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Additional Information

***Corema album* archaeobotanical remains in western Mediterranean basin.  
Assessing fruit consumption during Upper Palaeolithic in Cova de les Cendres  
(Alicante, Spain)**

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**KEYWORDS**

Pleistocene – Upper Palaeolithic – Climate dynamics – Western Europe – Vegetation dynamics – Gathering – *Corema album* – Vitamin C – Biogeographical disjunctions – seeds – pyrene – endangered species

1 **Abstract**

2 Information about plant gathering by Palaeolithic hunter-gatherers in Europe is scarce because of  
3 the problems of preservation of plant remains in archaeological sites and due to the lack of  
4 application of archaeobotanical analysis in many of them. Botanical macrorremains –wood  
5 charcoal, seeds, fruits, leaves, etc. – provide information not only about palaeoeconomy of hunter-  
6 gatherers, but also about climate, landscape and vegetation dynamics.

7 In Gravettian and Solutrean levels of Cova de les Cendres, *Corema album* pyrenes (*Empetraceae*  
8 or crowberries family) have been identified. On the contrary, wood charcoal of this species has  
9 not been documented among the remains of firewood. This differential presence of plant organs,  
10 together with the nutritional value of its fruits, which is presented here, make us hypothesize the  
11 systematic gathering of *C. album* fruits for human consumption. They have a high content in  
12 vitamin C, as well as potassium, magnesium and copper.

13 *Corema album* is a unique species, nowadays in danger of extinction. Its main population is  
14 located on the Atlantic coast of Iberian Peninsula, but in 1996 a small population was discovered  
15 on the Mediterranean Iberian coast (Benidorm, Spain). Archaeobotanical data from Cova de les  
16 Cendres (Teulada-Moraira, Spain) presented here point to a larger population of *camariña* during  
17 Upper Palaeolithic on the coast of Alicante. The harsh climatic conditions of the Last Glacial  
18 Maximum during Solutrean period, with colder temperatures and aridity increase, could explain  
19 the reduction of the presence of *C. album* remains until its absence in Magdalenian. The climatic  
20 amelioration during Upper Magdalenian did not mean the recovery of *camariña* population in the  
21 **Moraira headland area**. Probably, the rising of the sea level would affect them destroying its  
22 habitat in the dunes.

23

## 24 **1. Introduction**

25 Global climatic changes and human activities, among other elements, shape the landscape  
26 physiognomy throughout history. Landscape is the stage of human activity since Prehistory.  
27 There, human groups have found food, fuel, raw material, productive areas, etc. These uses imply  
28 an interrelation between two actors –humans and vegetation-, in a way that changes in vegetation  
29 condition human activity and human actions modify vegetation. Archaeological data evidence  
30 that these transformations take place since Pleistocene, and increasingly in the Holocene, when  
31 new more potent technologies generate anthropogenic landscapes (Boivin et al., 2016; Briggs et  
32 al., 2006; Erlandson and Braje, 2014; Ruddiman et al., 2015). This environmental impact has got  
33 worse fast in the last century. On the other hand, climatic changes throughout History as  
34 Pleistocene glacial and interglacial periods and finally Holocene have modified continuously the  
35 vegetation formations. Pleistocene flora distribution was different to Holocene once, especially  
36 in the coastal areas, where another factor must be kept in mind: sea level fluctuations.  
37 Archaeobotany, here understood as recovery, analysis, identification and interpretation of plant  
38 remains from archaeological sites, focus on the interrelation between human groups and  
39 vegetation in the past, as well as on paleolandscape and paleoclimatic conditions reconstruction.  
40 Hence, archaeobotanical information shows these transformations in the regional biodiversity and  
41 could be useful in the design of environmental management policy and conservation strategies.

42 Archaeobotanical studies also provide economic and cultural information. Plant foods  
43 provide some nutrients essential for human health: minerals as iron, calcium and magnesium  
44 among others, vitamin C, proteins and carbohydrates. A diet based only in animal protein causes  
45 health problems (Noli and Avery, 1988; Speth and Spielmann, 1983). Nevertheless, their role in  
46 Palaeolithic diet has been underestimated because of their scarce archaeological evidence,  
47 especially comparing with zooarchaeological remains. Moreover, plants can be used as raw  
48 material for basketry, weaving, ropemaking, etc. Only in the last 15 years a real effort has been  
49 carried out to go deep into the plant use by hunter-gatherers.

50 This question has been tackled by several analyses: dental calculus, phytoliths, stable  
51 isotopes, microwear analysis of tools, etc. (e. g. (Hardy, 2018; Henry et al., 2014; Revedin et al.,  
52 2015; Richards and Trinkaus, 2009). Macrofossil analyses have provided new and interesting data  
53 (e. g. (Baines et al., 2015; Holst, 2010; Lev et al., 2005; Melamed et al., 2016; Pryor et al., 2013;  
54 Weiss et al., 2004b), proving a relevant use of plant resource from Middle Palaeolithic to  
55 Mesolithic. Regarding Western Mediterranean Basin, in Iberian Peninsula, carpological analyses  
56 have been carried out in few Palaeolithic sites (Aura et al., 2005; Badal García, 2001; Freeman et  
57 al., 1988; Gale and Carruthers, 2000; Mason et al., 1999; Vidal-Matutano et al., 2018). In North  
58 Africa, interesting results have been recently published from Later Stone Age and Capsian sites  
59 (Carrión Marco et al., 2018; Morales, 2018; Morales et al., 2015). Cova de les Cendres (Teulada-  
60 Moraira, Alicante) has provided significant preliminary results (Badal and Martínez Varea, 2018;  
61 Martínez Varea and Badal, 2018; Villaverde et al., 2017). Here, part of the carpological  
62 assemblage from its Pleistocene levels is analyzed and interpreted from a palaeoethnobotany point  
63 of view, pointing to a possible human use of *C. album*, and from a palaeobotany perspective, to  
64 know the evolution of the distribution of this unique species, which is nowadays ‘In danger of  
65 extinction’ (Aguilella et al., 2009) in Valencian Community. This paper combines  
66 archaeobotanical and biological data in order to define the nexus between Upper Pleistocene and  
67 present on Alicante coast (Spain).

