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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

Les Equids du Pléistocène moyen à l'Holocène inférieur de la Péninsule des Pouilles (sud de l'Italie) : réévaluation taxonomique et biochronologique

Running head: Equids from Apulia Peninsula

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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 equid remains and its 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* in the Apulian Peninsula, from a few localities chronologically referred to late Middle Pleistocene. Most of the material from the late

37 Middle to the end of the Late Pleistocene is instead attributed to *Equus ferus*. The results
38 of this work thus add novel information on the biochronology of Italian fossil equids and on
39 their evolutionary history through the Middle and Late Pleistocene.

40

41

42 INTRODUCTION

43 The Italian Peninsula is considered a crossroads in the Mediterranean area, representing
44 a key area for the study of climatic changes and paleoenvironmental dynamics during the
45 Quaternary.

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

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

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

71 Several preliminary studies were conducted on the material from Cardamone (Rustioni
 72 1998), Cava Spagnulo (Mecozzi et al. 2017), Grotta del Cavallo (Sarti et al. 1998, 2002),
 73 Grotta Paglicci (Boscato 1994), Melpignano (Rustioni 1998) and Tana delle Iene (Conti et
 74 al. 2010) where the material were referred to *Equus ferus*. The material from San Sidero
 75 was attributed to the large-sized *Equus chosaricus* by Eisenmann (1991b) and *Equus*
 76 *ferus* by De Giuli (1983) and Rustioni (1998). The taxonomic attribution of other material
 77 from the AP was mainly based on the chronology of deposits and therefore frequently
 78 ascribed to *Equus ferus* (Tab. 1).

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

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

100 The postflexid index, calculated on lower teeth [$(\text{length of postflexid} \times 100) / \text{length of teeth}$],
 101 allows the comparison of teeth of various sizes to establish relative postflexid length (Caloi
 102 & Palombo 1987; Caloi, 1997; Boulbes, 2010).

103 In this scenario, we perform a comparison of protocone and postflexid indices in order to
 104 investigate the biometric variability and taxonomy through the Middle to Late Pleistocene

105 equids from AP. In this work, we present for the first time the craniodental material of fossil
106 *Equus* from late Middle to Late Pleistocene selected sites of the AP: Grotta di
107 Capelvenere, Grotta delle Tre Porte, Grotta Mario Bernardini, Grotta Uluzzo C,
108 Castellaneta, Grotta dei Giganti, Grotta Santa Croce, Grotta Laceduzza, Grotta Zinzulusa,
109 Fondo Focone and Santa Maria d'Agnano – esterno. In addition, the revision of the
110 material from Cardamone, Melpignano and San Sidero is carried out. The results allow us
111 to assemble a preliminary evolutionary framework for the horses during the Middle
112 Pleistocene to Early Holocene.

113

114 TAXONOMY OF MIDDLE-LATE PLEISTOCENE HORSES

115 After decades of debate, the systematics of caballoid horses has been recently redefined.
116 In 2003 the International Commission on Zoological Nomenclature proposed to use *Equus*
117 *ferus* Boddaert, 1785, a wild horse, to distinguish it from the domestic species *Equus*
118 *caballus* Linnaeus, 1758 (Gentry et al. 2004). Although many studies focused on caballoid
119 horses and their biostratigraphic importance, the taxonomic status of the Middle and Late
120 Pleistocene fossils is still a controversial topic (Forstén 1991; van Asperen 2012; Boulbes
121 & van Asperen 2019). The main issue concerns the interpretation of the morphological
122 changes and biometric variations as intra-specific variability or ecomorphotypes (Forstén
123 1988; Azzaroli 1983; Cramer 2002; van Asperen 2012; Boulbes & van Asperen 2019). The
124 diffusion of the first caballoid horses into Europe occurred in the early Middle Pleistocene
125 and led to the development of several ecomorphotypes through the Middle and Late
126 Pleistocene, including: *E. ferus mosbachensis*, *E. ferus germanicus*, *E. ferus gallicus*, *E.*
127 *ferus gmelini*. These subspecies of *E. ferus* are mainly distinguished by their overall size
128 and differences in skeletal proportions. According to van Asperen (2013), this inter- and
129 intraspecific variability cannot be explained by sexual dimorphism and/or age variability in
130 adult skeletal elements. Indeed, the author found no differences in size related to age and
131 sex variation in the extant specimens, assuming these factors have a very limited effect on
132 studies of fossil samples.

133 Based on the European fossil record, *Equus mosbachensis* is the first occurring caballine
134 *sensu lato* from the early Middle Pleistocene from the Germany localities of Mauer (MIS
135 17/15; 609 ± 40 ka; Wagner et al. 2011) and Süssenborn (MIS 16, 640 - 620 ka, Kahlke
136 2014) (Eisenmann et al. 1985; Langlois 2005; Boulbes & van Asperen 2019). This taxon
137 has been instituted by von Reichenau (1915) based on the material from the fossiliferous
138 sites of Mosbach (about 0.5 Ma) (Germany). Although the Mosbach horse (*E.*

139 *mosbachensis*) shared several features with the wild horse (*E. ferus*), it possesses some
 140 “archaic” morphological features (presence of the tendon insertion of the anterior brachialis
 141 muscle on the inner edge of the diaphysis of the radius, strong supraarticular tuberosities
 142 on metapodials) (Bonifay 1980; Eisenmann 1991a; Guadelli & Prat, 1995; Hadjouis 1998;
 143 Langlois 2005; Boulbes & van Asperen 2019). The affinity of the morphological features
 144 between *E. ferus* and *E. mosbachensis* suggests a close phyletic relationship between
 145 them, supported by the lack of clear craniodental diagnostic characters. This
 146 homogeneous overall morphology led some authors (van Asperen 2012) to refer the
 147 European Middle Pleistocene sample to a single species, *E. ferus* ssp., where the slight
 148 morphological and biometric variability is considered to reflect the adaptive responses to
 149 local climatic and palaeoenvironmental conditions. These differences could otherwise be
 150 considered to be due to normal population variability. However, there is a substantial
 151 consensus considering *Equus mosbachensis* as a distinct taxon because of its large-sized
 152 and robust build (Eisenmann et al. 1985; Hadjouis 1998; Langlois 2005, Uzunidis 2017;
 153 Boulbes & van Asperen 2019).
 154 In Italy, the first occurrence of large-sized and robust caballoid horses is reported in the
 155 Faunal Unit of Slivia (~ 0.9 Ma; Epivillafranchian Mammal Age) (Sala et al. 1992; Rustioni
 156 1998; Conti et al. 2010; Bellucci et al. 2014). Palombo & Alberdi (2017) suggested that the
 157 caballoid horses first appeared in the Ponte Galeria Unit (Cesi, about 0.7 Ma; Ficarelli et
 158 al. 1997). Moreover, Conti et al. (2010) suggests that the body size of this taxon
 159 decreased from the late Middle Pleistocene onwards (e.g., Malagrotta, Torre in Pietra).
 160 Other fossils from the Middle Pleistocene of Italy (0.8 - 0.3 Ma) have been referred *Equus*
 161 *caballus* ssp., *E. cf. E. mosbachensis*, *Equus caballus malatestai* and *Equus* sp.,
 162 highlighting the uncertainty of the taxonomic attribution and the difficulty to reconstruct the
 163 phylogeny of this group (Caloi & Palombo 1987; Caloi, 1997; Palombo & Alberdi 2017;
 164 Strani et al. 2018, 2019). In addition, Berzi (1972) attributed the astragalus from Monte
 165 Oliveto (Siena, Central Italy), chronologically referred to early Middle Pleistocene, to
 166 *Equus caballus* cf. *mosbachensis*, mainly based on its body size. Finally, Rustioni (1998)
 167 proposed to attribute large-sized fossil horses of the late Middle Pleistocene from the
 168 Italian Peninsula, to *E. mosbachensis*, and the small-sized ones from the Late Pleistocene
 169 to *E. ferus germanicus*.
 170 In this scenario, the taxonomic attribution of the European caballoid horse from Middle to
 171 Late Pleistocene (300 – 12 Ka) is still a controversial topic. The proliferation of the

172 subspecies reflects the homogeneous overall morphology and the lack of clear diagnostic
173 characters, which should allow the identification of the different taxa.

174

175 MATERIAL AND METHODS

176 The sample of *Equus* we have studied are part of several collections stored in different
177 Italian Institutions and Museums (Tab. 1).

178 The skull and dental features of Middle to Late Pleistocene *Equus* has been poorly
179 investigated, which prevents a large morphological comparison of the studied material. A
180 morphological description of the studied crania from San Sidero and Cardamone has been
181 reported in Supplementary Material 1 (SD1).

