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# Redrawing the History of *Celtis australis* in the Mediterranean Basin under Pleistocene–Holocene Climate Shifts

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**Abstract:** *Celtis australis* remains are usually present in Palaeolithic sites of the Mediterranean Basin. However, their uncharred state of preservation and the absence of wood charcoal remains of this species raise some doubts regarding the contemporaneity of the remains and the deposit wherein they were found. The mineral composition of their endocarps and their possible use as food lead us to discuss the available data of *Celtis australis* during Prehistory. In this paper, the history of this species from the Lower Pleistocene to the Middle Holocene is reconstructed, considering the impact of the Quaternary climatic changes on its geographical distribution. The nutritional composition of *Celtis australis* fruits is analysed to assess their current value and potential as food, especially in Palaeolithic contexts. Based on these issues, the doubts about its presence in these contexts are dispelled and possibly explained by intentional human gathering in some sites, considering the high content in carbohydrates, proteins and minerals of their fruits. The chronological and geographical distribution of the *Celtis* spp. remains shows a coherence, which only the variations in the distribution of this taxon according to the regional climatic conditions can explain, especially disturbed by cold fluctuations, such as MIS 10 or 2. The radiocarbon dating presented here demonstrates the unquestionable presence of *Celtis* sp. in the Iberian Mediterranean Basin during MIS 3.

**Keywords:** *Celtis australis*; archaeobotany; nutritional analysis; climatic dynamics; vegetation dynamics; Pleistocene; Holocene

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## 1. Introduction

In the Mediterranean region, tropical, Eurosiberian and genuinely Mediterranean taxa form the vegetation as a result of their adaptation to human impact and geological and climatic changes over the last million years [1–3]. Some of these taxa settled here during the Pliocene when subtropical climate conditions—warm and humid—fostered diverse and dense woody formations. Three plant groups are documented in the Pliocene and Lower Pleistocene European palaeobotanical sequences: laurisilva, temperate species and Mediterranean taxa [4].

During the Lower Pleistocene, the colder conditions and changing rainfall caused the reduction in the laurisilva in the Mediterranean Basin from which some taxa are present nowadays, such as *Laurus nobilis*, *Nerium oleander*, *Viburnum tinus* and *Arbutus*. The characteristic Mediterranean summer drought enabled the consolidation and expansion of xerophilic Mediterranean flora, such as evergreen *Quercus*, *Olea*, *Phillyrea*, *Pistacia*, *Artemisia* or *Ephedra fragilis*. Mesophilous trees growing in the region during the Lower Pleistocene can be classified into two groups: (A) genera that gradually disappeared from the Western Mediterranean Basin, such as *Carya*, *Pterocarya*, *Parrotia*, *Zelkova* or *Liquidambar* [5,6], and

(B) genera that currently grow in the basin, such as *Quercus*, *Fraxinus*, *Acer*, *Alnus*, *Carpinus*, *Tilia*, *Populus* or *Celtis*.

The Quaternary history of species is marked out by adaptations, extinctions and changes in their spatial distribution [5,7,8]. In this work, we focus on the history of *Celtis australis*, the interest in which lies in (1) its adaptation to glacial–interglacial cycles, (2) its resistance to summer droughts, (3) its ecological relevance in Mediterranean ecosystems and (4) the economic interest in its edible fruits to Pleistocene and Holocene human groups in the Mediterranean Basin. Moreover, knowing its history could help predict the future of this species under the climatic pressure of the Anthropocene [9]. To achieve these goals, all the available palaeobotanical information, including different types of remains (wood, charcoal, seeds, pollen and leaves), as well as evidence from other related taxa, such as *C. tournefortii*, is gathered. We add new data from Pleistocene Iberian sites and two new radiocarbon dates of *Celtis* endocarps. Second, through their chemical analysis, we assess the potential of its fruits as food, especially in hunter-gatherer contexts.

*Celtis australis: Species Description, Ecology and Traditional Uses*

*Celtis* is placed in the Cannabaceae family and comprises 66 different accepted species, growing in America, Africa, Asia and Europe [10,11]. In the Mediterranean Basin, nowadays, we can find *C. australis*, *C. occidentalis* (introduced), *C. glabrata* and *C. tournefortii*, the first being the only species growing in the Iberian Peninsula [12].

