous researches	Site	Abbrevations	MIS	Date	Reference	Data source
Equus ferus	Melpignano	Mel	MIS 9-8	Biochronology	Sala *et al.* 1992; Bologna *et al.* 1994; Mecozzi *et al.* 2019; this work	This work
Equus ferus - *Equus chosaricus*	San Sidero	SS	MIS 9-8	Biochronology	De Giuli 1983; Sala *et al.* 1992; Mecozzi *et al.* 2019; this work	This work
Equus ferus	Grotta di Capelvenere	GCv	MIS 9-8	Biochronology and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
Equus ferus – *Equus* sp.	Grotta delle Tre Porte	GTP	MIS 7-5	Biochronology and Stratigrpahy	Blanc 1958; this work	This work
Equus ferus	Grotta Mario Bernardini - VI	GMB - VI	MIS 7-5	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
Equus ferus	Grotta Uluzzo C - IV	GUC - IV	MIS 7-5	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
Equus ferus	Grotta del Cavallo	GCa - HI	MIS 5	Radiometric data	Sarti *et al.* 2002	Sarti *et al.* 2002
Unpublished	Castellaneta	Cas	MIS 5	Biochronology	This work	This work
Equus ferus	Grotta dei Giganti	GGi	MIS 4	Stratigraphy and Chrono-cultural	Blanc 1958; Aureli & Ronchitelli 2018	This work
Equus ferus	Grotta Santa Croce	GSC	MIS 4	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
Equus ferus	Grotta Laceduzza	Gla	MIS 4	Biochronology and Chrono-cultural	Mecozzi *et al.* 2019	This work
Equus ferus	Grotta Mario Bernardini - III	GMB - III	MIS 4	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
Equus ferus	Grotta Uluzzo C - III	GUC - III	MIS 4	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
Equus ferus	Grotta Mario Bernardini - II	GMB - II	MIS 3	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
Equus ferus	Grotta Uluzzo C - II	GUC - II	MIS 3	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
Equus ferus	Cava Spagnulo	CS	MIS 3	Biochronology and Chrono-cultural	Mecozzi *et al.* 2018	Mecozzi *et al.* 2018
Equus ferus	Fondo Cattìe	FCa	MIS 3	Biochronology and Chrono-cultural	Corridi 1989	Corridi 1989
Equus ferus	Grotta del Cavallo	GCa - F	MIS 3	Radiometric data	Sarti *et al.* 1998	Sarti *et al.* 1998
Equus ferus	Tana delle Iene	TI	MIS 3	Stratigraphy and Chrono-cultural	Conti *et al.* 2010	Conti *et al.* 2010
Equus ferus	Cardamone	Car	MIS 2	Biochronology and Chrono-cultural	Rustioni *et al.* 2003	This work
Equus ferus	Fondo Focone	FFo	MIS 2	Stratigraphy and Chrono-cultural	Cancellieri 2017; this work	This work
Equus ferus	Grotta Zinzulusa	GZi	MIS 2	Biochronology and Chrono-cultural	Blanc 1958; this work	This work
Equus ferus	Grotta Paglicci	GP	MIS 2	Radiometric data	Boscato 1994; Berto *et al.* 2017	Boscato 1994
Equus ferus	SMA-esterno - Gravettian	SMA - G	MIS 2	Radiometric data	Baills 2015; this work	This work
Equus ferus	Grotta delle Mura	GMu	MIS 1	Radiometric data	Bon & Boscato 1993	Bon & Boscato 1993

Hadjouis 1998; Langlois 2005, Uzunidis 2017; Boulbes & van Asperen 2019).

In Italy, the first occurrence of large-sized and robust caballoid horses is reported in the Faunal Unit of Slivia (~ 0.9 Ma; Epivillafranchian Mammal Age) (Sala *et al.* 1992; Rustioni 1998; Conti *et al.* 2010; Bellucci *et al.* 2014). Palombo & Alberdi (2017) suggested that the caballoid horses first appeared in the Ponte Galeria Unit (Cesi, about 0.7 Ma; Ficcarelli *et al.* 1997). Moreover, Conti *et al.* (2010) suggests that the body size of this taxon decreased from the late Middle Pleistocene onwards (e.g., Malagrotta, Torre in Pietra). Other fossils from the Middle Pleistocene of Italy (0.8-0.3 Ma) have been referred *Equus caballus* ssp., *E.* cf. *E. mosbachensis, Equus caballus malatestai* Caloi, 1997 and *Equus* sp., highlighting the uncertain of the taxonomic attribution and the difficult to reconstruct the phylogeny of this group (Caloi & Palombo 1987; Caloi 1997; Palombo & Alberdi 2017; Strani *et al.* 2018, 2019). In addition, Berzi (1972) attributed the astragalus from Monte Oliveto (Siena, central Italy), chronologically referred to early Middle Pleistocene, to *Equus caballus* cf. *mosbachensis*, mainly based on its body size. Finally, Rustioni (1998) proposed to attribute large-sized fossil horses of the late Middle Pleistocene from the

Italian Peninsula, to *E. mosbachensis,* and the small-sized ones from the Late Pleistocene to *E. ferus germanicus*.

In this scenario, the taxonomic attribution of the European caballoid horse from Middle to Late Pleistocene (300-12 Ka) is still a controversial topic. The proliferation of the subspecies reflects the homogeneous overall morphology and the lack of clear diagnostic characters, which should allow the identification of the different taxa.

MATERIAL AND METHODS

The sample of *Equus* studied in this work are part of several collections stored in different Italian Institutions and Museums (Table 1).

The skull and dental features of Middle to Late Pleistocene *Equus* has been poorly investigated, which prevents a large morphological comparison of the studied material. A morphological description of the studied crania from San Sidero and Cardamone has been reported in Appendix 1.

Following Eisenmann (1981), 5 cranial variables have been considered to be important for discriminating species of *Equus*: basilar length (BL), muzzle length (ML), length of the check teeth (P^2M^3LL), facial length (FaL), frontal length (FrL), muzzle breadth at the posterior borders of I^3 (MB) (Appendix 1). Following Eisenmann (1980), we also measured 24 for upper and lower teeth: length, breadth and length of protocone of the upper teeth (P^2L, P^2B, P^2Pr, $P^{3-4}L$, $P^{3-4}B$, $P^{3-4}Pr$, $M^{1-2}L$, $M^{1-2}B$, $M^{1-2}Pr$, M^3L, M^3B, M^3Pr) and length, breadth and length of postflexid of the lower teeth (P_2L, P_2B, P_2Pf, $P_{3-4}L$, $P_{3-4}B$, $P_{3-4}Pf$, $M_{1-2}L$, $M_{1-2}B$, $M_{1-2}Pf$, M_3L, M_3B, M_3Pf). The measurements were taken in occlusal view to the nearest 0.1 mm with a digital caliper. We used literature data on fossil horses from the Late Pleistocene to Early Holocene of the AP (Table 1).

We further assessed the degree of affinity between late Middle to Late Pleistocene *Equus* from Apulia by conducting a statistical analysis. First, in order to explore the affinity among the samples from different fossiliferous sites, we compared the upper and lower teeth from San Sidero to those from the other deposits. Specifically, we considered the length of the upper and lower premolars (P^2, P^{3-4}, P_2 and P_{3-4}) and molars (M^{1-2}, M^3, M_{1-2} and M_3). The dataset was subject to normality distribution verification using Shapiro test. We evaluated differences in length of the upper and lower premolars (P^2, P^{3-4}, P_2 and P_{3-4}) and molars (M^{1-2}, M^3, M_{1-2} and M_3) in the late Middle Pleistocene and Early Holocene, using linear model (Anova) with corner point parameterization testing the null hypothesis of no-differences between the mean of the San Sidero (SS) and the other samples (p.value > 0.05).

Taking into account the number of sites studied and the small sample size of some of the localities (i.e, Grotta Mario Bernardini – VI, Grotta Mario Bernardini – III, Grotta Mario Bernanrdini – II, Grotta Santa Croce, Grotta Uluzzo – IV, Grotta Uluzzo – II, Grotta Zinzulusa), the dataset has been assembled according to the MIS chronology. We considered the length of the upper and lower teeth of specimens referred from the late Middle Pleistocene (MIS 9-8) of AP and compared it to those referred to late Middle (MIS 7) and Early Holocene (MIS 1). This dataset was also subject to a test for normal distribution verification using the Shapiro test. We evaluated differences in upper and lower teeth in the late Middle Pleistocene to Early Holocene samples, using a linear model (Anova) with corner point parameterization testing the null hypothesis of no-differences between the mean of the MIS 9-8 and the other samples (p.value > 0.05). The statistical analysis was performed using the R software (Team 2000). Very worn teeth were excluded by statistical analysis.

In addition, in order to evaluate the dental variability in the considered samples, the protocone index [(length of protocone * 100)/length of teeth] and postflexid index [(length of postflexid * 100)/length of teeth] were compared. The protocone and postlfexid index is calculated as the mean of the upper and lower teeth respectively when the sample includes more than one specimen. The pattern of the protocone index assumes a taxonomical value for the identification of Middle Pleistocene to Early Holocene equids. In *E. mosbachensis* the protocone index displays an M^3 value higher than M^{1-2} one and P^{3-4} value higher or sub-equal than M^{1-2} one. In *E. ferus,* the M^{1-2} value is higher than both P^{3-4} and M^3. Finally, in *E. hydruntinus* the values of P^{3-4} and M^{1-2} are much lower than both *E. mosbachensis* and *E. ferus,* whereas those of P^2 and M^3 fall in the variability of the caballoid horse ones.

Finally, the ratio of the length and the breadth of the muzzle could represent an adaptation to climate, where the short and large muzzle should be found in specimens from sites attributed to glacial stage and *vice versa* (see Crégut-Bonnoure *et al.* 2018 for discussion). In order to investigate this adaptations we created standard bivariate plots of muzzle breadth at the posterior borders of I^3 (MB) and muzzle length (ML).

Institutional abbrevations

IGF	Museum of Natural History of the University of Florence, section of Geology and Paleontology, Florence (Italy);
IsIPU	Italian Institute of Human Paleontology, Anagni (Italy) ?;
ITCGC	Commercial Technical Institute “Galilei-Costa”, Lecce (Italy);
MPCCSM	Museum of Pre-Classical Civilizations of Southern Murgia, Brindisi (Italy);
MPUN	Paleontological Museum of the University of Naples Federico II, Naples (Italy);
PF	PaleoFactory Laboratory, Sapienza University of Rome, Rome (Italy).

LATE MIDDLE TO LATE PLEISTOCENE APULIAN FOSSIL EQUIDAE

Melpignano

The karst infilling deposits of Melpignano, locally known as “ventarole”, are located in the area of the village of Maglie. These karst deposits were firstly described by Mirigliano (1941), since then several Institutions, as the IsIPU

Fig. 2. — Crania in right view from late Middle to Late Pleistocene of Apulia: **A**, IGF16329, cranium of male of *Equus mosbachensis* von Reichenau, 1903 from San Sidero; **B**, CC467, cranium of female of *Equus ferus* from Cardamone; **C**, CC468, cranium of male of *Equus ferus* Boddaert, 1785 from Cardamone. Scale bars: 5 cm

and Italian Institute of Prehistory and Protohistory (IIPP), with the support of local Salentine Speleological groups, investigated this area (de Lorentiis 1962; Cardini 1962a). The "ventarole" are generally filled with reddish sediments (called "terre rosse") in the lower part, and brownish sediments (called "terre brune") in the upper, particularly rich in vertebrate fossil remains (Bologna *et al.* 1994) (Fig. 1). The *Equus* sample was recovered from the "terre rosse" of the "ventarole" of Mirigliano, Cava Nuzzo and Cava Bianco.

Repository and studied material

MPUN	Mirigliano collection – 17 upper teeth, 24 lower teeth;
Cava Nuzzo – PF	2 hemimandibles, 4 lower teeth (Fig. 3C);
Cava Bianco – PF	17 upper teeth, 2 hemimandibles, 9 lower teeth.

San Sidero

The "ventarole" of San Sidero are located along the state road (SS16) between the villages of Corigliano d'Otranto and Maglie. The first description of the deposit and its faunal assemblage was reported by Cardini (1962a). The mammal fauna from San Sidero was also studied by other authors (De Giuli 1980, 1983; Petrucci *et al.* 2012; Iurino *et al.* 2013, 2015). Similarly to the Melpignano sediments, these "ventarole" include "terre

FIG. 3. — Mandible of *Equus* from late Middle to Late Pleistocene of Apulia in labial (**1**), lingual (**2**) and occlusal (**3**) views: A1-A3, IGF16330, *Equus mosbachensis* von Reichenau, 1903 from San Sidero; B1-B3, CC414, *Equus ferus* Boddaert, 1785 from Cardamone; C1-C3, MPND396 (ex. Cur11), left hemimandible of *Equus mosbachensis* from Melpignano; D1-D3, C2 20b 77, right hemimandible from SMA-esterno; E1-E3, C2 20b 80, left hemimandible from SMA-esterno. Scale bars: 5 cm.

rosse” layers in the lower part and “terre brune” layers in the upper part. The Equidae sample was collected from the “terre rosse” of the “ventarole” called SS6 and Cava L.