182 Following Eisenmann (1981), 5 cranial variables have been considered to be important for
183 discriminating species of *Equus*: basilar length (BL), muzzle length (ML), length of the
184 check teeth (P^2M^{3L}), facial length (FaL), frontal length (FrL), muzzle breadth at the posterior
185 borders of I^3 (MB) (Tab. SD1). Following Eisenmann (1980), we also measured 24 for
186 upper and lower teeth: length, breadth and length of protocone of the upper teeth (P^2L ,
187 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
188 and length of postflexid of the lower teeth (P_2L , P_2B , P_2Pf , $P_{3-4}L$, $P_{3-4}B$, $P_{3-4}Pf$, $M_{1-2}L$, $M_{1-2}B$,
189 $M_{1-2}Pf$, M_3L , M_3B , M_3Pf) variables have been considered. The measurements were
190 taken in occlusal view to the nearest 0.1 mm with a digital caliper. We used literature data
191 on fossil horses from the Late Pleistocene to Early Holocene of the AP (Tab. 1).

192 We further assessed the degree of affinity between late Middle to Late Pleistocene *Equus*
193 from Apulia by conducting a statistical analysis. First, in order to explore the affinity among
194 the samples from different fossiliferous sites, we compared the upper and lower teeth from
195 San Sidero to those from the other deposits. Specifically, we considered the length of the
196 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
197 dataset was subject to normality distribution verification using Shapiro test. We evaluated
198 differences in length of the upper and lower premolars (P^2 , P^{3-4} , P_2 and P_{3-4}) and molars
199 (M^{1-2} , M^3 , M_{1-2} and M_3) in the late Middle Pleistocene and Early Holocene, using linear
200 model (Anova) with corner point parameterization testing the null hypothesis of no-
201 differences between the mean of the San Sidero (SS) and the other samples (p.value >
202 0.05).

203 Taking into account the number of sites studied and the small sample size of some of the
204 localities (i.e. Grotta Mario Bernardini – VI, Grotta Mario Bernardini – III, Grotta Mario
205 Bernanrdini – II, Grotta Santa Croce, Grotta Uluzzo – IV, Grotta Uluzzo – II, Grotta

206 Zinzulusa), the dataset has been assembled according to the MIS chronology. We
207 considered the length of the upper and lower teeth of specimens referred from the late
208 Middle Pleistocene (MIS 9-8) of AP and compared it to those referred to late Middle (MIS
209 7) and Early Holocene (MIS 1). This dataset was also subject to a test for normal
210 distribution verification using the Shapiro test. We evaluated differences in upper and
211 lower teeth in the late Middle Pleistocene to Early Holocene samples, using a linear model
212 (Anova) with corner point parameterization testing the null hypothesis of no-differences
213 between the mean of the MIS 9-8 and the other samples (p.value > 0.05). The statistical
214 analysis was performed using the R software (Team 2000). Very worn teeth were
215 excluded by statistical analysis.

216 In addition, in order to evaluate the dental variability in the considered samples, the
217 protocone index [(length of protocone *100)/length of teeth] and postflexid index [(length of
218 postflexid *100)/length of teeth] were compared. The protocone and postflexid index is
219 calculated as the mean of the upper and lower teeth respectively when the sample
220 includes more than one specimen. The pattern of the protocone index assumes a
221 taxonomical value for the identification of Middle Pleistocene to Early Holocene equids. In
222 *E. mosbachensis* the protocone index displays an M^3 value higher than M^{1-2} one and P^{3-4}
223 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}
224 and M^3 . Finally, in *E. hydruntinus* the values of P^{3-4} and M^{1-2} are much lower than both *E.*
225 *mosbachensis* and *E. ferus*, whereas those of P^2 and M^3 fall in the variability of the
226 caballoid horse ones.

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

232

233 INSTITUTIONAL ABBREVIATIONS

234 IGF: Museum of Natural History of the University of Florence, section of Geology and
235 Paleontology.

236 IsIPU: Italian Institute of Human Paleontology.

237 ITCGC: Commercial Technical Institute “Galilei-Costa”

238 MPCCSM: Museum of Pre-Classical Civilizations of Southern Murgia.

239 MPUN: Paleontological Museum of the University of Naples Federico II.

240 PF: PaleoFactory Laboratory, Sapienza University of Rome.

241

242 LATE MIDDLE TO LATE PLEISTOCENE APULIAN FOSSIL EQUIDAE

243 *Melpignano*

244 The karst infilling deposits of Melpignano, locally known as “ventarole”, are located in the
245 area of the village of Maglie. These karst deposits were firstly described by Mirigliano
246 (1941), since then several Institutions, as the IsIPU and Italian Institute of Prehistory and
247 Protohistory (IIPP), with the support of local Salentine Speleological groups, investigated
248 this area (de Lorentiis 1962; Cardini 1962a). The “ventarole” are generally filled with
249 reddish sediments (called “terre rosse”) in the lower part, and brownish sediments (called
250 “terre brune”) in the upper, particularly rich in vertebrate fossil remains (Bologna et al.,
251 1994) (Fig. 1). The *Equus* sample was recovered from the “terre rosse” of the “ventarole”
252 of Mirigliano, Cava Nuzzo and Cava Bianco.

253 *Repository and studied material*

254 MPUN: Mirigliano collection - 17 upper teeth, 24 lower teeth.

255 Cava Nuzzo - PF: 2 hemimandibles, 4 lower teeth (Fig.3-3).

256 Cava Bianco - PF: 17 upper teeth, 2 hemimandibles, 9 lower teeth.

257

258 *San Sidero*

259 The “ventarole” of San Sidero are located along the state road (SS16) between the
260 villages of Corigliano d’Otranto and Maglie. The first description of the deposit and its
261 faunal assemblage was reported by Cardini (1962a). The mammal fauna from San Sidero
262 was also studied by other authors (De Giuli 1980, 1983; Petrucci et al. 2012; Iurino et al.
263 2013, 2015). Similarly to the Melpignano sediments, these “ventarole” include “terre rosse”
264 layers in the lower part and “terre brune” layers in the upper part. The Equidae sample was
265 collected from the “terre rosse” of the “ventarole” called SS6 and Cava L.

266 *Repository and studied material*

267 SS6 - IGF: 1 skull (Fig. 2a), 11 upper teeth, 10 lower teeth (Fig. 3-1).

268 Cava L- PF: 5 upper teeth, 1 hemimandible, 6 lower teeth.

269

270 *Grotta di Capelvenere*

271 The site, located near the town of Santa Caterina (Lecce), occurs in a Cretaceous
272 limestone (Calcari di Melissano Formation) at 20 m a.s.l. and about 100 m from the current
273 seashore. The cave was discovered in 1960 and was only partially excavated in 1971, 1974

274 and 1975 (Borzatti von Löwenstern 1961; Giusti 1979, 1980). Outside the cave, a nearby
275 conglomerate deposit at about 8 m a.s.l. has been referred to Tyrrhenian beach
276 (MIS 5) (Patriarchi 1980). The stratigraphic sequence can be divided into two main
277 complexes separated from a speleothem: in the upper part, the brownish sediment, where
278 domestic fauna, ceramics and artefacts appeared, has been referred to Iron age. Instead,
279 in the lower part ten levels including vertebrate fossils and artefacts have been referred to
280 Mousterian facies (Borzatti von Löwenstern 1961; Giusti 1979, 1980; Patriarchi 1980). The
281 studied sample comes from the lower part of the sedimentary succession.

282 *Repository and studied material*

283 IGF: 18 upper teeth, 5 hemimandibles, 26 lower teeth.

284

285 *Grotta delle Tre Porte*

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

291 *Repository and studied material*

292 IsIPU: 8 upper teeth, 1 hemimandible, 9 lower teeth.

293

294 *Grotta Mario Bernardini*

295 The cave located along the Ionian coast near the village of Santa Caterina, also known as
296 Grotta di Santa Margherita, was discovered in 1961 (Borzatti von Löwenstern 1970, 1971)
297 (Fig. 1). The stratigraphic succession consists of four main archeological levels: D, C, B
298 and A, excepted for the top of the sequence, where ceramic and artefacts were referred to
299 Iron and Bronze age (Borzatti von Löwenstern 1970, 1971; Carmigiani & Romagnoli
300 2017). From the complex VI-III artefacts referred to Mousterian facies were found,
301 whereas those from the complex II were attributed to Uluzzian (Borzatti von Löwenstern
302 1970, 1971; Carmigiani & Romagnoli 2017). The volcanic material recovered in the top of
303 complex IV (firstly indicated as α) can be correlated with that found in the level G of the
304 Grotta del Cavallo dated approximately to $109,100 \pm 900$ ka (Sarti et al. 2002; Spinapolice
305 2008; Douka & Spinapolice 2012; Spinapolice 2018; Zanchetta et al. 2018). Instead, the
306 volcanic material from the bottom of the complex II (initially indicated as β) can be
307 correlated with that found at the top of the level F of the Grotta del Cavallo dated

308 approssimatively to $45,700 \pm 1,000$ ka (Sarti et al. 2002; Spinapolice 2008; Douka &
309 Spinapolice 2012; Spinapolice 2018; Zanchetta et al. 2018). Albeit the mammal remains
310 have never been studied in detail, a preliminary mammal list was provided by Borzatti von
311 Löwenstern (1970, 1971). *Equus* is found from different levels (VI, IV, III, II), where also
312 lithic artefacts referred to Middle Palaeolithic from the complexes VI-III and Upper
313 Palaeolithic from the complex II were found (Tab. 1, Fig. SD1).