## 68 2. Regional setting

69 Cova de les Cendres (Teulada-Moraira, Alicante, Spain) is located at the cliffs of the  
70 Moraira headland, at 60 m.a.s.l., just at the coastline (Fig. 1a). A wide archaeological sequence  
71 has been documented. Pleistocene levels have been dated to Aurignacian, Gravettian, Solutrean  
72 and Magdalenian periods (Table 1) (Villaverde et al., 2017, 2012). Along the whole sequence,  
73 archaeobotanical analyses have been carried out (Badal and Carrión, 2001; Badal and Martínez  
74 Varea, 2018; Martínez Varea and Badal, 2018; Villaverde et al., 2017).

75 From Cap de la Nau to Moraira headland, strike-slip and normal faults shape the coast  
76 with promontories of flat summits and subvertical cliffs, known as “*morres*”. They are interposed  
77 by inlets and beaches, besides Eemian eolianites dated by thermoluminescence in  $112000 \pm 17000$   
78 BP (Fumanal, 1995; Fumanal et al., 1993a; Fumanal and Viñals, 1988). These fossil dunes were  
79 formed during the Last Interglacial (MIS 5e) when the position of the seashore was near to the  
80 current. They extend under the sea, probably because they were part of a bigger dune system on  
81 the continental shelf (Fumanal et al., 1993a).

82 The current bioclimatic conditions of the Moraira headland are thermomediterranean  
83 (Rivas Martínez, 2007), with a mean annual temperature of 17 °C and a mean annual precipitation  
84 around 500 mm. The landscape is characterized as an impoverished shrubland, composed mainly  
85 by heliophilous shrubs as *Rosmarinus officinalis*, *Erica multiflora*, *Lavandula dentata* and  
86 *Ephedra distachya*. There are some taxa characteristic of maquis as *Olea europaea* var. *sylvestris*,  
87 *Pistacia lentiscus*, *Quercus coccifera* and *Chamaerops humilis*. Moraira headland is a botanical  
88 microreserve (Laguna et al., 2004), where some endangered species are present (*Silene hifacensis*,  
89 *Helianthemum caput-felis*, *Convolvulus valentinus*, among others).

### 90 3. Material and methods

91 A multidisciplinary approach has been applied in this research so different materials have  
92 been analysed. Archaeobotanical remains have been processed first and given the obtained results,  
93 we have carried out analysis of fresh material of *C. album*.

#### 94 3.1. Archaeobotanical methods

95 Archaeological samples from Gravettian (XVIa and XV), Solutrean (XIII), Middle (XII)  
96 and Upper Magdalenian (XI) levels of Cova de les Cendres have been analysed. All the sediment  
97 was processed with a flotation machine with a 1 mm sieve cloth mesh for the heavy residue and  
98 a 0.25 mm sieve cloth mesh for the light fraction. Both fractions were **splited** with a sieve stack  
99 with 4, 2, 1, 0.5 and 0.25 mm sieve meshes to make easier the sorting of plant remains. This was

100 carried out under a low power stereo microscope (Leica M165C) and fruits, seeds, leaves and  
101 other charred, mineralised and uncharred plant remains were recovered (Martínez Varea, 2016).  
102 The identification of the archaeobotanical remains was done based on morphology and anatomy  
103 compared with the reference collection of the Laboratori d'Arqueologia of Universitat de  
104 València and of Servicio de Vida Silvestre-CIEF of Generalitat Valenciana and with specialized  
105 bibliography (Bojnánský and Fargašová, 2007; Cappers et al., 2006). Photographs were taken  
106 with a Leica DFC425 camera and with Leica Application Suite V3 and Helicon Focus 3.10.3  
107 software.

### 108 3.2. Fresh material analysis

109 The number of pyrenes by fruit has been checked with the analysis of 100 *C. album* fruits  
110 from the current population of National Park of Doñana (Huelva, Spain) (Table 2) in order to  
111 calculate the minimum number of fruits that were carried to the cave in each archaeological level.

112 On the other hand, chemical composition of *C. album* fruits from National Park of Doñana  
113 was analysed in order to know their chemical properties. Moisture was determined using the fruit  
114 samples weight before and after drying at constant weight, using the formula  $100 * (\text{water weight}/\text{fresh weight})$ . Soluble solids (SS) were measured refractometrically using a drop of juice  
115 using a hand-held refractometer. The pH was determined in juice using an automatic pHmeter.  
116 Total titratable acidity was determined potentiometrically by titrating a 100 ml diluted (1:5)  
117 sample of juice with 0.5 N NaOH to pH 8.1, and expressed as percentage of citric acid. The  
118 ripening index was determined as the quotient between the soluble solids and the titratable acidity.  
119 Ascorbic acid (mg/100 g fresh fruit) was determined by potentiometric titration with a Titrino  
120 702 (Metrohm, Herisau, Switzerland) using a Metrohm 6.0420.100 combined Pt selective  
121 electrode and a 0.005 M chloramine T as standard.  
122

123 Protein content was calculated as  $N * 6.25$  from the N content values determined with the  
124 Kjeldahl method (Foss Tecator, Högamäs, Sweden). For the analysis of minerals, 2 g of the dry

125 fruit samples were calcined in a furnace at 450 °C for 2 h. Subsequently they were weighted and  
126 dissolved in 2 mL of HCl. The mixture was heated until vapors appeared, after which immediately  
127 several mL of distilled water were added. After filtration, the extract volume was brought to 100  
128 mL with distilled water. The following methodologies were used for the different minerals: P was  
129 determined by spectrometry (UV-VIS Jenway 6305) using the molibdovanadate method, K by  
130 flame photometry (Jenway PFP7, Essex, United Kingdom), and Ca, Mg, Fe, Cu and Zn by atomic  
131 absorption spectrophotometry (Thermo Elemental SOLAAR AA, Cambridge, United Kingdom).  
132 All minerals results of composition determinations are reported on a 100 g fresh weight basis.  
133 The fiber content (%) is determined by extraction with a hot neutral detergent solution and  
134 subsequent calcinations.

135 Total phenolics (mg caffeic acid.kg<sup>-1</sup> fresh fruit) were determined according to the Folin–  
136 Ciocalteu procedure after extraction with acetone (70% v/v) and acetic acid (0.5% v/v).  
137 Absorbance was measured at 750 nm and caffeic acid (Sigma–Aldrich Chemie) was used as a  
138 standard. Antioxidant activity was estimated using the colourimetric DPPH (1,1-diphenyl-2-  
139 picrylhydrazyl) and expressed as Trolox (6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic  
140 acid) equivalents.