*Celtis australis*, commonly known as Mediterranean hackberry or nettle tree, is a deciduous tree that can grow 30 m in height, with a broad and dense crown and thin and erect branches. The bark of its trunk is smooth and grey. Their leaves are alternate, petioled, lance-shaped to oval-lanceolate, acuminated and serrated, and they have an asymmetric base. The small hackberry flowers are axillary and solitary, although they occasionally form small clusters of two or three flowers. They have a pentamerous perianth, five stamina and a unilocular ovary. This species is andromonoecious, and its pollination occurs through anemophily. *Celtis australis* fructifies in sub-spherical drupes, 8.5–12 mm in diameter, green unripe, blackish when ripe, with a long stem. Inside its sandy flesh, a woody endocarp contains the seed [13].

The Mediterranean hackberry grows in the south of Europe, west of Asia and north of Africa, in woods, ravines, riverbanks and rock fissures, on fresh or humid, light or rocky soils, although it is indifferent to the substratum (Figure 1). It is a heliophilous species, which avoids cold and frosts [13,14]. It is usually documented in mixed woods, growing with *Quercus pubescens*, *Fraxinus ornus*, *Corylus avellana* and *Acer* spp., as well as with evergreen *Quercus* and *Pinus halepensis*. *Celtis australis* also forms gallery forests with *Salix* spp., *Populus* spp. and *Ulmus* spp. [15]. Since it is cultivated as an ornamental tree, it is usually found feral. In gardens and parks, we can find other species of this genus from America or Asia [16]. Primary shoot growth spans from March to May, and diameter growth is higher from spring to early summer, as a response to water availability [9,17]. The hackberry flowers over one month in spring, from April to May, and fructifies at the end of summer. The fruits ripe in autumn, but they can remain on the tree until winter. Frugivorous vertebrates disperse the seeds, favouring the propagation of the plant by sowing the seeds as soon as they ripe, although vegetative reproduction is also possible via root suckers [15,18]. Leaf shedding starts in November.

Regarding its traditional uses, its wood is highly valued due to its flexibility, hardness and resistance, being an excellent raw material for the manufacture of boats and paddles, farm equipment, such as pitchforks, sticks and handles, bowls and mortars, musical instruments, as well as door and window lintels [19–21], even from the 4th century BC, when Theophrastus characterised it as "incorruptible" in *De historia plantarum* (V, 4, 2 and V, 5, 6). This traditional use was widely spread in many regions of the Kingdom of Valencia during the 18th century, as pointed out by Cavanilles in his *Observaciones sobre la Historia Natural*. This tradition hardly continues to date. The use of hackberry wood for construction was archaeologically documented in the Castle of Turís [22]. Its wood has

also been employed in cabinetmaking and to create sculptures in Florence. Hackberries are planted in Toscane and Sicily as vine-growing guides [23]. Its wood and its wood charcoal are considered good fuel. The bark from the stems and roots contains a yellow pigment used, as already indicated by Dioscorides, for dying silk [14,16]. Hackberry leaves and bark have been used as fodder. For instance, in the Central Himalayan region, *Celtis australis* is cultivated around the fields in order to use its leaves in April and May as green fodder for cattle, since they are nutritious, palatable and free from tannins [24]. In the Iberian Peninsula, the dry leaves of the hackberry are eaten by sheep in autumn [14,25].