Repository and studied material

SS6 – IGF	one skull (Fig. 2A), 11 upper teeth, 10 lower teeth (Fig. 3A);
Cava L – PF	five upper teeth, one hemimandible, six lower teeth.

Grotta di Capelvenere

The site, located near the town of Santa Caterina (Lecce), occurs in a Cretaceous limestone (Calcari di Melissano Formation) at 20 m a.s.l. and about 100 m from the current seashore. The cave was discovery in 1960 and was only partially excavated in 1971, 1974 and 1975 (Borzatti von Löwenstern 1961; Giusti 1979, 1980). Outside the cave, a nearby conglomerate deposit at about 8 m a.s.l. has been referred to Tyrrhenian beach (MIS 5) (Patriarchi 1980). The stratigraphic sequence can be divided into two main complexes separated from a speleothem: in the upper part, the brownish sediment, where domestic fauna, ceramics and artefacts appeared, has been referred to Iron age. Instead, in the lower part ten levels including vertebrate fossils and artefacts have been referred to Mousterian (Borzatti von Löwenstern 1961; Giusti 1979, 1980; Patriarchi 1980). The studied sample comes from the lower part of the sedimentary succession.

Repository and studied material

IGF	18 upper teeth, five hemimandibles, 26 lower teeth.

Grotta delle Tre Porte

The fossiliferous site was discovered in 1936 during a field survey of the IsIPU conducted by Gian Alberto Blanc (Blanc 1958) (Fig. 1). The coastal cave, located at Punta Ristola, includes three different saloons, but only two contained Pleistocene deposits, Antro del Bambino and Grotta Titti. The *Equus* material was collected from the level F of Antro del Bambino, associated to Middle Palaeolithic artefacts.

Repository and studied material

IsIPU	eight upper teeth, one hemimandible, nine lower teeth.

Grotta Mario Bernardini

The cave located along the Ionian coast near the village of Santa Caterina, also known as Grotta di Santa Margherita, was discovered in 1961 (Borzatti von Löwenstern 1970, 1971) (Fig. 1). The stratigraphic succession consists of four main archeological levels: D, C, B and A, excepted for the top of the sequence, where ceramic and artefacts were referred to Iron and Bronze age (Borzatti von Löwenstern 1970, 1971; Carmigiani & Romagnoli 2017). From the complex VI-III artefacts referred to Mousterian facies were found, whereas those from the complex II were attributed to Uluzzian (Borzatti von Löwenstern 1970, 1971; Carmigiani & Romagnoli 2017). The volcanic material recovered in the top of complex IV (firstly indicated as ß) could be correlated with that found in the level G of the Grotta del Cavallo dated approximately to 109 100 ± 900 ka (Sarti *et al.* 2002; Spinapolice 2008; Spinapolice 2018; Douka & Spinapolice 2012; Zanchetta *et al.* 2018). Instead, the volcanic material from the bottom of the complex II (initially indicated as ß*)* can be correlated with that found at the top of the level F of the Grotta del Cavallo dated approssimatively to 45 700 ± 1 000 ka (Sarti *et al.* 2002; Spinapolice 2008, 2018; Douka & Spinapolice 2012; Zanchetta *et al.* 2018). Albeit the mammal remains have never been studied in detail, a preliminary mammal list was provided by Borzatti von Löwenstern (1970, 1971). *Equus* is found from different levels (VI, IV, III, II), where also lithic artefacts referred to Middle Palaeolithic from the complexes VI-III and Upper Palaeolithic from the complex II were found (Table 1; Appendix 1).

Repository and studied material

IGF	27 upper teeth, one hemimandible, 27 lower teeth.

Grotta Uluzzo C

The cave is located in the Uluzzo Bay near the village of Nardò, opening into the Cretaceous limestone. The stratigraphic succession was described by Borzatti von Löwestern (1965, 1966) and Borzatti von Löwestern & Magaldi (1969). In particular, the green volcanic sand from the bottom of the complex II could be correlated with the tephra found at the top of the level F of Grotta del Cavallo, dated at 45 700 ± 1000 ka by Zanchetta *et al.* (2018). Instead, the complex II-I transition, consisting of a grey volcanic sand, could be correlated with the Ignimbrite Campana (CI) identified at the bottom of the level C of Grotta del Cavallo, dated at 39 850 ± 140 ka Zanchetta *et al.* (2018). The presence of a reworked tephra in the top of the complex IV could represent a marker for the lower deposit. Further investigations needed to confirm the age of these volcanic levels. Moreover, Borzatti von Löwestern (1965, 1966) reported a preliminary list of the fossil mammals recovered from this locality. The studied sample come from the complex IV, III and II (Table 1; Appendix 2). Whereas, artefacts from the complex IV and III were attributed to Middle Palaeolithic, instead those from the complex II to early Upper Palaeolithic.

Repository and studied material

IGF	21 upper teeth, two hemimandibles, 33 lower teeth.

Castellaneta

The Castellaneta deposit is a karst infilling into the Pleistocene Calcarenite (Monte Castiglione Formation) (De Giorgi 1877). The fossil material was recovered during the geological survey in the area conducted by Cosimo De Giorgi in the 1870s. Albeit the author delegated the study of the collected sample to Ulderigo Botti, the remains from the karst fissure were never described.

Repository and studied material

ITCGC	28 upper teeth, 1 hemimandible, 28 lower teeth.

Grotta dei Giganti

The coastal cave, located between Punta Ristola and Punta Marchiello, was discovered by the Italian Institute of Human

Paleontology during a field survey conducted by Gian Alberto Blanc in the 1930s (Blanc 1958). The authors also reported a mammal faunal list. In addition, Alessio *et al.* (1978) attempted to carry out radiocarbon dating without success. However, the fossil material was found associated to Middle Palaeolithic artefacts.

Repository and studied material

IsIPU	12 upper teeth, 20 lower teeth;
ITCGC	four upper teeth, three lower teeth.

Grotta Santa Croce

The cave, located near the small village of Bisceglie, was discovered in the 1937 (Segre & Cassoli 1987). The first systematic excavations directed by Luigi Cardini were carried out by Italian Institute of Human Palaeontology (IsIPU) during the 1950s (Mallegni *et al.* 1987; Segre & Cassoli 1987; Boscato *et al.* 2006). The sedimentary succession includes several levels attributed to Middle and Upper Paleolithic and Neolithic (Segre & Cassoli 1987; Arrighi *et al.* 2009; Ranaldo *et al.* 2017). Radiocarbon dated indicated an age of 24 900 ± 150 BP for the level B and 31 500 ± 400 BP for the level C (Arrighi *et al.* 2009; Ranaldo *et al.* 2017). There are no radiocarbon dating results for levels H-D that are referred to MIS 5 and MIS 4, respectively (Arrighi *et al.* 2009; Ranaldo *et al.* 2017). The fossil remains of mammals from the level D were studied by Segre & Cassoli (1987). Recently, new material also was discovered from this level and *Equus ferus* and *Bos primigenius* Bojanus, 1827 were identified (Boscato *et al.* 2006). The studied material was recovered from the level D, associated with lithic artefacts attributed to Middle Palaeolithic.

Repository and studied material

IsIPU	seven upper teeth, seven lower teeth.

Grotta Laceduzza

The cave deposit, located near the village of San Michele Salentino, was discovered by the "Gruppo Speleologico Salentino Pasquale de Lorentiis" in 1970 (Coppola 2005, 2012). The lower part of the sedimentary succession includes fossil remains of mammals and artefacts referred to Middle Palaeolithic. A preliminary mammal list was recently reported, including a rich sample of *Meles meles* (Linnaeus, 1758) (Mecozzi *et al.* 2019). The *Equus* material was recovered from the lower part of the deposit, associated to Middle Palaeolithic artefacts.

Repository and studied material

MPCCSM	nine upper teeth, 12 lower teeth.

Grotta Zinzulusa

The cave is located along the Adriatic coast near the town of Castro. In 1793, Francesco Antonio Del Duca, bishop of the diocese of Castro described the cave in a letter to Ferdinando IV, king of the Kingdom of the Two Sicilies. Nevertheless, the Pleistocene infilling deposit was presented only after a century from the discovery by Botti (1874). The cave consists of several saloons, where Pleistocene deposits were found (Blanc 1962). The sedimentary succession can be divided in two complexes, the lower part, the level B6, where fossil remains of mammals and artefacts referred to Middle Palaeolithic were found, and the upper part, the levels B5-3 including fossil remains of mammals and artefacts referred to Upper Palaeolithic. The *Equus* material comes from the levels B5-3, where also artefacts referred to Middle Palaeolithic were found.

Table 2. — Table of p-values for the linear model of the upper teeth with corner point parameterization testing the null hypothesis of no-differences between the mean of the MIS 9-8 and the other samples (p-value > 0.05).

	Number of specimen				P-value			
Age	**P^2**	**P$^{3-4}$**	**M$^{1-2}$**	**M^3**	**P^2**	**P$^{3-4}$**	**M$^{1-2}$**	**M^3**
MIS 9-8	5	19	20	6	–	–	–	–
MIS 7-5	3	6	1	–	0.14	0.00	0.01	–
MIS 5	3	9	8	4	0.10	0.00	0.00	0.57
MIS 4	7	12	9	4	0.09	0.00	0.00	0.80
MIS 3	14	39	16	20	0.03	0.00	0.00	0.01
MIS 2	37	76	66	13	0.01	0.00	0.00	0.00
MIS 1	3	5	3	1	0.10	0.00	0.01	0.13

Repository and studied material

IsIPU	B5-6 upper teeth, five lower teeth.

Cardamone

The karst infilling deposit was discovered by Cosimo De Giorgi in 1872 (Botti 1890). The site is located in a region where several quarries are opened for the extraction of a Plio-Pleistocene calcarenite, and, unfortunately, the deposit was destroyed. The mammal assemblage from Cardamone, initially described by Botti (1890), was recently revised by Rustioni *et al.* (2003). Based on the presence of the wholly rhino (*Coelodonta antiquitatis* (Blumenbach, 1799)) and the wholly mammoth (*Mammuthus primigenius* (Blumenbach, 1799)), the association was referred to "*Mammuthus-Coelodonta* Faunal Complex" and chronologically attributed to climax of the Last Glacial Maximum (22-18 kyr).

Repository and studied material

IGF	16 upper teeth, 33 lower teeth;
ITCGC	two crania (Fig. 2B, C), 13 maxillaries, 83 upper teeth, four hemimandibles, 112 lower teeth (Fig. 3B).

Fondo Focone

The site, discovered during a survey conducted by Decio de Lorentiis in the early 1960s, is located near the village of Ugento. The first excavation campaign was carried out by Luigi Cardini (Cardini 1962b). The fieldwork, direct by Eugenia Segre Naldini, continued during the 1970s, who opened a trench, 3 × 3 m, called "Trincea B" (Cancellieri 2017). Fossil remains of mammals and the artefacts referred to Upper Palaeolithic (early Epigravettian) were found (Cardini 1962b; Cancellieri 2017).

TABLE 3. — Table of p-values for the linear model of the lower teeth with corner point parameterization testing the null hypothesis of no-differences between the mean of the MIS 9-8 and the other samples (p-value > 0.05).

	Number of specimen				P-value			
Age	P_2	P_{3-4}	M_{1-2}	M_3	P_2	P_{3-4}	M_{1-2}	M_3
MIS 9-8	14	20	19	11	–	–	–	–
MIS 7-5	3	4	8	2	0.74	0.34	0.00	0.11
MIS 5	3	12	19	12	0.18	0.00	0.00	0.00
MIS 4	7	17	12	8	0.01	0.00	0.00	0.00
MIS 3	26	57	48	22	0.02	0.00	0.00	0.00
MIS 2	42	55	72	30	0.04	0.00	0.00	0.00
MIS 1	3	8	10	3	0.04	0.00	0.00	0.01

Repository and studied material

IsIPU — one maxillary, 37 upper tooth, one hemimandible, 27 lower teeth.

Santa Maria d’Agnano – esterno (SMA-esterno)

The Grotta di Santa Maria di Agnano, located near the village of Ostuni, on the north-western margin of Risieddi promontory, was discovered during the 1960s by the Associazione Studi e Ricerche (Studies and Research Association) (Coppola 2012). The excavations in the cave deposit started in 1991 and continued still today, whereas from 2007 the area outside the cave, known as SMA-esterno, was also investigated (Coppola 1992, 2012 ; Vacca *et al.* 1992; Vacca & Coppola 1993; Baills 2015; Coppola *et al.* 2017; Chakroun *et al.* 2018). The fossil remains come from level 8, dated 25221-24549 cal BP and 26338-25779 cal BP, and levels 6A-4C dated 18013-17587 cal BP and 16745-16401 cal BP with radiocarbon method (Renault-Miskovsky *et al.* 2011; Baills 2015).

