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► To cite this version:

Antigone Uzunidis, Montserrat Sanz, Joan Daura. Sub-speciation processes of equids in the Iberian Peninsula: ecological strategies and refuge areas. *Quaternary Science Reviews*, 2024, 325, pp.108473. 10.1016/j.quascirev.2023.108473 . hal-04751993

HAL Id: hal-04751993

<https://hal.science/hal-04751993v1>

Submitted on 24 Oct 2024

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1 **Sub-speciation processes of equids in the Iberian Peninsula: ecological strategies and**
2 **refuge areas.**

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4
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9

10 **Abstract**

11

12 *Equus* is a genus that have generated a lot of debate among the scientific community. Its
13 complex taxonomy led to the set-up of many forms that are questioned nowadays. In Upper
14 Pleistocene Europe, several subspecies have been described in order to qualify chronological
15 evolutions or geographical adaptations. In Peninsulas, while several subspecies have been
16 defined, their connection to the main continental equids are not well-known. The site of
17 Canyars in northeastern Iberian Peninsula has yield numerous remains of *Equus caballus* and
18 *Equus hydruntinus* in very good preservation state. According to the mortality profile of *E.*
19 *caballus*, it is likely that they experienced a catastrophic death before being scavenged by
20 biological agencies, such as hyenas. While the European donkey can be attributed to the
21 subspecies *E. h. davidi*, the horse seems to differ from the continental sub-contemporaneous
22 cohorts. The differentiation in the sub-speciation processes between *E. hydruntinus* and *E.*
23 *caballus* may be related to their ecological strategies and dependence to refuge areas.

24

25 **Highlights**

26

27 Canyars' horse morphometric characteristics do not fit in the *E. germanicus-gallicus-arcelini*
28 scheme.

29

30 Canyars *E. hydruntinus* can be attributed to *E. h. davidi* subspecies.

31

32 Iberian Peninsula is part of the core territory of *E. hydruntinus* and is peripheric for *E.*
33 *caballus*.

34

35 Catastrophic events led to the death of Canyars equids

36

37 **Keywords**

38

39 *Equus caballus*; *Equus hydruntinus*; Late Pleistocene; Morphometry; Demography;
40 Palaeoecology

41

42 **1. Introduction**

44 *Equus* is a widespread genus since the Early Pleistocene in Europe (Azzaroli, 1990; Bernor et
45 al., 2021; Cirilli et al., 2022). During the Upper Pleistocene, it is very commonly found in
46 archaeological and palaeontological sites and has been very often predated by human groups,
47 especially Neanderthals (Guadelli, 1987; Rendu et al., 2023; Uzunidis, 2020). At this period,
48 it is represented by two species: *E. caballus* (Linnaeus, 1758) and *E. hydruntinus* (Regalia,
49 1907), the former being often well represented and abundant and the latter, a lot rarer. Both
50 species have been the subject of intense taxonomic debates and many subspecies, morpho- or
51 ecotypes have been described or criticized (Azzaroli, 1990; Cirilli et al., 2022; Eisenmann,
52 1991a; Forsten, 1988; Prat, 1968; Van Asperen, 2013).

53 Cabaloid horses are present in Europe since at least 0.5 Ma (0.6 if we consider the very
54 fragmented specimen from Vallparadis, Spain, Aurell-Garrido et al., 2010; Madurell-
55 Malapeira et al., 2010) in Mauer, Germany, and attributed to the species *E. mosbachensis*
56 (Reichenau, 1915) (Eisenmann, 2006a). The metric variability of Middle and Late Pleistocene
57 horses appears to be similar than the one of *E. przewalskii* or than the one of domestic forms
58 (Van Asperen, 2013) which conduct authors to consider all the cabaloid horses to belong to
59 the same species (Cirilli et al., 2022; Van Asperen, 2013). Qualitative and quantitative
60 observations of teeth and post-cranial bones, however, reveal a higher proportion of stenoian
61 traits in Middle Pleistocene horses that distinguish them from Upper Pleistocene ones such as
62 the proportionally most elongated protocone on the upper third molar compare to the second
63 one, the recurrence of narrow lingual grooves on the lower teeth and of elongated vestibular
64 grooves on the lower molars, a better isometry between the two facets for the navicular bone
65 on the distal view of the talus, the higher rate of absence of the facets for the third cuneiform
66 on the metatarsal and of the trapezoid on the metacarpal (Uzunidis-Boutillier, 2017). During
67 the Upper Pleistocene, several subspecies have been described in continental Western
68 European assemblages, among others: *E. caballus germanicus* (Nehring, 1884), *E. caballus*
69 *gallicus* (Prat, 1968) and *E. caballus arcelini* (Guadelli, 1991). *Equus c. germanicus* is a
70 robust cabaloid horse of medium size which appear during MIS 5 (Boulbes and van Asperen,
71 2019). A reduction of size in horses was observed from MIS 4 to the end of the Pleistocene
72 (Boulbes and van Asperen, 2019; Forsten, 1993; Magniez and Boulbes, 2014) that motivates
73 authors to distinguish steps in this quite linear evolution (Bignon et al., 2005; Guadelli, 1991,
74 1987; Prat, 1968). Other authors, however, consider that the morphological proximity
75 between the three forms is too significant to distinguish subspecies (Eisenmann, 2022), or
76 recognize only two forms, elevated at the specific rank: *E. germanicus* and *E. arcelini*
77 (Eisenmann, 1991a) Here, the subspecies will be considered as illustration of chrono-
78 geographical expression of horses' variability. In the Upper Pleistocene of Iberia one, two
79 cabaloid taxa have been described, both dated from MIS 2: *E. caballus casarensis* (Altuna,
80 1973) in la Cueva de los Casares (Guadalajara, Spain) and *E. caballus antunesi* (Cardoso and
81 Eisenmann, 1989) from several sites (Algar de João Ramos, Fontainhas and Pedreira de
82 Salemas) in Portugal. *Equus c. casarensis* was described from a single distal portion of a
83 metatarsal and its diagnosis rely on the slenderness of the bone and very weak distal width.
84 While *E. c. casarensis* has been included in other works (Alonso, 2015; Maldonado, 1996;
85 Martínez Valle and Fernández Peris, 1989), we have considered here that its description is too
86 scarce and based on too few material to be considered as sufficient. The *E. c. antunesi*

87 subspecies characterisation rely also on very poor material quantity that come from three
88 different locations (Cardoso and Eisenmann, 1989). It is therefore difficult to ensure that the
89 observed characters are representative of a *E. caballus* local evolution, i.e. that a majority of
90 specimens express them within a population. Indeed, in an equid population, it is common to
91 see “archaic” characters reappear (Eisenmann, 2004; Guadelli, 1991; Uzunidis-Boutillier,
92 2017) and a reliable determination can be made only by taking into account their proportions.
93 This subspecies has been considered valid in other works (Fourvel et al., 2015; Iñigo et al.,
94 1998; Maldonado, 1996) but should be re-evaluated in the light of new material. Here, it will
95 be included with cautious for comparison purpose.

96 *E. hydruntinus*, or European wild donkey is a small and slender equid that have been related
97 to *E. hemionus* through genetic analysis (Bennett et al., 2017; Orlando et al., 2009, 2006).
98 More recent ones suggest, however, that they may have been sister taxa (Özkan et al., 2023).
99 Moreover, several morphological features, distinguish them both (Boulbes and van Asperen,
100 2019; Cirilli et al., 2022) and it will be considered here as distinct from *E. hemionus*. In
101 Western Europe, subspecies have also been described for this taxon: *E. hydruntinus minor*
102 (Bonifay, 1991) (Lunel-Viel, France, MIS 7), *E. hydruntinus hydruntinus* (Stehlin and
103 Graziosi, 1935) (Romanelli, Italie, MIS 2) and *E. hydruntinus davidi* (Alimen, 1946) (Saint-
104 Agneau, France, MIS 3). *Equus h. minor* marks the very reduce size of the species which
105 affiliation has been questioned (Azzaroli, 1990; van der Made et al., 2017). *Equus h. davidi*
106 and *E. h. hydruntinus* would be geographical subspecies that can be distinguished by the
107 length of the protocone on the upper teeth more significant in *E. h. davidi* and the reduction of
108 the depth of vestibular groove on lower molars (Alimen, 1946; Boulbes, 2009; Boulbes and
109 van Asperen, 2019; Prat, 1968). From MIS 3 (maybe MIS 4?), the two subspecies would have
110 been separated by the Alps mountain range and experienced independent evolution (Guadelli
111 and Delpech, 2000). The form *davidi* have been found in Upper Pleistocene sites from France,
112 Spain and Portugal (Álvarez-Lao et al., 2017; Boulbes, 2009; Cardoso, 1995).

113 The complexity of equids evolution, especially during the Pleistocene, is related to its eco-
114 morphological flexibility (Forsten, 1988; Uzunidis, 2021; van Asperen, 2010). The taxonomic
115 position of specimens originating from peninsulas is particularly difficult to assess. In Iberia,
116 for Middle and Upper Pleistocene, a least three taxa have been described: *E. caballus*
117 *torralbae* (Prat, 1977), *E. c. casarensis* and *E. c. antunesi*. The connexion between those taxa
118 and the ones describe for continental Europe is unclear. Prat, 1977 indicate that *E. c. torralbae*
119 might correspond to a local expression of *E. steinheimensis*, *E. antunesi* seems to share a
120 proximity with Italian horses from Valdichiana (Eisenmann, 2022). The description of *E. c.*
121 *casarensis* rely on a unique fragmented metacarpal bone and, therefore, cannot be considered
122 as sufficient.

123 The site of Terrasses de la Riera dels Canyars (henceforth Canyars), Gavà, Barcelona, has
124 yield a numerous collection of equids bones in a very good preservation state corresponding
125 to a caballoid horse and *E. hydruntinus* (Daura et al., 2013; Sanz-Royo et al., 2020). The
126 description and comparison of this assemblage with contemporaneous sites will make it
127 possible to account for the specificities of Iberian equids compared to continental specimens.
128 It will thus allow us to question the position of *E. caballus* and *E. hydruntinus* in the
129 framework described for sub-contemporary continental horses. Moreover, the exceptional

130 preservation of the bones has allowed to conduct a demographical study in order to question
131 the conditions of their accumulation.

132

133 **2. Materials and methods**

134

135 *2.1 Terrasses de la Riera dels Canyars site*

136

137 Canyars is located near the city of Gavà (Barcelona, Catalunya, Spain) and is an open-air
138 deposit in the terrace of the Canyars stream (**Supplementary Fig. S1**). The site was excavated
139 in 2007 by the Grup de Recerca del Quaternari (GRQ). Seventeen layers were recognised in
140 the site with the main fossiliferous area being identify as Cala A-Rasa D. More than 5 000
141 large mammals remains were discover in a single sedimentary unit (layer I) corresponding to
142 a filled paleochannel. The unit was radiocarbon dated 34.6 ¹⁴C (~39.6 cal) ka BP,
143 corresponding to Heinrich Stadial (HS) 4 episode, during the MIS 3 and is thought to have
144 been accumulated during a time interval comprised between several decades and less than a
145 millennium (Daura et al., 2013).

146 The assemblage is dominated by equids (*E. caballus* and *E. hydruntinus*), followed by *Bos*
147 *primigenius*, *Cervus elaphus*, *Coelodonta antiquitatis*, *Sus scrofa*, *Capra pyrenaica* and
148 elephantids. Carnivores are also present: *Lynx pardinus*, *Crocuta Crocuta*, *Panthera leo*,
149 *Panthera pardus*, *Ursus arctos*, *Canis lupus*, *Felis silvestris*, *Cuon alpinus* and *Vulpes vulpes*.

150 The site is interpreted as the result of a hyena den in an abandoned meander with a probable
151 contribution of other small predators (Daura et al., 2013; Jimenez et al., 2019; Rosado-
152 Méndez et al., 2015). Some evidence of human activities are also represented by the presence
153 of a few stone tool ascribed to the Aurignacian techno-complex and a bone used as a punch
154 board (Daura et al., 2013; Doyon et al., 2023).

155

156 *2.2 The equids material from Canyars*

157

158 The equids from Canyars have already been the subject of a previous study presenting the
159 differences in the dental morphology of *E. caballus* and *E. hydruntinus* (Sanz-Royo et al.,
160 2020). It is a large collection of at least 27 horses (Minimum Number of Individuals) and four
161 European donkey (Daura et al., 2013) with a very good preservation state. Almost all the
162 bones are well-represented with the notable exception of the smallest ones like the
163 carpal/tarsal or sesamoid bones (**Tabl. 1**).

164

Skeletal element	<i>Equus caballus</i>						<i>Equus hydruntinus</i>						
	Juvenile			Adult			Juvenile			Adult			
	Left	Right	Indet.	Left	Right	Indet.	Left	Right	Indet.	Left	Right	Indet.	
Skull				1	1	2							
Mandibula		1			1	2						2	
D2	7	8						1					
D3-4	11	13						2					
P2				5	4								
P3-4				20	17								
M1-2				18	14								
M3				5	5						1		
d2	3	2						1					
d3-4	5	6						2					
p2				3	2						1	1	
p3-4				8	4						2	4	
m1-2				7	6						2	2	
m3				2	2						1	1	
Scapula				8	2								
Humerus	1			10	10						1	2	
Radius	1			7	10						1	1	
Triquetrum					1						1	1	
Hamatum				1	1						1	1	
Capitatum				2	1						1	1	
Trapezoid				3								1	
Lunatum	1	1		2							2	1	
Scaphoid				3	1						1		
Pisiform				1								1	
Metacarpal		1		23	14						4	1	1
Ph I anterior	1	1		7	2						3	2	
Ph II anterior				6	2						1	4	
Coxal female				6	9								
Coxal male				6	3								
Coxal indet.	3	1		9	7								
Femur	2	1		9	5							2	
Tibia	2	4		13	11	1					3		
Calcaneus	5	3		12	11							2	
Talus	3	2		10	9							4	
Navicular	2	2		2	12							1	
Cuboid	1	1		4	7							2	
First cuneiform	1	2		8	5							4	
Third cuneiform				2	3						1		
Metatarsal	1	2		13	19							4	1
Ph I post	2	1		5	8							2	
Ph II post				5	12							2	
Ph I indet.	2		3			3					1	1	
Ph II indet.		2	2		1	4							

Ph III	1	1	13	15	1	3	2	2
--------	---	---	----	----	---	---	---	---

165 Tabl. 1: Number of identifiable specimens (NISP) of *E. caballus* and *E. hydruntinus* from
166 Canyars par age-class and laterality.