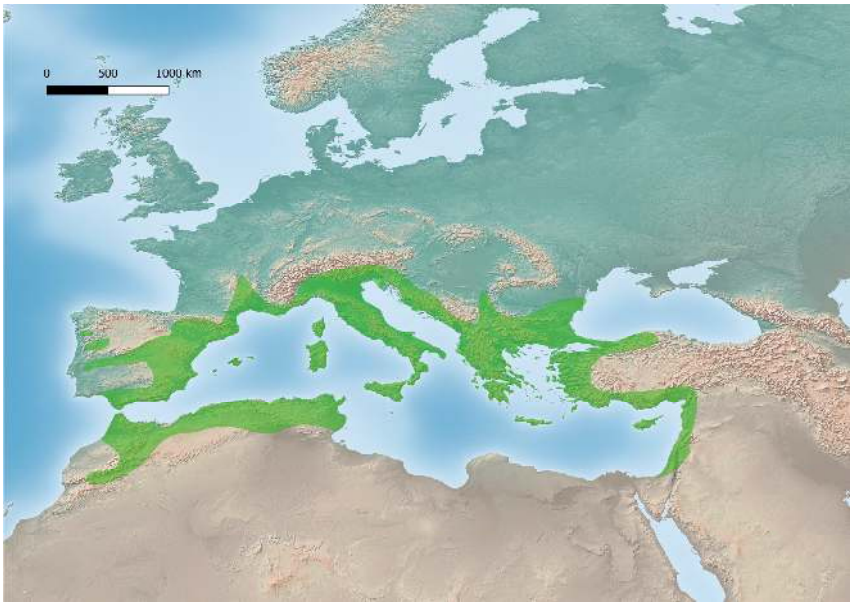



**Figure 1.** Current distribution of *Celtis australis* (redrawn from Ref [15] using QGIS version 3.4.13; Source: Natural Earth Data).

Hackberry fruits are edible when ripe but are considered toxic when unripe. Although their flavour is rough and they are dry and astringent, they have high sugar content; therefore, the Greeks call them "honey fruits". Due to their sweetness, they are especially attractive for kids, and they have been used to produce liquors, as well as a source of sugar during shortage periods [14,16,26,27]. Their seeds are also edible, and they can be used to extract oil [28].

Some medical properties were attributed to the hackberry by Dioscorides as early as the 1st century. For example, fruits and leaves are used to reduce blood pressure, prevent diarrhoea, reduce cholesterol and regulate menstrual flow or for diuretic purposes [14].

*Celtis australis* is currently an ornamental tree, as in Roman times, considering the history of Lucius Crassus, in whose garden in the Palatine there were six Mediterranean hackberries [29]. According to the agricultural treatises from Al-Andalus times, the Mediterranean hackberry was used to construct irrigation canals and mills and protect some parts of the gardens from the dew [30].

## 2. Materials and Methods

To achieve the raised objectives, we explored several methodological lines:

- We conducted literature searches to gather all the palaeobotanical finds of *Celtis* spp., from Lower Pleistocene to Middle Holocene. Regarding the geographical setting, we focused on the Mediterranean Basin and northern Europe, although we considered the findings in other regions, which could enrich our discussion. We gathered the documentation of macro—-wood, leaves, wood charcoal and seeds—and micro-remains—pollen and phytoliths—recovered in archaeological and natural sites.

- The palaeobotanical data are presented in Tables 1–5, chronologically arranged. The chronology shown is that of the level or structure where the remains were recovered, not a direct dating (with exceptions). Where possible, the abundance of the taxon in the assemblage is noted, expressed as percentage or number of remains, as is published in the checked works.
- To check the antiquity of *Celtis* remains, we carried out two radiocarbon datings on uncharred endocarps from two Middle Palaeolithic Iberian sites: Abrigo de la Quebrada (Chelva, Valencia) and Cueva del Arco (Cieza, Murcia). Hackberry endocarps formed naturally with carbonate, which reflects the $C^{14}$ atmospheric values of only one growing season. Therefore, endocarps are suitable for obtaining reliable dating [31]. However, the integrity of the mineral composition of the fossil specimen must be evaluated previously. The carpological remains were first washed with deionised water to remove organic sediments and debris. After crushing them, they were subjected to HCl etches to eliminate secondary carbonate components [32].
- The presence or absence of *Celtis* wood charcoal in archaeological sites is analysed to assess the specialised use of this taxon, considering the frequent presence of fruit remains as opposed to the absence of wood in most sites.
- A chemical analysis of the current fruits of *Celtis australis* was carried out to assess their nutritional value.

### 2.1. Celtis Endocarps Description

*Celtis australis* fruits contain a stony endocarp, which encloses the seed. This endocarp presents four marked ridges growing from the apex. Two of them encircle the endocarp, whereas the other opposite two are along its upper half. The space among the ridges is covered by a pronounced reticulate. Although with some difficulties, the taxa within this genus can be differentiated based on the density of this reticulate and the more or less pronounced ridges [33]. However, frequently, an identification of archaeobotanical remains within the species range is not possible due to the state of the surface or the absence of reference material. In these cases, ecological criteria are usually applied.

The walls of the endocarps of *Celtis* spp. fruits are composed mainly of aragonite (40–70 wt%), a form of calcium carbonate [31,34–36], one of the more frequent biogenic minerals [37]. In addition, opal and organic matter are present [31,38].