141 In order to analyze the anatomical features of *C. album*, a wood fragment 10 cm long and  
142 2 cm diameter from the current population of National Park of Doñana (Huelva, Spain) was  
143 charred in an open fire. The resultant wood charcoal fragments were analyzed under an incident  
144 light microscope (Leica DM6000M). Specific features and pictures were taken with a scanning  
145 electron microscope (Hitachi S-4100) with spotlight of field emission and digital image  
146 acquisition system QUANTAX 200, held at the Servicio Central de Soporte a la Investigación  
147 (SCSIE) at Universitat de València. Wood anatomy of *C. album* was checked with the  
148 descriptions of vegetal anatomy atlas (Schweingruber, 1990).

#### 149 **4. *Corema album***



150           The genus *Corema* has been traditionally placed into *Empetraceae* –crowberries family–  
151 , a small family of heath-like shrubs having flesh fruits, containing only 3 genus (*Empetrum*,  
152 *Corema* and *Ceratiola*) and 4-6 species, and showing major biogeographical disjunctions (Moore,  
153 1998). *Corema* comprises 2 species: *C. conradii* Torrey, which occurs in the eastern coast of  
154 North America (Martine et al., 2005; McEwen, 1894; Redfield, 1884), and *C. album* (L.) D. Don  
155 ex Steudel, living in the Atlantic coasts of the Iberian Peninsula, from Gibraltar to Finisterre  
156 (subsp. *album*, see (Boratyński and Vera de la Puente, 1994; Villar, 1993; Webb, 1972)), and in  
157 the Azores (subsp. *azoricum* Pinto da Silva, see (Clavijo et al., 2002; Pinto da Silva, 1966)). In  
158 1996, a small and extreme disjunct population of *C. album* was found in the Mediterranean basin,  
159 in the coastal cliffs of Serra Gelada near Benidorm (Alicante, Spain) (Aguilella et al., 2009;  
160 Solanas and Crespo, 2001). Serra Gelada is placed more than 550 km far from the closest Atlantic  
161 population, in Tarifa sands, near the Strait of Gibraltar (Fig. 1a).

162           Despite *Empetraceae* has been maintained as an independent family since its description  
163 by Hooker and Lindley (Hooker, 1821), Wood and Channell (1959) recommended its inclusion  
164 into the *Ericaceae*, and recent phylogenetic studies based on morphological and molecular  
165 characters (Anderberg, 1994; Kron et al., 1991; Kron and Chase, 1993; Li et al., 2002) and  
166 comparative morphology and embryology (Reveal and Chase, 2011) demonstrate its better  
167 inclusion into this family.

168           *Corema album* is described as a dioecious perennial shrub although some hermaphrodite  
169 individuals are known in the southern populations of its biogeographical area (Díaz-Barradas et  
170 al., 2000; Zunzunegui et al., 2006). This plant is a perennial medium-size shrub, up to 1 meter in  
171 height, with numerous branches and flowers grouped in closely packed racemose inflorescences,  
172 bearing scented leaves and stems. The linear leaves are in whorls of three or four, and give the  
173 plant a heath aspect. The fruits are berry-like drupes, white or pale pink, 5-8 mm in diameter,  
174 often containing 3 seeds -pyrenes-, c. 0.5 cm long, with a thick woody endocarp. Flowering occur  
175 from March to April and fruiting from April to September (Fig. 1b and c). On its Atlantic Iberian  
176 distribution area (subsp. *album*), this species grows on sites ranging from the

177 thermomediterranean to the mesomediterranean and thermotemperate termotypes, under dry-  
178 subhumide to hyperhumide ombrotypes, according to the classification of Rivas-Martínez (2007).  
179 Annual rainfall on its Atlantic distribution ranges from 550 to 1600 mm. It is a dominant species  
180 in several types of coastal shrublands on sand dunes (Rivas Martínez et al., 2002).

181           On its unique Mediterranean site, the most relevant for this article, *C. album* is only spread  
182 on a small sector of the coastal mountain Serra Gelada in Benidorm, colonizing relict fossil dunes,  
183 where it characterizes the plant association *Coremato albi-Juniperetum macrocarpae* Alcaraz, M.  
184 Costa, M.B. Crespo, De la Torre & Solanas 2002. It deals with an endemic open shrubland,  
185 exclusive from Serra Gelada ( Solanas and Crespo, 2001; Aguilera et al., 2009; Rivas Martínez  
186 et al., 2002). This site is strongly different than the Atlantic areas for the same species, due to its  
187 extreme aridity -annual rainfall around 300 mm-. It is placed on the northernmost range of the so-  
188 called Spanish Southeastern desert. The Mediterranean population is extremely small and is  
189 placed on an extremely inaccessible place. According to our data, only 11 very aged individuals  
190 (4 female and 7 male, last census in 2016) grow on 400 m<sup>2</sup> and rarely produce viable seeds .  
191 Although the population has been regularly visited since its discovery, no young plants have been  
192 found (Aguilella et al., 2009).

193           On the basis of the IUCN criterion D2 (IUCN, 2012), the Mediterranean population of *C.*  
194 *album* can be evaluated as “Critically Endangered” (see Aguilera et al., 2009). Consequently,  
195 both species and the site are significantly protected by the environmental authority of the  
196 Valencian Community. The whole population is included in the Plant Micro-reserve “Serra  
197 Gelada Sud”. The mountain range Serra Gelada, its coastal cliffs and close small islands are  
198 enclosed into the boundaries of a Natural Park, which is additionally included in the European  
199 Union’s Natura 2000 network of protected sites –as Site of Community Importance, SCI “Serra  
200 Gelada”-. The species is strictly protected in the Valencian region at the highest legal category  
201 ‘In danger of extinction’, included in the Valencian Catalogue of Threatened Plant Species  
202 (Aguilella et al., 2009). In order to ensure its surviving, the Centre for Forestry Research and  
203 Experimentation (CIEF) of the Valencian Community, started in 2009 a recovery program

204 through propagation by seeds in order to obtain new seeds/plants for its maintenance in the CIEF's  
205 nurseries as mother plants to produce new seedlings.