167

168 In this study we will mainly focus on the analysis of the teeth and metapodials morphology
169 that provide a good discrimination between population/species (Bignon et al., 2005; Bignon
170 and Eisenmann, 2006; Eisenmann, 1991b, 1980, 1979, 1979; Uzunidis-Boutillier, 2017). The
171 notation terminology used for metapodials is metacarpal as Mtc and metatarsal as Mtt, for
172 teeth the abbreviation of premolars and molars as P and M respectively with capital letter for
173 upper and lower case for lower followed by the tooth number (e.g. second lower molar = m2;
174 second upper molar = M2).

175 We have described the morphology of both decidual and adult teeth. In each case, we have
176 discarded from the analysis the teeth not enough or too worn. Thus, we have included only the
177 teeth with the occlusal surface fully abraded and discard the ones with erased or partially
178 erased morphological features due to age following the recommendations of (Boulbes, 2010;
179 Cirilli et al., 2023; Fernandez, 2006; Savoy et al., 2012). For bones, we only have considered
180 the ones belonging to fully fused adults. In order to interpret the mortality event(s) that have
181 led to the horses' death, we have compared Canyars patterns to five populations with known
182 death conditions. We have used two modern populations: the horse living one from Pryor
183 Mountains (Montana, USA) and the zebra catastrophic mortality from Akagera (death in a
184 bush fire, Akagera, Rwanda) (Fernandez et al., 2006). Also, three fossil horses' cohorts were
185 compared: two anthropic accumulations, Combe-Grenal (Dordogne, France) and Bau de
186 l'Aubesier (Vaucluse, France) and one hyena den, Fouvent (Haute-Saône, France). All of
187 them were published by (Fernandez et al., 2006) (**Tabl. 2**).

188 The horse cohort from Canyars was compared metrically to ten Upper Pleistocene western
189 European fossil cohorts corresponding to several subspecies or forms: *E. c. germanicus* (Villa
190 Seckendorff, Cave aux Endives, Portel-Ouest), *E. c. gallicus* (Siréjol, Jaurens, Solutré), *E. c.*
191 *arcelini* (Solutré), *E. c. antunesi* (Algar de João Ramos, Fontainhas, Pedreira de Salemas,
192 Cueva de la Carihuela) and one other catalan locality (Teixoneres) (**Tabl. 2**).

193 The *E. hydruntinus* was also compared to nine other sites that have yield different subspecies:
194 *E. h. minor* (Lunel-Viel), *E. h. hydruntinus* (Tana delle Iene, Romanelli) and *E. h. davidi*
195 (Valorgues, Félines-Termenès, Teixoneres, Cornille, La Balauzière and Flandin 2) (**Tabl. 2**).

196

Site	Location	Chronology	Species	Type of analysis	References
Villa Seckendorff	Germany	MIS 5/4	<i>E. c. germanicus</i>	Palaeontological	(Cramer, 2002; Forsten and Ziegler, 1995)
Portel-Ouest	France	MIS 3	<i>E. c. germanicus</i>	Palaeontological	(Vezian, 2014)
Cave aux Endives	France	MIS 3	<i>E. c. germanicus</i>	Palaeontological	A. Uzunidis, unpublished data
Siréjol	France	MIS 3	<i>E. c. gallicus</i>	Palaeontological	(Eisenmann, n.d.)
Teixoneres	Spain	MIS 3	<i>E. caballus</i>	Palaeontological	A. Uzunidis, unpublished data
Jaurens	France	MIS 3/2	<i>E. c. gallicus</i>	Palaeontological	(Eisenmann, n.d.; Mourer-Chauviré, 1980)
Algar de João Ramos, Fontainhas, Pedreira de Salemas	Portugal	MIS 2	<i>E. c. antunesi</i>	Palaeontological	(Cardoso and Eisenmann, 1989)
Cueva de la Carihuela	Spain	MIS 2	<i>E. c. antunesi</i>	Palaeontological	(Maldonado, 1996)
Solutré_Solutrean levels	France	MIS 2	<i>E. c. gallicus</i>	Palaeontological	(Guadelli, 1991)
Solutré_Magdalenian levels	France	MIS 2	<i>E. c. arcelini</i>	Palaeontological	(Guadelli, 1991)
Lunel-Viel	France	MIS 7	<i>E. h. minor</i>	Palaeontological	(Bonifay, 1991; N. Boulbes database)
Tana delle Iene	Italy	MIS 4	<i>E. h. hydruntinus</i>	Palaeontological	(Conti et al., 2010)
Teixoneres	Spain	MIS 3	<i>E. h. davidi</i>	Palaeontological	A. Uzunidis, unpublished data
Flandin 2	France	MIS 3	<i>E. h. davidi</i>	Palaeontological	A. Uzunidis, unpublished data
Romanelli	Italy	MIS 2	<i>E. h. hydruntinus</i>	Palaeontological	(Eisenmann, n.d.; Stehlin and Graziosi, 1935)
Balauzière	France	MIS 2	<i>E. h. davidi</i>	Palaeontological	(Bonifay, 1966)
Valorgues	France	MIS 2	<i>E. h. davidi</i>	Palaeontological	(Boulbes and Rillardon, 2010)
Cornille	France	MIS 2	<i>E. h. davidi</i>	Palaeontological	(Bonifay and Lecourtois-Ducgoninaz, 1976)
Félines-Termènes	France	MIS 1	<i>E. h. davidi</i>	Palaeontological	(Eisenmann and Patou, 1980)
Bau de l'Aubesier	France	MIS 7/6	<i>E. mosbachensis</i>	Demographical	(Fernandez et al., 2006)
Combe-Grenal	France	MIS 5/3	<i>E. c. germanicus</i>	Demographical	(Fernandez et al., 2006)
Fouvent	France	MIS 3	<i>E. c. germanicus</i>	Demographical	(Fernandez et al., 2006)
Pryor Mountains	USA	Actual	<i>E. caballus</i>	Demographical	(Fernandez et al., 2006)
Akagera	Rwanda	Actual	<i>Equus burchelli bohemi</i>	Demographical	(Fernandez et al., 2006)

199 **Tabl. 2: Summary of the sites used in this work with their geographical positions, date, type of**
200 **analysis they were used for and the references of the original works.**

201
202 *2.3 Methods*

203
204 *E. caballus* is also lately refer to as *E. ferus*, following the guidelines of the International
205 Commission on Zoological Nomenclature (ICZN (International Commission on Zoological
206 Nomenclature), 2003). The goal of the ICZN was to refer to the species according to the first
207 description of a wild specimen. In the case of the horse, the description selected was the one
208 made by Boddaert in 1784 of tarpans (Boddaert, 1784). The description suggested by
209 Boddaert was rather limited to the colour of the coat of two castrated individuals. Thus, this
210 too-brief description does not seem to concern wild animals and the change of name and
211 holotype do not meet the objective of the ICZN like other work already underlined (Brugal et
212 al., 2020; Eisenmann, 2006b; Guadelli and Delpech, 2000). In this work, we will thus,
213 conserve the old nomenclature and refer to the horses as *E. caballus*.

215 All the measurements were made using a digital calliper. All the statistical analysis were
216 performed using R v. 4.2-Rstudio v4.1.3.

217

218 2.3.1 Age estimation and mortality pattern

219

220 The mortality curves were build using the Number of Identified Specimens (NISP) (Lyman,
221 2008) that allow to consider more individuals than the MNI since sample size around 30
222 individuals are necessary to interpret demographic features (Kurtén, 1954a, 1954b, 1953). The
223 NISP is also regularly used in other similar works (Fernandez et al., 2006; Fernandez and
224 Boulbes, 2010; Pérez-Pérez et al., 2021). We took into account isolated upper teeth and cheek
225 teeth set in the maxilla. We used the method published by (Fernandez and Legendre, 2003) to
226 estimate the age of the individuals. This method uses the height of each type of tooth (P2, P3-
227 4...) to assign them to an age interval through regression analysis. An uncertainty is also
228 given for each age estimation. The crown height was measured on the mesostyle. In this work,
229 juvenile correspond to the age-class 0-3 years, sub-adult from 3 to 6 years (mean age of the
230 first pregnancy for mares), adult encompass 6 to 18 years (period of sexual activity) and the
231 senile are above 18 years when the reproduction is less common (Ransom et al., 2016).

232 The mortality pattern of Canyars horses was analysed using four indicators (frequency,
233 mortality, survival and killing factor) and following the methodology published by Fernandez
234 et al., 2017, 2006. The frequency rate corresponds to the proportion of individuals of the
235 cohort dying in each age interval. The mortality rate refers to the mortality that occur from
236 one age group to the next (from x to x+1). The survival rate indicates the rate of individuals
237 that survived from age x to age x+1. The killing factor is an index of the “intensity” of
238 mortality per each age group.

239

240 2.3.2 Sexual determination

241

242 Sexual dimorphism is almost absent in equids (Barone, 1986; Van Asperen, 2013). Some
243 criteria, however, allow a sexual determination but require a very good preservation as this is
244 the case in Canyars.

245 For *E. hydruntinus*, we use the presence of canine as a criterion to discriminate male from
246 female. This tooth is present in stallion and usually absent, or very reduced in mares (Barone,
247 1986).

248 For *E. caballus*, we made qualitative observations on the coxal bones that were more
249 numerous than the canines. Three criteria were used (Barone, 1986; Coumont, 2006): 1) the
250 semi-lunar surface is well exposed on the ischium bone in males, whereas it is not in females;
251 2) the pubic spine is rounded, thick and convex on its dorsal side in males. In females the
252 pubic bone is flattened dorsoventrally with a sharp cranial edge and a concave endopelvic
253 surface; 3) the sciatic spine is less marked in males than in females.

254

255 2.3.3 Morphometrical analysis

256

257 All the measurements were taken according to the protocol established by Véra Eisenmann
258 (Eisenmann et al., 1988), published on her website (Eisenmann, n.d.) and already used in

259 numerous works (Boulbes, 2010; Cirilli et al., 2022; Eisenmann, 1979; Uzunidis, 2021;
260 Uzunidis-Boutillier, 2017). The teeth were measured on the enamel without the cement.
261 The qualitative observations rely on morphological criteria already discussed in previous
262 works: (Azzaroli, 1990; Bonifay, 1991, 1980, 1966; Boulbes, 2010, 2009; Brugal et al., 2020;
263 Cramer, 2002; Eisenmann, 1980, 1979; Fernandez, 2006; Guadelli, 1991, 1987; Guadelli and
264 Prat, 1995; Langlois, 2005; Prat, 1968; Uzunidis-Boutillier, 2017).

265

266 2.3.4 Statistical analysis

267

268 The relative proportions of the limb bones were analysed using log-ratio diagrams (Simpson,
269 1941). This graphic allows us to compare the differences in size and conformation between
270 different populations based on measurements standardised on a referenced population. Here,
271 the standard used for comparison is *E. hemionus hemionus*, published by V. Eisenmann on her
272 website (Eisenmann, n.d.). This analysis was used to include comparative populations only
273 published through mean data.

274 The morphometrical variability on equid metapodial was investigate though Principal
275 Component Analysis (PCA) using a spearman coefficient which is more suitable for small
276 effective. Since PCA do not accept incomplete data, several bones were rejected prior to the
277 analysis. For *E. hydruntinus*, we focus only on the distal part of the metapodials in order to
278 avoid too much rejection. This includes four measurements: the sus-articular and articular
279 breadth and the distal extremity, the depth of the sagittal crest and greatest depth of the medial
280 condyle.

281 To identify clusters of related populations, we used the Rstudio function *hclust* to perform a
282 hierarchical agglomerative clustering (HAC) with the Ward's minimum variance method
283 using the squared Euclidian distance and the first two components of the PCA that in all case
284 represented at least 70% of the variance. This last analysis was performed only for *E. caballus*
285 for which enough comparative populations were available.

286

287 **3. Results**

288

289 *3.1 Demographical description of the Equus caballus and Equus hydruntinus from Canyars*

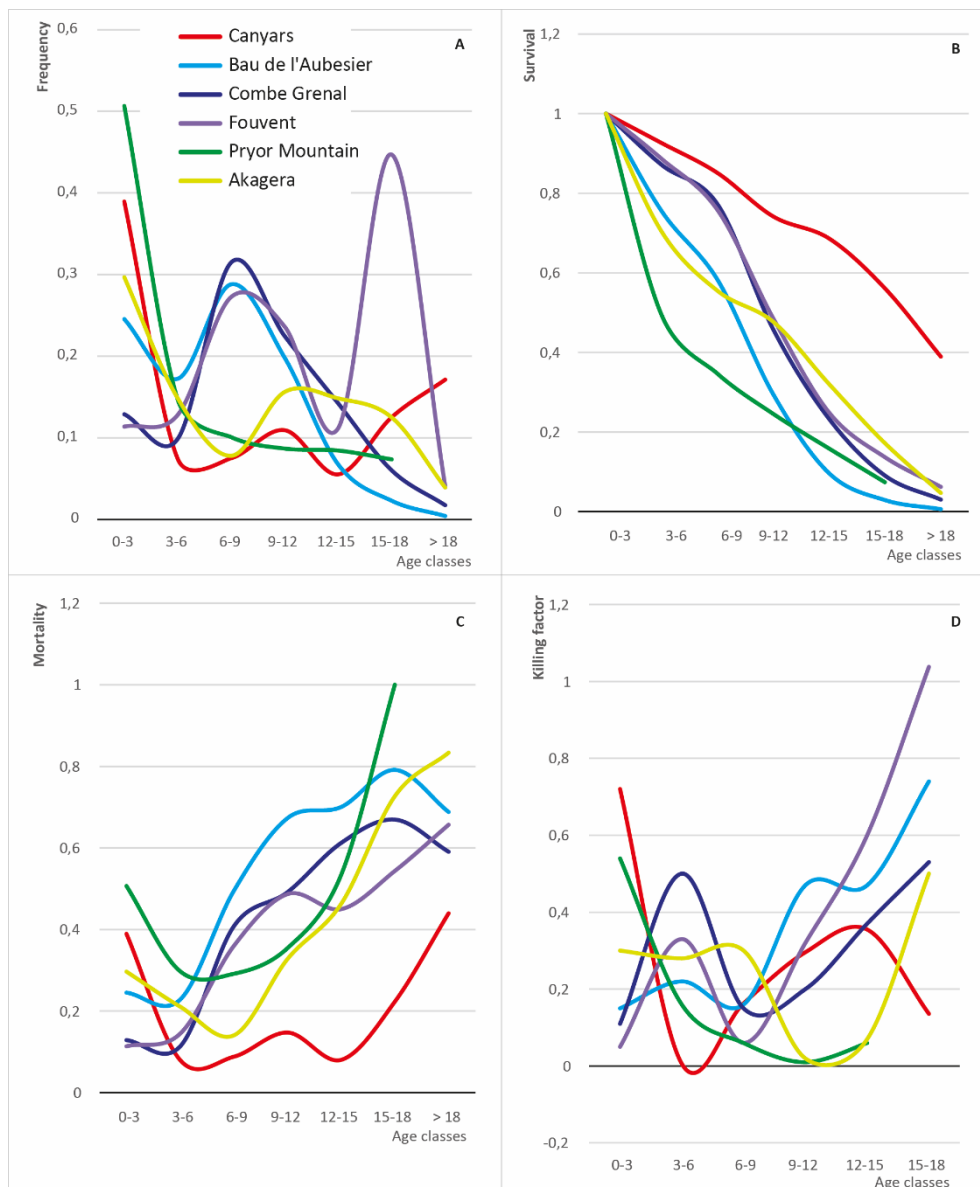
290

291 According to the metapodials, the minimum number (MNI) of horses in Canyars is estimated
292 to be 27 individuals (Daura et al., 2013). The number of identified specimens (NISP)
293 according to the teeth is almost similar with at least 28 individuals.