### 2.2. Challenges in Wood Celtis Identification

A relevant issue regarding *Celtis* wood, which is barely identified in the Pleistocene, is to assess whether it can be mistaken for other species due to the similarity of their wood anatomy. Indeed, *Celtis* spp. can sometimes be challenging to differentiate from *Ulmus* spp. based on their wood anatomy. According to wood anatomy atlases [39], both genera have ring-porous, with pores in latewood grouped in long, tangential to oblique, bi- to four-seriate bands together with vascular tracheids and parenchyma. In the earlywood, *Celtis* spp. has a generally uniseriate pore ring, while *Ulmus* spp. has 1 to 3 rows of earlywood pores. In the tangential section, they have spiral thickenings in small vessels. The rays are generally homogeneous to heterogeneous with one row of square marginal cells in *Ulmus* spp. and slightly heterogeneous with few rows of square and upright cells in *Celtis* spp. Regarding multiseriate rays, they are generally 4- to 5-seriate (occasionally narrower or wider) in *Ulmus* spp. and 4- to 8-seriate in *Celtis* spp.

To evaluate whether these genera can be discriminated in prehistoric charcoal, we performed a comparative study of both species (on current carbonised wood from the reference collection) through a scanning electron microscope (SEM) (Figure 2). We focused on the most probable criteria for distinguishing between both genera—pore distribution in earlywood ring and ray morphology (width and heterogeneity)—thus confirming the criteria described above. However, it should be noted that in archaeological wood charcoal (sometimes of small size and with preservation problems), these criteria might not be observable, or they might overlap. For this reason, some references where the taxon

*Ulmus*/*Celtis* was identified were also considered in Tables 1–5 as a possible but not certain presence of *Celtis*.