206 Growing pressure from human activities and climate change impacts, threat the functional  
207 integrity of the coastal ecosystem affecting *C. album* populations, which decline in different areas  
208 of the western coast of the Iberian Peninsula (Fernández de la Cigoña, 1988; Parra et al., 2000),  
209 although the current distribution of this species remains constant (Gil-López, 2011). Sand dune  
210 ecosystems are affected since early twentieth century by large plantations of pine trees, causing  
211 the reduction of incident sunlight, the presence of nitrophilous invasive plants, as well as the  
212 recession of specialized fauna for seed dispersal. These reasons conduced to a considerable  
213 decrease in fruit production of *C. album* and were decisive in the cessation of its traditional  
214 commercial activity (Gil-López, 2011). Facing the ongoing habitat loss and disturbance in *C.*  
215 *album* communities, natural regeneration of this species is really low. Seed ecology has  
216 extensively been studied and reports low germination under natural (Álvarez-Cansino et al., 2016;  
217 Zunzunegui et al., 2006) or controlled laboratory conditions (Sousa et al., 2014), presenting  
218 physiological dormancy (at least 1 or 2 years in natural habitats), which is partially broken after  
219 consumption by vertebrates like seagulls, rabbits, and foxes. Also, the coastlines face high risks  
220 of damage from certain types of natural disasters as strong winds, hurricanes or cyclones.

221 *Corema album* branches and fruits have traditionally played a useful role for local people  
222 in the Atlantic side of the Iberian Peninsula. The plant was used to make rustic brushes, which  
223 may explain the origin of the generic name, from Greek verb '*korema*' which means 'broom'  
224 (Huxley, 1992). The fruits, commonly known as '*camariña*' or '*camarinha*', are edible, slightly  
225 acid and traditionally consumed in some parts of Portugal (Andrade et al., 2017a) and Spain (Gil-  
226 López, 2011), either in the raw state or transformed into acid-tasting lemonades, jams or liquors,  
227 being also used for cooking preparations or as appetizers (León-González et al., 2013b). They  
228 constitute an important source of water, fibers and sugars (Andrade et al., 2017a). The extracts of  
229 their leaves and fruits are rich in polyphenols and phenolic acids (León-González et al., 2012,  
230 2013b) which are becoming relevant because of their bioactive and medical properties as

231 vermifugal and febrifugal (Andrade, 2016; Andrade et al., 2017a, 2017b), and particularly as  
232 chemotoxic for carcinomes (León-González et al., 2012, 2013a; Macedo et al., 2015), and  
233 neuroprotective against Parkinson's disease (Gonçalves, 2014; Jardim, 2012). In fact, due to its  
234 relevant properties and edible fruits, *C. album* has been proposed as a new crop (Oliveira and  
235 Dale, 2012). No **ethnobotanical** references about ancient *C. album* uses in Mediterranean coast  
236 have been found.

237 **Regarding archaeological evidences, a compilation of finds has been carried out by I.**  
238 **López-Dóriga (2018). Up to now, the most ancient evidences of *C. album* in Iberian Peninsula**  
239 **come from Portuguese Early Neolithic sites. It has been also documented in some later**  
240 **archaeological sites until Medieval period on the Atlantic coast. The only evidence that predates**  
241 **these chronologies comes from the British Pleistocene site Pakefield-Kessingland, dated to**  
242 **700,000 years (although a possible contamination with recent material could not be dismissed).**  
243 **Having said that and as it is indicated by the author, the lack of evidence from Mediterranean sites**  
244 **could be explained by a misidentification of the remains of *camariña* (López-Dóriga, 2018).**

## 245 **5. Results**

### 246 5.1. Archaeological results

247 **The Pleistocene sequence of Cova de les Cendres is extremely rich in archaeobotanical**  
248 **remains, specially in charcoal and seeds. Regarding carpological remains, the density varies from**  
249 **28.98 remains/litre of sediment in the richest level (XVIA) to 0.77 remains/litre in the poorest**  
250 **(XIII). At least 90 different species have been documented, being *C. album* one of the most**  
251 **abundant of the assemblage. *Corema album* pyrenes (see Fig. 2) have been identified abundantly**  
252 **in three of the five Palaeolithic analyzed levels. Nevertheless, its presence is not homogenous**  
253 **throughout the sequence. In fact, a clear decrease from the bottom to the upper part of the**  
254 **sequence is detected. Together with the pyrenes, few leaves fragments have been identified, but**  
255 **no wood charcoal fragments of *C. album* have been documented.**

256 In the Gravettian level XVIA, 5936 pyrenes have been recovered, that is the 21.83% of  
257 the carpological assemblage. This high quantity of remains is equivalent to a minimum of 1061.58  
258 fruits of *C. album*. In level (XV), also dated to Gravettian, the presence of *C. album* starts to  
259 decrease, with 871 remains (16.97% of the assemblage), and representing 131.5 fruits. This drop  
260 in the number of remains consolidates in the Solutrean level XIII. There, only 32 remains of *C.*  
261 *album* have been identified (8.63%), so the minimum number of fruits is 5.42 (table 3; Fig. 3).

262 Finally, *C. album* remains are not present in the Middle and Upper Magdalenian levels.  
263 This absence is not due to a sampling bias, since an amount of litres of sediment similar to level  
264 XV was analysed. The explanation of its decrease and final disappearance must be looked for in  
265 their availability evolution on the Moraira headland.

## 266 5.2. Composition of *C. album*

267 The nutritional characterization of *C. album* fruit has been evaluated by moisture, soluble  
268 solids (SS), total titratable acidity, pH, ripening index, vitamin C, fiber, protein, mineral content  
269 (phosphorus, potassium, calcium, magnesium, iron, copper and zinc), total phenolic compounds  
270 and antioxidant activity, differentiating in some parameters between complete fruit (including  
271 seeds) and fruit without seeds (Table 4).

272 The moisture of the fruit without seeds is superior to the humidity of the fruit with seeds.  
273 In both cases, the water levels of the fruit are higher than indicated by Santos et al. (2014) (83.4%),  
274 possibly because the fruit is more mature, which is corroborated by increased soluble solids  
275 content, the lower acidity and higher index of maturity compared to what described previously  
276 (Santos et al., 2014).