294 Of these 28 individuals, 40% would correspond to the juvenile age class, between 0 and 3
295 years. Almost 16% would be senile (over 18 years old). The sub-adult (3-6 years) and adult
296 (6-18 years) age groups represent a combined 44.6% but rarely exceed 10% per 3-year age
297 group (**Fig. 1**)

298 Thus, in Canyars horse population, the very young and very old individuals are better
299 represented in term of frequency (Fig. 1A). It indicates a higher mortality in this 0-3 years-old
300 age class as well as for the individuals older than 15 years old (Fig. 1B). Also, among the
301 younger adults, there is a slightly higher mortality for the 9-12 years old age class. The
302 survivorship obtained for Canyars is abnormal since the mortality in the 3-9 years age-classes

303 appears to be higher than in natural mortality events (in Pryor Mountains and Akagera) but
 304 not as significant in carnivore dens (Fouvent) or anthropic sites (Bau de l'Aubesier, Combe-
 305 Grenal) (Fig. 1C). So, as expected, the killing factors are distorted in Canyars compare to
 306 living population (Pryor Mountain) (Fig. 1D). The young adults (3-6 years old) are under-
 307 represented in comparison with the other age-classes, especially the very young and above 15
 308 years old age classes. The stability index R_0 in Canyars is also a strong indicator of the
 309 instability of the population since it corresponds to 1.99 (**Supplementary Tabl. S1**). It is thus
 310 very high in comparison with the living population without distortion of Pryor Mountain and
 311 it is closer to the values of the catastrophic event of Akagera.
 312



313
 314 **Fig. 1:** Mortality and survivorship curves of fossil horses from Canyars compare to
 315 Neandertal contexts (Bau de l'Aubesier, Combe-Grenal), a hyena den (Fouvent) and feral
 316 horse populations (Akagera, Pryor Mountain). A: frequency; B: survival; C: mortality; D:
 317 killing factor.
 318

319 Since the bones from Canyars were exceptionally well preserved, it was possible to estimate
320 the sex of some horses based on their coxal morphology. We only focus on totally fused coxal
321 bones belonging to fully adult horses, meaning for this bone, above 5 years old (Barone,
322 1986). Nine left coxal bones were attributed to mares and six right coxal bones were
323 attributed to stallions. Thus, for a cohort of at least 28 individuals (from all age class), it was
324 possible to determine the sex of 15 adult individuals giving a sex-ratio of 1:0.66 in favour of
325 females.

326

327 The European donkey, *Equus hydruntinus* is not as well represented as the horse in Canyars
328 with a MNI of four individuals according to the metapodials (Daura et al., 2013). Based on
329 the teeth, it was possible to estimate the age of three of them. One individual is a juvenile of
330 less than 3 years, another is a full adult of about 13,9 years ($\pm 1,01$ year) and the last a senile
331 of about 24,9 years ($-2,3/+2,25$ years). Thus, the *E. hydruntinus* cohort of Canyars is quite
332 heterogeneous in its age repartition.

333 The presence or the absence of canines have been observed on two mandibula symphyses.
334 Since, canines are exceptional in equids female (Barone, 1986), symphyses without any were
335 attributed to female and symphyses with well-expressed canines, to male. Thus, at least one
336 male and one female are represented in Canyars *E. hydruntinus* cohort.

337

338 *3.2 Morphometrical description of the Equus caballus from Canyars*

339

340 3.2.1 The skull

341

342 A fragmented horse skull was discovered in Canyars with the entire jugal teeth row complete,
343 the maxilla as well as the frontal bone conserved (**Fig. 2**). The nasal bones, orbits and
344 zygomatic arches are partial. On the caudal part of the nasal bone, from a dorsal point of
345 view, a very light depression in the middle of the bone is visible while it appears to be better
346 expressed at least in the Middle Pleistocene caballine from Lunel-Viel, Les Rameaux and
347 Camp-de-Peyre (Bonifay, 1980; Guadelli and Prat, 1995; Uzunidis-Boutillier, 2017). From a
348 lateral point of view, the frontal bone is straight without any frontal bulge that can be frequent
349 in zebra or Middle Pleistocene horses (Guadelli and Prat, 1995; Uzunidis-Boutillier, 2017).
350 The zygomatic and preorbital fossa are not very well marked. The vertical line from the
351 rostral edge of the orbit meets the maxillary bone right above the metastyle of the M3 like it is
352 common in current horses while it passes way backward the tooth for *E. stenonis* or Middle
353 Pleistocene horses (Bonifay, 1980; Gromova, 1949; Guadelli and Prat, 1995; Uzunidis-
354 Boutillier, 2017).

355

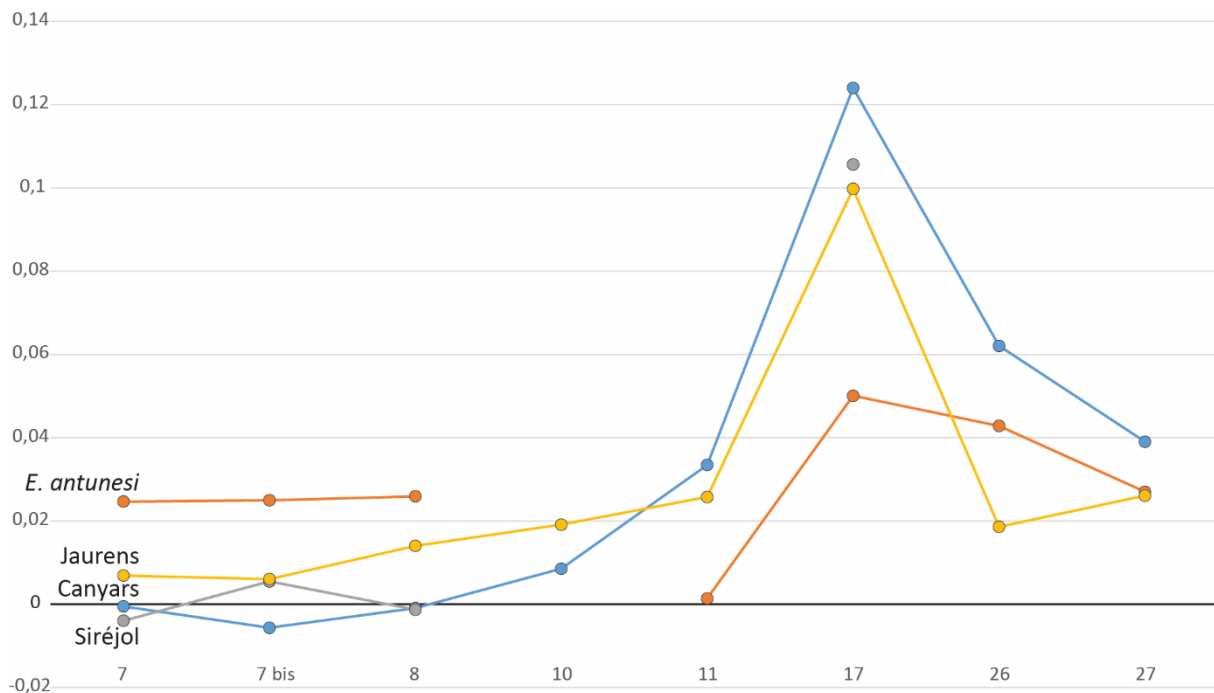


356
 357 **Fig. 2:** *Equus caballus* skull (site #2924) and mandibles (site #1659) from Canyars. A.
 358 Ventral view. B. Left lateral view. C. Dorsal view of skull. D Right lateral view of the
 359 mandibles. E Occlusal view. F Detailed occlusal view of upper dentition. G Detailed occlusal
 360 view of lower dentition (right side).

361
 362 Metrically, the skull size of the individual from Canyars is comparable to the ones from the *E.*
 363 *c. gallicus* of Jaurens and Siréjol (**Fig. 3; Supplementary Tabl. S2**). They are also
 364 comparable in proportion: they are characterised by a relatively short jugal teeth row with a
 365 similar ratio between the premolar and molar rows. The facial breadth taken at the rostral end
 366 of the facial crests is wide. While the skull of *E. c. antunesi* is comparable by size to the other
 367 ones, it displays very different proportion with a longer tooth row compare to a very narrow
 368 facial breadth.

369 Also, the horse from Canyars, Jaurens and Siréjol are characterized by a wide muzzle when it
 370 is very narrow for *E. c. antunesi*.

371



372 Fig. 3: Log ratio diagram comparing the dimensions of the horse's skull from Canyars,
 373 Fontaihnas, Siréjol and Jaurens. Reference *E. hemionus* (Eisenmann, n.d.). References for the
 374 measurements: V. Eisenmann (Eisenmann, n.d.): 7: premolar length; 7bis: molar length; 8:
 375 length of the cheek teeth; 10: greatest choanal breadth; 11: facial breadth; 17: muzzle breadth
 376 at the posterior border of the I3; 26: facial height between P4 and M1; 27: facial height behind
 377 M3.
 378

379
 380 3.2.2 The upper teeth
 381

382 On the upper teeth, the interstylar portion of the paracone is almost only convex on the D2
 383 (90%) and P2 (88,88%) while it is often concave on the P3-4 (70,59%), M1-2 (80,64%) and
 384 the M3 (66,66%) (**Fig. 2; Supplementary Fig. S2**). The interstylar portion of the metacone is
 385 more often concave on the D2 (60%), P2 (50,55%), P3-4 (79,41%) and the M1-2 (77,42%)
 386 and more regularly flat on the D3-4 (87,5%) and the M3 (44, 44%). The protocone is almost
 387 always elongated and bilobed on the D2 (54,55%), D3-4 (75%), P3-4 (82,35%), M1-2
 388 (62,5%) and the M3 (55,55%). On the P2, it is more regularly round (66,67%). The parastyle
 389 is always board and can be double on the D2 and the D3-4 (100%) as well on the P3-4
 390 (82,35%). On the P2 (55,55%), M1-2 (96,77%) and M3 (88,89%) it is more often simple. The
 391 mesostyle is always board on the D2, D3-4, P2 and P3-4 and mostly on the M1-2 (93,75%)
 392 and the M3 (88,88%). It is always double on the D2, D3-4 and P2 and mostly double on the
 393 P3-4 (91,43%). It is more regularly simple on the M1-2 (90,62%) and the M3 (66,66%). The
 394 metastyle is always simple and narrow. The fossette inside the paracone are not very wrinkled
 395 with a mean of three folds on its distal portion for all the teeth. The “pli caballine” is mostly
 396 well expressed on the D2 (55,55%), D3-4 (71,43%), P2 (66,67%) and the P3-4 (78,12%). It is
 397 absent on almost all the M1-2 (86,67%) and not well-marked on the M3 (62,5%). On the two
 398 M2 from the skull (#2924), the hypoglyphs appear isolated (**Fig. 2**) but discrete features were
 399 mostly absent in Canyars cohort.

400 The evolution of the protoconic index of the horse from Canyars shows a moderate increasing
401 of the index from the P3-4 to the M1-2 which is comparable to the one display by *E. c.*
402 *germanicus* (Portel-Ouest, Cave aux Endives) and the others Iberian horses (Cueva de la
403 Carihuela, *E. c. antunesi* and Teixoneres) (**Supplementary Fig. S3**). It is however, more
404 significant than for *E. c. arcelini* (Solutré) and *E. c. gallicus* (Siréjol) and less significant than
405 for other cohorts of *E. c. gallicus* (Jaurens, Solutré). Like generally for Upper Pleistocene
406 caballoid horses, the index decrease on the M3 (Boulbes, 2010; Guadelli, 1987; Uzunidis-
407 Boutillier, 2017). This is not the case for several cohorts and among them *E. c. antunesi*. The
408 length of the protocone on M3 on this taxon was used as a criteria to describe it (Cardoso and
409 Eisenmann, 1989). Other authors, however, warn to be cautious with this index when few
410 teeth were available suggesting that considering the high variability in horses' morphology,
411 only the tendencies of a large cohort could display trustful results (Guadelli, 1991, 1987).