Repository and studied material

MPCCSM — level eight – 10 maxillary, 59 upper tooth, 35 hemimandibles, 67 lower teeth (Fig. 3D-E).

RESULTS

Equus samples from the late Middle Pleistocene to Early Holocene of AP show a large variation in dental dimensions and proportions. In particular, the length of P^2 and M^3 are highly variable both within and between samples (Appendices 3; 4; 7). On the contrary, the length of P^{3-4} from San Sidero is closer (p-value > 0.05) to those from Cava Spagnulo, Grotta di Capelvenere, Grotta Mario Bernardini – II and Grotta Uluzzo C (Appendix 7). The length of M^{1-2} from San Sidero is similar (p-value > 0.05) to those from Castellaneta, Fondo Cattìe, Grotta di Capelvenere, Grotta Mario Bernardini – III, Grotta Santa Croce, Grotta Zinzulusa, Melpignano and Tana delle Iene (Appendix 7). As in the case of the upper teeth, even the length of P_2 and M_3 show a huge variability (Appendices 5; 6). The P_{3-4} from San Sidero is closer (p-value > 0.05) to those from Grotta di Capelvenere, Grotta dei Giganti, Grotta Mario Bernardini – IV, Grotta delle Tre Porte, Grotta Zinzulusa and Tana delle Iene (Appendices 5; 6; 8). Whilst, the M^{1-2} from San Sidero is closer (p-value > 0.05) to Grotta Santa Croce, Grotta delle Tre Porte, Grotta Zinzulusa, Grotta Uluzzo C – II, Melpignano and Tana delle Iene (Appendices 5; 6; 8).

Considering the MIS chronology, the length of P^2 and M^3 of the sample from MIS 9-8 is larger only of samples from MIS 3 (P^2, p-value < 0.05; M^3 p-value < 0.05) and MIS 2 (P^2, p-values < 0.05; M^3 p-value < 0.05). Whilst, the length of P^{3-4} and M^{1-2} of the sample from MIS 9-8 are larger than those from the late Middle Pleistocene (MIS 7) to Early Holocene (MIS 1) (p-values < 0.05). In the lower dentition, the length of the teeth from MIS 9-8 are larger than those from Late Pleistocene (MIS 5) to Early Holocene (MIS 1) (p-values < 0.05), whereas they are similar to those from late Middle to early Late Pleistocene (MIS 7-5) in the P^2 (p-value > 0.05), P^{3-4} (p-value > 0.05) and M^3 (p-value > 0.05) (Fig. 5, Table 3).

The protocone index of the Grotta di Capelvenere, Melpignano and San Sidero shows a trend closer to that reported for *E. mosbachensis*, with M^3 value higher than M^{1-2} one and P^{3-4} value higher or sub-equal than M^{1-2} one (Fig. 6). On the contrary, the pattern of the other samples is closer to that reported for *E. ferus*, with M^{1-2} value higher than both P^{3-4} and M^3. Finally, the sample from Tana delle Iene and Grotta delle Mura possesses a well different values compared to the others, resembling those reported for *Equus hydruntinus*. In fact, in *E. hydruntinus* the values for P^{3-4} and M^{1-2} are significantly lower than those of both *E. mosbachensis* and *E. ferus*, whereas they are similar in P^2 and M^3 values.

Whereas, the postflexid index has been investigated, but no trend can be detected through the time and/or differences among the considered taxa (Fig. 7).

Finally, in the standard bivariate plot of muzzle proportions (Fig. 8), two groups can be recognized. The first includes the specimen from the fossiliferous sites referred to glacial stages (Appendix 9), which display a large muzzle in relation to their length. An exception is the cranium of *Equus ferus antunesi* Cardoso and Eisenmann, 1989 from Fontainhas (Portugal), where the muzzle is longest. The specimen from Cardamone falls in the variability of the glacial horses, and is similar to that from Cuane de l’Arago (Fig. 8). A second group is composed by crania from deposits referred to interglacial stages, where the muzzle is narrow compared to its total length. The cranium from San Sidero falls in this variability.

DISCUSSION

The taxonomy of Middle to Late Pleistocene European *Equus* remains controversial (Forstén 1991; van Asperen 2012). The large variability of the morphological features and biometric traits of caballoid horses has been the subject of controversy amongst many authors. No consensus exists on how to define this variability, as it is either treated as being intra-specific or inter-specific events (Azzaroli 1983; Forstén 1988; Cramer 2002; van Asperen 2012). This unresolved taxonomic issue has led a proliferation of taxa, identified as either species or subspecies (*E. mosbachensis, E. steinheimensis* Von Reichenau, 1915*, E. achenheimensis* Nobis, 1971*, E. taubachensis* Freudenberg, 1911) (see van Asperen 2012 for discussion). In the Italian fossil record, the specific attribution of the fossil samples from Middle Pleistocene sites reflects this

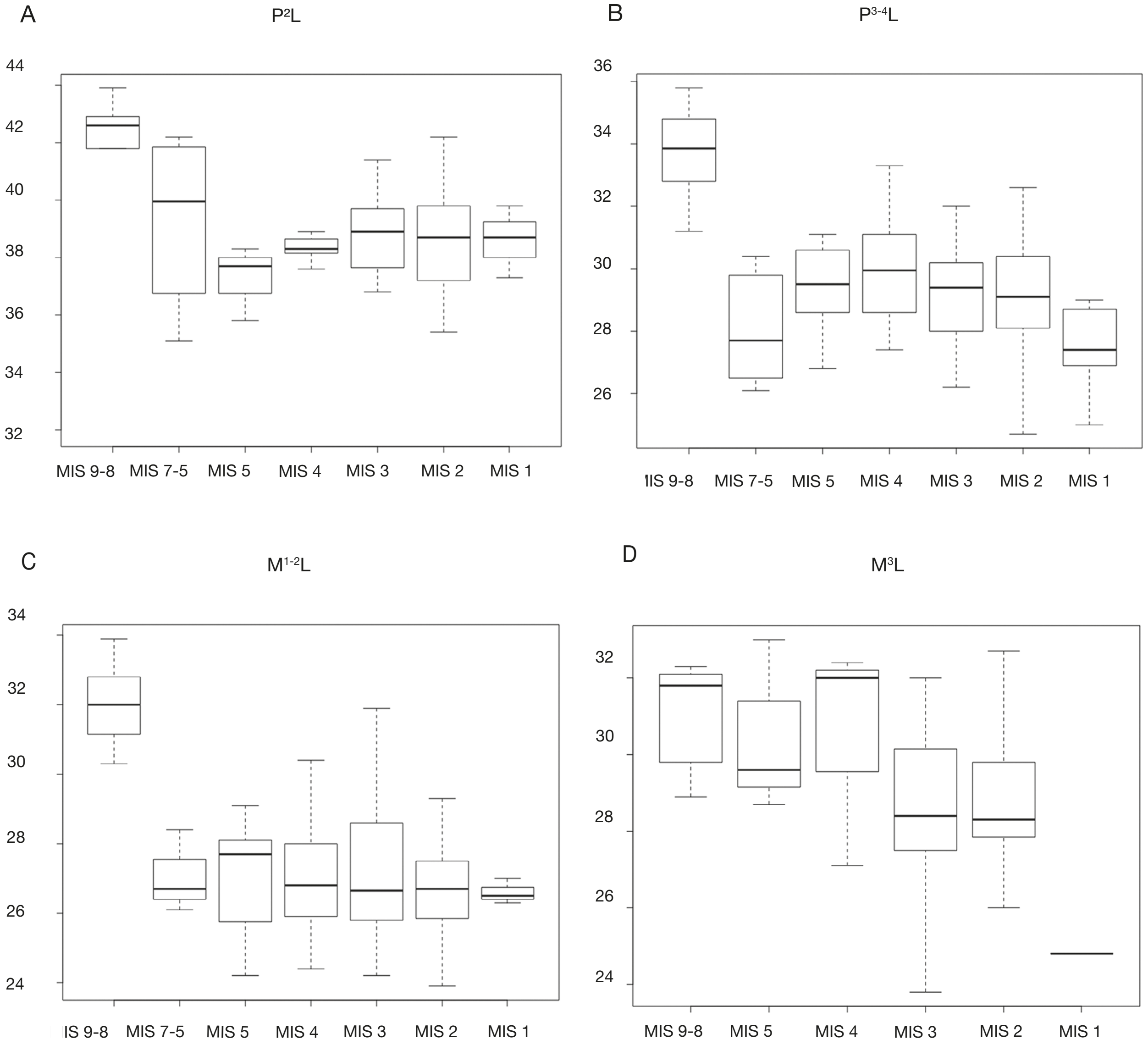

Fig. 4. — Boxplot of the length of the lower teeth considered for chronology: **A,** second premolar (P_2L); **B**, third-fourth premolar ($P_{3-4}L$); **C**, first-second molar ($M_{1-2}L$); **D,** third molar (M_3L). For the groups, see Table 1.

uncertainty (*Equus altidens* von Reichenau, 1915*, Equus* aff. *sussebornensis, Equus caballus* ssp., *E.* cf. *E. mosbachensis Equus caballus* cf. *mosbachensis* and *Equus* sp.) (Berzi 1972; Caloi & Palombo 1987; Strani *et al.* 2018, 2019). Preliminary studies on *Equus* samples from several AP sites led to the identification of *E. ferus* from the deposits of Cardamone (Rustioni 1998), Cava Spagnulo (Mecozzi *et al.* 2018), Grotta del Cavallo (Sarti *et al.* 1998, 2002), Grotta Paglicci (Boscato 1994), Melpignano (Rustioni 1998) and Tana delle Iene (Conti *et al.* 2010), whereas the previous taxonomic attribution of the material from San Sidero has been questioned. In the revision of the Middle to Late Pleistocene *Equus* material from Europe, Eisenmann (1991b) attributed the material from San Sidero to the large-sized *Equus chosaricus*, whereas other authors (De Giuli 1983; Rustioni 1998) classified it as *Equus ferus*. Unlike, the results of the statistical analysis and the comparison of the protocone index carried out in this work allow to refer the material from San Sidero to *E. mosbachensis*.

In this scenario, the analysis of a relatively large sample of *Equus* fossils from late Middle to Late Pleistocene localities of AP allows us to reassess the taxonomy and the evolutionary trend of local horse species. Based on the results of the statistical analyses and the comparison of the protocone indexes, *E. mosbachensis* is identified for the first time from few Apulian fossiliferous sites, among which are included San Sidero, Melpignano and Grotta di Capelvenere. *Equus mosbachensis* possesses larger upper and lower teeth than those of *E. ferus* (Figs 4, 5; Tables 2, 3) and different values of the P^{3-4}, M^{1-2} and M^3 protocone index (Fig. 6). The Grotta di Capelvenere, Melpignano and San Sidero samples displays a M^{1-2} protocone index value lower than those both P^{3-4} and M^3 (Fig. 6). The