277 Levels of vitamin C are especially high, in contrast to the value of 5.4 mg / 100 g reported  
278 elsewhere (Pimpão et al., 2013). The state of maturation, the ecotype, the edaphoclimatic  
279 conditions and the methodology used, can be at the origin of these differences.

280 The fruit is rich in fiber, coinciding with the results of Andrade et al. (2017a). Fiber levels  
281 are 90% higher in fruits with seeds. Protein levels are low, and similar to those found in citrus  
282 fruits. The protein content is higher in the fruit with seeds, due to the greater accumulation in this  
283 part of the fruit.

284 The total polyphenolic content is higher than that reported by León-González et al.  
285 (2013b) for this species, but lower than levels of other berries. These results are explained by the  
286 lack of anthocyanins in *C. album* fruits, since they are the main substances responsible for the  
287 polyphenolic concentration and the colors of most of the berries fruits, contrasting with the  
288 whitish color of the *C. album* fruits. The antioxidant activity of the fruits is superior to that  
289 recorded in the literature.

290 This work is unprecedented in the contribution of data on mineral content, so our results  
291 are compared to mineral concentration of a similar fruit, cranberry (BEDCA, n.d.). The mineral  
292 concentration is higher in the fruit with seeds, except for potassium, magnesium and copper,  
293 where the pulp concentrates higher percentage contents of these minerals. In comparison with  
294 cranberry, *C. album* fruits present lower content of phosphorus and iron, but the concentrations  
295 of the rest of minerals are higher.

296 In conclusion, *C. album* is a fruit, very rich in vitamin C, with an adequate antioxidant  
297 capacity and a very balanced mineral concentration, which is more important in the fruits with  
298 seeds.

### 299 5.3. Wood anatomy of *Corema album*

300 *C. album* has a heterogeneous wood with diffuse-porous to slightly semi-ring-porous,  
301 pores very small (10-15  $\mu\text{m}$  diameter), numerous, solitary or in small groups. Growth ring  
302 boundaries are very distinct and rays in transverse section rather indistinct. In longitudinal  
303 sections, *C. album* has uniseriate and homogeneous rays, composed only by procumbent cells.

304 The vessels have scaleriform perforation plates with ten or twelve bars, visible in the three  
305 sections of wood (Fig. 4).

306 *Corema album* wood is really particular and it has genuine features, such as the  
307 scaleriform perforation plates, so it could not go unnoticed within the Palaeolithic charcoal  
308 assemblage of Cova de les Cendres.

## 309 **6. Discussion**

### 310 6.1. Paleolandscape of the Moraira headland

311 The archaeobotanical analysis of the Pleistocene sequence of Cova de les Cendres (Badal  
312 and Carrión, 2001; Badal and Martínez Varea, 2018; Villaverde et al., 2017), as well as the studies  
313 of the evolution of the coastline (Fumanal et al., 1993a, 1993b; Fumanal and Viñals, 1988;  
314 Hernández-Molina et al., 1994) prove the existence of an Upper Pleistocene landscape on the  
315 Moraira headland extremely different from the current one (Fig. 5).

316 Nowadays, Cova de les Cendres is located just on the coastline. However,  
317 geomorphological analyses have revealed that during Upper Pleistocene the coastline was far  
318 away from the cave entrance. During the Last Glacial Maximum (23500-21800 cal BP),  
319 coinciding more or less with the Solutrean period, sea level was 120 m less than the current, so  
320 the seashore was 15-20 km away from the current position (Fumanal et al., 1993b). On the  
321 emerged continental shelf, there were a paleovalley, a small hill and some ponds. Sandspits and  
322 restingas developed on the coast of the light sloped platform and talus deposits next to the cliffs  
323 made easier the access to the karst formations (Fumanal et al., 1993a).

324 In 11500 BP, with the sea level rise, coastline advanced gradually until 4-9 km to the  
325 cave, where it remained until 9000 BP. In 6000 BP the current coastline was configured, with its  
326 characteristic cliffs (Fumanal and Viñals, 1988). The Holocene marine transgression covered and  
327 destroyed the eolianites so that nowadays just a small part of the Eemian dune system is visible

328 along the coast or submerged under the sea (Cova Tallada, Portet de Moraira, Torre de Moraira,  
329 Serra Gelada, etc.) (Fumanal et al., 1993a, 1993b; Fumanal and Viñals, 1988).

330 The identified flora among archaeobotanical remains fits perfectly with these  
331 geomorphological results. Through the Palaeolithic anthracological sequence, 8736 wood  
332 charcoal fragments have been analyzed and 21 woody taxa have been identified. This list  
333 increases to 26 taxa with the identification of seeds of five *Juniperus* species (Badal and Martínez  
334 Varea, 2018). Anthracological sequence is dominated by cryophilous pines, followed by  
335 *Juniperus* and shrub taxa, some of them clearly Mediterranean, such as *Rosmarinus officinalis*,  
336 *Pistacia* spp., *Erica multiflora* or *Ephedra* spp. The most xeric moments with the most open  
337 landscape are documented at the bottom of the diagram (XVIC) and during Middle Magdalenian  
338 (XII), as the significant increase of *Juniperus* spp. and shrub plant shows (Fig. 6). Maximum  
339 expansion of woodland is documented in Gravettian levels XVIA and B and during Upper  
340 Magdalenian (XI and IX), which must be the most humid moments of the sequence.

341 Pine forests would develop on rocky and limestone soils, together with *Juniperus sabina*  
342 and *J. thurifera*. The spread of these formations changes slightly throughout the sequence. The  
343 understory would be formed by *Fabaceae*, *Cistaceae*, *Lamiaceae* and other thermophile shrubs.  
344 A coastal dune system was developed, as the presence of *C. album* prove, especially during  
345 Gravettian. Other species documented in the archaeobotanical assemblage would grow there, as  
346 *Buglossoides arvensis* or *Echium vulgare* (*Boraginaceae* family). Some *Juniperus* species grow  
347 also in coastal sand dunes, as *J. oxycedrus* subsp. *macrocarpa* and *J. phoenicea* subsp. *turbinata*.  
348 Some *Cyperaceae* would grow at the edges of the ponds on the continental shelf.