412
413 In term of general size, the P3-4 and M1-2 of the horses from Canyars are quite small and
414 similar in size to the other populations from Iberia (Cueva de la Carihuela, *E. c. antunesi* and
415 Teixoneres) as well as the French ones from Jaurens (**Supplementary Tabl. S3;**
416 **Supplementary Fig. S4**). The teeth from the other French populations of *E. c. germanicus*
417 (Portel-Ouest, Cave aux Endives), *E. c. gallicus* (Siréjol, Solutré) and *E. c. arcelini* (Solutré)
418 are larger, both by the total length of the teeth and the length of their protocone.

419

420 3.2.3 The lower teeth

421

422 On the decidual lower teeth, the lingual groove is well-open ($d2 = 100\%$; $d3-4 = 81,82\%$), the
423 vestibular groove does not often cross the isthmus ($d2 = 100\%$; $d3-4 = 62,5\%$) and the pli
424 ptychostylid is always well-developed. The protostylid is never present.

425 On the definitive lower teeth (**Fig. 2**), the lingual groove is flared on the p2 (100%) and the
426 m3 (75%), can be equally sharp or flared on the p3-4 (50%) and mostly sharp on the m1-2
427 (60%). The hypoconid is always concave on the p2 and p3-4 and mostly concave on the m1-2
428 (69.23%). On the m3, it is mostly flat (50%). The protoconid is always convex on the p2, p3-4
429 and m3 and can be concave on the m2 (8.33%). The metastylid is mostly triangular ($p2 =$
430 100% ; $p3-4 = 83,33\%$; $m1-2 = 90\%$; $m3 = 75\%$). The pli ptychostylid is lightly expressed ($p2 =$
431 75% ; $p3-4 = 50\%$; $m3 = 75\%$) or can be totally absent on the m2 (present = 11.1%; lightly
432 expressed = 44.44%; absent = 44.4%). The vestibular groove never crosses the isthmus on the
433 p2 and rarely on the p3-4 (72.72%). On the m2, it is mostly elongated, beyond the isthmus
434 (88.89%) while it can be equally short (do not cross the isthmus) or elongated on the m3
435 (50%). The pli protostylid is always present on the p2, p3-4 and m1-2 and almost always on
436 the m3 (66.67%). The protostylid is never present.

437 The size of the p3-4 and m1-2 display the same characteristics as their upper counterpart
438 (**Supplementary Tabl. S4; Supplementary Fig. S5**). The size of the specimens from the
439 Iberian Peninsula and of some French localities like Jaurens is reduced compare to the *E. c.*
440 *germanicus* from the Portel-Ouest.

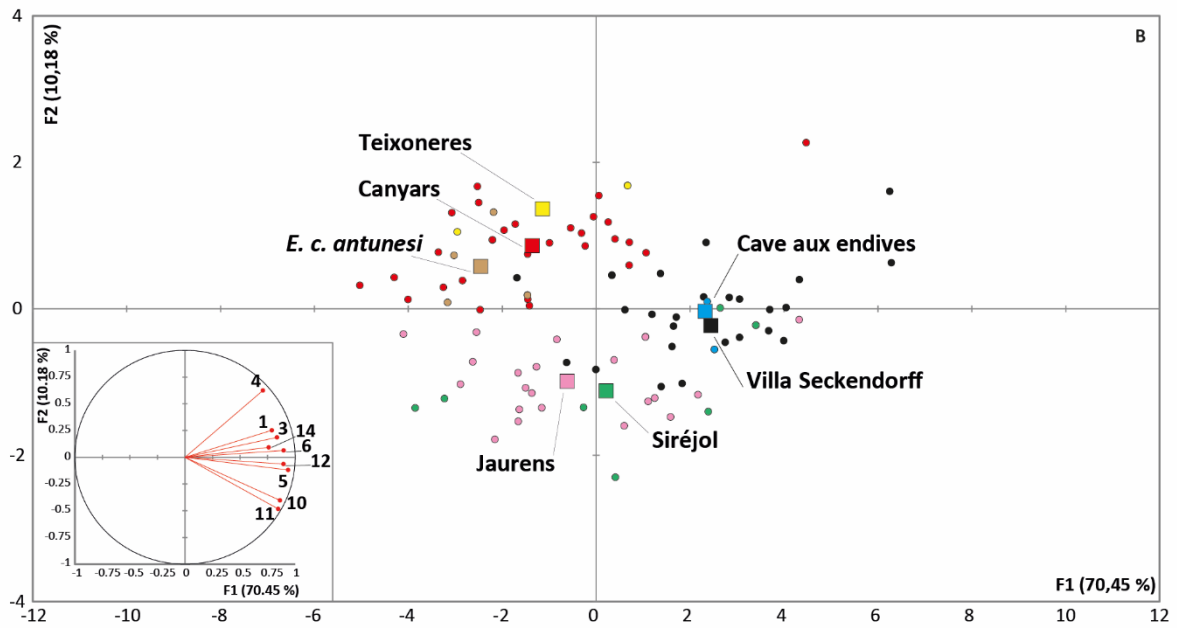
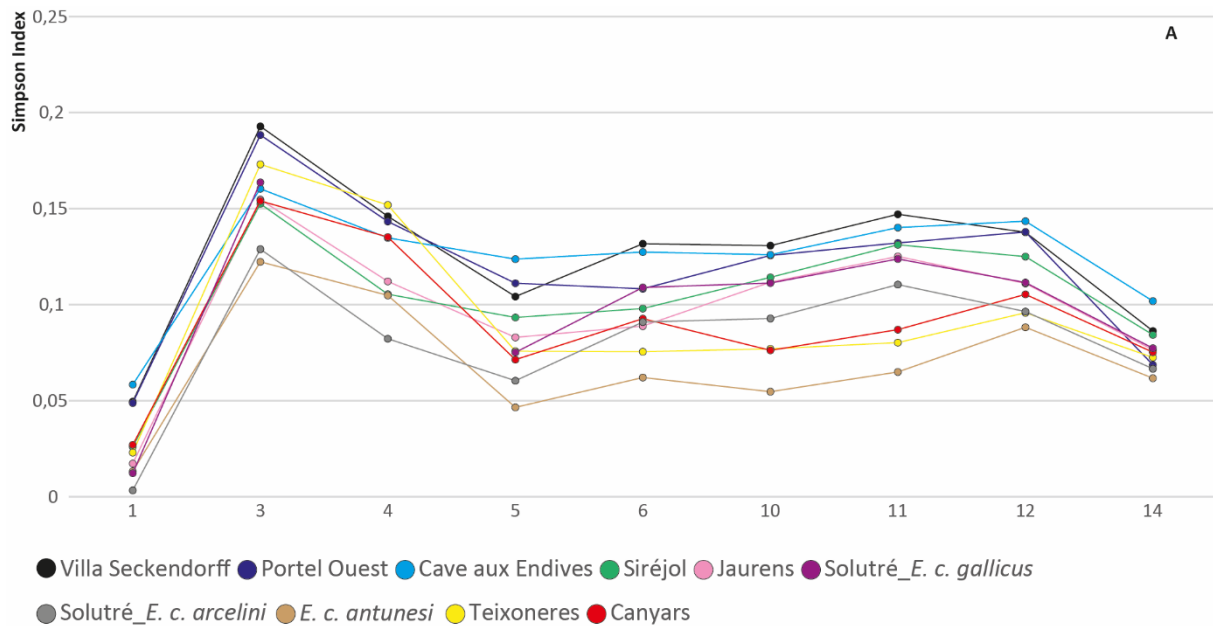
441

442 3.2.4 The metacarpal bones

443

444 On the metacarpal bones (**Supplementary Fig. S6**), the palmar depression on the distal
445 portion of the diaphysis is almost never expressed (71.87%) like it is the case on true
446 caballoid horse by opposition with stenonian or Middle Pleistocene ones (Boulbes, 2010;
447 Gromova, 1949; Prat, 1980; Uzunidis-Boutillier, 2017). The facet in connexion with the
448 trapezoid is also mostly present and well-expressed (78.95%) and the facet for the hamatum
449 bone, always inclined. Only one vestigial metacarpal (a second one) was found fused to the
450 third metacarpal.

451 The metacarpal bones of the horses from Canyars are short, of a similar size of the other
452 Iberian horses from Teixonerres and *E. c. antunesi* and of the *E. c. gallicus* from jaurens,
453 Siréjol and Solutré. They are smaller compare to the *E. c. germanicus* from Villa Seckendorff,
454 Cave aux Endives and Portel-Ouest but larger compare to the *E. c. arcelini* from Solutré
455 (**Supplementary Tabl. S5; Fig. 4**). Compare to the German and French specimens, the
456 Iberian ones from Canyars, Teixonerres and *E. c. antunesi* are characterised by a rounder form
457 in general with proportionally a larger thickness of the proximal and distal extremities andof
458 the diaphysis (**Fig. 4**).



459
 460
 461 Fig. 4: A: Log ratio diagram comparing the dimensions of the horse's metacarpals bones from
 462 Canyars to other Western European Upper Pleistocene cohorts. Reference *E. hemionus*
 463 (Eisenmann, n.d.). B: Principal component analysis (PCA) with measurements of horse third
 464 metacarpal from Canyars and other Western European Upper Pleistocene cohorts. Circle =
 465 individuals; square = centroid of each cohort. 1: maximal length; 3: breadth at the middle of
 466 the diaphysis; 4: depth of the diaphysis at the same level; 5: maximal proximal breadth; 6:
 467 maximal proximal depth; 10: Distal sus-articular breadth; 11: distal articular breadth; 12:
 468 depth of the sagittal crest; 14: greatest depth of the medial condyle.

469
 470 The ratio between the distal sus-articular width and the largest articular width, or “caballine
 471 index” can also be a good indicator of the evolution status of horses' cohorts. Like generally
 472 for the Upper Pleistocene horses, this value is below 100, meaning that the articulation is

473 wider than the tubercles over it (**Supplementary Fig. S7**). More “archaic” horses usually
474 display a more significant value (Boulbes and van Asperen, 2019; Eisenmann, 1979;
475 Fernandez, 2006; Sondaar, 1968; Uzunidis-Boutillier, 2017).

476 The metacarpal bones of the horses from Canyars are robust like this is the case for the horse
477 from Teixoneres which display an even larger slenderness index (**Supplementary Fig. S7**).
478 This is not the case for *E. c. antunesi* which is very slender. Among French and German
479 specimens, the slenderness index is variable with robust metacarpal comparable with those
480 from Teixoneres and Canyars at Portel-Ouest, Jaurens, Siréjol and Villa Seckendorff, and
481 more slender ones like at Cave aux Endives. The metacarpal slenderness variations have been
482 linked to ecomorphological adaptations (Boulbes and van Asperen, 2019; Eisenmann, 1984;
483 Gromova, 1949; Uzunidis, 2021).

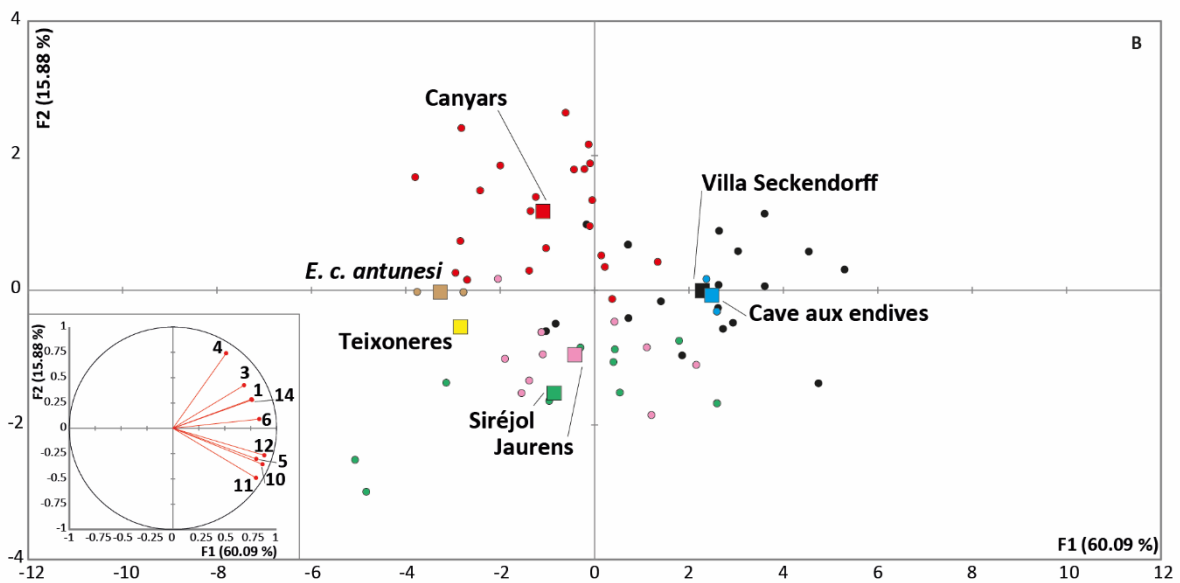
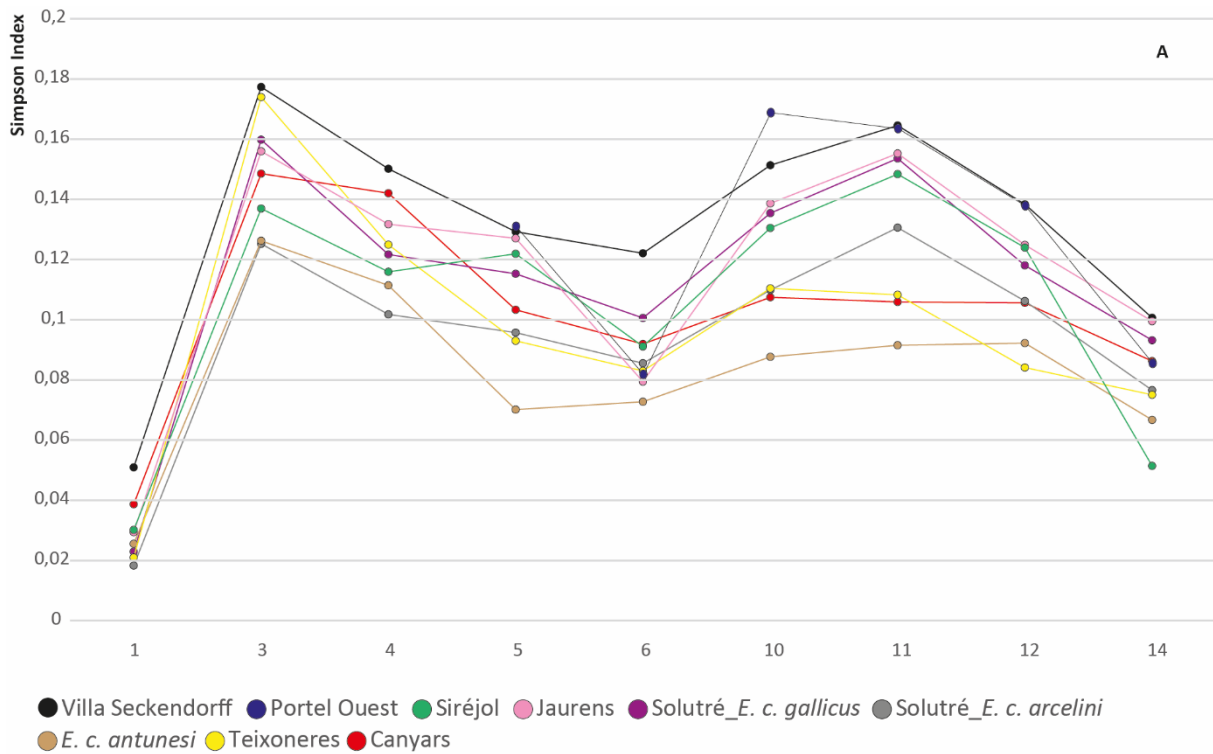
484

485 3.2.5 The metatarsal bones

486

487 Like for the metacarpal bones, the palmar distal depression is almost never expressed
488 (96.15%). The facet in connexion with the third cuneiform is mostly developed (92.3%)
489 which is usually not the case in “archaic” Middle Pleistocene horses (Guadelli and Prat, 1995;
490 Uzunidis-Boutillier, 2017) and the facet for the cuboid bone is always present. The anterior
491 and posterior articular facets for the first cuneiform can be in connexion (47.82%). Only one
492 vestigial metatarsal (a second one) was found fused with the third metatarsal among 30 bones
493 (96.67%) (**Supplementary Fig. S8**).