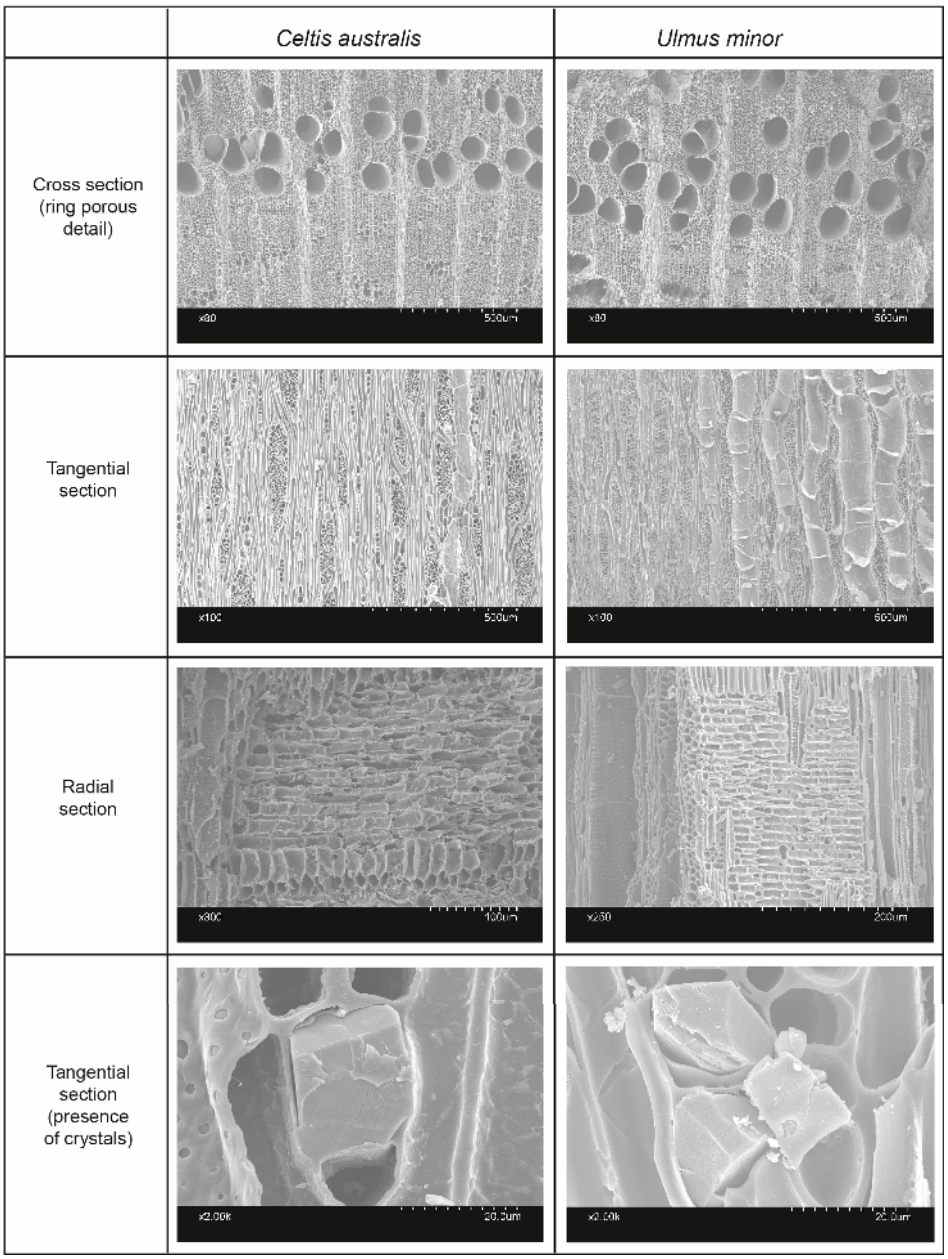



**Figure 2.** Comparison of the wood anatomy of *Celtis* and *Ulmus*.

### 2.3. Chemical Composition Analysis

*Celtis australis* fruits are edible, but composition and nutritional analyses are scarce. Knowing these data is essential in order to assess their potential use as food and to discuss their use during Prehistory or even favour their consumption nowadays. To carry out these analyses, 1.8 kg of fruits of an individual was gathered on 14 November 2021 near Cheste (Valencia, Spain) (39°29′50.43″ N; 0°39′07″ W) at 218 m a.s.l. The climatic conditions in the gathering area are classified as BSk following the Köppen–Geiger system, with a mean annual precipitation of around 456 mm and a mean annual temperature of 16.1 °C. Under these conditions, thermo-Mediterranean flora develops, with *Nerium oleander*, *Olea europaea* var. *sylvestris*, *Rhamnus lycioides*, *Chamaerops humilis* and *Quercus coccifera*. *Celtis australis* concentrate in the more humid spaces, such as talwegs, fields' edge or ravines. The criteria applied for the selection of the sampled tree were: (1) a young tree whose size

allow climbing to the top and (2) standing in a natural environment, not much altered by humans. Fruits are abundant and remain on the tree until the beginning of the winter when the flesh is dry, and the fruits are disseminated by gravity or by the birds. Fruit gathering is laborious, since they do not fall easily knocking down the branches. Moreover, under the selected tree, there was a dense understorey of tall grasses and thorny bushes. For this reason, the knocking down was not performed because we would need to put a net around the trunk to collect the fruits. We do not rule out the use of this gathering method during Prehistory, but we wanted to check the cost with the minimum technology used in the collection. Therefore, for the current experimentation, we decided to harvest the fruits manually. To collect about 2 kg of fruit, a person spent 3 h.

#### 2.3.1. Morphological Parameters

The morphological parameters of hackberry fruits (*Celtis australis*), such as unit weight, pulp weight, seed weight, diameter (D), height (H), volume (V), geometric mean diameter ($D_g$), degree of sphericity (Ø) and the surface area (S) of the fruit, are noted. The weights were measured with an analytical balance (CB-Junior, Cobos) with an accuracy of ±0.001 g. The fruit's dimensions were measured using an electronic digital slide gauge (model CD-15 DC; Mitutoyo (UK) Ltd., Telford, UK) within 0.01 mm accuracy. The volume of the fruit was calculated using the adapted formula of a sphere: $V = \frac{3}{2} * \pi * \left(\frac{H}{2} + \frac{D}{2}\right) * D^2$. The geometric mean diameter of the fruit was calculated by using the formula $D_g = (HD^2)^{1/3}$, where the degree of sphericity can be expressed as $Ø = D_g/H$, and the surface area (S) of the fruit was calculated by using the formula $S = \pi {D_g}^2$ [40]. Thirty random fruits were selected for morphological measurements, since the variability of the parameters was low.