314 *Repository and studied material*

315 IGF: 27 upper teeth, 1 hemimandible, 27 lower teeth.

316

317 *Grotta Uluzzo C*

318 The cave is located in the Uluzzo Bay near the village of Nardò, opening into the
319 Cretaceous limestone. The stratigraphic succession was described by Borzatti von
320 Löwenstern (1965, 1966) and Borzatti von Löwenstern & Magaldi (1969). In particular, the
321 green volcanic sand from the bottom of the complex II can be correlated with the tephra
322 found at the top of the level F of Grotta del Cavallo, dated at $45,700 \pm 1,000$ ka by
323 Zanchetta et al. (2018). Instead, the complex II-I transition, consisting of a grey volcanic
324 sand, can be correlated with the Ignimbrite Campana (CI) identified at the bottom of the
325 level C of Grotta del Cavallo, dated at $39,850 \pm 140$ ka Zanchetta et al. (2018). The
326 presence of a reworked tephra in the top of the complex IV could represent a marker for
327 the lower deposit, but further investigations needed to confirm its age. Moreover, Borzatti
328 von Löwenstern (1965, 1966) reported a preliminary list of the fossil mammals recovered
329 from this locality. The studied sample come from the complex IV, III and II (Tab. 1, Fig.
330 SD2). Whereas, artefacts from the complex IV and III were attributed to Middle
331 Palaeolithic, instead those from the complex II to early Upper Palaeolithic.

332 *Repository and studied material*

333 IGF: 21 upper teeth, 2 hemimandibles, 33 lower teeth.

334

335 *Castellaneta*

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

341 *Repository and studied material*

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

343

344 *Grotta dei Giganti*

345 The coastal cave, located between Punta Ristola and Punta Marchiello, was discovered by
346 the Italian Institute of Human Paleontology during a field survey conducted by Gian Alberto
347 Blanc in the 1930s (Blanc et al. 1958). The authors also reported a mammal faunal list. In
348 addition, Alessio et al. (1978) attempted to carry out radiocarbon dating without success.
349 However, the fossil material was found associated to Middle Palaeolithic artefacts.

350 *Repository and studied material*

351 IsIPU: 12 upper teeth, 20 lower teeth.

352 ITCGC: 4 upper teeth, 3 lower teeth.

353

354 *Grotta Santa Croce*

355 The cave, located near the small village of Bisceglie, was discovered in the 1937 (Segre &
356 Cassoli 1987). The first systematic excavations directed by Luigi Cardini were carried out
357 by Italian Institute of Human Palaeontology (IsIPU) during the 1950s (Segre & Cassoli
358 1987; Mallegni et al. 1987; Boscato et al. 2006). The sedimentary succession includes
359 several levels attributed to Middle and Upper Paleolithic and Neolithic (Segre & Cassoli
360 1987; Arrighi et al. 2009; Rinaldo et al. 2017). Radiocarbon dated indicated an age of
361 $24,900 \pm 150$ BP for the level B and $31,500 \pm 400$ BP for the level C (Arrighi et al. 2009;
362 Rinaldo et al. 2017). There are no radiocarbon dating results for levels H-D that are
363 referred to MIS 5 and MIS 4, respectively (Arrighi et al. 2009; Rinaldo et al. 2017). The
364 fossil remains of mammals from the level D were studied by Segre & Cassoli (1987).
365 Recently, new material also was discovered from this level and *Equus ferus* and *Bos*
366 *primigenius* were identified (Boscato et al. 2006). The studied material was recovered from
367 the level D, associated with lithic artefacts attributed to Middle Palaeolithic.

368 *Repository and studied material*

369 IsIPU: 7 upper teeth, 7 lower teeth.

370

371 *Grotta Laceduzza*

372 The cave deposit, located near the village of San Michele Salentino, was discovered by
373 the “Gruppo Speleologico Salentino Pasquale de Lorentiis” in 1970 (Coppola 2005, 2012).
374 The lower part of the sedimentary succession includes fossil remains of mammals and
375 artefacts referred to Middle Palaeolithic. A preliminary mammal list was recently reported,

376 including a rich sample of *Meles meles* (Mecozzi et al. 2019). The *Equus* material was
377 recovered from the lower part of the deposit, associated to Middle Palaeolithic artefacts.

378 *Repository and studied material*

379 MPCCSM: 9 upper teeth, 12 lower teeth.

380

381 *Grotta Zinzulusa*

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

392 *Repository and studied material*

393 IsIPU: B5 - 6 upper teeth, 5 lower teeth.

394

395 *Cardamone*

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

404 *Repository and studied material*

405 IGF: 16 upper teeth, 33 lower teeth.

406 ITCGC: 2 crania (Fig. 2b,c), 13 maxillaries, 83 upper teeth, 4 hemimandibles, 112 lower
407 teeth (Fig. 3-2).

408

409

410 *Fondo Focone*

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

417 *Repository and studied material*

418 IsIPU: 1 maxillary, 37 upper tooth, 1 hemimandible, 27 lower teeth.

419

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

421 The Grotta di Santa Maria di Agnano, located near the village of Ostuni, on the north-
422 western margin of Risieddi promontory, was discovered during the 1960s by the
423 Associazione Studi e Ricerche (Studies and Research Association) (Coppola 2012). The
424 excavations in the cave deposit started in 1991 and continued still today, whereas from
425 2007 the area outside the cave, known as SMA-esterno, was also investigated (Coppola
426 1992; Vacca et al.1992; Vacca & Coppola, 1993; Coppola 2012; Bails 2015; Coppola et al.
427 2017; Chakroun et al. 2018). The fossil remains come from level 8, dated 25221-24549 cal
428 BP and 26338-25779 cal BP, and levels 6A-4C dated 18013-17587 cal BP and 16745-
429 16401 cal BP with radiocarbon method (Renault-Miskovsky et al. 2011; Bails 2015).

430 *Repository and studied material*

431 MPCCSM: level 8 - 10 maxillary, 59 upper tooth, 35 hemimandibles, 67 lower teeth (Fig. 3-
432 4,5).

433

434 RESULTS

435 *Equus* samples from the late Middle Pleistocene to Early Holocene of AP show a large
436 variation in dental dimensions and proportions. In particular, the length of P^2 and M^3 are
437 highly variable both within and between samples (Fig. SD3-SD4; Tab. SD1). On the
438 contrary, the length of P^{3-4} from San Sidero is closer (p.value > 0.05) to those from Cava
439 Spagnulo, Grotta di Capelvenere, Grotta Mario Bernardini –II and Grotta Uluzzo C (Tab.
440 SD1). The length of M^{1-2} from San Sidero is similar (p.value > 0.05) to those from
441 Castellaneta, Fondo Cattie, Grotta di Capelvenere, Grotta Mario Bernardini –III, Grotta
442 Santa Croce, Grotta Zinzulusa, Melpignano and Tana delle Iene (Tab.SD1). As in the case
443 of the upper teeth, even the length of P_2 and M_3 show a huge variability (Fig. SD5-SD6).

444 The P_{3-4} from San Sidero is closer (p.value > 0.05) to those from Grotta di Capelvenere,
 445 Grotta dei Giganti, Grotta Mario Bernardini – IV, Grotta delle Tre Porte, Grotta Zinzulusa
 446 and Tana delle Iene (Fig. SD5-SD6; Tab. SD2). Whilst, the M_{1-2} from San Sidero is closer
 447 (p.value > 0.05) to Grotta Santa Croce, Grotta delle Tre Porte, Grotta Zinzulusa, Grotta
 448 Uluzzo C – II, Melpignano and Tana delle Iene (Fig. SD5-SD6; Tab. SD2).
 449 Considering the MIS chronology, the length of P^2 and M^3 of the sample from MIS 9-8 is
 450 larger only of samples from MIS 3 (P^2 , p.value < 0.05; M^3 p.value < 0.05) and MIS 2 (P^2 ,
 451 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
 452 MIS 9-8 are larger than those from the late Middle Pleistocene (MIS 7) to Early Holocene
 453 (MIS 1) (p.values < 0.05). In the lower dentition, the length of the teeth from MIS 9-8 are
 454 larger than those from Late Pleistocene (MIS 5) to Early Holocene (MIS 1) (p.values <
 455 0.05), whereas they are similar to those from late Middle to early Late Pleistocene (MIS 7-
 456 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, Tab. 3).
 457 The protocone index of the Grotta di Capelvenere, Melpignano and San Sidero shows a
 458 trend closer to that reported for *E. mosbachensis*, with M^3 value higher than M^{1-2} one and
 459 P^{3-4} value higher or sub-equal than M^{1-2} one (Fig. 6). On the contrary, the pattern of the
 460 other samples is closer to that reported for *E. ferus*, with M^{1-2} value higher than both P^{3-4}
 461 and M^3 . Finally, the sample from Tana delle Iene and Grotta delle Mura possesses a well
 462 different values compared to the others, resembling those reported for *Equus hydruntinus*.
 463 In fact, in *E. hydruntinus* the values for P^{3-4} and M^{1-2} are significantly lower than those of
 464 both *E. mosbachensis* and *E. ferus*, whereas they are similar in P^2 and M^3 values.
 465 Whereas, the postflexid index has been investigated, but no trend can be detected through
 466 the time and/or differences among the considered taxa (Fig. 7).
 467 Finally, in the standard bivariate plot of muzzle proportions (Fig. 8), two groups can be
 468 recognized. The first includes the specimen from the fossiliferous sites referred to glacial
 469 stages (Tab. SD3), which display a large muzzle in relation to their length. An exception is
 470 the cranium of *Equus ferus antunesi* from Fontainhas (Portugal), where the muzzle is
 471 longest. The specimen from Cardamone falls in the variability of the glacial horses, and is
 472 similar to that from Cuane de l'Arago (Fig. 8). A second group is composed by crania from
 473 deposits referred to interglacial stages, where the muzzle is narrow compared to its total
 474 length. The cranium from San Sidero falls in this variability.
 475
 476
 477