494 The metrical characteristics of the horses’ metatarsals from Canyars are similar to the
495 metacarpal ones. They are short, in the size range of *E. c. gallicus* and of the other Iberian
496 specimens, smaller than the *E. c. germanicus* and larger than *E. c. arcelini*. They also are
497 rounder than the French and German individuals with proportionally more important values in
498 the antero-distal measurements of the proximal and distal extremities(**Supplementary Tabl.**
499 **S6; Fig. 5**).



500
501

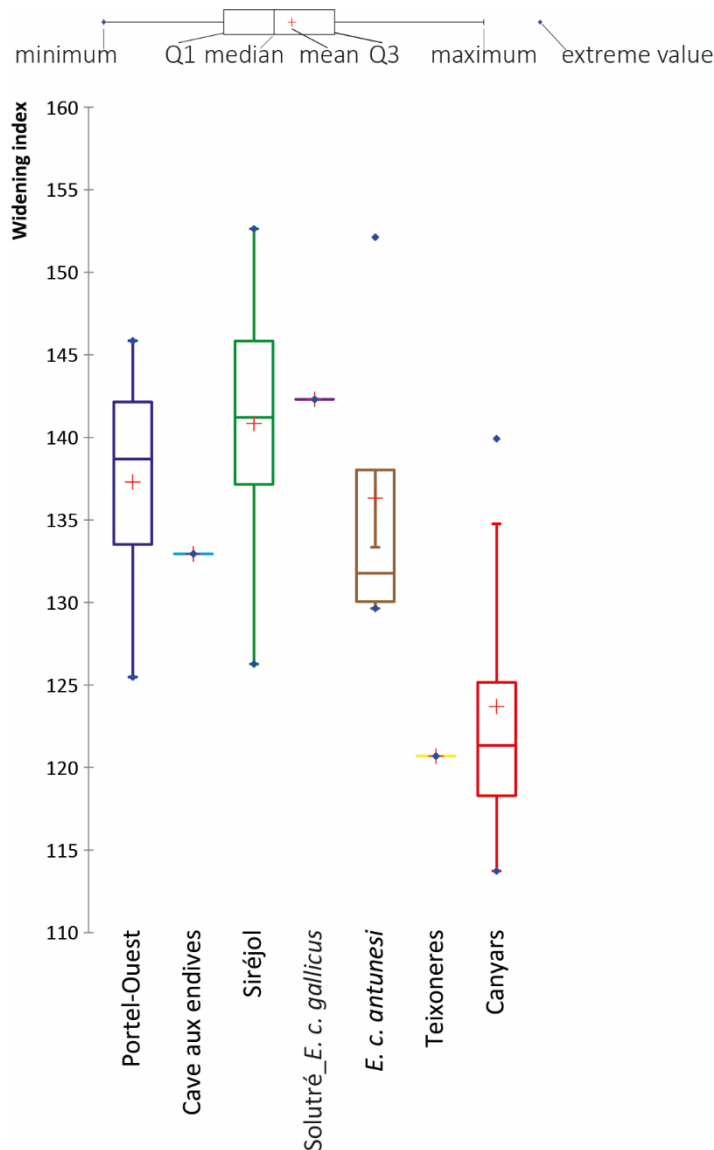
502 Fig. 5: A: Log ratio diagram comparing the dimensions of the horse's metatarsal bones from
503 Canyars to other Western European Upper Pleistocene cohorts. Reference *E. hemionus*
504 (Eisenmann, n.d.). B: Principal component analysis (PCA) with measurements of horse third
505 metatarsal from Canyars and other Western European Upper Pleistocene cohorts. Circle =
506 individuals; square = centroid of each cohort. 1: maximal length; 3: breadth at the middle of
507 the diaphysis; 4: depth of the diaphysis at the same level; 5: maximal proximal breadth; 6:
508 maximal proximal depth; 10: Distal sus-articular breadth; 11: distal articular breadth; 12:
509 depth of the sagittal crest; 14: greatest depth of the medial condyle.

510

511 3.2.6 The third phalanx

512

513 The anterior and posterior third phalanges were grouped together. The ratio between the
 514 greatest width of the third phalanges and its greatest length allow to evaluate the enlargement
 515 of this bone. The third phalanges of the horses from Canyars are among the most tapered ones
 516 with the specimens from Teixoneres and Cave aux Endives (**Fig. 6**). The width of the third
 517 phalanges of *E. c. antunesi* is moderate while it is very important at Portel-Ouest, Siréjol and
 518 the *E. c. gallicus* of Solutré. The plantar surface of the third phalanges of horses is considered
 519 as an adaptation to the hardness of the substrate (Bignon and Eisenmann, 2006; Foronova,
 520 2006; Uzunidis, 2021).
 521



522
 523
 524 Fig. 6: Box plot comparing the widening index (greatest wide/greatest length*100) of the
 525 horses third phalanges from Canyars to other Western European Upper Pleistocene cohorts.

526
 527 3.2.7 Morphological comments on other bones

528
 529 *Humerus*

530 Two proximal extremities were observable in the Canyars collection (**Supplementary Fig.**
531 **S9**). The deltoidian tuberosity is curved forward and the tubercles majus and intermedius are
532 separated by a deep groove that is common in caballoid horses (Bonifay, 1980). Eleven distal
533 extremities were observable also displaying common caballoid features (Bonifay, 1980): the
534 upper edge of the distal articulation below the coronoidian fossette form an irregular line
535 while the fossette is elongated from the mesial to the lateral parts of the bone. On the lateral
536 side of the coronoidian fossette, there is a rounded protrusion.

537

538 *Radius*

539 On the proximal articulation, the medial glenoidal cavity is mostly rectangular (81.81%) that
540 is more common in recent horses (Langlois, 2004). The tendon groove on the mesial side of
541 the proximal portion of the radius can be absent (28.57%), lightly expressed (42.86%) or
542 present (28.57%) while it is rarely present in currant horses (Guadelli and Prat, 1995). On the
543 distal part of the bone, there is never a posterior depression while it is common on stenonian
544 and Middle Pleistocene horses (Bonifay, 1980; Uzunidis-Boutillier, 2017). The diaphysis is
545 always straight (**Supplementary Fig. S9**).

546

547 *Carpal bones*

548 On the trapezoids, there is a supplementary facet for the capitatum on the posterior part of the
549 bone. On the capitatum, three facet are present: two on the anterior part and one on the
550 posterior (**Supplementary Fig. S10**).

551

552 *Talus*

553 All the morphological characteristic of the horses from Canyars place it among caballoid
554 horses (Bonifay, 1980). Its width is always superior to its high. The articulations for the
555 navicular and cuboid bones are separated by a smooth crest. On the anterior view, the internal
556 articulation tends to be straight while on stenonian horses, it folds inwards (**Supplementary**
557 **Fig. S10**).

558

559 *First Phalanges*

560 All the first phalanges (**Supplementary Fig. S10**) of the horses from Canyars, regardless if
561 there are anterior or posterior, have a very strong ligament insertion draw on the plantar face
562 of the bones. This morphology is common for the modern horses while the Middle
563 Pleistocene ones display flatter plantar surface (Guadelli and Prat, 1995).

564

565 3.2.8 Proportion of horse limb length

566

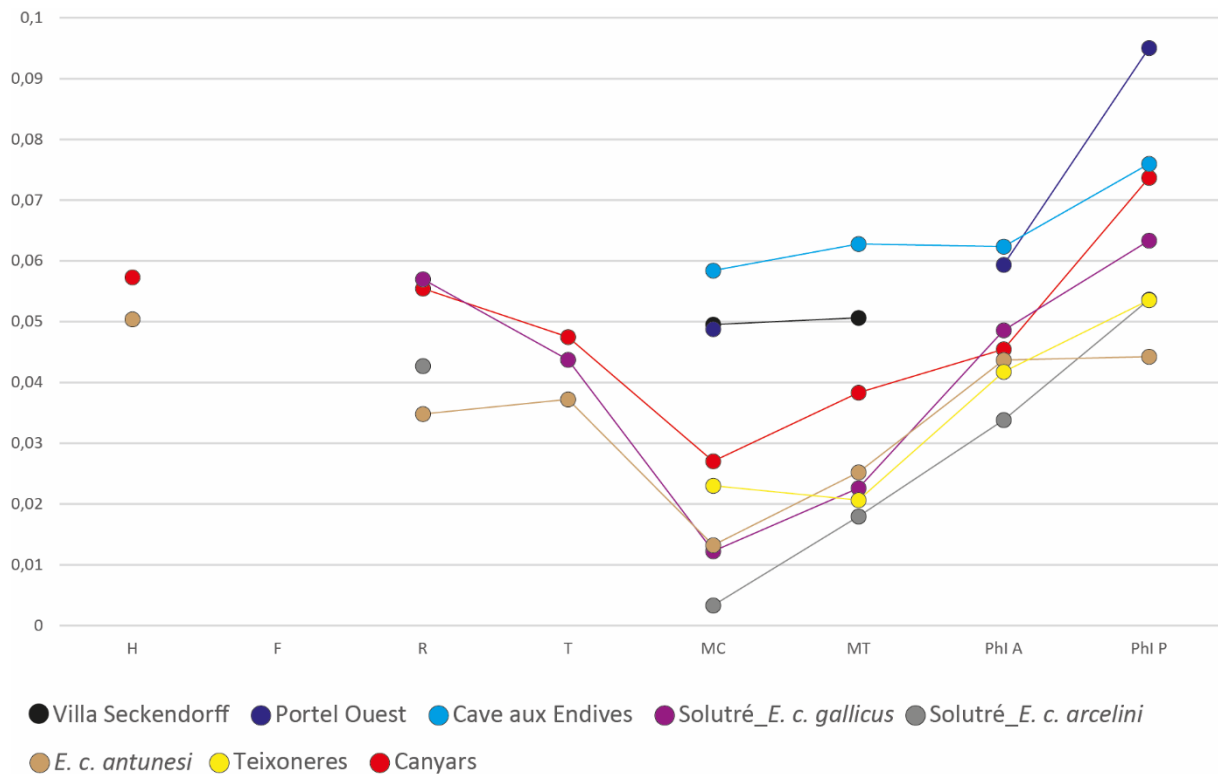
567 The limb bone lengths of the horse from Canyars are more similar to the Iberian horses from
568 Teixoneres and *E. c. antunesi* and to the smalls *E. c. gallicus* (Solutré) and *E. c. arcelini*
569 (Solutré). The specimens attributed to *E. c. germanicus* (Villa Seckendorff, Portel-Ouest,
570 Cave aux Endives) are larger, especially on the metapodials (**Fig. 7**).

571 For the front limbs, the radius of the specimens from Canyars is well-developed, the
572 metacarpal is proportionally less elongated and the first phalanx, long compare to *E. hemionus*

573 (that is the reference in the analysis). For the back limbs, the tibia is relatively short while the
 574 metatarsal and the first phalanx are more elongated.

575 These proportions are similar in Teixoneres or for the *E. c. gallicus* lineage but are inverted in
 576 *E. c. antunesi*. Indeed, it is characterized by short radius and metacarpal with long first
 577 phalanx and by a long tibia and metatarsal with short first posterior phalanges.

578



579

580 Fig. 7: Log ratio diagram of humerus, femur, radius, tibia, third metacarpal and metatarsal,
 581 first anterior and posterior phalanges greatest length of Canyars horses compare to other
 582 Western European Upper Pleistocene cohorts. Reference *E. hemionus* (Eisenmann, n.d.).

583

584 3.3 Morphometrical description of the *Equus hydruntinus* from Canyars

585

586 3.3.1 The upper and lower teeth

587

588 The dental material of *E. hydruntinus* from Canyars consist of one M3 isolated, three isolated
 589 upper decidual teeth and three mandibula fragments bearing teeth (**Supplementary Fig. S3**).

590 On the upper decidual teeth, the interstylar portion of the paracone and the metacone are
 591 always convex. The protocone is round on the D2 et more elongated on the D3-4. The
 592 parastyle can be double or simple on the D3-4 (50%) but it is always board. The mesostyle is
 593 always board and simple and the mesostyle, always thin and simple on the D2 and D3-4. The
 594 inner fossettes of the paracone are very simple with only one fold on its distal portion. The
 595 “pli caballine” is absent on the D2 and D3-4 and the hypoglyph can be close for at least the
 596 D2. Other examples of closed hypoglyphs have been documented even on definitive teeth for
 597 this species (Boulbes, 2009).