#### 2.3.2. Nutritional Parameters

For nutritional characteristics, fruits were transversely cut in half. The pulp and peel were manually separated from the seeds and weighed, and the seeds were eliminated. Moisture and dry matter were determined for the whole fruit and for the pulp and peel. The rest of the parameters were determined in pulp plus peel (since fruits are usually ingested unpeeled).

Proximal composition was carried out following the official methods (Official Method of Analysis of the Association of Official Analytical Chemists International): moisture [41] (984.25), proteins [41] (984.13), fat [41] (983.23), fibre [41] (991.43) and ashes [41] (923.03). The carbohydrate (CH) content was calculated by the difference. The results are expressed as g·100 $g^{-1}$ of fresh weight (fw). Energy (kcal 100 $g^{-1}$) was calculated by multiplying the grams of fat by 9 kcal and the grams of protein and carbohydrates of each 100 g of fruit by 4 kcal.

To determine the pH, soluble solids content (SSC) and titratable acidity (TA) of the peel and pulp of the hackberries, 5 g of the sample plus 15 mL of distilled water was crushed with a domestic blender to obtain a juice-like substance. The pH determination was made by direct potentiometric measurement of the homogenised peel and pulp with pH and Ion-metro GLP 22 (CRISON). The SSC in the juice was carried out using refractometric techniques [41] (932.12). The material used in this determination is a hand-held refractometer with a range of 0–32 °Brix. The determination of total acidity (TA) consists of the potentiometric titration of the sample with an alkaline solution (0.5 *N* NaOH) up to pH = 8.1 [41] (942.15). The results are expressed in grams of citric acid for 100 g of the sample.

The mineral composition was determined by the previous digestion of the samples following the method AOAC 985.35 [41]. The samples were calcined in a Carbolite CWF 1100 muffle at 550 °C. The mineralised samples were analysed by inductively coupled plasma emission spectroscopy (ICP-EOS) to determine the mineral elements. The equipment used is Agilent ICP-EOS 710 (700 series ICP-OES, Mulgrave, Victoria, Australia). The wavelengths selected for each element are the following: 317.933 nm for Ca determination, 324.754 nm for Cu determination, 238.204 nm for Fe, 769.897 nm for K, 285.213 nm for Mg, 257.610 nm for Mn, 589,592 nm for Na, 177,434 nm for P, 196.026 nm for Se, 213.857 nm for

Zn, 249.678 nm for B and 281.615 nm for Mo determination. The results are expressed in mg of the mineral element per 100 g of fresh fruit.

Total polyphenols (TP) were determined in an aliquot of methanolic extract with a modification of the Folin–Ciocalteu assay, according to a previously published protocol [42], using gallic acid as the reference standard. The results are expressed in mg of gallic acid for 100 g of fresh fruit weight (mg EAG 100 $g^{-1}$ fw). To measure the extract's effect on the DPPH radical, the optimised method of Brand-Williams et al. [43] is adapted. This measure of the total antioxidant (AOT) capacity is carried out by employing methanol: HCl (99:1) as dissolvent. The results are expressed in terms of activity equivalent to Trolox of fresh fruit weight (µmol Trolox 100 $g^{-1}$ fw).

Thirty fruits were used for the morphological measurements, and the rest of the parameters were analysed in triplicate. The obtained data were processed using Statgraphics Plus version 5.1, which computed the means and standard errors to summarise a single sample of data.

## 3. Results

### *3.1. Palaeobotanical Remains*

*Celtis* remains were identified in 51 archaeological sites and 35 palaeobotanical sites of the Mediterranean Basin (Tables 1–5), chronologically and geographically unevenly distributed.

Following Palamarev [44], the group *Celtis lacunosa*, which includes the ancestry taxa of *Celtis australis* (*C. lacunosa*, *C. japetii*, *C. begonioides*, *C. vulcanica* and *C. cernua*), appeared during the Oligocene, and it was present during this period, the Miocene and the Pliocene in most parts of Europe (France, Germany, Czech Republic, Poland, Hungary, Austria, Bulgaria and Moldavia) with some geographic disjunctions.

From the Lower Pleistocene, only 10 sites provide information. *Celtis* sp. has been documented in the archaeological sites Gran Dolina (Spain) (936.000 BP), where both endocarps and pollen were identified [45], Dmanisi (Georgia) [46] and Grotte du Vallonet (France) [47]. We must highlight that the remains found in Dmanisi are probably *Celtis tournefortii*, based on ecological criteria. In Gran Dolina, the remains come from a level dated to MIS 25, one of the warmest stadials of the Günz glaciation. Moreover, pollen and leaves of *Celtis* sp. were recovered in seven palaeobotanical sites in Western Mediterranean (Table 1, Figure 3).