478 DISCUSSION

479 The taxonomy of Middle to Late Pleistocene European *Equus* remains controversial
480 (Forstén 1991; van Asperen 2012). The large variability of the morphological features and
481 biometric traits of caballoid horses has been the subject of controversy amongst many
482 authors. No consensus exists on how to define this variability, as it is either treated as
483 being intra-specific or inter-specific events (Forstén 1988; Azzaroli 1983; Cramer 2002;
484 van Asperen 2012). This unresolved taxonomic issue has led a proliferation of taxa,
485 identified as either species or subspecies (*E. mosbachensis*, *E. steinheimensis*, *E.*
486 *achenheimensis*, *E. taubachensis*) (see van Asperen 2012 for discussion). In the Italian
487 fossil record, the specific attribution of the fossil samples from Middle Pleistocene sites
488 reflects this uncertainty (*Equus altidens*, *Equus* aff. *sussebornensis*, *Equus caballus* ssp.,
489 *E. cf. E. mosbachensis* *Equus caballus* cf. *mosbachensis* and *Equus* sp.) (Berzi 1972;
490 Caloi & Palombo 1987; Strani et al. 2018, 2019). Preliminary studies on *Equus* samples
491 from several AP sites led to the identification of *E. ferus* from the deposits of Cardamone
492 (Rustioni 1998), Cava Spagnulo (Mecozzi et al. 2017), Grotta del Cavallo (Sarti et al.
493 1998, 2002), Grotta Paglicci (Boscato 1994), Melpignano (Rustioni 1998) and Tana delle
494 Iene (Conti et al. 2010), whereas the previous taxonomic attribution of the material from
495 San Sidero has been questioned. In the revision of the Middle to Late Pleistocene *Equus*
496 material from Europe, Eisenmann (1991b) attributed the material from San Sidero to the
497 large-sized *Equus chosaricus*, whereas other authors (De Giuli, 1983; Rustioni, 1998)
498 classified it as *Equus ferus*. Unlike, the results of the statistical analysis and the
499 comparison of the protocone index carried out in this work allow to refer the material from
500 San Sidero to *E. mosbachensis*.

501 In this scenario, the analysis of a relatively large sample of *Equus* fossils from late Middle
502 to Late Pleistocene localities of AP allows us to reassess the taxonomy and the
503 evolutionary trend of local horse species. Based on the results of the statistical analyses
504 and the comparison of the protocone indexes, *E. mosbachensis* is identified for the first
505 time from few Apulian fossiliferous sites, among which are included San Sidero,
506 Melpignano and Grotta di Capelvenere. *Equus mosbachensis* possesses larger upper and
507 lower teeth than those of *E. ferus* (Figs. 4-5; Tabs. 2-3) and different values of the P^{3-4} ,
508 M^{1-2} and M^3 protocone index (Fig. 6). The Grotta di Capelvenere, Melpignano and San
509 Sidero samples displays a M^{1-2} protocone index value lower than those both P^{3-4} and M^3
510 (Fig. 6). The taxonomic attribution to *E. ferus* of the material from other considered sites
511 chronologically referred from late Middle Pleistocene (MIS 7) to the end of Late

512 Pleistocene (MIS 2) is confirmed, based on the medium-size of the specimens and the
 513 values of the protocone index. In fact, besides displaying smaller upper and lower teeth
 514 than those of *E. mosbachensis* (Figs. 4-5; Tabs. 2-3), the protocone index in the materials
 515 of *E. ferus* displays M^{1-2} value higher than those both P^{3-4} and M^3 (Fig. 6). Furthermore, for
 516 the samples from Tana delle Iene and Grotta delle Mura, the protocone index differs. The
 517 values of P^{3-4} and M^{1-2} are much lower than those of caballoid horses. This atypical profile
 518 of IP index in the fossil materials of Tana delle Iene and Grotta della Mura could be due to
 519 the small size of the available samples.

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

524 Whereas *E. mosbachensis* is widespread in Europe during the Middle Pleistocene, its
 525 presence in Italian Peninsula was quite scarce (Gliozzi et al. 1997), and documented only
 526 from few sites: Cesi (Ficcarelli et al. 1997), Venosa-Notarchirico (Palombo & Alberdi
 527 2017), Fontana Ranuccio (Biddittu et al. 1979). In AP, the Mosbach horse is identified for
 528 the first time in a few localities, which unfortunately lack of absolute radiometric
 529 determinations. As for the European material, in the AP the Mosbach horse was well-
 530 distinct for its large teeth sized, which is larger to the wild horse (*E. ferus*) (Figs. 4-5; Tabs.
 531 2-3) and display different values of the protocone index (Fig. 6). According to (Guadelli
 532 2007; Uzunidis 2017), the last occurrence of *E. mosbachensis* took place during the late
 533 Middle Pleistocene, probably during the MIS 6 (Guadelli 2007; Uzunidis 2017) although no
 534 general consensus was reached (Boulbes & van Asperen 2019). However, the first
 535 historical appearance of *E. ferus* in AP is from Grotta del Cavallo during the early Late
 536 Pleistocene (< 109 ka) (Zanchetta et al. 2018). Therefore, a new dispersal of *Equus*
 537 species could have taken place during the late Middle Pleistocene. This possible scenario
 538 is consistent with the results of the aDNA analysis performed on *E. ferus*, which revealed
 539 that the wild horse originated at about 240,000 years ago (late Middle Pleistocene),
 540 differing therefore from the earlier form of *Equus* (George & Rider 1986). Unfortunately,
 541 the taxonomic uncertainty for the Middle Pleistocene sample from Italian Peninsula record
 542 prevents an in-depth reconstruction of the caballoid horse lineage (Berzi 1972; Caloi &
 543 Palombo 1987; Strani et al. 2018, 2019, Strani 2020).

544 The last occurrence of *E. ferus* in the Italian Peninsula took place during the end of Late
 545 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 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 extinction 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 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; Crègut-Bonnouire 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

580 attributed to glacial stages ($n = 15$) display a short and wide muzzle as in the cases of the
581 Middle Pleistocene sites of Cuane de l'Arago (MIS 14-12) (France) (Eisenmann et al.
582 1985) and Igue des Rameaux (MIS 10-9) (France) (Uzunidis 2017) or Late Pleistocene
583 ones of Coulet des Roches (MIS 2) (France) (Crégut-Bonnouire et al. 2018), Jaurens (MIS
584 3) (France) (Guerin, 1999) and Sirejol (MIS 3) (France) (Philippe et al. 1980) (Tab. SD3).
585 Whereas, the crania from interglacial stages ($n = 2$) possess an elongated and narrow
586 muzzle, as the specimens from Middle Pleistocene sites of Lunel-Viel (MIS 11) (France)
587 (Bonifay 1980; Eisenmann et al. 1985) and Mosbach (MIS 13) (Germany) (Maul, 2000)
588 (Fig. 8; Tab. SD3). An exception is represented by the cranium from Last Glacial (MIS 2;
589 $22,730 \pm 835$ ka) of Fontainhas (Portugal), since its proportions fall outside the variability
590 of the glacial caballoid horses (Fig. 8; Tab SD.3). The proportions of the two studied skulls,
591 San Sidero and Cardamone specimens, corroborated the glacial/interglacial separation.
592 Indeed, the skull from Cardamone biochronologically referred to Last Glacial falls in the
593 variability of the glacial group, representing one of the largest specimens (Fig. 8; Tab.
594 SD3). Contrary, the proportions of the skull from San Sidero (MIS 9-8) differ from those of
595 the glacial group, and are similar to those of Mosbach and Lunel-Viel ones (Fig. 8; Tab.
596 SD3). Finally, considering the large variability of the skull size of caballoid horses during
597 the Middle and Late Pleistocene, no evolutionary trend can be recognized. Nevertheless,
598 based on the proportions of the muzzle, two groups are identified from the Middle to Late
599 Pleistocene of Europe, which reflect an adaptation to climate (glacial and interglacial
600 stages). Therefore, the proportions of the muzzle of caballoid horse clearly reveal
601 important information on climatic conditions and palaeoenvironment.