598 The interstyler portion of the paracone and the metacone on the M3 are convex. The
599 protocone is flat and elongated. The parastyle and the mesostyle are broad and simple while
600 the metastyle is thin and simple. The fossette inside the paracone bear a number of folds
601 similar to the ones found on horses with three folds on its distal part. The “pli caballine” is
602 absent and the post-fossette, open. A deep and wide groove is present on all the height of the
603 distal part of the crown like it is always the case for *E. hydruntinus* (Boulbes, 2009).

604 The size of the M3 from Canyars is in the variability of the ones from Teixoneres and of the
605 other Upper Pleistocene/Holocene location of Valorgues and Félines-Termenès attributed to
606 *Equus hydruntinus davidi* (**Supplementary Fig. S11**). The general size of the M3 is
607 comparable among all *E. hydruntinus* cohort but display a more elongated protocone in
608 comparison with the Middle Pleistocene *E. hydruntinus minor* from Lunel-Viel.

609
610 On the decidual lower teeth (**Supplementary Fig. S2**), the lingual groove is always very
611 narrow, the vestibular groove always crosses the isthmus and is in connexion with the lingual
612 groove. The pli ptychostylid is never developed and the metaconulid has been observed
613 disconnected on one d3-4.

614 On the definitive lower teeth (p2, p3-4, m1-2, the m3s being too altered to be described), the
615 lingual groove is always very narrow, the protoconid is always convex, the metastylid
616 triangular, the vestibular groove never crosses the isthmus, the entostylid is always expressed
617 and the pli protostylid, absent. The hypoconid is flat on the p2 and convex on the p3-4 (75%)
618 and the m1-2 (100%).

619 The size of the lower definitive teeth is less discriminant than the upper teeth to distinguish
620 European donkey species or cohort (**Supplementary Tabl. S7; Supplementary Fig. S12**). It
621 is, nonetheless, worthy to observe that the proportions in length and within p2, p3-4 and m1-2
622 of the *E. hydruntinus* from Canyars is very close to the ones from Teixoneres and La
623 Balauzière. Also, both Iberian specimens (Canyars and Teixoneres) are characterized in
624 general by thinner teeth (weak DVL), especially on the m1-2.

625

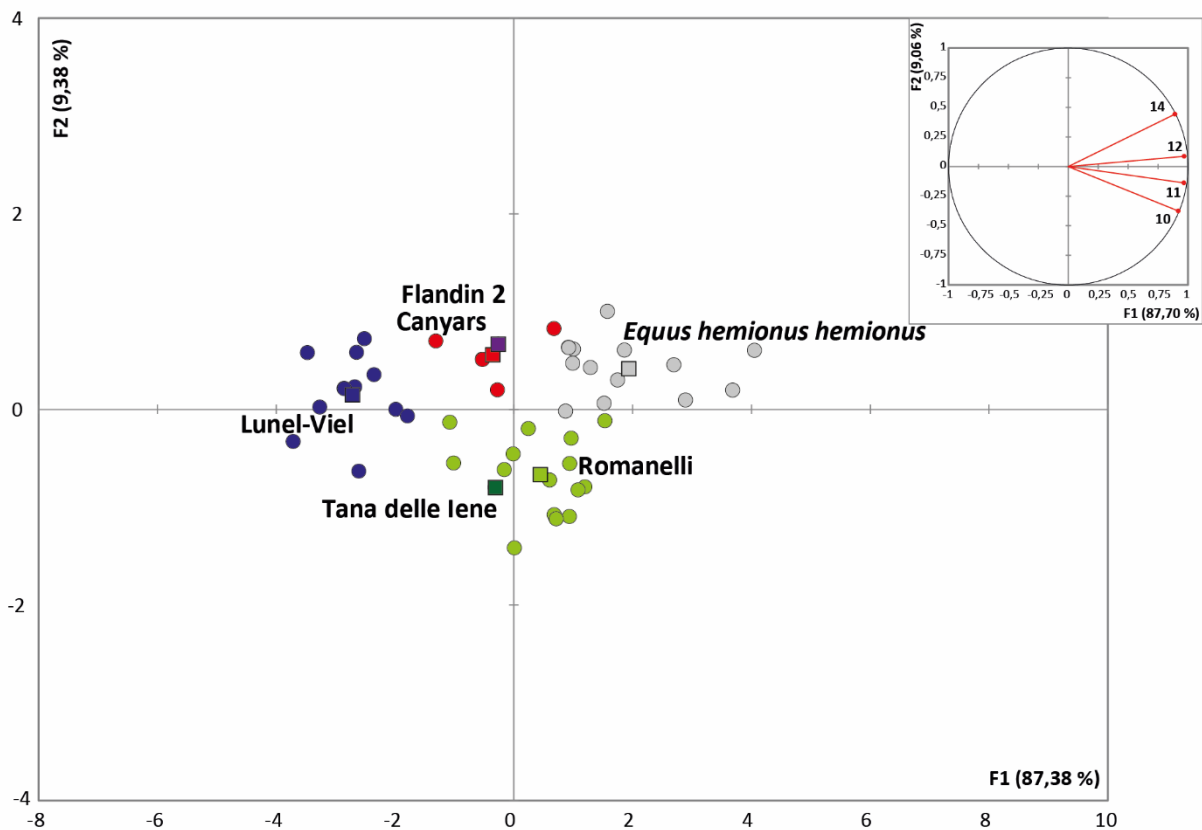
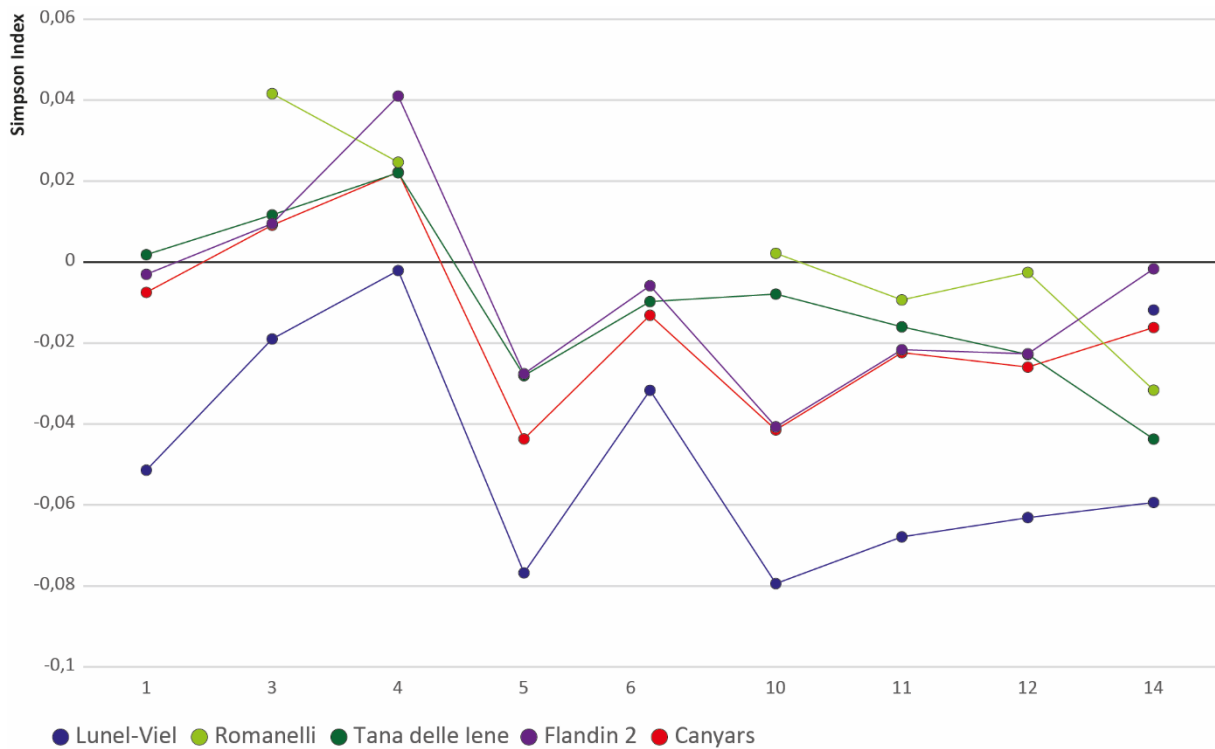
626 3.3.2 The metacarpal bones

627

628 On Canyars European donkey metacarpal bones (**Supplementary Fig. S6**), the palmar
629 depression on the distal portion of the diaphysis is always deep and wide while this part of the
630 bones is almost flat for the horses. The facet in connexion with the trapezoid bone is absent on
631 five of the bones and very reduced one the last one. The facet for the hamatum is always
632 inclined. Of the six third metacarpal bones attributed to *E. hydruntinus* at Canyars, two of
633 them are fused with the second vestigial metacarpal.

634 The third metacarpal of the specimens from Canyars are in the size variability of the *E.*
635 *hydruntinus davidi* from Flandin 2 and of the *E. hydruntinus hydruntinus* from Romanelli and
636 Tana della Iene (**Supplementary Tabl. 8; Fig. 8**). *Equus hydruntinus minor* from Lunel-Viel
637 is smaller. Due to the breakage of the bones, it was possible to conduct a PCA only on the
638 distal measurements of the metacarpals which appear to be a discriminant portion of the bone
639 to distinguish the *E. hydruntinus* subspecies (**Fig. 8**). The depth at the medial condyle is
640 proportionally large for *E. h. minor* and the sagittal crest is well-expressed; the distal and,
641 especially sus-articular breadths are very reduced. The current *E. h. hemionus* display similar

642 proportion of the distal part of the metacarpal but with larger dimensions than *E. h. minor*. In
643 comparison with *E. h. davidi* (Flandin 2), *E. h. hydruntinus* (Romanelli, Tana della Ierne)
644 appear to have a proportionally wider sus-articular width associated with a narrower bone at
645 the level of the distal articulation. Also, the distal articulation depth is proportionally weak
646 and the distal sagittal crest is well expressed. The *E. hydruntinus* from Canyars metacarpal
647 proportions are very similar to the *E. h. davidi* representatives (**Fig. 8**).
648



649
 650 Fig. 8: Log ratio diagram comparing the dimensions of the *E. hydruntinus* metacarpal bones
 651 from Canyars to other Western European cohorts. Reference *E. hemionus* (Eisenmann, n.d.).
 652 B: Principal component analysis (PCA) with measurements of European donkey third
 653 metatarsal from Canyars, other Western European Pleistocene cohorts and *Equus hemionus*
 654 *hemionus* (Eisenmann, n.d.). Circle = individuals; square = centroid of each cohort. 1:
 655 maximal length; 3: breadth at the middle of the diaphysis; 4: depth of the diaphysis at the

656 same level; 5: maximal proximal breadth; 6: maximal proximal depth; 10: Distal sus-articular
657 breadth; 11: distal articular breadth; 12: depth of the sagittal crest; 14: greatest depth of the
658 medial condyle.

659

660 It is striking to observe that the ratio between the distal sus-articular width and the largest
661 articular width, or “caballine index” differentiate well *E. h. hydruntinus* (Romanelli, Tana
662 della Ierne) and *E. h. davidi* (Flandin 2) (**Supplementary Fig. S13**). The first are
663 characterized by high indexes, above 100 while the latter display weak indexes comparable to
664 caballoid horses, below 100. The *E. h. minor* from Lunel-Viel and the current *E. h. hemionus*
665 display an intermediary position between *E. h. hydruntinus* and *E. h. davidi*. The European
666 donkeys from Canyars are displayed among the *E. h. davidi* variability.