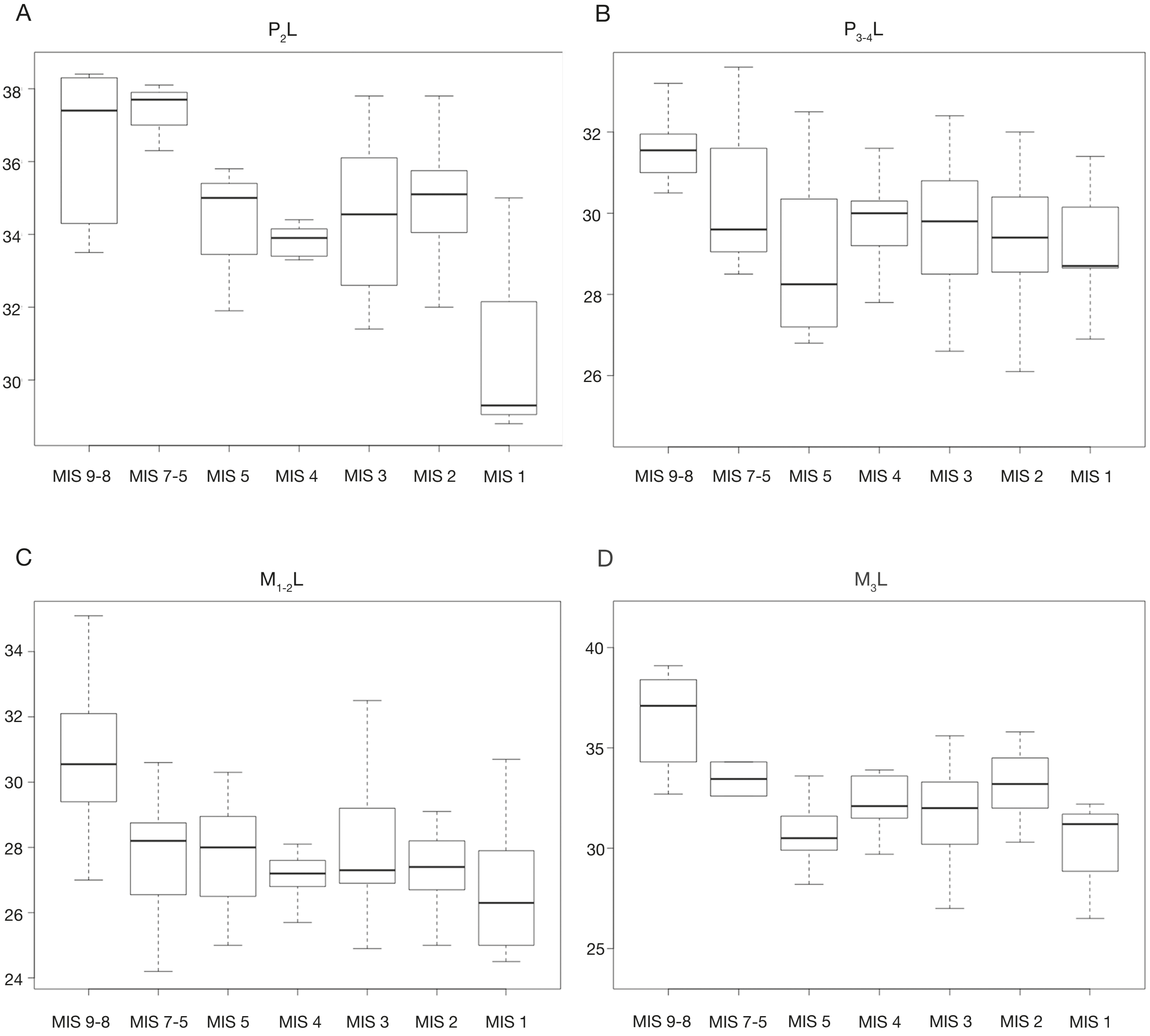

FIG. 5. — Boxplot of the length of the upper teeth considered for chronology: **A**, second premolar (P_2L); **B**, third-fourth premolar ($P_{3-4}L$); **C**, first-second molar; ($M_{1-2}L$); **D**, third molar (M_3L). For the groups see Table 1.

taxonomic attribution to *E. ferus* of the material from other considered sites chronologically referred from late Middle Pleistocene (MIS 7) to the end of Late Pleistocene (MIS 2) is confirmed, based on the medium-size of the specimens and the values of the protocone index. In fact, besides displaying smaller upper and lower teeth than those of *E. mosbachensis* (Figs 4, 5; Tables 2, 3), the protocone index in the materials of *E. ferus* displays M^{1-2} value higher than those both P^{3-4} and M^3 (Fig. 6). Furthermore, for the samples from Tana delle Iene and Grotta delle Mura, the protocone index differs. The values of P^{3-4} and M^{1-2} are much lower than those of caballoid horses. This atypical profile of IP index in the fossil materials of Tana delle Iene and Grotta della Mura could be due to the small size of the available samples.

Finally, following the literature, the postflexid index fails to discriminate *Equus* species from Middle to Late Pleistocene and no trend can be observed (Fig. 7). In accordance with Boulbes (2010), the significant variation of the postflexid index could be related to tooth ontogeny (relative wear).

Whereas *E. mosbachensis* is widespread in Europe during the Middle Pleistocene, its presence in Italian Peninsula was quite scarce (Gliozzi *et al.* 1997), and documented only from few sites: Cesi (Ficcarelli *et al.* 1997), Venosa-Notarchirico (Palombo & Alberdi 2017), Fontana Ranuccio (Biddittu *et al.* 1979). In AP, the Mosbach horse is identified for the first time in a few localities, which unfortunately lack of absolute radiometric determinations. As for the European material, in the AP the Mosbach horse was well-distinct for its large teeth sized, which is larger to the wild horse (*E. ferus*) (Figs 4, 5; Tables 2, 3) and display different values of the protocone index (Fig. 6). According to several authors (Guadelli 2007; Uzunidis 2017),

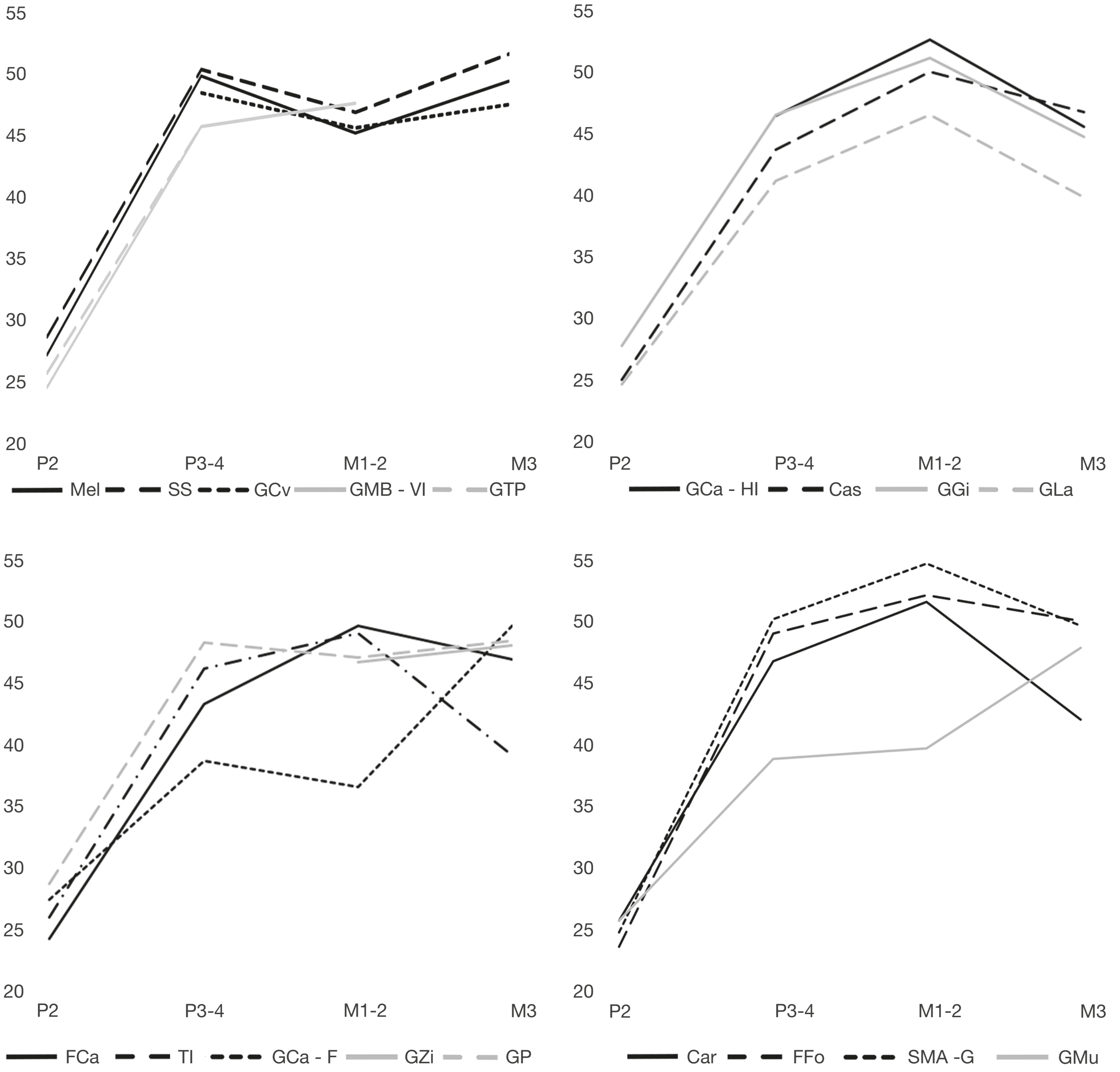

FIG. 6. — Protocone index of the upper teeth of *Equus* species from the late Middle Pleistocene to Early Holocene sites of the Apulia. Abbreviations: see Table 1.

the last occurrence of *E. mosbachensis* took place during the late Middle Pleistocene, probably during the MIS 6, although no general consensus was reached (Boulbes & van Asperen 2019). However, the first historical appearance of *E. ferus* in AP is from Grotta del Cavallo during the early Late Pleistocene (< 109 ka) (Zanchetta *et al.* 2018). Therefore, a new dispersal of *Equus* species could have taken place during the late Middle Pleistocene. This possible scenario is consistent with the results of the aDNA analysis performed on *E. ferus*, which revealed that the wild horse originated at about 240.000 years ago (late Middle Pleistocene), differing therefore from the earlier form of *Equus* (George & Rider 1986). Unfortunately, the taxonomic uncertainty for the Middle Pleistocene sample from Italian Peninsula record prevents an in-depth reconstruction of the caballoid horse lineage (Berzi 1972; Caloi & Palombo 1987; Strani *et al.* 2018, 2019, Strani 2020).

The last occurrence of *E. ferus* in the Italian Peninsula took place during the end of Late Pleistocene to Early Holocene (18-9.1 ka BP). During the end of Late Pleistocene (16-12 ka BP), *E. ferus* was well diffused across the Italian Peninsula, as documented by Leonardi *et al.* (2018) at Grotta delle Mura, Grotta Paglicci, Palidoro, Romito and Vado Arancio. During the Early Holocene however, its presence was exclusively reported from Grotta delle Mura (Bon & Boscato 1993) (Leonardi *et al.* 2018). The radiometric dating of level 3 indicates an age ranging from 17913-1738 to 13009-12688 cal BP, whereas that of level 2 varies between 9451-9125 to 9527-8982 cal

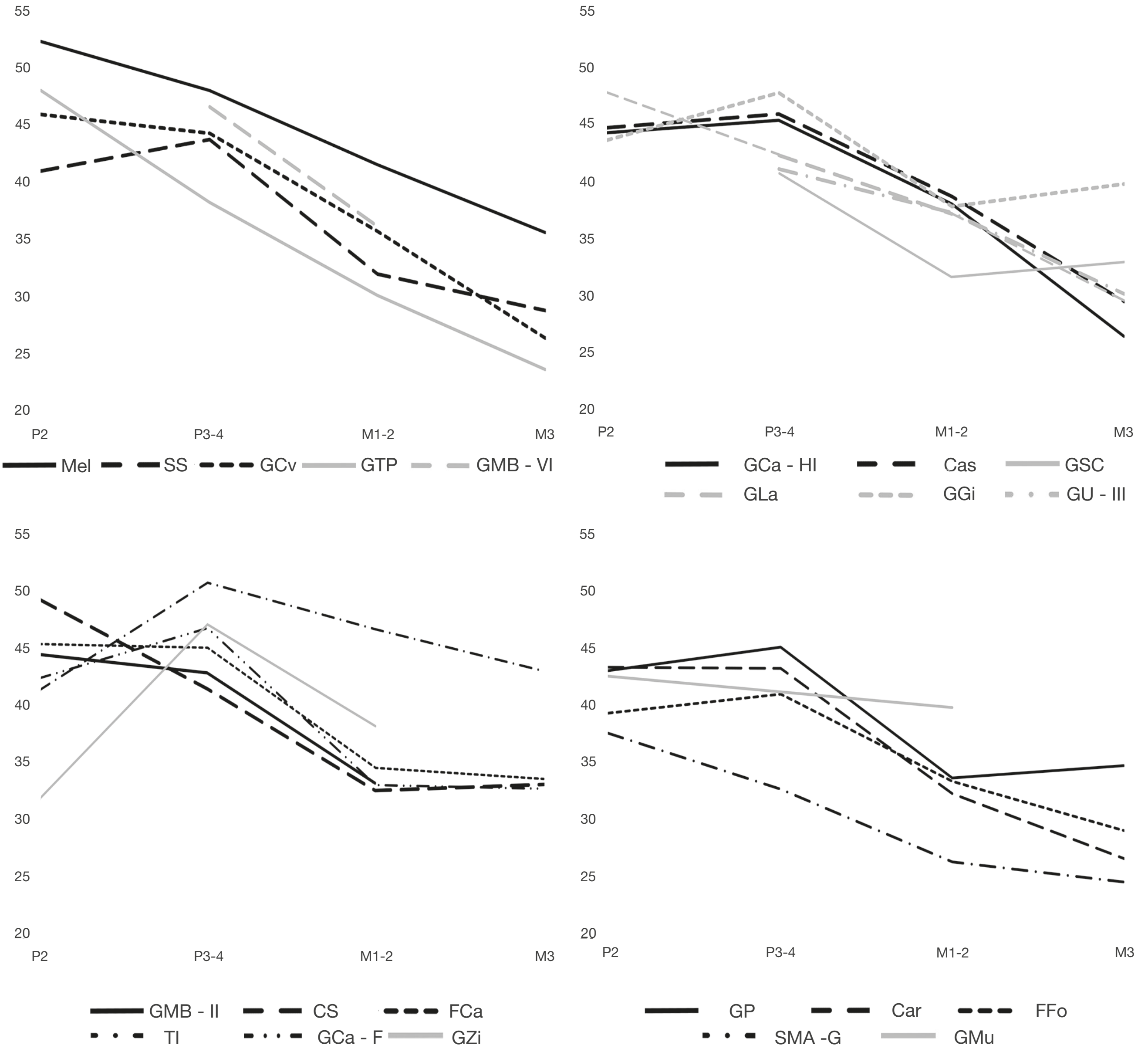

Fig. 7. — Postflexid index of the lower teeth of *Equus* species from the late Middle Pleistocene to Early Holocene sites of the Apulia. Abbreviations : see Table 1.