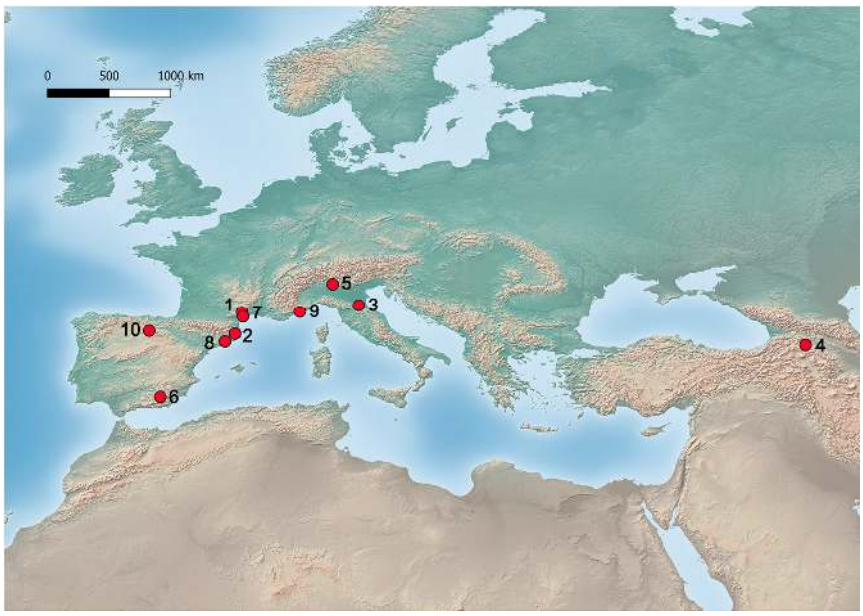



**Figure 3.** Lower Pleistocene sites where *Celtis* remains were reported (numbers in the figure correspond to ID numbers in Table 1) (map generated using QGIS version 3.4.13; Source: Natural Earth Data).

**Table 1.** Lower Pleistocene sites where *Celtis* remains were reported (types of remains: endocarp (E), leaves (L), pollen (P)).

| ID | Site | Location | Chronology | Cultural Adscription | Taxa | Type | NR | Reference |
|---|---|---|---|---|---|---|---|---|
| 1 | Bernasso | Lunas, France | 2.2 Ma–2.1 Ma (MIS 82–78) Pollen zone II = Interglacial | | *Celtis* sp.<br>*Celtis* cf. *australis/caucasica* | P<br>L | <15% | [48–50] |
| 2 | Tres Pins | Porqueres, Spain | Early Pleistocene (interglacial) | | *Celtis* sp. | P | <2% | [51] |
| 3 | Lamone Valley | Lamone Valley, Italy | 1.8–1.4 Ma (MIS 64-46) | | *Celtis* sp. | P | <5% | [52] |
| 4 | Dmanisi | Kvemo Kartli, Georgia | 1.8 ± 0.05 Ma | Early Palaeolithic | *Celtis* sp. (cf. *C. tournefortii*) | E | 3 | [46] |
| 5 | Leffe Basin | Leffe, Italy | MIS 53-52 or 51-50 | | *Celtis* sp. | P | <2% | [53] |
| 6 | Palominas | Baza, Spain | 1.8–1.1 Ma | | *Celtis* sp. | P | 10% | [8] |
| 7 | Saint-Macaire maar | Servian, France | 1.4–0.68 Ma | | *Celtis* sp. | P | <1% | [54] |
| 8 | Cal Guardiola | Terrassa, Spain | 1.2–0.8 Ma | | *Celtis* sp. | P | 0.2% | [55] |
| 9 | Grotte du Vallonnet | Roquebrune-Cap-Martin, France | 1,370,000 ± 120,000–910,000 ± 60,000 BP (Donau-Günz Interglacial) | | *Celtis* sp.<br>cf. *Celtis australis* | E<br>P | <5% | [47,56] |
| 10 | Gran Dolina | Atapuerca, Spain | 936,000 BP (MIS 25) | Lower Palaeolithic | *Celtis* cf. *australis* | E<br>P | 91 | [45,57] |