667

668 3.3.3 The metatarsal bones

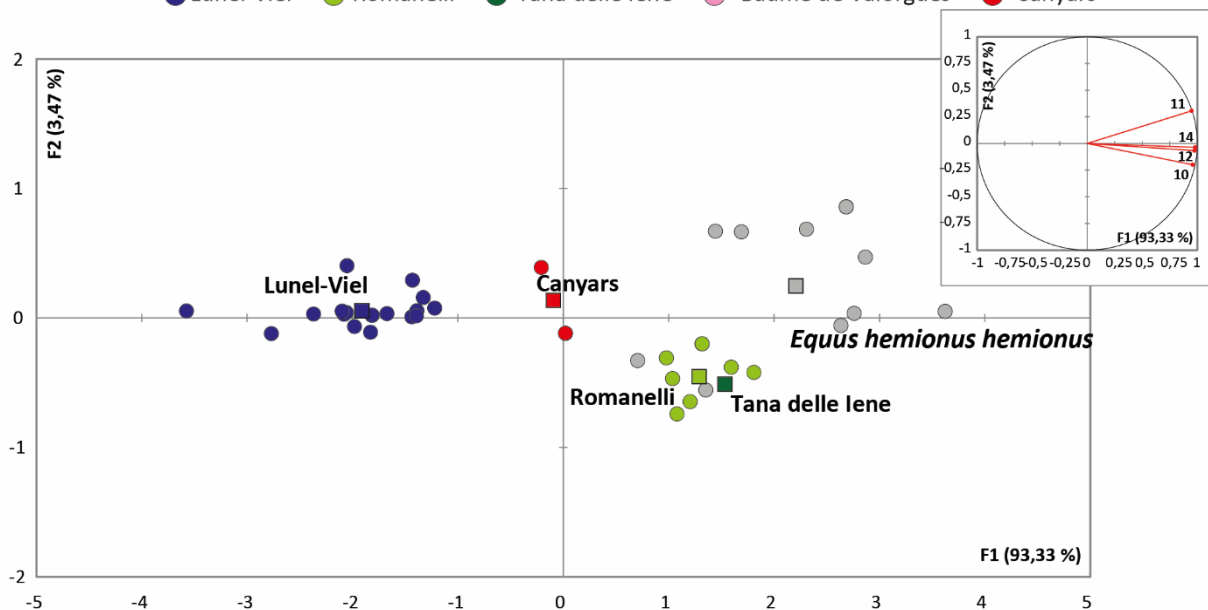
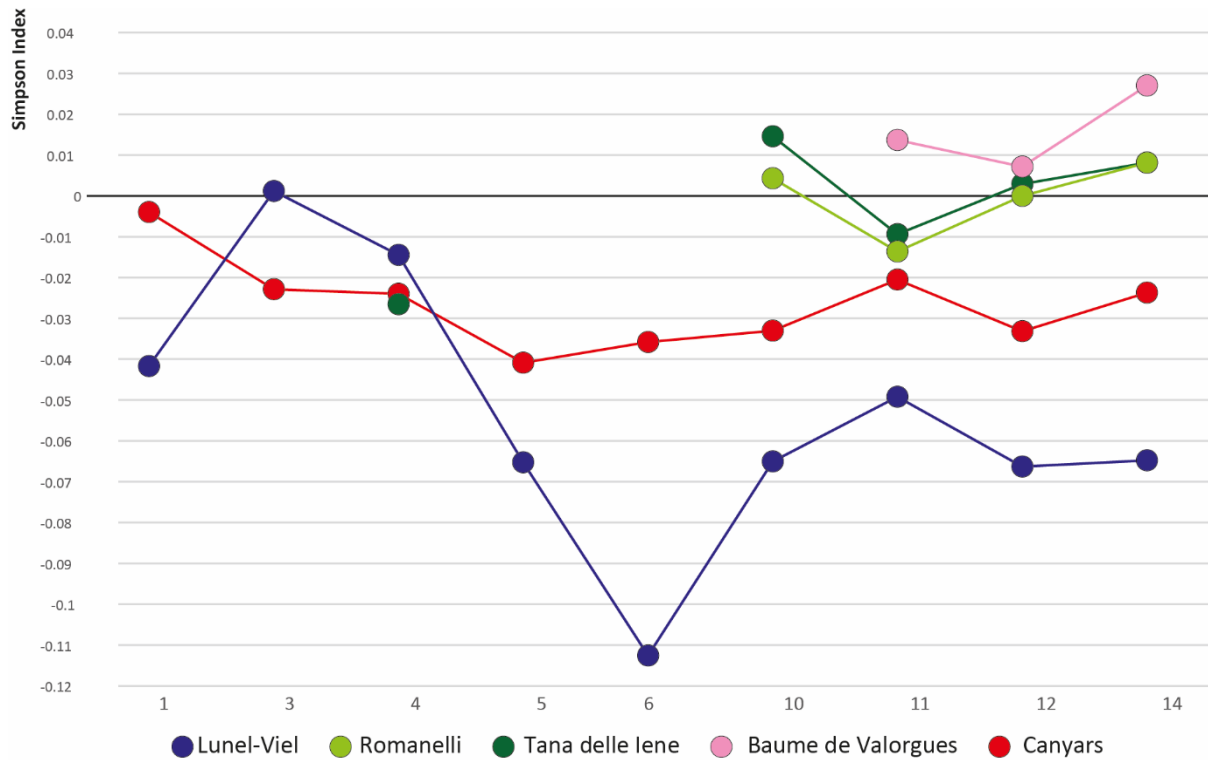
669

670 Like for the metacarpal bones and unlike the horses metapodials, the palmar distal depression
671 is always well expressed (**Supplementary Fig. S8**). The facet in connexion with the third
672 cuneiform and the one in connexion with the cuboid bone are always present. The anterior
673 and posterior facets for the first cuneiform can equally be in connexion or not. No vestigial
674 metatarsal was found fused with the third metatarsal.

675 The metrical characteristics of the European donkeys’ metatarsals from Canyars are similar to
676 the metacarpal ones. Indeed, they are longer than the ones from Lunel-Viel but slender. On
677 the distal part, they are thick and wide on the articulation with a weak sagittal crest (**Fig. 9**).
678 The caballine index is weak and similar to the true horses one in comparison with the index
679 display by *E. h. hydruntinus* (**Supplementary Tabl. S9; Supplementary Fig. S13**).

680

681



682
 683 Fig. 9: Log ratio diagram comparing the dimensions of the *E. hydruntinus* metatarsal bones
 684 from Canyars to other Western European cohorts. Reference *E. hemionus* (Eisenmann, n.d.).
 685 B: Principal component analysis (PCA) with measurements of European donkey third
 686 metatarsal from Canyars, other Western European Pleistocene cohorts and *Equus hemionus*
 687 *hemionus* (Eisenmann, n.d.). Circle = individuals; square = centroid of each cohort. See
 688 **Supplementary Table S6** for the description of the variables.

689
 690 **4. Discussion**

691
 692 *4.1 Demographical composition of the equid cohorts from Canyars*

693

694 While adults are present, especially among the 9-12 age-class, the horse cohort in Canyars is
695 dominated by young and above 15 years old individuals. Usually, in cohorts assembly by
696 predators, prime adults are the better represented age-group (Levine, 1983). This is the case
697 both for carnivore-accumulated assemblages (Fernandez et al., 2006; Levine, 1983; Pérez-
698 Pérez et al., 2021) and human-accumulated assemblages (Burke and Cinq-Mars, 1998;
699 Fernandez et al., 2006; Fernandez and Legendre, 2003; Marín et al., 2017). The juvenile and
700 senile dominated-curves are more similar to the living population of Pryor Mountain and the
701 catastrophic event of Akagera where zebras died in a bush-fire (**Fig. 1**).

702 Social structure in equids has been separated in two sociotypes: harem-forming equids with
703 female defence polygyny (Type I, Klingel, 1975, 1974), and territorial equids with resource
704 defence polygyny (Type II, Klingel, 1975, 1974; Rubenstein, 1986). Type I social groups
705 correspond to harem with one or more adult males and one or more adult females, young
706 animals of both sexes not yet dispersed, and the foals of the year (Linklater, 2000) and
707 bachelor groups composed by nonbreeding males (Klingel, 1974; Rubenstein, 1986) that
708 occur within the same territory. Currently, horses correspond to the type I. The sex was
709 estimated for 15 individuals and is in favour of females with a sex-ratio of 1:0.66, indicating
710 the presence of individuals from both the harem and bachelor socio-groups. While at birth, the
711 sex ratio in equid species is generally of 1:1 (Ransom et al., 2016), unbalance can be observe
712 at adult age in a territory that encompass both harem and bachelor groups. Male or female can
713 surpass in number their counterpart depending of environmental conditions and social
714 constraints. For example, in North America a similar sex-ratio (between 0.61 and 0.77:1 male
715 per female) was observed in the reproductive age classes (Garrott, 1991). The higher male
716 mortality was attributed to the high energy cost in the rut period (fights and reproduction). In
717 general, a sex ratio in favour of female is observed in resource-stress populations (Ransom et
718 al., 2016).

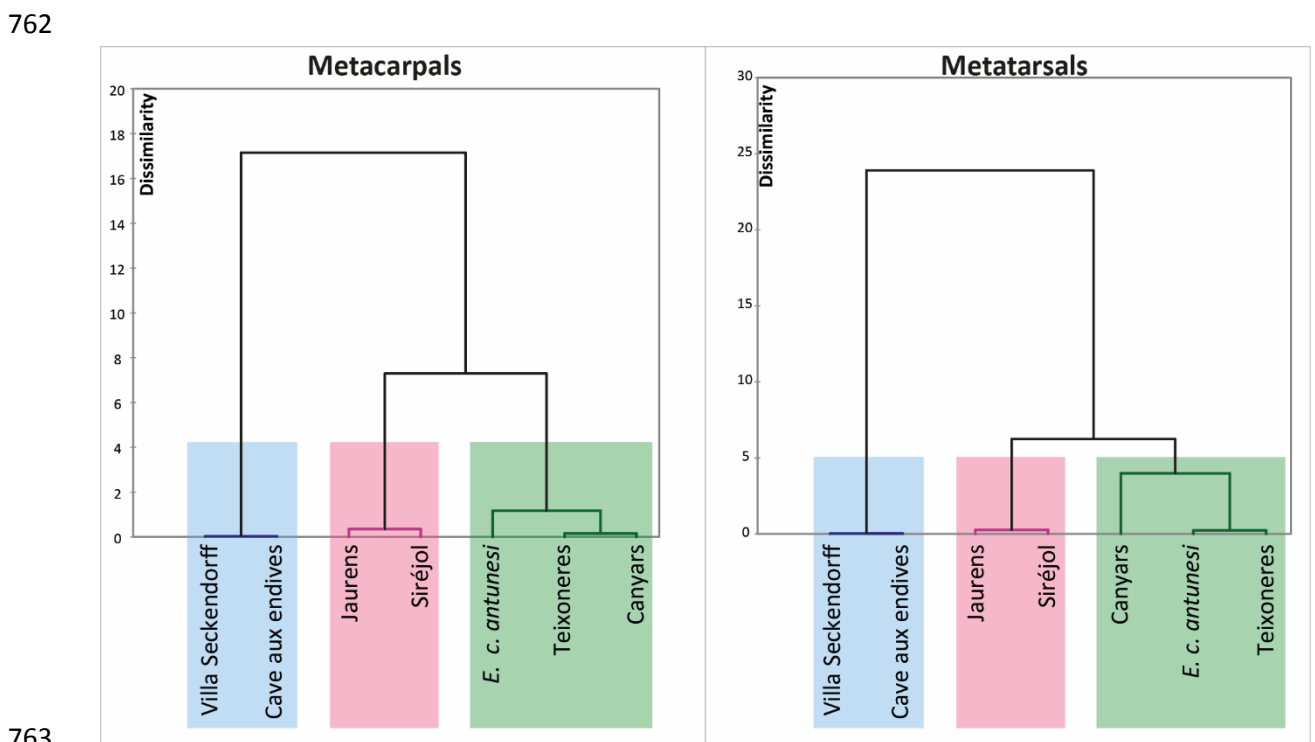
719 The Canyars assemblage is accumulated by diverse agents and processes being the carnivores
720 the main agencies, such as hyenas and lynxes for large mammals and lagomorpha,
721 respectively. In a lesser degree, some bones concentrated at the site could be related to
722 expected riverside thanatocoenosis and a possible human camp site in the surrounding area
723 (Daura et al., 2013). Among them, hyena would have been the most likely possibility since
724 large predators are the main responsible in equid predation (Boyce and McLoughlin, 2021).
725 While some examples of sexual-biases hyena attacks on equids have been observed (Kruuk,
726 1972), horse age profile, however, is not consistent with predation pattern. This would suggest
727 that horse death would have occur for other reasons before the carnivores, acted as scavenger
728 and consume the corpses opportunely. Currently, the main mortality factor in Mongolian feral
729 horse populations is starvation, predation being only the second factor in order of significance
730 (Usukhjargal and Namkhai, 2013). The horse mortality around Canyars site could also be
731 related with the nearby two paleo-rivers and with the flood events that have repeatedly
732 occurred in the region during the Upper Pleistocene (Daura et al., 2013). Indeed, high *K*
733 factors associated with a no-predated mortality are found in catastrophic events (such as in
734 Akagera) while populations with a mortality without saliant events display a weaker index
735 (Fernandez et al., 2006). In this scenario, the condition of the Canyars accumulation would be
736 comparable to Untermassfeld fluvial site (Lower Pleistocene, Germany) (Kahlke and
737 Gaudzinski, 2005). The higher number of females could also be related with the presence of

738 the rivers. Pregnant and lactating mares have a higher frequency of drinking (Schoenecker et
739 al., 2016), increasing the probability of female horses dying nearby a water source.

740
741 The *E. hydruntinus* cohort in Canyars is represented at least by one juvenile, one full adult,
742 one senile individual and at least one male and one female. While no age or sex selection
743 seem to have been made for this species, it is too scarcely represented to allow any
744 hypothesis. It is, however, interesting to observe, that the scarcity of this specie is common: it
745 is, regularly represented in fossil collection but almost always by a very few specimen (with
746 the notable exception of a few locations such as Lunel-Viel (Bonifay, 1991). *Equus*
747 *hydruntinus* has been associated with the equid sociotype II characterized by unstable groups
748 of variable composition that occupy small territories and may have been more difficult to hunt
749 by Human (Burke et al., 2003). In Canyars however, Human or other carnivores weren't
750 probably responsible of the equids killing. The scarcity of *E. hydruntinus* in palaeontological
751 record may reflect simply their scarcity in western European Pleistocene landscape as it is
752 already hypothesised through genomics studies (Özkan et al., 2023)

753 754 4.2 *Equus caballus* and *Equus hydruntinus* from Canyars inside the European lineages

755
756 Based on the metapodials bones, the Upper Pleistocene horses can be separate in three groups
757 (**Fig. 10**): *E. c. germanicus* from Villa Seckendorff and Cave aux Endives characterized by
758 long and thick bones, *E. c. gallicus* from Siréjol and Jaurens that share the same proportion of
759 the previous group but belong to smaller individuals. The last group is composed by horses
760 from Canyars, Teixoneres and *E. c. antunesi* that are in size comparable to *E. c. gallicus* but
761 have proportionally larger metacarpal in the antero-distal direction.



763

764 Fig. 10: Cluster analysis (Ward's method) of the first two components of the PCAs describing
765 the metacarpal and metatarsal bones of the horses from Canyars and other Western European
766 Upper Pleistocene cohorts.

767

768 Thus, Iberian horses share a morphometrical proximity, on their limb bone, mainly due to
769 their short and thick metapodials on the antero-distal direction. The deepness of the
770 metapodial was already observed for *E. c. antunesi* and used as a criteria to describe the
771 subspecies (Cardoso and Eisenmann, 1989; Eisenmann, 2022). The general limb bone ratios,
772 however, is quite different between *E. c. antunesi* and the horse from Canyars which is closer
773 to Teixoneres specimens and the French cohorts.