BP (Leonardi *et al.* 2018; recalibrated using Oxcal v. 4.4, IntCal20 curve). Recently, new radiometric analysis has been performed on Grotta dei Cervi, which records the presence of *E. ferus* at 10175-9701 cal BP (De Grossi Mazzorin & Montefinese 2017) (recalibrated using Oxcal v. 4.4, IntCal20 curve). A long gap was detected in the horse fossil record, between the occurrences from Grotta delle Mura and Grotta dei Cervi and those from the bronze age localities of Santa Rosa di Roviglio (4149-4112 to 3492-3355 cal BP) and Montale (4089-3057 to 3370-3219 cal BP) (recalibrated using Oxcal v. 4.4, IntCal20 curve). This gap has been interpreted as the local excinction of wild *E. ferus*, which was later reintroduced in the Italian Peninsula by recent human populations. This disappearance during the Early Holocene could be linked to a marked reduction of steppe- and tundra-like landscapes (Leonardi *et al.* 2018).

The wild horse is a common element of the mammal assemblages from AP during the late Aurelian, showing a homogenous body size through the time. According to van Asperen (2012), size oscillations of *E. ferus* can occur in response to climatic change, with the specimens from glacial stages being smaller and more robust, possibly as an adaptation to colder environmental conditions (Mayr 1956; James 1970; Lindstedt & Boyce 1985; Blackburn *et al.* 1999). On the contrary, interglacial horses could be larger with more slender limb proportions. Some populations of interglacial *E. ferus* can also be characterized by small and robust individuals (always less robust than glacial ones). The body-size of *E. ferus* of the Apulia region during the MIS 7-5 to MIS 2 is quite constant and no changes can be detected. According to van Asperen (2010), this stasis could suggest that the wild horse

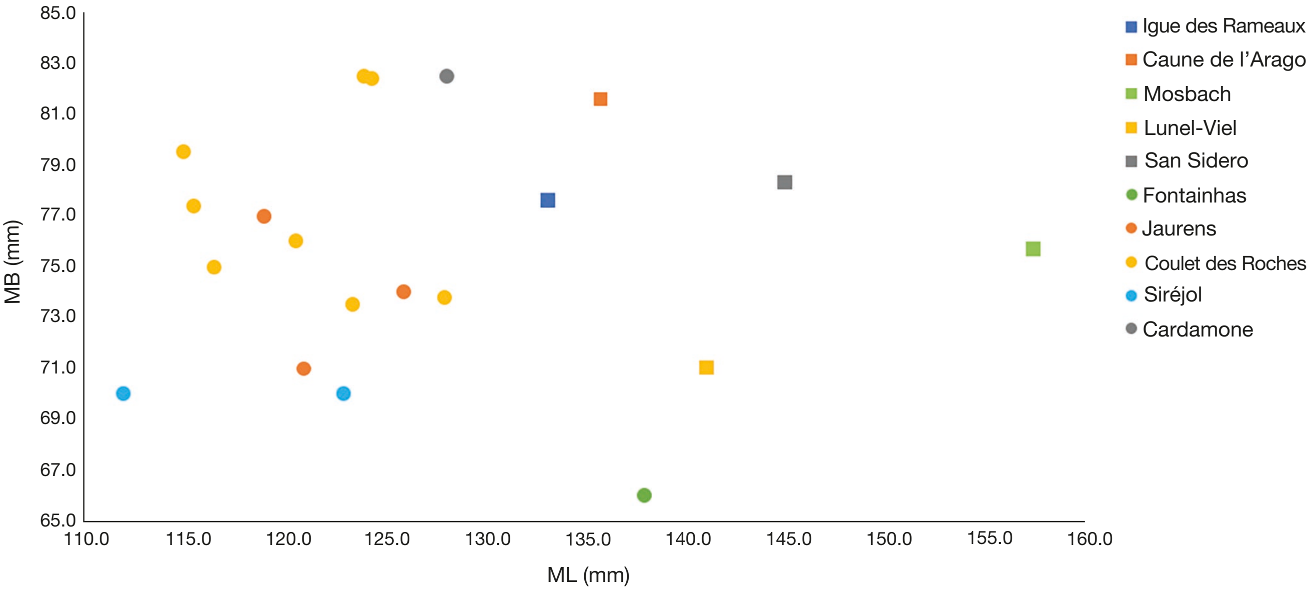

Fig. 8. — Standard bivariate plot of muzzle length (ML) and muzzle breadth at the posterior borders of I^3 (MB) of caballoid horses from Middle to Late Pleistocene of Europe (Appendix 9). Symbol: **square**, Middle Pleistocene specimens; **circle**, Late Pleistocene specimens.

was in low competition for resources in a stable landscape constantly dominated by open-environments (i.e, steppe-like and/or grasslands). Another feature which could fluctuate as response to climatic change is the proportion of the muzzle, where the skulls from glacial stages possess a wide and short muzzle and *vice versa* (Eisenmann 2014; Crégut-Bonnoure *et al.* 2018; Boulbes & van Asperen 2019). Moreover, there is no chronological differences among cranial proportions of caballoid horse through the Middle to Late Pleistocene of Europe (Fig. 8), despite a possible evolutionary trend for explaining these different cranial proportions was proposed. Specimens from deposits attributed to glacial stages (n = 15) display a short and wide muzzle as in the cases of the Middle Pleistocene sites of Cuane de l'Arago (MIS 14-12) (France) (Eisenmann *et al.* 1985) and Igue des Rameaux (MIS 10-9) (France) (Uzunidis 2017) or Late Pleistocene ones of Coulet des Roches (MIS 2) (France) (Crégut-Bonnoure *et al.* 2018), Jaurens (MIS 3) (France) (Guérin 1999) and Sirejol (MIS 3) (France) (Philippe *et al.* 1980) (Appendix 9). Whereas, the crania from interglacial stages (n = 2) possess an elongated and narrow muzzle, as the specimens from Middle Pleistocene sites of Lunel-Viel (MIS 11) (France) (Bonifay 1980; Eisenmann *et al.* 1985) and Mosbach (MIS 13) (Germany) (Maul *et al.* 2000) (Fig. 8; Appendix 9). An exception is represented by the cranium from Last Glacial (MIS 2; 22, 730 ± 835 ka) of Fontainhas (Portugal), since its proportions fall outside the variability of the glacial caballoid horses (Fig. 8; Appendix 9). The proportions of the two studied skulls, San Sidero and Cardamone specimens, corroborated the glacial/interglacial separation. Indeed, the skull from Cardamone biochronologically referred to Last Glacial falls in the variability of the glacial group, representing one of the largest specimens (Fig. 8; Appendix 9). Contrary, the proportions of the skull from San Sidero (MIS 9-8) differ from those of the glacial group, and are similar to those of Mosbach and Lunel-Viel ones (Fig. 8; Appendix 9). Finally, considering the large variability of the skull size of caballoid horses during the Middle and Late Pleistocene, no evolutionary trend can be recognized. Nevertheless, based on the proportions of the muzzle, two groups are identified from the Middle to Late Pleistocene of Europe, which reflect an adaptation to climate (glacial and interglacial stages). Therefore, the proportions of the muzzle of caballoid horse clearly reveal important information on climatic conditions and palaeoenvironment.

CONCLUSIONS

Our results highlight as the application of statistical analysis and the reconstruction of the protocone index in a large dataset represents a potential tool to redefine taxonomical attribution of equid fossil material in order to improve current biochronological information on key localities and areas of the Italian Peninsula. Most of the examined material originates from archeological sites where human exploitation produced a strong impact on fossil remains, which are often highly fragmented. Furthermore, *Equus* material from these localities was not studied from a paleontological perspective and most of the samples was taxonomical ascribed to *Equus ferus* according to the chronology of the deposit.

Therefore, our results allow us to redefine the taxonomical attribution of the material from Grotta di Capelvenere, Melpignano and San Sidero, which is referred to *Equus mosbachensis*. For the fossil material from the deposits attributed from the late Middle Pleistocene (MIS 7-6), Late Pleistocene (MIS 5-2) and Early Holocene the attribution to *E. ferus* is confirmed.

The presence of *E. mosbachensis* is reported from few AP localities, which lack of absolute radiometric dating, whereas the first historical appearance of *E. ferus* is from the early Late Pleistocene of Grotta del Cavallo (MIS 5). Therefore, the Mosbach horse could disappear during the late Middle Pleistocene. In addition, in accordance with Leonardi *et al.* (2018), the last occurrence of *E. ferus* in Italian fossil record is from Early Holocene sites of Grotta delle Mura and Grotta dei Cervi.

Finally, the proportions of the muzzle of caballoid horses fluctuate as response to climate, where wide and short muzzle was found in specimens from deposits attributed to glacial stages and *viceversa.*