602

603 CONCLUSIONS

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

612 Therefore, our results allow us to redefine the taxonomical attribution of the material from
613 Grotta di Capelvenere, Melpignano and San Sidero, which is referred to *Equus*

614 *mosbachensis*. For the fossil material from the deposits attributed from the late Middle
615 Pleistocene (MIS 7-6), Late Pleistocene (MIS 5-2) and Early Holocene the attribution to *E.*
616 *ferus* is confirmed.

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

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

626

627

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Caption

972 Fig. 1 – Location of the considered Apulian sites: 1 - Grotta Santa Croce; 2 - SMA-esterno;
 973 3 - Grotta Laceduzza; 4 - Castellaneta; 5 - Cardamone; 6 - Grotta Mario Bernardini -
 974 Grotta Uluzzo C - Grotta di Capelvenere; 7 - San Sidero - Melpignano; 8 - Grotta
 975 Zinzulusa; 9 - Fondo Focone; 10 -Grotta dei Giganti Grotta delle Tre Porte.

976 Fig. 2 –Crania in right view from late Middle to Late Pleistocene of Apulia: a - IGF16329,
 977 cranium of male of *Equus mosbachensis* from San Sidero; b - CC467, cranium of female

978 of *Equus ferus* from Cardamone; c - CC468, cranium of male of *Equus ferus* from
979 Cardamone.

980 Fig. 3 – Mandible of *Equus* from late Middle to Late Pleistocene of Apulia in labial (a-b)
981 and occlusal (c) views: 1a-c - IGF16330, *Equus mosbachensis* from San Sidero; 2a-c -
982 CC414, *Equus ferus* from Cardamone; 3a-b, MPND396 (ex. Cur11), left hemimandible of
983 *Equus mosbachensis* from Melpignano; 4a-b - C2 20b 77, right hemimandible from SMA-
984 esterno; 5a-b – C2 20b 80, left hemimandible from SMA-esterno.

985 Fig. 4 – Boxplot of the length of the upper teeth considered for chronology: a – second
986 premolar (P^2L); b - third-fourth premolar ($P^{3-4}L$); c - first-second molar; ($M^{1-2}L$); d - third
987 molar (M^3L). For the groups see Tab. 1.

988 Fig. 5 - Boxplot of the length of the lower teeth considered for chronology: a – second
989 premolar (P_2L); b - third-fourth premolar ($P_{3-4}L$); c - first-second molar ($M_{1-2}L$); third molar
990 (M_3L). For the groups see Tab. 1.

991 Fig. 6 – Protocone index of the upper teeth of *Equus* species from the late Middle
992 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1

993 Fig. 7 - Postflexid index of the lower teeth of *Equus* species from the late Middle
994 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1

995 Fig. 8 – Standard bivariate plot of muzzle length (ML) and muzzle breadth at the posterior
996 borders of I^3 (MB) of caballoid horses from Middle to Late Pleistocene of Europe (Tab.
997 SD3). Symbol: circle – Middle Pleistocene specimens; squared – Late Pleistocene
998 specimens.

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1000 Table

1001 Tab. 1 – *Equus* fossil material from the late Middle to Early Holocene of the Apulian
1002 Peninsula.

1003 Tab. 2 - Table of p-values for the linear model of the upper teeth with corner point
1004 parameterization testing the null hypothesis of no-differences between the mean of the
1005 MIS 9-8 and the other samples (p-value > 0.05).

1006 Tab. 3 - Table of p-values for the linear model of the lower teeth with corner point
1007 parameterization testing the null hypothesis of no-differences between the mean of the
1008 MIS 9-8 and the other samples (p-value > 0.05).

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1011 Supplementary data

1012 **Supplementary information**

1013 SI.1 - Morphological description of crania from late Middle to Late Pleistocene of AP

1014 **Figures**

1015 Fig. SD1 – Schematic stratigraphic log of Grotta Mario Bernardini (modified from Borzatti
1016 von Löwenstern 1970)

1017 Fig. SD2 - Schematic stratigraphical log of Grotta Uluzzo C (modified from Borzatti von
1018 Löwenstern & Magaldi 1969).

1019 Fig. SD3 - Boxplot of length of upper premolars (a – P^2L ; b – $P^{3-4}L$) from the late Middle
1020 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1

1021 Fig. SD4 - Boxplot of length of upper molars (a – $M^{1-2}L$; b – M^3L) from the late Middle
1022 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1

1023 Fig. SD5 - Boxplot of length of lower premolars (a – P_2L ; b – $P_{3-4}L$) from the late Middle
1024 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1

1025 Fig. SD6 - Boxplot of length of lower molars (a – $M_{1-2}L$; b – M_3L) from the late Middle
1026 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1

1027

1028 **Table**

1029 Tab. SD1 – Table of p-values for the linear model of the upper teeth with corner point
1030 parameterization testing the null hypothesis of no-differences between the mean of the
1031 San Sidero (SS) and the other samples (p-value > 0.05).

1032 Tab. SD2 - Table of p-values for the linear model lower teeth with corner point
1033 parameterization testing the null hypothesis of no-differences between the mean of the
1034 San Sidero (SS) and the other samples (p-value > 0.05).

1035 Tab. SD3 – *Equus* crania from Middle to Late Pleistocene of Europe.

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Supplementary data

Morphological description of crania from late Middle to Late Pleistocene of AP

San Sidero

The IGF16329 is a splanchnocranium 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 tooththrows 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 groove 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 groove 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 groove 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.

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1110 **Figures**

1111 Fig. SD1 – Schematic stratigraphical log of Grotta Mario Bernardini (modified from Borzatti
1112 von Löwenstern 1970)
1113 Fig. SD2 - Schematic stratigraphical log of Grotta Uluzzo C (modified from Borzatti von
1114 Löwenstern & Magaldi 1969).

1115 Fig. SD3 - Boxplot of length of upper premolars (a – P^2L ; b – $P^{3-4}L$) from the late Middle
 1116 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1
 1117 Fig. SD4 - Boxplot of length of upper molars (a – $M^{1-2}L$; b – M^3L) from the late Middle
 1118 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1
 1119 Fig. SD5 - Boxplot of length of lower premolars (a – P_2L ; b – $P_{3-4}L$) from the late Middle
 1120 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1
 1121 Fig. SD6 - Boxplot of length of lower molars (a – $M_{1-2}L$; b – M_3L) from the late Middle
 1122 Pleistocene to Early Holocene sites of the Apulia. For the abbreviations see Tab. 1

1123 **Table**

1124 Tab. SD1 – Table of p-values for the linear model of the upper teeth with corner point
 1125 parameterization testing the null hypothesis of no-differences between the mean of the
 1126 San Sidero (SS) and the other samples (p-value > 0.05).
 1127 Tab. SD2 - Table of p-values for the linear model lower teeth with corner point
 1128 parameterization testing the null hypothesis of no-differences between the mean of the
 1129 San Sidero (SS) and the other samples (p-value > 0.05).
 1130 Tab. SD3 – Equidae crania from Middle to Late Pleistocene of Europe.

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Fig. 1



Fig. 2



Fig. 3



Fig. 4



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1161 Fig. 5
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Fig. 6