774 The horse from Canyars can be characterised by its flat frontal bone, the weak depression on
775 its nasal and that its orbit is located in an anterior position. Also, on the upper teeth, the
776 interstylar portions of the paracone and the metacone are mostly concave, the parastyle and
777 the mesostyle are large and double on the premolar teeth and simple on the molar ones. The
778 “pli caballine” is well expressed and the protocone is elongated with a protoconic index more
779 significant on the M1-2 than on the M3. On the lower teeth, the lingual groove is mostly well-
780 open, the protoconid is concave and the metastylid triangular. On the metapodials, the
781 caballine index is weak and all the facets in connexion with carpal or tarsal bones are present
782 (and consequently are also expressed on the carpal/tarsal bones) that indicate a positioning of
783 the leg less flexed than for Middle Pleistocene and stenoian horse (Uzunidis-Boutillier,
784 2017). Thus, the horse from Canyars displays the characteristics of a caballoid horse with
785 very few reminders of the stenoian lineage both on the skeleton and the dental remains. The
786 horse from Canyars share a lot of similarities with the specimens from Teixoneres that display
787 the same metrical characteristic on the metapodials (deep diaphysis and extremities, small
788 size, a caballine index below 100) and on the teeth (elongated protocone on the M1-2 and
789 shorter on the M3, small upper and lower teeth). This is not the case for *E. c. antunesi* which
790 bear some characteristics most often expressed in archaic Middle Pleistocene horses such a
791 greater caballine index on the metacarpals or an elongated protocone on the M3 (Bonifay,
792 1980; Boulbes, 2010; Eisenmann, 1991a; Fernandez, 2006; Guadelli, 1987; Guadelli and Prat,
793 1995; Uzunidis-Boutillier, 2017). Moreover, the cranial general organisation differ from the
794 Canyars and French skulls that are wider and shorter than *E. c. antunesi* ones. Based on its
795 metric characteristics, V. Eisenmann suggested a relation between *E. c. antunesi* and Italian
796 horses from Valdichiana and distinguished it from the French specimens as well (Eisenmann,
797 2022). Horses from Canyars (and Teixoneres) can, therefore, be distinguished from *E. c.*
798 *antunesi*.

799

800 The horses from Canyars and Teixoneres share also similarities, mentioned above, with the *E.*
801 *c. germanicus-gallicus-arcelini* from the North of the Pyrenees but do not fit in their
802 evolutionary pattern. *Equus c. germanicus* was described from a specimen discovered in
803 Remagen, Germany (Nehring, 1884). *Equus c. gallicus* and *E. c. arcelini* were describe later
804 to distinguish steps in the gradual reduction of the size of horses that occur during the Upper
805 Pleistocene (Bignon et al., 2005; Cramer, 2002; Forsten and Ziegler, 1995; Gromova, 1949;
806 Guadelli, 1991, 1987; Prat, 1968; Tournepiche, 1982). This lineage is widespread across
807 Europe and its representative were described for example in France, Belgium, Germany,

808 Switzerland, Czech Republic, Serbia, Bulgaria or Russia (Dimitrijević et al., 2014; Forsten
809 and Ziegler, 1995; Gautier et al., 1998; Guadelli, 1991; Guadelli and Delpéch, 2000; Magniez
810 and Boulbes, 2014; Oppliger and Becker, 2010; Pokorný et al., 2018; Prat, 1968; Savoy et al.,
811 2012). Canyars horses have deeper metapodials and smaller teeth than *E. c. germanicus*. They
812 are, therefore, not morphometrically similar to the representative of the *germanicus-gallicus-*
813 *arcelini* lineage on the teeth and metapodial bones that are considered the best diagnostic part
814 for taxonomic interpretations (Bignon et al., 2005; Eisenmann, 1986). The size of the horse
815 from Canyars according to the length of its limb bone is similar to the Teixoneres specimens
816 and intermediary between *E. c. germanicus* and *E. c. gallicus* (**Fig. 7**). Thus, in addition to the
817 morphometrical differences described above, Canyars' horses, as well as Teixoneres ones, do
818 not fit in the size pattern modelled for Upper Pleistocene European horses.

819
820 Canyars *E. caballus* metapodials are robust in comparison with *E. c. antunesi* or *E. c. arcelini*
821 for example (**Fig. 4 and 5**) which can be correlated with humid climate or very cold periods
822 (Eisenmann, 1984; Gromova, 1949; Uzunidis, 2021; van Asperen, 2010). In Canyars, several
823 paleoenvironmental indicators indicate a dry climate (Daura et al., 2013) suggesting that the
824 robustness of the bones are more likely to be related with the cold condition of the Heinrich
825 Stadial 4 (Rivals et al., 2017). The ecomorphological adaptations of the muzzle and the third
826 phalanx are in accordance with this interpretation. The muzzle of Canyars horses is very wide,
827 similar to the values of the *E. caballus* from Jaurens and Siréjol (**Fig. 2 and 3**). This
828 morphology type is linked to an adaptation to a cold and dry climate (Caloi, 2002; Crégut-
829 Bonnoure et al., 2018; Eisenmann et al., 1985; Uzunidis, 2021) and a grazing diet that have
830 been found for this population (Rivals et al., 2017). Finally, the third phalanx is very narrow
831 (**Fig. 6**) that could reflect an habitat with a dry substrate (Bignon and Eisenmann, 2006;
832 Crégut-Bonnoure et al., 2018; Uzunidis, 2021). The robustness of the metapodials and the
833 enlargement of the muzzle of the *E. caballus* in Canyars are comparable to the values display
834 by French specimens indicative of rather similar adaptations. Only the width of the third
835 phalanx separate Canyars (and Teixoneres) specimens from the more northerner ones. This
836 could indicate a snow cover more frequent North from the Pyrenees (Uzunidis, 2021).

837 Thus, ecological adaptations do not support the hypothesis of the occupation of a quite
838 distinct inhabited environment and do not explicate satisfactorily the differentiation between
839 the European and the Iberian lineages. This differentiation seems to have occurred since the
840 Middle Pleistocene since other horse species have been described for this period, *E. c.*
841 *torralbae* in Torralba (MIS 7), and failed to have been linked to the contemporaneous
842 European lineages (Prat, 1977, 1968). The recurrent speciation phenomenon in Spain could
843 therefore 1) correspond to an early separation and an evolution from, at least, *E. c. torralbae*
844 to the *E. caballus* from Canyars or; 2) illustrate periodic isolations of mammal populations
845 South of the Pyrenees that would have induced morphometric differentiation. Such a
846 phenomena has been already described for red deer (Uzunidis et al., 2022) and could have
847 occurred with the opening and closing of the western and eastern Pyrenean corridors during
848 glacial and interglacial periods (Álvarez-Lao and García, 2011a, 2011b).

849
850 The *E. hydruntinus* from Canyars is characterized by the significant length of the protocone
851 on the M3 (**Supplementary Fig. S11**). Those characteristics are typical of the subspecies *E.*

852 *hydruntinus davidi* (Alimen, 1946) (Boulbes, 2009; Boulbes and van Asperen, 2019) and the
853 specimens from Canyars can be attributed to this form. *Equus hydruntinus* is most often
854 describe from its teeth or skull and its post-cranial bones are not so well known (Boulbes,
855 2009; Burke et al., 2003; Sanz-Royo et al., 2020). The study of Canyars European donkey
856 bones brings, however, insights in the distinction between sub-species post-cranial bones. On
857 the metapodial bones in particular, the “caballine index” is more significant in Romanelli or
858 Tana delle Iene with indexes above 100 in comparison with specimens from Flandin 2 and
859 Canyars that display indexes below 100 (**Supplementary Fig. S13**). *Equus h. davidi*
860 metapodials are also larger in an antero-posterior direction on the distal extremity with a
861 lesser expressed distal articular sagittal crest (**Fig. 8 and 9**).

862
863 *E. hydruntinus* is known through several subspecies. In Western Europe, three have been
864 described: *E. h. minor*, *E. h. hydruntinus*, *E. h. davidi*. *Equus h. minor* is a very small form
865 known in Lunel-Viel (Bonifay, 1991) which affiliation has been challenged (Azzaroli, 1990;
866 van der Made et al., 2017). The species and subspecies, *E. h. hydruntinus* was first described
867 in the level MIS 2 of Romanelli (Italy) (Regalia, 1907; Stehlin and Graziosi, 1935) and is,
868 probably an Upper Pleistocene species. *Equus h. davidi* was defined in Saint-Agneau
869 (Charente, France), dated from the Upper Pleistocene by (Alimen, 1946). It was, latter,
870 observed in several location dated between MIS 3 and MIS 1 in the South of France (Boulbes,
871 2009; Boulbes and van Asperen, 2019; Guadelli, 1995; Prat, 1968) and the Iberian Peninsula
872 (Álvarez-Lao et al., 2017; Cardoso, 1995). Thus, from MIS 3, a separation can be observed
873 between Western and Eastern *E. hydruntinus* populations with the apparition of *E. h. davidi*
874 west and the maintenance of *E. h. hydruntinus* east. The Alps may have acted as an
875 ecological barrier between eastern and western populations and induce a speciation (Guadelli
876 and Delpech, 2000).

877
878 The morphometrical characters of the *E. caballus* from Canyars indicate that this cohort do
879 not fit in the *E. c. germanicus* lineage. While *E. c. germanicus* was described in localities all
880 across Europe, horses from Canyars must have been separated from the main continental aera
881 of expansion. It suggests that the Pyrenees must have limited the exchanges of populations
882 north and south of the mountain range. The *E. hydruntinus*, however, was attributed to the
883 subspecies *davidi* and shares a morphometrical proximity with the cohorts West from the
884 Alps. For this species, the Pyrenees do not seem to have induce a segregation while it was the
885 case for the Alps. The two equids appear not to have experienced the same geographical
886 limitations. The different trend between the two species may be related to the fragmentation
887 of Southwestern Europe in climatic refuges during Pleistocene (Stewart et al., 2010). While
888 *Equus caballus* seems to have been able to maintain its presence in most of the European
889 continent during glacial and interglacial periods, *E. hydruntinus* may have undergone phases
890 of withdrawal and recolonisation from southern refuges (Boulbes, 2009). Thus, while the
891 *Equus caballus* cohort from Canyars may consist in a margin of the general geographical
892 repartition of horses, the *E. hydruntinus* one may correspond to the core territory for this
893 species, the Iberian peninsula being considered as a refuge for temperate species during
894 glacial periods (Álvarez-Lao and García, 2011b; Stewart et al., 2010). Therefore, the
895 extension-contraction model which view European southern peninsulas as refugia for

896 temperate-adapted species (Bennett and Provan, 2008; Provan and Bennett, 2008; Stewart et
897 al., 2010; Stewart and Lister, 2001) did not operate similarly for the two equid species. While
898 *E. hydruntinus* seems to have followed this pattern, *E. caballus*, probably due to its highest
899 ecological flexibility and the persistence of local suitable biotopes have persisted within and
900 beyond the peninsulas as it has already been suggested for other small and large mammals
901 (Bilton et al., 1998; Croitor and Brugal, 2007; Leonardi et al., 2022).

902

903

904 **5. Conclusions**

905

906 Two equids are represented in Canyars: *E. caballus* and *E. hydruntinus davidi*. The horse
907 cohort is represented by at least 28 (NISP) mainly young and old individuals and is dominated
908 by female. The European donkey cohort correspond to four individuals of all age and all sex.
909 The equids mortality profile is more consistent with catastrophic events that would suggest an
910 opportunistic scavenging of their bones by biological agencies, mainly by hyenas. While the
911 horses morphometrical features indicate a differentiation with specimen northern from the
912 Pyrenees, the European donkeys are very similar to their French counterparts. This
913 observation suggests that the two species experienced different limitation to their repartition.
914 It draws also the picture of a fragmented Pleistocene South-western Europe where the Iberian
915 Peninsula could have corresponded to a peripheric territory for horses while it could have
916 been one of the core territories for *E. hydruntinus*.

917

918 **Acknowledgements**

919 This research benefited from financial support by the following agencies: Ramon y Cajal
920 postdoctoral grant (RYC2021-032999-I) with financial sponsorship from the Spanish
921 Ministry of Science and Innovation and the European Union NextGenerationEU (MS);
922 CNRS-INEE International Research Network programme (grant # IRN0871TaphEN);
923 Departament de Cultura de la Generalitat de Catalunya (grant #
924 CLT/2022/ARQ001SOLC/128) and AGAUR (SGR2021-00337); Knowledge Generation
925 projects (PID2020-113960GB-100 Spanish Ministry of Science and Innovation). Fieldwork
926 was sponsored by GTI (Gavanenca de Terrenys i Inmobles, Ajuntament de Gavà). Thanks to
927 Castelldefels city council for the Guixera laboratory (Castelldefels). The authors would like to
928 thanks Nicolas Boulbes for sharing the raw data of the metapodials of the *E. hydruntinus* from
929 Lunel-Viel, Véra Eisenmann for sharing freely her data on her website and Alicia Sanz-Royo
930 for her previous work on equids. The authors would like also to thanks the three anonymous
931 reviewers for their comments that increase the quality of this paper.

932

933 **Data availability**

934 The raw data are available at the following link: <https://zenodo.org/records/10091780>

935

936 **Author's contribution**

937 AU collected the data, designed and conducted the research, wrote the main manuscript and
938 prepared all the figures, tables and supplementary information. MS and JD conducted the
939 archaeological work, the curation of the material, organized the collection for the

940 paleontological study, provided contextual information and the figures illustrating the equid
941 material and the site. All authors reviewed, commented and participated in improving the
942 manuscript.

943

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945

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1426 OpenStreetMap licensed under ODD 1.0 (<https://openstreetmap.org/copyright>) by the OpenStreetMap
1427 Foundation (OSMF). OpenStreetMap contributors (<https://openstreetmap.org/>).

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1518 Supplementary Fig. S13: Box plot comparing the caballine index ($10*100/11$) of the metacarpal and
1519 metatarsal bones of the *E. hydruntinus* from Canyars to other Western European cohorts.

1520 Supplementary Tabl. S9: Summary of the measurements of the metatarsal bones of the *E. hydruntinus*
1521 from Canyars compare to other Western European cohorts. References for measurements: V.
1522 Eisenmann (Eisenmann, n.d.). n: effective; m: mean; s: standard deviation; min: minimum; max:

1523 maximum; 1: maximal length; 3: breadth at the middle of the diaphysis; 4: depth of the diaphysis at
1524 the same level; 5: maximal proximal breadth; 6: maximal proximal depth; 10: Distal sus-articular
1525 breadth; 11: distal articular breadth; 12: depth of the sagittal crest; 14: greatest depth of the medial
1526 condyle; CI: caballine index; SI: slenderness index.