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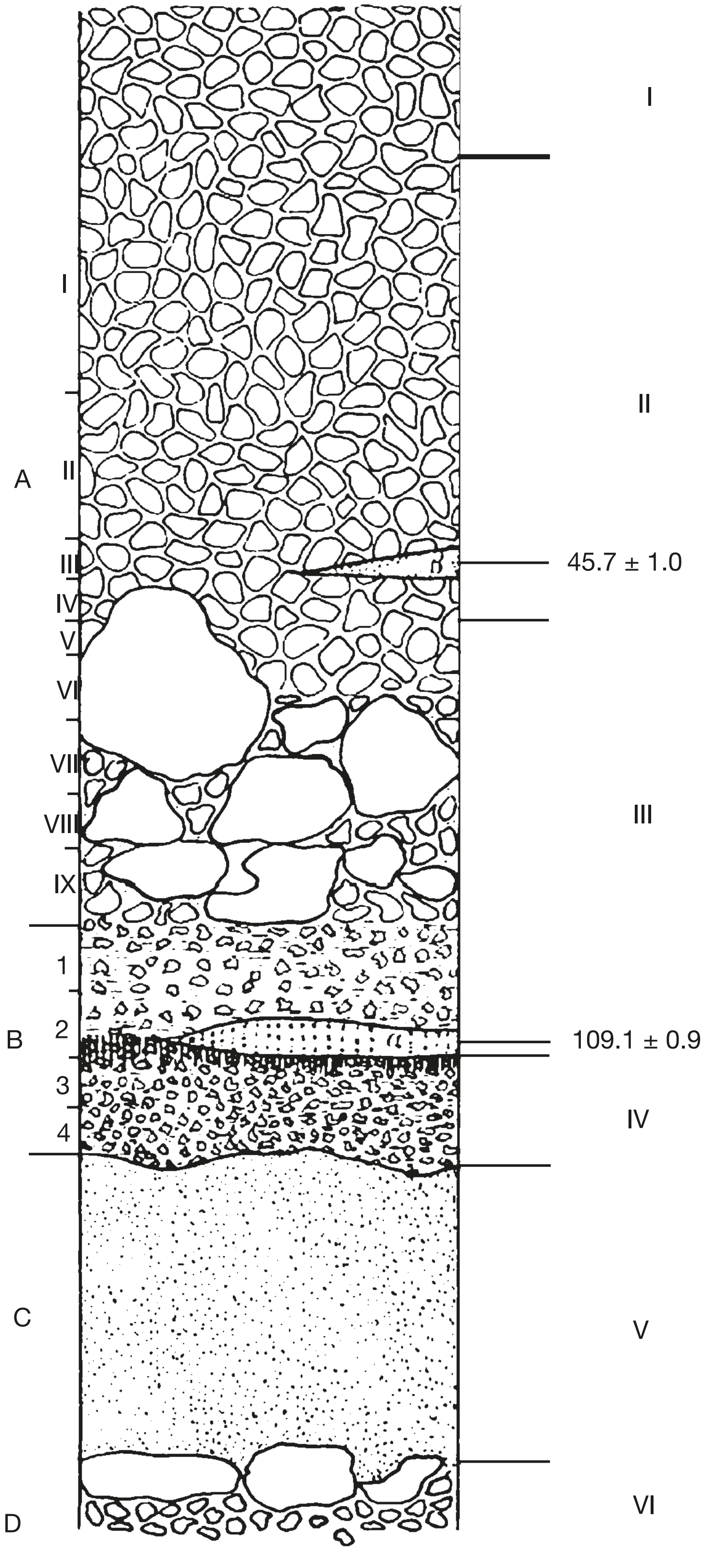
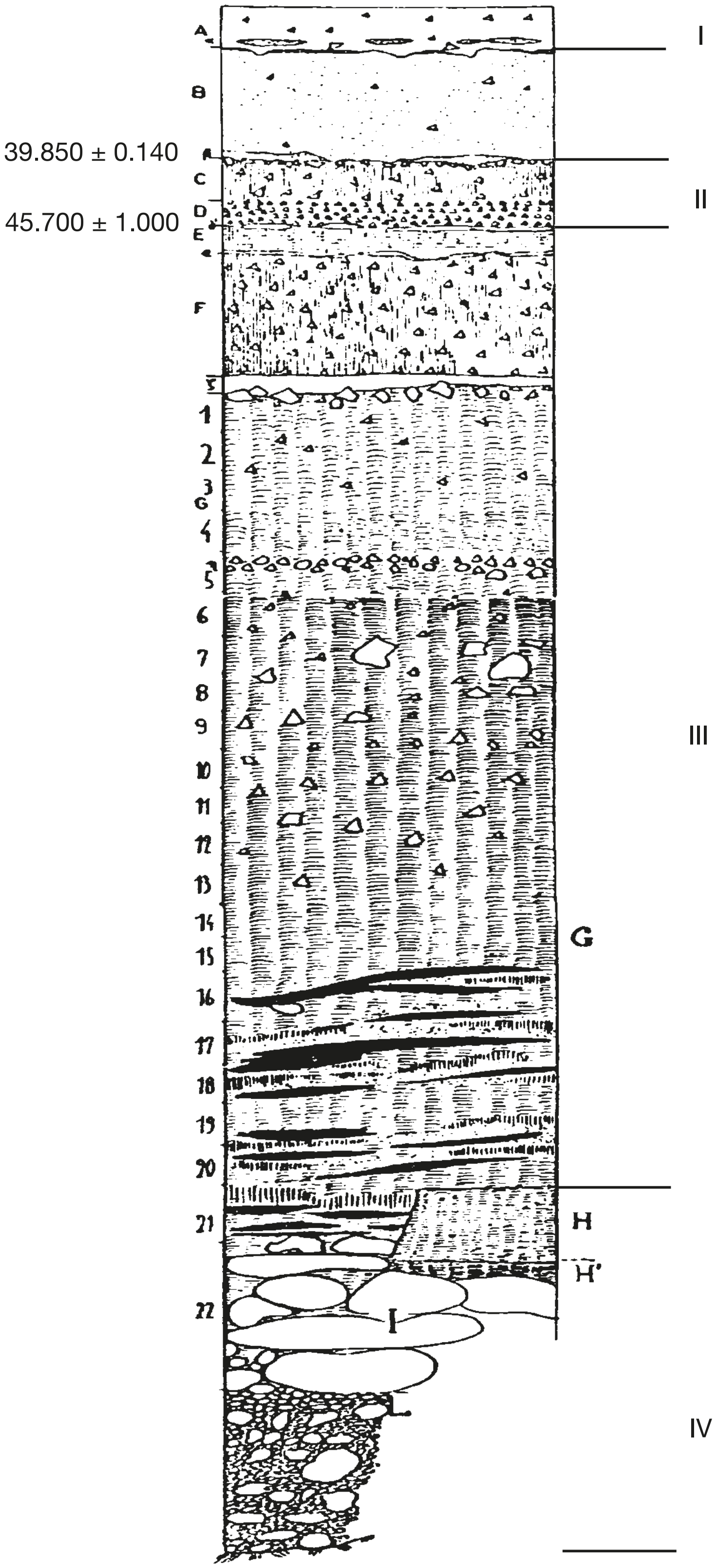
Appendices. — Morphological description of crania from late Middle to Late Pleistocene of Apulian Peninsula.

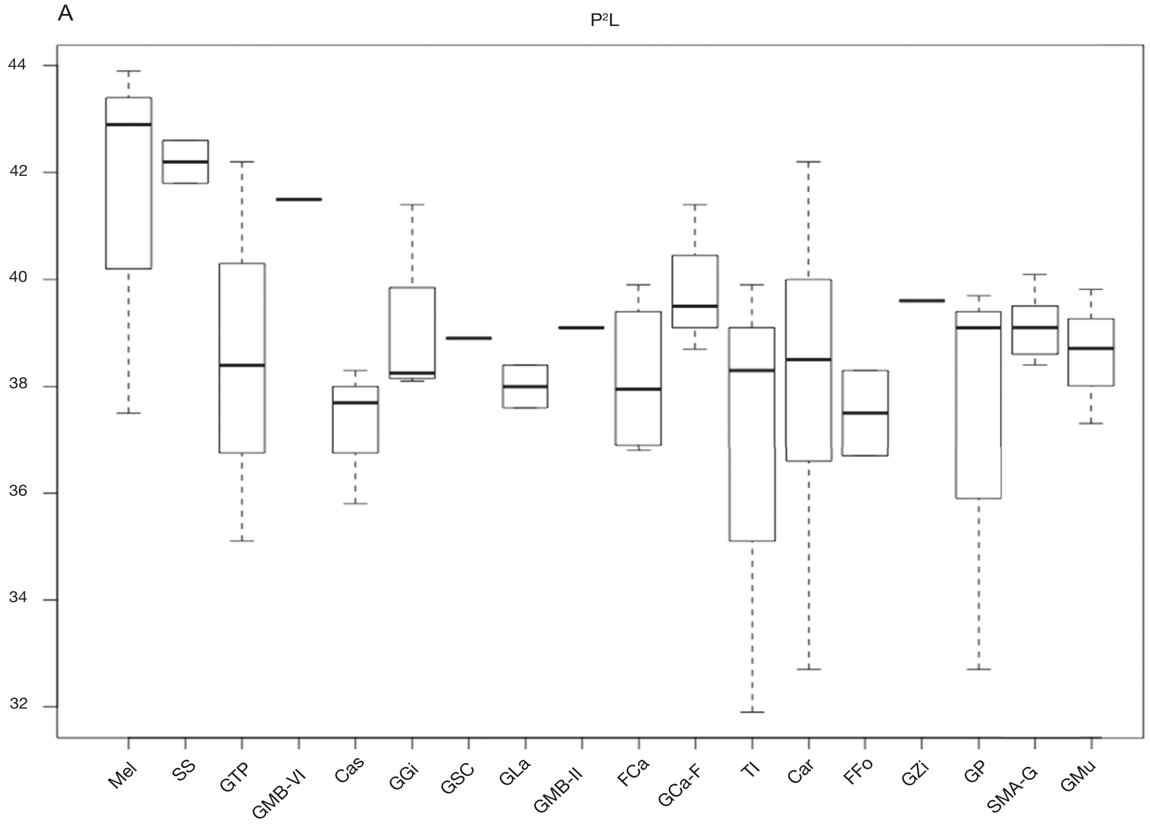
Appendix 1. — Schematic stratigraphic log of Grotta Mario Bernardini (modified from Borzatti von Löwenstern 1970).

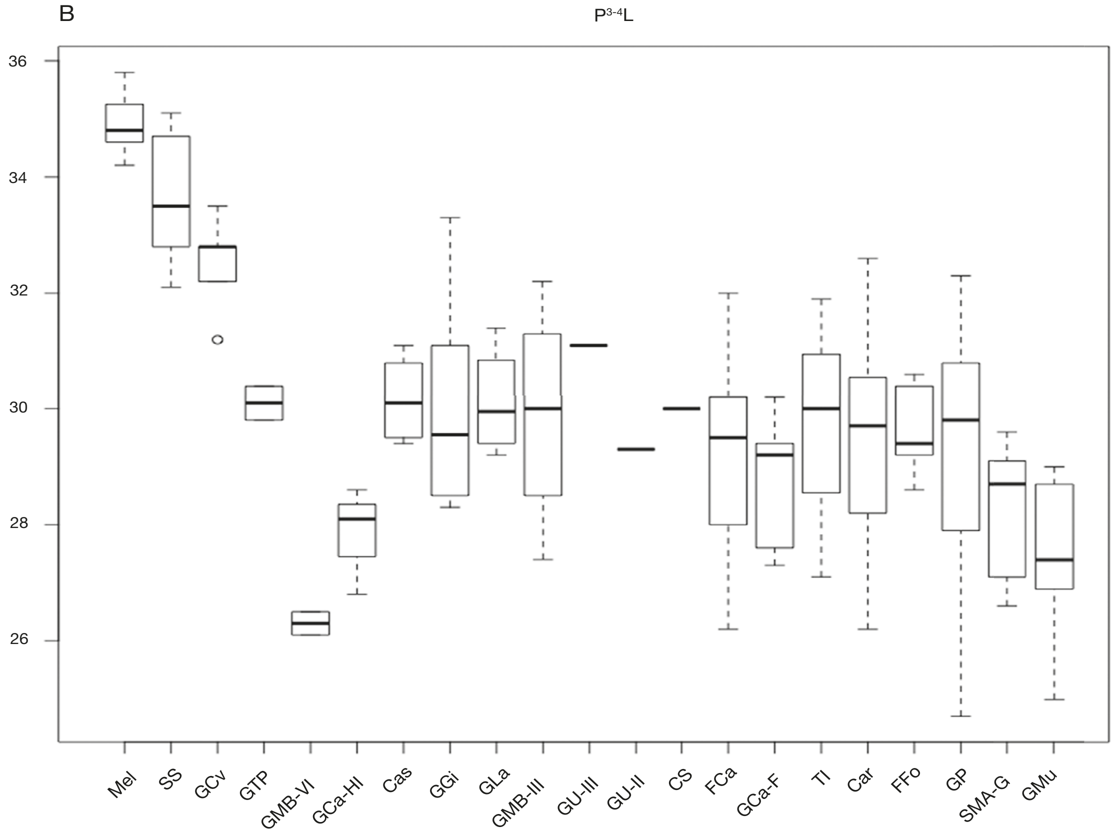


APPENDIX 2. — Schematic stratigraphical log of Grotta Uluzzo C (modified from Borzatti von Löwenstern & Magaldi 1969).