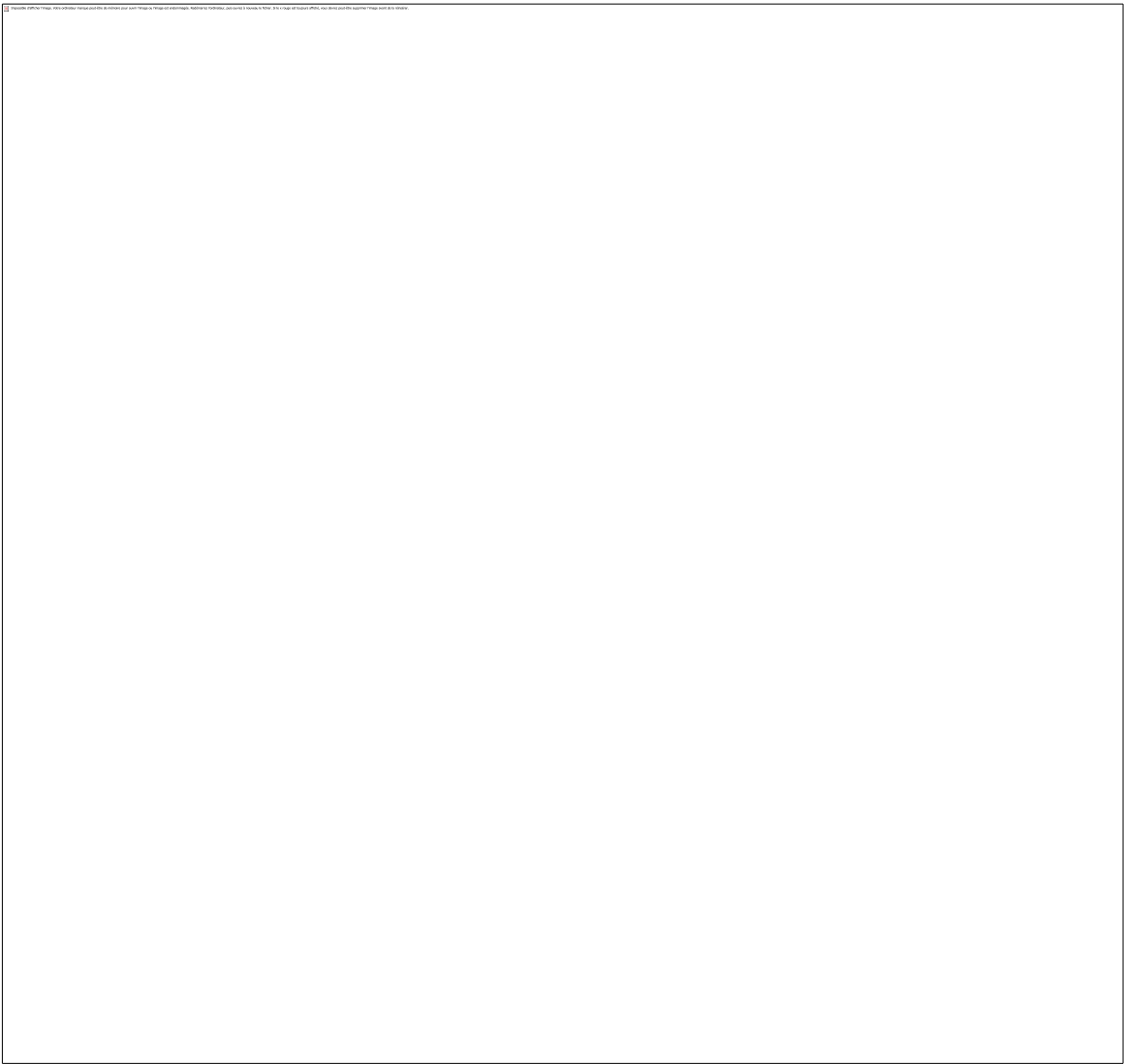


Fig. 7

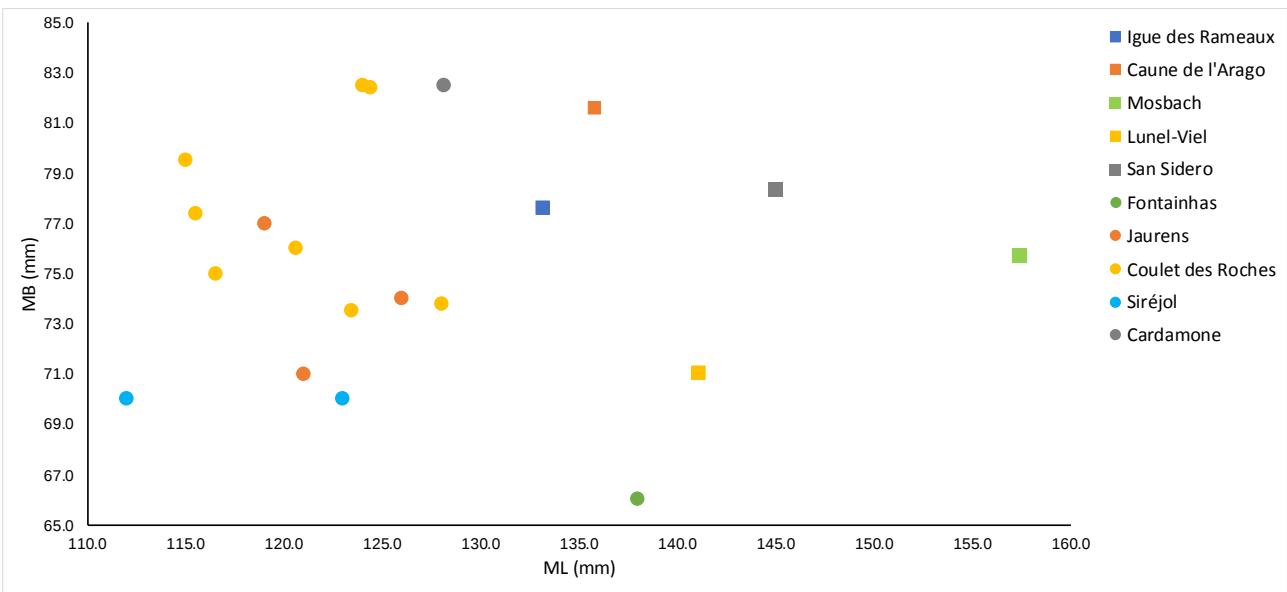


Fig. 8

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Species reported in previous researches	Site	Abbreviations	MIS	Date	Reference	Data source
<i>Equus ferus</i>	Melpignano	Mel	MIS 9-8	Biochronology	Bologna et al. 1994; Sala et al. 1992; Mecozzi et al. 2019; this work	This work
<i>Equus ferus</i> - <i>Equus chosaricus</i>	San Sidero	SS	MIS 9-8	Biochronology	De Giuli 1983; Sala et al. 1992; Mecozzi et al. 2019; this work	This work
<i>Equus ferus</i>	Grotta di Capelvenere	GCv	MIS 9-8	Biochronology and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
<i>Equus ferus</i> - <i>Equus</i> sp.	Grotta delle Tre Porte	GTP	MIS 7-5	Biochronology and Stratigraphy	Blanc 1958; this work	This work
<i>Equus ferus</i>	Grotta Mario Bernardini - VI	GMB - VI	MIS 7-5	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
<i>Equus ferus</i>	Grotta Uluzzo C - IV	GUC - IV	MIS 7-5	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
<i>Equus ferus</i>	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
<i>Equus ferus</i>	Grotta dei Giganti	GGi	MIS 4	Stratigraphy and Chrono-cultural	Blanc 1958; Aureli & Ronchitelli 2018	This work
<i>Equus ferus</i>	Grotta Santa Croce	GSC	MIS 4	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
<i>Equus ferus</i>	Grotta Laceduzza	Gla	MIS 4	Biochronology and Chrono-cultural	Mecozzi et al. 2019	This work
<i>Equus ferus</i>	Grotta Mario Bernardini - III	GMB - III	MIS 4	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
<i>Equus ferus</i>	Grotta Uluzzo C - III	GUC - III	MIS 4	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
<i>Equus ferus</i>	Grotta Mario Bernardini - II	GMB - II	MIS 3	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
<i>Equus ferus</i>	Grotta Uluzzo C - II	GUC - II	MIS 3	Stratigraphy and Chrono-cultural	Aureli & Ronchitelli 2018; this work	This work
<i>Equus ferus</i>	Cava Spagnulo	CS	MIS 3	Biochronology and Chrono-cultural	Mecozzi et al. 2018	Mecozzi et al. 2018
<i>Equus ferus</i>	Fondo Cattle	FCa	MIS 3	Biochronology and Chrono-cultural	Corridi 1987	Corridi 1987
<i>Equus ferus</i>	Grotta del Cavallo	GCa - F	MIS 3	Radiometric data	Sarti et al. 1998	Sarti et al. 1998
<i>Equus ferus</i>	Tana delle Iene	TI	MIS 3	Stratigraphy and Chrono-cultural	Conti et al. 2010	Conti et al. 2010
<i>Equus ferus</i>	Cardamone	Car	MIS 2	Biochronology and Chrono-cultural	Rustioni et al. 2003	This work
<i>Equus ferus</i>	Fondo Focene	FFo	MIS 2	Stratigraphy and Chrono-cultural	Cancellieri 2017; this work	This work
<i>Equus ferus</i>	Grotta Zinzulusa	GZi	MIS 2	Biochronology and Chrono-cultural	Blanc 1958; this work	This work
<i>Equus ferus</i>	Grotta Paglicci	GP	MIS 2	Radiometric data	Boscato 1994; Berto et al. 2017	Boscato 1994
<i>Equus ferus</i>	SMA-esterno - Gravettian	SMA - G	MIS 2	Radiometric data	Baillis 2015, 2016; this work	This work
<i>Equus ferus</i>	Grotta delle Mura	GMu	MIS 1	Radiometric data	Bon & Boscato 1993	Bon & Boscato 1993

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Tab. 1

Age	Number of specimen				P.value			
	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