349 The presence of *C. album* in the archaeological sequence of Cova de les Cendres shows  
350 a clear descending evolution, from Gravettian levels (XVIA and XV) when it constitutes one of  
351 the most frequent taxa, with a great reduction during Solutrean occupations and a final absence  
352 in Middle and Upper Magdalenian (Fig. 3). Harsh climatic conditions of Last Glacial Maximum  
353 during Solutrean, with colder temperatures and, specially, an aridity increase, which increment



354 during Middle Magdalenian, could affect the regeneration of *C. album*. The climatic amelioration  
355 during Upper Magdalenian did not mean the recovery of *C. album* population in the Moraira  
356 headland area, as probably the sea level rise would affect them destroying its habitat. In fact, this  
357 was the period of its final disappearance. The impact of the sea level changes on landscape and  
358 resources availability has been recently evaluated also in the Eastern Mediterranean site Franchthi  
359 Cave (Asouti et al., 2018).

360 Up to now, evidences to explain the presence of the unique Mediterranean population of  
361 *C. album* in Serra Gelada (Benidorm) were scarce. Different hypothesis were considered:  
362 originated by a bird migration input or relictual population. Nowadays, thanks to its preservation  
363 in Cova de les Cendres, at least since 29170 cal BP, we know the existence of a population near  
364 the Moraira headland, so being its ancient Mediterranean distribution larger than today, as it has  
365 also been suggested by López-Dóriga (2018). Probably, during Magdalenian, the Eemian inland  
366 dunes were already lithificated, so *C. album* populations faced with sea level rise could not  
367 migrate to them and their regeneration was limited to the better preserved dunes, maybe in the  
368 Serra Gelada area. In fact, the most developed *C. album* populations nowadays grow in sand dunes  
369 in the National Park of Doñana and along the Portuguese coast. Nevertheless, more  
370 archaeobotanical research in this region is essential to know the real extension of the ancient *C.*  
371 *album* populations and its reduction process until the current situation, probably related to the  
372 Last Glacial Maximum climatic conditions and the Holocene marine transgression.

## 373 6.2. Origin of the assemblage

374 The interpretation of the archaeobotanical assemblage must be found on a correct  
375 definition of its origin, that is, the routes of entry of the remains. Defining the deposition processes  
376 is not easy. Three different origins can be considered in the case of *C. album* in Cova de les  
377 Cendres: natural, biological and human processes.

378 -Natural deposition: *C. album* is not an anemochore plant. The morphological configuration of  
379 the cave and the possible distribution of *C. album* plants in the environment, far from the cavity,  
380 make us reject also a natural deposition by water.

381 -Animal deposition: *C. album* fruits are consumed by different animals. In fact, this is its seed  
382 dispersal mechanism (Calviño-Cancela, 2004). Microsedimentological analyses have  
383 documented the presence of insectivorous bats in some moments of Gravettian and Upper  
384 Magdalenian, as well as the presence of birds only in some Gravettian phases. Although we do  
385 not completely discard that these birds carried some seeds to the cave, we consider that they were  
386 not the main agent of introduction, since their presence is not frequent. In the archaeological levels  
387 analyzed here, there is no evidence of activity of other mammals (Villaverde et al., 2017). Another  
388 possibility is the incorporation of the grains within the stomach of the preys (Vaquer and Ruas,  
389 2009).

390 -Human deposition: based on the large number of remains, especially in Gravettian levels, the  
391 charred state of most of them and its undeniable alimentary usefulness, we consider that *C. album*  
392 remains were carried to the cave intentionally by humans. It would be illogical that human groups  
393 that visited Cendres discarded the use of these fruits, keeping in mind their vitamin C richness  
394 and their easy gathering. Moreover, the lack of *C. album* wood charcoal suggest a protection of  
395 these plants, avoiding their use as firewood.

### 396 6.3. Palaeoeconomy

397 Plants (fruits, seeds, leaves or stems) provide essential nutrients, some of which are not  
398 found in other types of food. In plants we found minerals as calcium, magnesium, manganese,  
399 iron and potassium. Plant foods are source of carbohydrates, fiber, fatty acids, amino acids and  
400 proteins (Slavin and Lloyd, 2012). A diet based principally on animal protein intake is cause of  
401 serious health problems (Butterworth et al., 2016; Noli and Avery, 1988) and diseases as rabbit  
402 starvation (Speth and Spielmann, 1983), hyperammonemia, hyperaminoacidemia or calciura

403 (Hardy, 2010, pp. 666–667). In fact, the under-consumption of some of these vegetable nutrients  
404 has serious consequences for fertility, pregnancy and post-partum (Hockett, 2012). Among the  
405 vitamins of vegetable origin, vitamin C stands out, since humans need ingest it, as we cannot  
406 produce **ascorbate acid** (Milton, 1999). In this sense, we found specially interesting that *C. album*  
407 fruits have a high content in vitamin C (97 mg/100 g). Moreover, they have a high content in  
408 potassium, magnesium and copper. So, Palaeolithic hunter-gatherers of Cova de les Cendres  
409 could find near the cave a vitamin, antioxidant and high-mineral-content fruit. *Corema album*  
410 fruits are also vermifuge and antipyretic, and they quench the thirst (León-González et al., 2012,  
411 2013b).

412 *Corema album* fruits gathering **could have had** an important role in Cendres hunter-  
413 gatherers' diet, especially during Gravettian, when they represent more than 21% of the  
414 carpological assemblage. *Camariña* fruits, as other plant foods, are stable, predictable -available  
415 during summer-, and easily gathered -knocked down to a container- and consumed. **Their flesh**  
416 can be ingested raw, throwing away their hard endocarp, maybe to the hearths, making possible  
417 their archaeological detection. It is also possible that hunter-gatherer prepared some kind of  
418 beverage with the fruits juice, discarding the pyrenes as by-products of processing, which could  
419 be thrown to the fire. These are just hypothesis, as we cannot prove the mode of consumption of  
420 the *C. album* fruits. **Therefore, these fruits could have been an important source of vitamin C, and**  
421 **minerals. Moreover, their vermifugal and febrifugal properties could have been known by hunter-**  
422 **gatherers. Their key role in the diet of the groups that visited the cave could explain why no *C.***  
423 ***album* pieces of charcoal have been identified within the anthracological assemblage, which is**  
424 **not due to problems in the identification, as its anatomy is really characteristic (Fig. 4). Gatherers**  
425 **may have managed the species that provided them food, they probably protected the plant,**  
426 **avoiding cutting down it for fuel, despite the high calorific power of its wood (López-Dóriga,**  
427 **2018). Only some parts of the plant were selected and carried to the cave. This behaviour was**  
428 **detected in Cueva de Nerja with *Pinus pinea* (Aura et al., 2010; Badal García, 2001).**