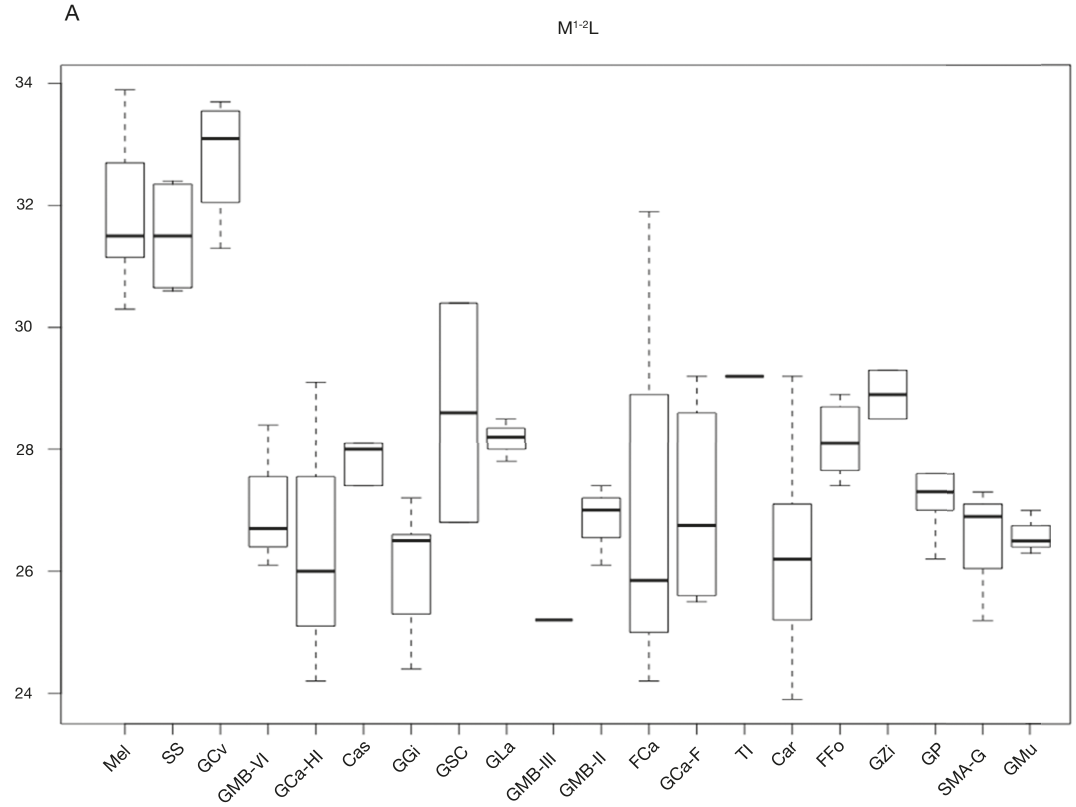


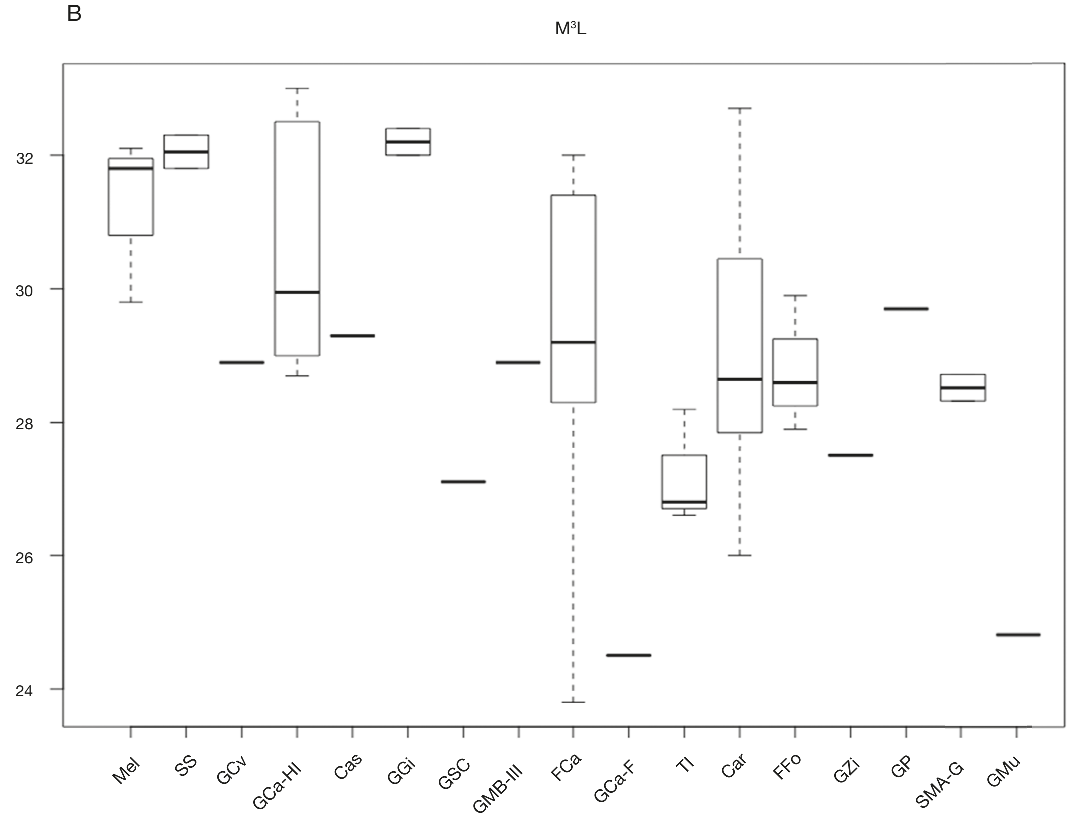
Appendix 3. — Boxplot of length of upper premolars (**A,** P2L; **B,** P3-4L) from the late Middle Pleistocene to Early Holocene sites of the Apulia. For the abbreviations : see Table 1.



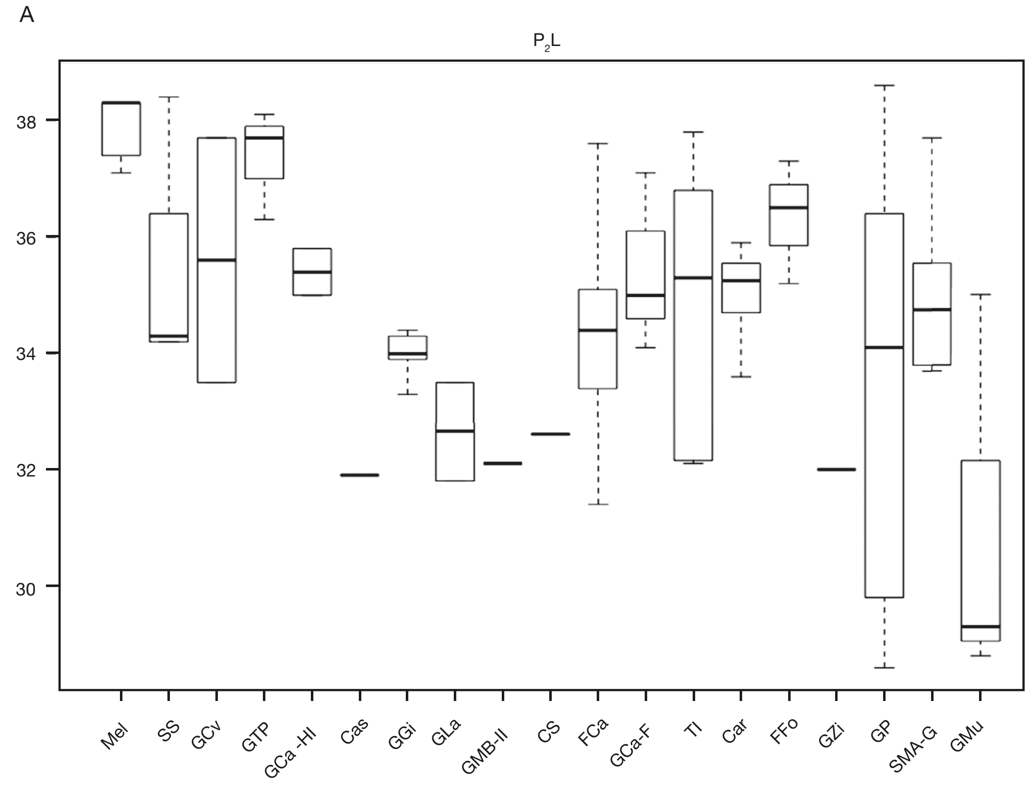


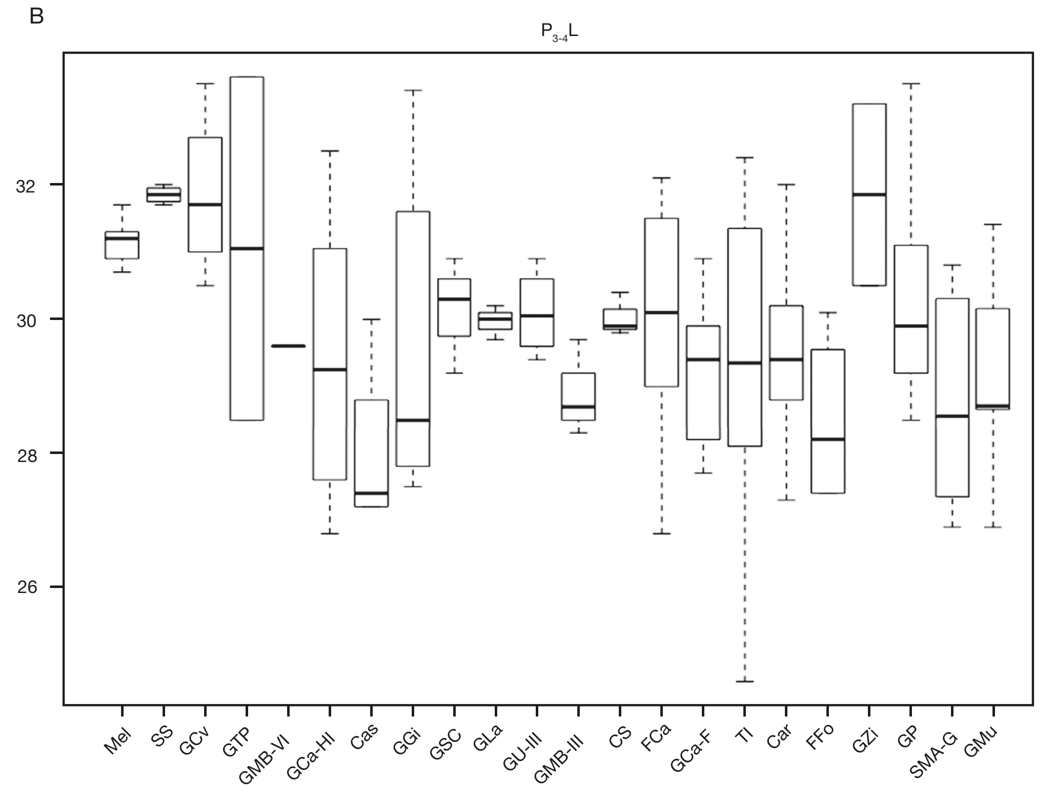
APPENDIX 4. — Boxplot of length of upper molars (**A,** M1-2L; **B,** M3L) from the late Middle Pleistocene to Early Holocene sites of the Apulia. Abbreviations : see Table 1.



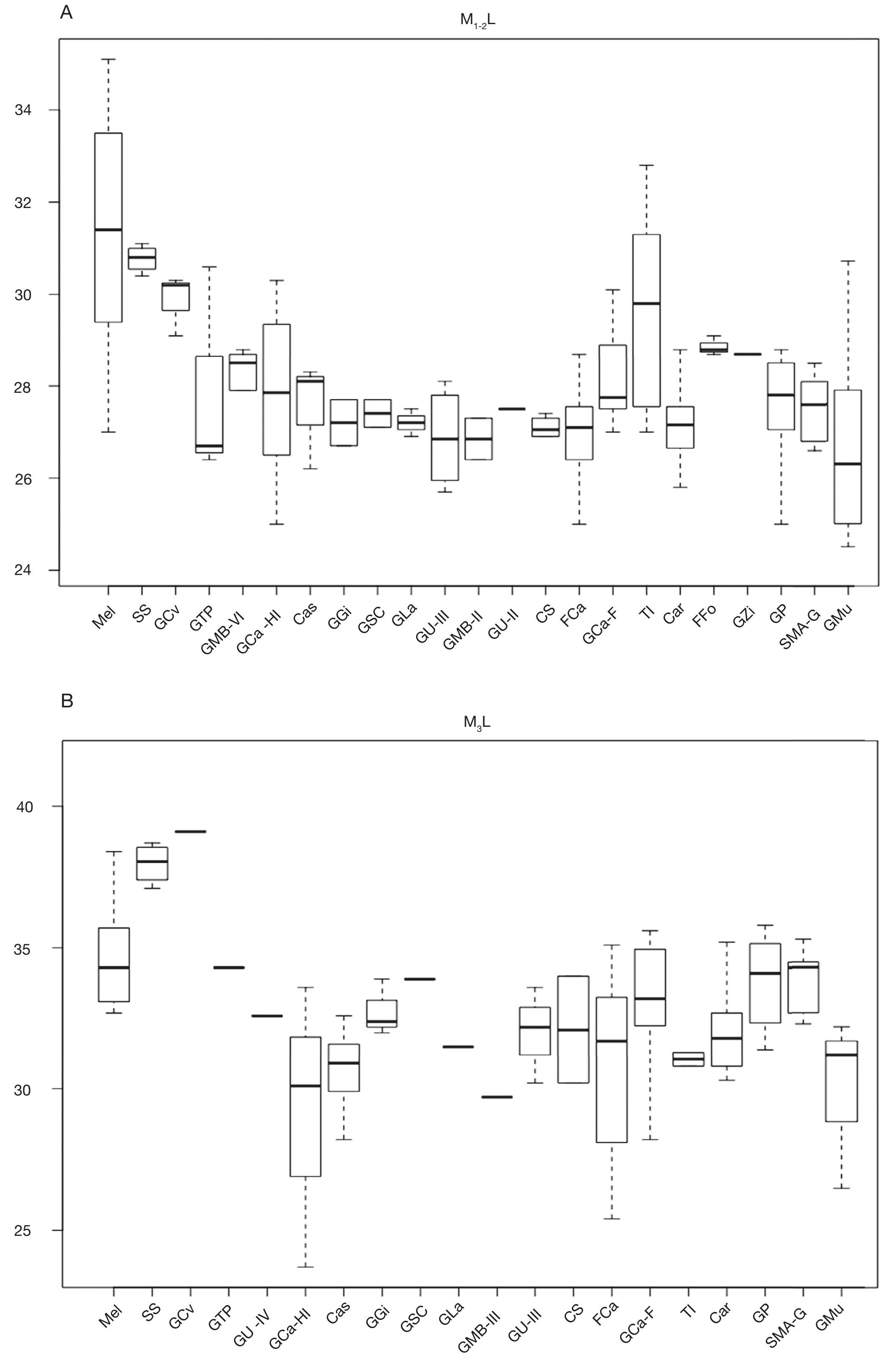


Appendix 5. — Boxplot of length of lower premolars (**A**, P_2L; **B**, $P_{3\text{-}4}L$) from the late Middle Pleistocene to Early Holocene sites of the Apulia. Abbreviations see : Table 1.