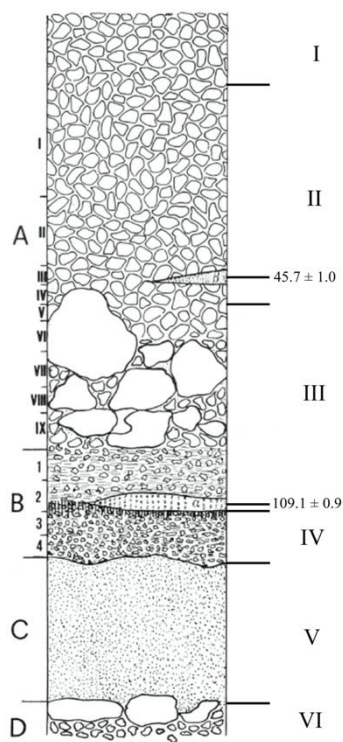
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Tab. 2

Age	Number of specimen				P.value			
	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

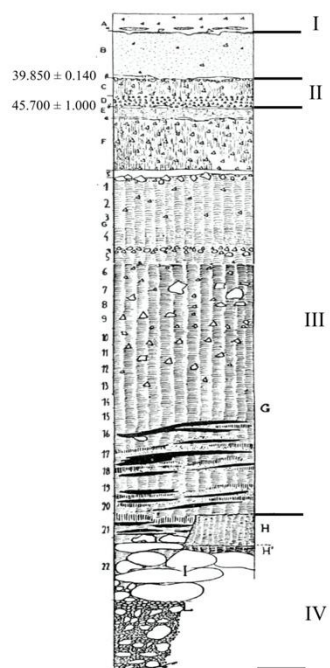
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Tab. 3



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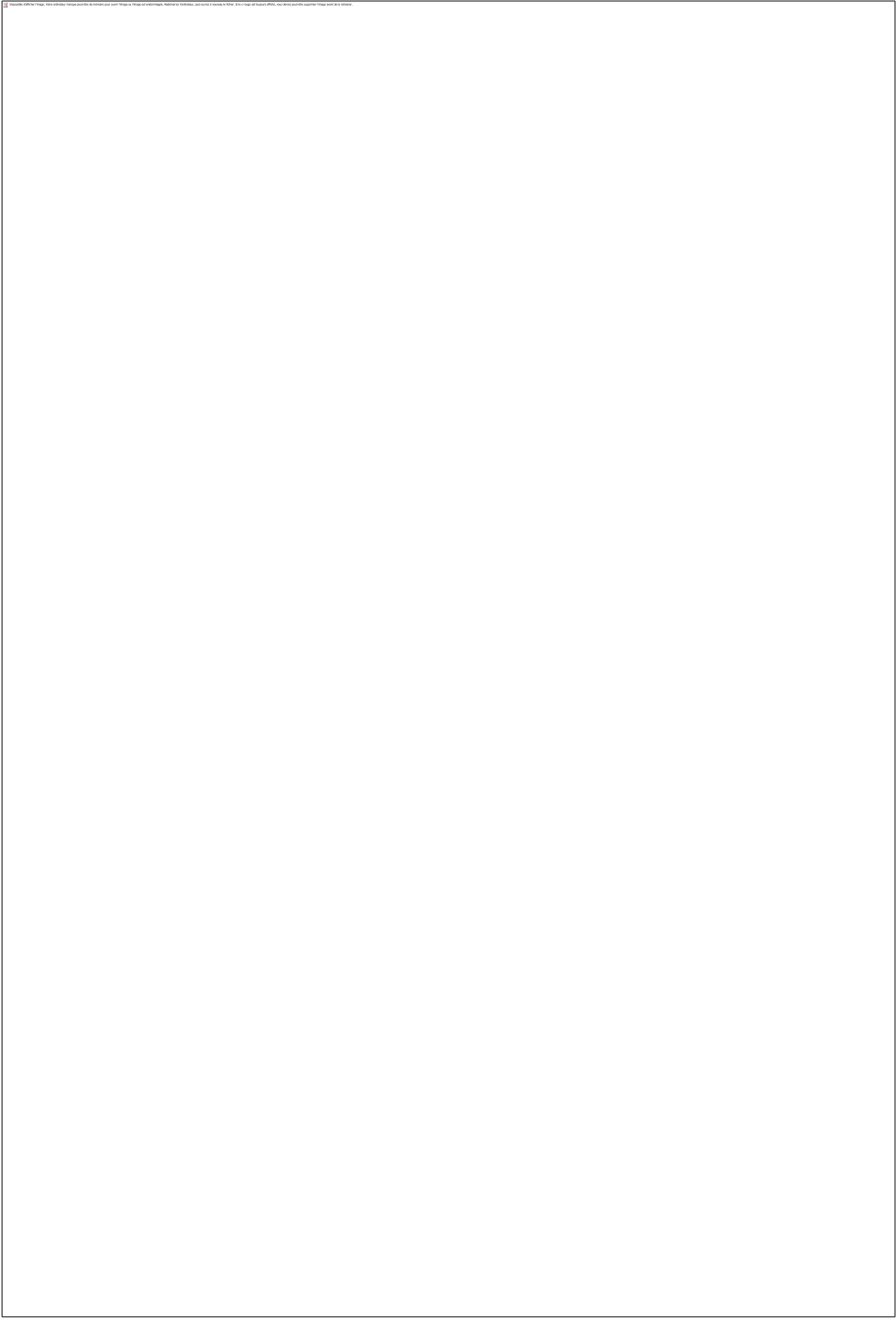
1184 Fig. SD1