429 Through the sequence, the gathering of other fleshy fruits has been documented, as *Sorbus*  
430 *spp.*, *Sambucus nigra/racemosa* and *Ficus carica*, although its presence is reduced (Martínez  
431 Varea and Badal, 2018; Villaverde et al., 2017). *Rosaceae* family, specially genus as *Prunus spp.*,  
432 *Malus spp.*, *Sorbus spp.* or *Rubus spp.*, is frequently documented in Palaeolithic and Mesolithic  
433 sites where they have been considered as an essential component of diet: Santa Maira (Aura et  
434 al., 2005), Aizpea (Zapata, 2001), Balma Guilanyà (Allué et al., 2012), Tybrind Vig (Kubiak-  
435 Martens, 1999) or Öküzini (Martinoli and Jacomet, 2004). In Cendres just a few remains of  
436 *Rosaceae* have been documented, probably because of its scarce availability in the environment  
437 of the cave. Thus, we hypothesize that the role of *Rosaceae* fruits in other sites was played by *C.*  
438 *album* fruits during Gravettian and Solutrean. In Grotte de l’Abeurador and Theopetra a similar  
439 situation has been detected, as the more frequent fleshy fruit is *Hippophaë rhamnoides*, which, as  
440 *C. album*, is rich in vitamin C (Kotzamani, 2009; Vaquer and Ruas, 2009).

441 Together with *Rosaceae* fruits, seeds of *Poaceae* and *Fabaceae* are commonly present in  
442 Palaeolithic and Mesolithic sites. Small-grained wild grasses gathering seems to undergo a  
443 gradual rise during the Palaeolithic and Mesolithic, which could be related to the detected increase  
444 of food processing intensity (de Beaune, 2000; Power and Williams, 2018). They have been  
445 documented in Ghar e-Boof (Baines et al., 2015) or Franchthi Cave (Hansen, 1980), but they form  
446 the bulk of the gathered plants in Ohalo II (Weiss et al., 2004a), where they could have been even  
447 cultivated (Snir et al., 2015). Wild legumes were widely used as food since Middle Palaeolithic  
448 in different regions, as the results of Franchthi Cave (Hansen, 1980), Theopetra and Schisto  
449 (Kotzamani and Livarda, 2014), Ghar-e Boof (Baines et al., 2015), Taforalt (Humphrey et al.,  
450 2014) or Santa Maira (Aura et al., 2005) show. *Fabaceae* and *Poaceae* remains have been  
451 documented in Cendres as well. These three types of plant food – fleshy fruits, grains and  
452 legumes–, provided carbohydrates, fiber, proteins, minerals and vitamins to prehistoric hunter-  
453 gatherers.

454 In the last years, the increasing evidences disclosed by different disciplines strengthen the  
455 role of plants in prehistoric hunter-gatherers' economies. Nevertheless, an effort on the  
456 application of sampling methodologies and new research questions are needed to leave the biased  
457 image of Palaeolithic groups which emphasized the role of hunting activities behind.

## 458 7. Conclusion

459 Plants provide nutrients and minerals that humans cannot find in other sources. Therefore,  
460 combining meat intake with other elements, as plant food, is essential to health. Palaeolithic  
461 hunter-gatherers would not elude that, and unlike what traditional research shows, they probably  
462 combined different food sources: hunt, fishing, shellfishing and plant gathering. The carpological  
463 analysis of Cova de les Cendres evidences the consumption of *C. album*, among other plant foods,  
464 by human groups that visited it, at least since Gravettian until the end of Solutrean, being an  
465 essential part of diet. Moreover, these groups managed their ecosystem, since *C. album* is not  
466 present among the residues of domestic fires: they avoided cutting down it for fuel, as this plant  
467 provides them with fruits rich in vitamin C and minerals.

468 These data not only provide palaeoeconomic information, but also palaeoecological and  
469 palaeobotanical, as they shed light on the presence of the unique Mediterranean population of *C.*  
470 *album* and on the Upper Pleistocene coastal dune systems of Alicante. The dynamic of the most  
471 sensitive species to climatic and geographic changes, as *C. album*, can be correlated with global  
472 climatic changes of the Last Glacial Maximum and subsequent periods. The destruction of the  
473 coastal dunes by sea level rise and the lithification of the inner dune system probably prevent the  
474 regeneration of *C. album* populations, which became restricted to more limited areas on the  
475 Mediterranean coast, whose last refuge is Serra Gelada (Benidorm). More research in these terms  
476 is required in order to better know the real ancient extension of *camariña* populations, and genetic  
477 analysis could be carried out on the archaeological uncharred pyrenes of *Corema*.

478           Several reasons uphold the importance of preserving endangered species. Maintaining the  
479 biological and genetic diversity is required for the conservation of ecosystem or habitat where  
480 plants and animals live. In nature, each species plays a role in the ecosystem. The loss of a plant  
481 or animal species could yield serious consequences for the ecosystem -affecting the interspecific  
482 relationships, unbalancing trophic functions, etc.-, even collaterally endangering other species. Its  
483 impact is not always evident and sometimes can be difficult to be predicted at short and mid time.  
484 A second main reason to preserve an endangered species is to keep its genetic variability, as its  
485 progressive or sudden reduction can increase its risk of extinction. The conservation of genetic  
486 variability is also crucial to adapt the individuals to new environments, including those derived  
487 from climate change. Finally, the endangered species must be maintained as a future source of  
488 promissory benefits to humans, as already indicated for *C. album* regarding its medicinal uses.

489           An interdisciplinary research where botanists and archaeologists work together is  
490 essential to understand how ecosystems have changed through history, how humans have had to  
491 adapt to these changes and how human activities have altered the landscape.

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839  
840 **Figure legends:**

841 Fig. 1. a- Cova de les Cendres location and current distribution of *Corema album* in bioclimatic  
842 belts (based on [www.anthos.es](http://www.anthos.es)); b- *C. album* on dunes of Doñana, and c- detail of fruits.