Appendix 6. — Boxplot of length of lower molars (**A**, $M_{1\text{-}2}L$; **B**, M^3L) from the late Middle Pleistocene to Early Holocene sites of the Apulia. Abbreviations see : Table 1.



Appendix 7. — Table of p-values for the linear model of the upper teeth with corner point parameterization testing the null hypothesis of no-differences between the mean of the San Sidero (SS) and the other samples (p-value > 0.05).

		Number of specimen				P.value			
Site	**Abbreviations**	P^2	P^{3-4}	M^{1-2}	M^3	P^2	P^{3-4}	M^{1-2}	M^3
San Sidero	SS	2	7	4	2	1.00	1.00	1.00	1.00
Melpignano	Mel	3	7	12	3	0.56	0.04	0.36	0.37
Grottadi Capelvenere	CPv	–	5	4	1	–	0.14	0.08	0.44
Grottadelle Tre Porte	GTP	3	2	–	–	0.25	0.04	–	–
Grotta Mario Bernardini-VI	GMB-VI	1	4	1	–	0.22	0.04	0.03	–
Grottadel Cavallo-HI	GCa-HI	–	3	3	3	–	0.02	0.03	0.22
Castellaneta	Cas	3	6	5	1	0.08	0.00	0.10	0.22
Grottadei Giganti	GGi	4	6	5	2	0.06	0.01	0.01	–
Grotta Santa Croce	GSC	1	1	1	1	0.22	–	0.06	0.22
Grotta Laceduzza	GLa	2	4	3	1	0.06	0.00	0.00	–
Grotta Mario Bernardini-III	GMB-III	–	–	1	–	–	–	0.16	–
Grotta Uluzzo-III	GUC-III	–	1	–	–	–	0.02	–	–
Grotta Mario Bernardini-II	GMB-II	2	1	3	–	0.22	0.13	0.03	0.22
Grotta Uluzzo-II	GUC-II	–	3	2	1	–	0.13	–	–
Cava Spagnulo	CS	–	1	–	1	–	0.13	–	0.04
Fondo Cattìe	FCa	6	25	4	14	0.06	0.00	0.08	0.08
Tanadelle Iene	TI	3	3	1	3	0.08	0.02	0.16	0.08
Grottadel Cavallo-F	GCa-F	3	6	6	1	0.08	0.00	0.01	0.50
Grotta Zinzulusa	GZi	1	–	2	1	0.22	–	0.06	0.22
Grotta Paglicci	GP	3	9	5	1	0.08	0.00	0.01	0.22
Cardamone	Car	18	42	36	3	0.03	0.00	0.00	0.05
Fondo Focone	FFo	2	5	7	5	0.12	0.01	0.01	0.22
SMA-Esterno-Gravettiano	SMA-G	9	13	13	2	0.03	0.00	0.00	0.05
Grottadelle Mura	GMu	3	5	3	1	0.08	0.01	0.03	0.22

Age	P^2	P^{3-4}	M^{1-2}	M^3
MIS 9-8	1	1	1	1
MIS 7-5	0.14	0	0.1	
MIS 5-4	0.05	0	0	0.74
MIS 3	0.03	0	0	0.1
MIS 2	0.01	0	0	0
MIS 1	0.1	0	0.01	0.13

APPENDIX 8. — Table of p-values for the linear model lower teeth with corner point parameterization testing the null hypothesis of no-differences between the mean of the San Sidero (SS) and the other samples (p.value > 0.05).

		Number of specimen				P.value			
Site	**Abbreviations**	P_2	P_{3-4}	M_{1-2}	M_3	P_2	P_{3-4}	M_{1-2}	M_3
San Sidero	SS	7	5	4	4	1.00	1.00	1.00	1.00
Melpignano	Mel	5	7	11	6	0.99	**0.01**	0.79	**0.04**
Grotta di Capelvenere	CPv	2	8	4	1	0.35	0.82	**0.03**	0.16
Grotta delle Tre Porte	GTP	3	2	3	1	0.98	0.98	0.08	0.16
Grotta Mario Bernardini -VI	GMB-VI	–	1	5	1	–	0.16	**0.01**	–
Grotta Uluzzo - VI	GUC-VI	–	–	–	1	–	–	–	0.16
Grotta del Cavallo - HI	GCa-HI	3	8	16	3	1.00	**0.04**	**0.00**	**0.03**
Castellaneta	Cas	1	4	3	6	0.16	**0.02**	**0.03**	**0.01**
Grotta dei Giganti	GGi	5	6	2	6	0.07	0.09	**0.06**	**0.03**
Grotta Santa Croce	GSC		4	2	1		**0.02**	0.06	0.16
Grotta Laceduzza	GLa	2	3	3	3	0.06	**0.03**	**0.03**	0.06
Grotta Mario Bernardini -III	GMB-III	–	–	1	–	–	–	–	0.16
Grotta Uluzzo - III	GUC III	–	4	4	3		**0.02**	**0.02**	**0.03**
Grotta Mario Bernardini -II	GMB-II	1	3	2	–	0.16	**0.03**	**0.06**	–
Grotta Uluzzo - II	GUC-II	–	1	–	–	–	–	0.16	–
Cava Spagnulo	CS	2	3	4	2	0.06	**0.03**	**0.02**	**0.06**
Fondo Cattìe	FCa	7	26	20	11	0.22	**0.02**	**0.01**	0.00
Grotta del Cavallo - F	GCa-F	10	9	10	7	0.76	**0.01**	**0.02**	**0.01**
Tana delle Iene	TI	7	16	12	2	0.26	0.06	0.15	0.06
Cardamone	Car	15	29	25	7	**0.85**	**0.00**	**0.00**	**0.00**
Fondo Focone	FFo	3	2	3	2	1.00	**0.02**	**0.03**	–
Grotta Paglicci	GP	13	9	19	8	0.13	**0.03**	**0.01**	**0.01**
Grotta Zinzulusa	GZi	1	2	1	–	0.16	0.98	0.16	–
SMA-Esterno - Gravettiano	SMA-G	8	8	14	–	9.00	**0.01**	**0.00**	**0.03**
Grotta delle Mura	GMu	3	8	10	3	0.16	**0.01**	**0.01**	**0.03**

Site	P_2	P_{3-4}	M_{1-2}	M_3
MIS 9-8	1	1	1	1
MIS 7-5	0.75	0.36	0	0.11
MIS 5-4	0	0	0	0
MIS 3	0	0	0	0
MIS 2	0.01	0	0	0
MIS 1	0.03	0	0	0.01

Appendix 9. — *Equus* crania from Middle to Late Pleistocene of Europe.

Species	**Site**	**Specimen number**	**Age**	**Reference**	**ML**	**MB**
Equus mosbachensis	Igue des Rameaux	–	Middle Pleistocene	Uzunidis (2017)	133.2	77.6
Equus mosbachensis tautavelensis	Caune de l'Arago	–	Middle Pleistocene	Bellai (1998)	135.8	81.6
Equus mosbachensis	Mosbach	–	Middle Pleistocene	Gromova (1949)	157.4	75.7
Equus mosbachensis	Lunel-Viel	10110	Middle Pleistocene	Eisenmann (1985)	141.1	71.0
Equus mosbachensis	San Sidero	IGF16329	Middle Pleistocene	This work	145.0	78.3
Equus ferus antunesi	Fontainhas	–	Late Pleistocene	Cardoso & Eisenmann (1989)	138.0	66.0
Equus ferus gallicus	Jaurens	FSL 303 486	Late Pleistocene	https://vera-eisenmann.com/	121.0	71.0
Equus ferus gallicus	Jaurens	FSL 303 482	Late Pleistocene	https://vera-eisenmann.com/	126.0	74.0
Equus ferus gallicus	Jaurens	FSL 303 468	Late Pleistocene	https://vera-eisenmann.com/	119.0	77.0
Equus ferus gallicus	Coulet des Roches	N5.106	Late Pleistocene	Crégut-Bonnoure *et al.* (2014)	120.6	76.0
Equus ferus gallicus	Coulet des Roches	N4.289.1	Late Pleistocene	Crégut-Bonnoure *et al.* (2014)	124.0	82.5
Equus ferus gallicus	Coulet des Roches	M4.546	Late Pleistocene	Crégut-Bonnoure *et al.* (2014)	115.0	79.5
Equus ferus gallicus	Coulet des Roches	L4+M4 878 + 879	Late Pleistocene	Crégut-Bonnoure *et al.* (2014)	116.5	75.0
Equus ferus gallicus	Coulet des Roches	L6-41	Late Pleistocene	Crégut-Bonnoure *et al.* (2014)	128.0	73.8
Equus ferus gallicus	Coulet des Roches	L5-78	Late Pleistocene	Crégut-Bonnoure *et al.* (2014)	115.5	77.4
Equus ferus gallicus	Coulet des Roches	M6 437-1	Late Pleistocene	Crégut-Bonnoure *et al.* (2014)	124.4	82.4
Equus ferus gallicus	Coulet des Roches	M7 97	Late Pleistocene	Crégut-Bonnoure *et al.* (2014)	123.4	73.5
Equus ferus gallicus	Siréjol	100.854	Late Pleistocene	https://vera-eisenmann.com/	112.0	70.0
Equus ferus gallicus	Siréjol	100.856	Late Pleistocene	https://vera-eisenmann.com/	123.0	70.0
Equus ferus	Cardamone	CC467	Late Pleistocene	This work	128.1	82.5

APPENDIX 10. — Supplementary data: Morphological description of crania from late Middle to Late Pleistocene of AP.

San Sidero

The IGF16329 is a splancnocranium in poor state of preservation. The sutures are completely fused. In dorsal view, the nasal is narrow with the anterior part getting thinner, whereas the muzzle is long and broad. In lateral view, the frontal and nasal bones are flat, where the nasal incisive fossa opens at the level of the posterior border of P^2. In ventral view, the palatal is large at the level of M^2-M^3.

The specimen IGF16329 has permanent teeth and the right and left cheek toothrows are complete. The presence of the canines allows to refer the cranium to male. The incisors are disposed in semicircular, where the I^1 and I^2 are buccolingually elongated whereas the I^3 is mesiodistally elongated. The canine is mesiodistally elongated, with an evident crest along the margin of the teeth. Generally, the sketch of the caballine and protoconule folds is low complicated. The hypoconal grove is more pronounced in the premolars (P^3 and P^4) than that of the molars (M^1 and M^2), instead the protoconal groove is pronounced.

Cardamone

The CC467 is a well-preserved cranium, except for parietal, frontal, nasal, zygomatic and vomer bones, which are incomplete. The cranium is elongated rostrocaudally with the nasal and frontonasal sutures not completely fused. In dorsal view, the nasal bones are narrow and the frontal bone became wider at the zygomatic processes. In lateral view, the frontal is flat and the zygomatic process is robust. The nasal incisive fossa opens at the level of the middle part of P^2, whereas the infraorbital foramen is large and opens at around the middle part of P^4. In ventral view, the incisive bone is narrow, the palatine fissurae is long and the interincisive canal is large. The palatal is wide at the level of M^2-M^3, the basisphenoid is robust as well as the basal part of occipital bone. The retroarticular process is robust, the mandibular fossa is marked and hypoglossal foramen is large and mesiodistally elongated. The specimen CC468 has permanent teeth and the canine is not present, therefore the cranium can be attributed to female. The incisors are not preserved, whereas the left and right cheek toothrow are complete. Generally, the sketch of the caballine and protoconule folds is low complicated. The hypoconal grove is more pronounced in the premolars (P^3 and P^4) than that of molars (M^1 and M^2), whereas the protoconal groove is low pronounced.

The CC468 is very well-preserved cranium, only lacking the anterior part of incisive bone. The cranium is elongated rostrocaudally with the sutures completely fused. In dorsal view, the nasal is narrow with the anterior part getting thinner, whereas the zygomatic processes of the frontal bone are robust from which diverged the two temporal lines ending posteriorly to a short sagittal crest. In posterior view, nuchal crest is well-developed and the braincase has a rough surface. In lateral view, the frontal bone is flat, whereas the nasal and parietal bones are slightly convex. The infraorbital foramen is large and open around the posterior border of P^4. The zygomatic process is robust and the occipital bone is posteriorly directed.

In ventral view, the palatal bone is larger at the level of M^2-M^3, the basisphenoid bone and the basal part of occipital bone are robust, whereas the vomer bone is thin. The mandibular fossa is marked, the retroarticular process is robust and hypoglossal foramen is large and mesiodistally elongated.

The specimen CC468 has permanent teeth, which includes the presence of left canine. Therefore, the cranium can be referred to male. The canine is mesiodistally elongated, with an evident crest along the margin of the teeth. The left and right cheek toothrow are complete, excepted for incisors. Generally, the sketch of the caballine and protoconule folds is low complicated. The hypoconal grove is more pronounced in the premolars (P^3 and P^4) than that of molars (M^1 and M^2). whereas the protoconal groove is low pronounced.