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1186 Fig. SD2

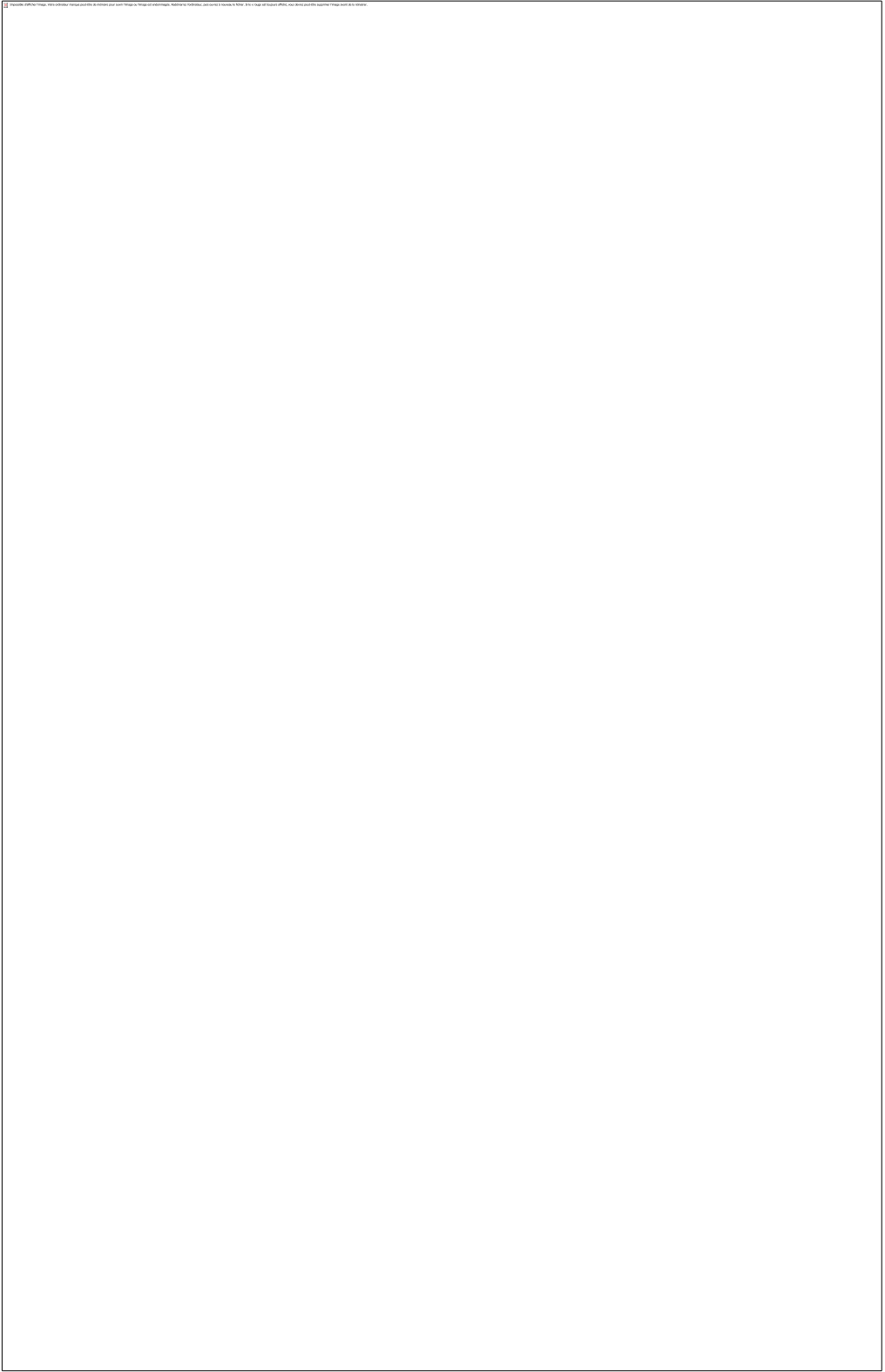
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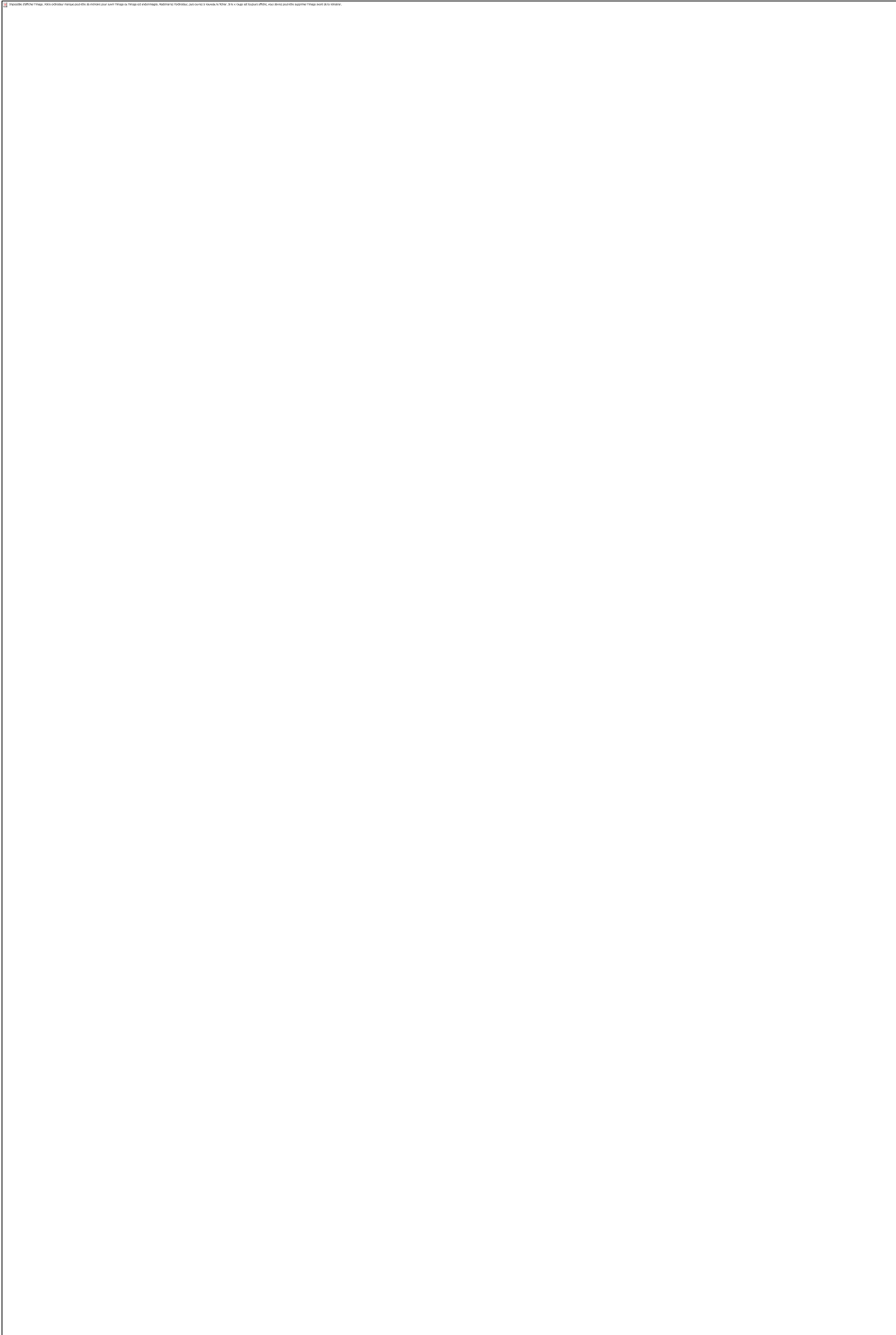
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Fig. SD3



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1191 Fig. SD4



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1193 Fig. SD5

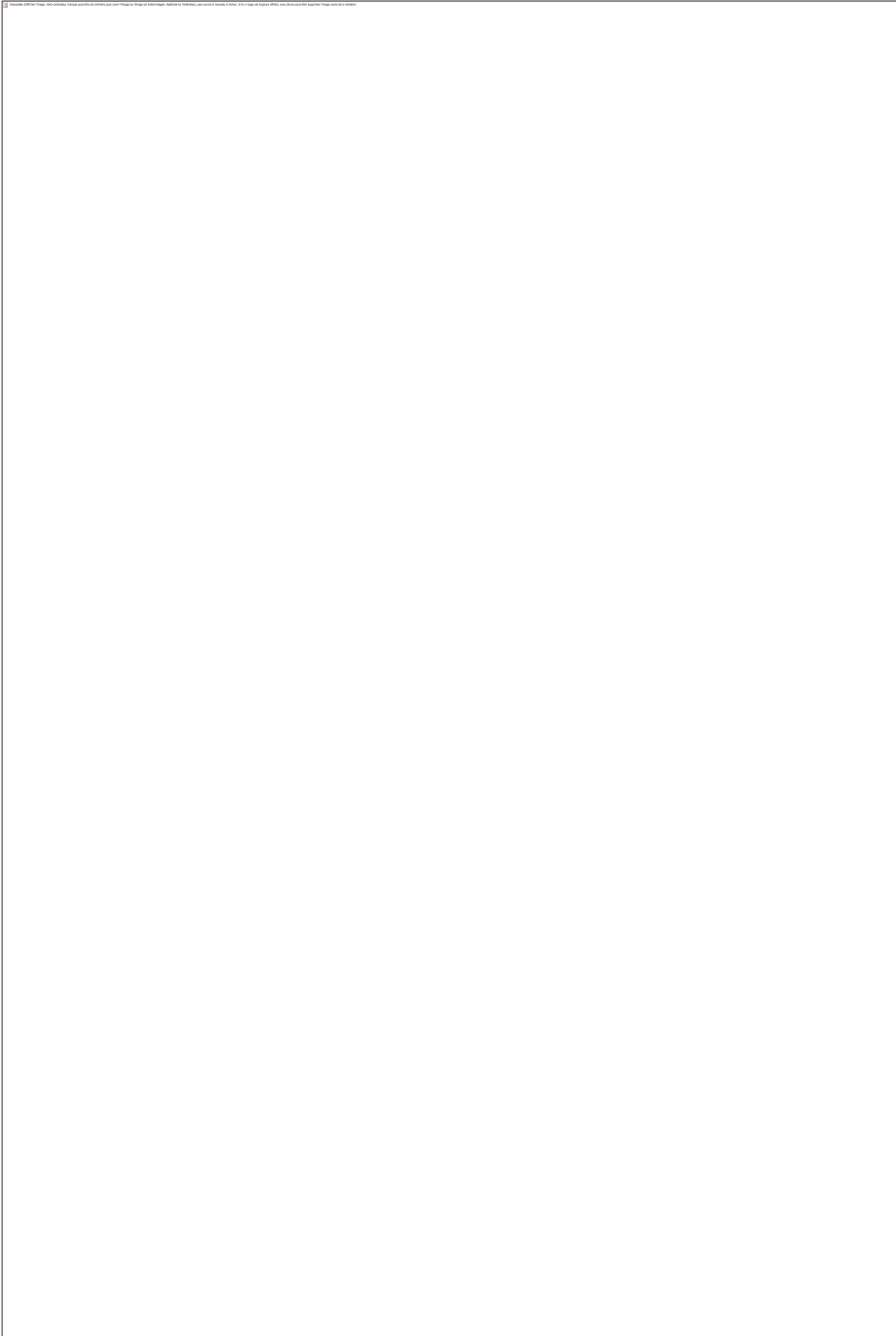


Fig. SD6

Site	Abbreviations	Number of specimen				P.value			
		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
Grotta di Capelvenere	CPv		5	4	1		0.14	0.08	0.44
Grotta delle Tre Porte	GTP	3	2			0.25	0.04		
Grotta Mario Bernardini -VI	GMB - VI	1	4	1		0.22	0.04	0.03	
Grotta del 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
Grotta dei 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 Cattie	FCa	6	25	4	14	0.06	0.00	0.08	0.08
Tana delle Iene	TI	3	3	1	3	0.08	0.02	0.16	0.08
Grotta del 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
Grotta delle Mura	GMu	3	5	3	1	0.08	0.01	0.03	0.22

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1201 Tab. SD1

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Site	Abbreviations	Number of specimen				P.value			
		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 -IV	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 Cattie	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

Tab. SD2

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

Tab. SD3