843 Fig. 2. *Corema album*: fresh (a), archaeological charred (b) and mineralised (c) pyrenes.

844 Fig. 3. Evolution of *Corema album* remains through Cendres Palaeolithic sequence.

845 Fig. 4. Wood anatomy of *Corema album*: a-Transversal section: growth ring boundaries are  
846 distinct; b- Transversal section, scalariform perforation in vessel (detail); c-Radial section,  
847 scalariform perforation in vessel with several bars; d- Tangential section with uniseriate rays.

848 Fig. 5. Current topography and coastline of Moraira area (a) and geomorphology of the  
849 continental shelf (results of the geosismic surveys of 1993) (redrawn from Fumanal et al., 1993a)  
850 (b).

851 Fig. 6. Anthracological diagram of Cova de les Cendres.

852

853

Archaeological Level	Cultural adscription	Lab ID	Material	Age BP	Level age cal BP (95%)
IX	Final Upper Magdalenian	Beta-142284	<i>Pinus nigra/sylvestris</i> (charcoal)	12470±100	15180 - 14100
X	Steril				
XI	Upper Magdalenian	Beta-189079	<i>Pinus nigra/sylvestris</i> (charcoal)	13120±60	16240 - 15530
		Beta-287538	<i>Pinus nigra/sylvestris</i> (charcoal)	13350±50	
XII	Middle Magdalenian	Beta-118022	<i>Pinus nigra/sylvestris</i> (charcoal)	13690±120	19570 - 16140
		Beta-287541	<i>Pinus nigra/sylvestris</i> (charcoal)	16030±60	
XIII	Solutrean	Beta-287542	<i>Pinus nigra/sylvestris</i> (charcoal)	16790±60	23230 - 20050
		Beta-118026	<i>Pinus nigra/sylvestris</i> (charcoal)	18920±180	
XIV	Solutrean	Beta-287545	<i>Pinus nigra/sylvestris</i> (charcoal)	20200±80	24620 - 24030
		Beta-287544	<i>Pinus nigra/sylvestris</i> (charcoal)	20280±80	
XV	Gravettian	Beta-142282	<i>Pinus nigra/sylvestris</i> (charcoal)	21230±80	26700 - 25340
		Beta-437194	<i>Pinus nigra/sylvestris</i> (charcoal)	22190±80	
XVIA	Gravettian	Beta-437195	<i>Pinus nigra/sylvestris</i> (charcoal)	22750±110	29170 - 26750
		Beta-437196	<i>Pinus nigra/sylvestris</i> (charcoal)	24850±110	
XVIB	Gravettian	Beta-437823	<i>Acer</i> sp. (charcoal)	25590±100	31000 - 29350
		Beta-437198	<i>Pinus nigra/sylvestris</i> (charcoal)	26580±90	
XVIC	Late/Evolved Aurignacian	VERA-6428ABOxSC	<i>Pinus nigra/sylvestris</i> (charcoal)	27560±240	34140- 31020
		VERA-6427ABOxSC	<i>Pinus nigra/sylvestris</i> (charcoal)	29490±260	
XVID	Late/Evolved Aurignacian	Beta-458346	<i>Juniperus</i> spp. (charcoal)	31080±170	35340 - 34620
XVII	Cultural adscription pending				

854

855 Table 1. Chronological limits and cultural adscription of Palaeolithic archaeological levels of  
856 Cova de les Cendres (Villaverde et al., 2017) (Calibration obtained with CalPal-IntCal 13).

857

<b>Number of seeds/fruit</b>	<b>Number of individuals</b>
1	2
2	30
3	68
<b>Total of fruits</b>	<b>100</b>
<b>Number of seeds</b>	<b>266</b>
<b>Mean number of seeds/fruit</b>	<b>2.66</b>
<b>Mode</b>	<b>3</b>

858

859 Table 2. Number of seeds per fruit of *Corema album*

860



	Level XI	Level XII	Level XIII	Level XV	Level XVIIA
Litres of sediments	270	138	483	198	938,4
Reproductive remains	1730	843	371	5131	27192
Total <i>Corema album</i> remains	0	0	32	871	5936
<i>Corema album</i>	Charred endocarp		11	257	2284
	Charred endocarp fragment		17	550	3579
	Charred seed		1	31	12
	Charred seed fragment		0	23	2
	Mineralised endocarp		1	0	4
	Mineralised endocarp fragment		0	0	9
	Mineralised seed		0	0	12
cf. <i>Corema album</i>	Charred endocarp		0	0	1
	Charred endocarp fragment		2	10	26
	Mineralised endocarp fragment		0	0	0
	Charred seed		0	0	6
	Mineralised seed		0	0	0
	Mineralised seed fragment		0	0	1
<b>MNI <i>Corema album</i></b>			16,25	394,5	3184,75
<b>MNF</b>			5,42	131,5	1061,58

861

862 Table 3. *Corema album* remains in Cova de les Cendres (MNI: Minimum Number of Individuals  
863 or endocarps; MNF: Minimum Number of Fruits).

864

	<b>Fruit with seeds</b>	<b>Fruit without seeds</b>
<b>Moisture (%)</b>	97,66	98,32
<b>Soluble solids (°Brix)</b>		8,5
<b>Total titratable acidity (% citric)</b>		0,89
<b>Ripening index</b>		9,55
<b>pH</b>		3,3
<b>Vitamin C (mg/100 g)</b>		97
<b>Fiber (%)</b>	10,43	1,04
<b>Protein (%)</b>	0,44	0,19
<b>Phosphorus (mg/100 g)</b>	3,75	1,4
<b>Potassium (mg/100 g)</b>	121,3	129,1
<b>Calcium (mg/100 g)</b>	21,36	17,88
<b>Magnesium (mg/100 g)</b>	4,78	7,35
<b>Iron (mg/100 g)</b>	0,29	0,13
<b>Copper (mg/100 g)</b>	0,19	0,22
<b>Zinc (mg/100 g)</b>	0,22	0,09
<b>Total phenolic compounds (mg caffeic acid/kg)</b>		1801,55
<b>Antioxidant activity (μmoles ET/g)</b>		70,2

865

866 Table 4. Results of the chemical analysis of *Corema album* fruits.

867