For the Middle Pleistocene, the evidence increases, with data from 9 archaeological sites, such as Grotte de l'Escale, Caune de l'Arago or Grotte du Lazaret in France, or even in Germany, in Kärlich [58,59], De Lumley in Refs [60,61], and 18 palaeobotanical sites, showing a larger distribution (Table 2, Figure 4). For this period, the expansion of *Celtis* to northern Europe must be highlighted, reaching the north of Germany. Most of these remains were reported in levels dated to warm MIS 11 (Holstein interglacial). Only Grotte de l'Escale is clearly placed in a cold period (Middle or Upper Mindel glaciation). MIS 10 represents one of the coldest moments in Europe, so this period must be critical for *Celtis* in northern Europe. Afterwards, *Celtis* is documented in Lazaret and during MIS 9 and 7 in Cova del Bolomor [62].

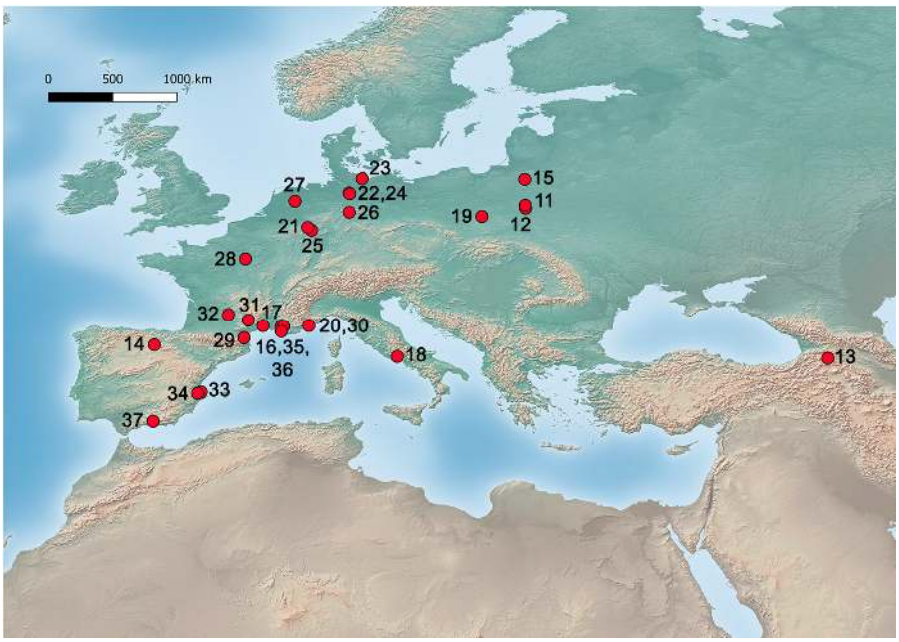



**Figure 4.** Middle Pleistocene sites where *Celtis* remains were reported (numbers in the figure correspond to ID numbers in Table 2) (map generated using QGIS version 3.4.13; Source: Natural Earth Data).

**Table 2.** Middle Pleistocene sites where *Celtis* remains were reported (types of remains: wood charcoal (C), endocarp (E), leaves (L), pollen (P), wood (W)).

| ID | Site | Location | Chronology | Cultural Adscription | Taxa | Type | NR | Reference |
|---|---|---|---|---|---|---|---|---|
| 11 | Łuków | Łuków, Poland | Ferdynandovian I interglacial (MIS 15–MIS 13) | | *Celtis* sp. | P | | [63] |
| 12 | Zdany | Zdany, Poland | Ferdynandovian I interglacial (MIS 15–MIS 13) | | *Celtis* sp. | P | | [63] |
| 13 | Achalkalakai | Achalkalakai, Georgia | Early Middle Pleistocene | | *Celtis* sp. | E | | [64] |
| 14 | Galería | Atapuerca, Spain | Final Middle Pleistocene | Lower Palaeolithic | *Celtis* sp. | P | 2% | [65] |
| 15 | Krzyżewo | Krzyżewo, Poland | Augustovian interglacial (cf. Late Cromerian) | | *Celtis* sp. | P | <1% | [66] |
| 16 | Grotte de l'Escale | Saint-Estève-Janson, France | Middle and Upper Mindel | Without adscription | *Celtis* sp. | E | | [59] |
| 17 | Grotte nº1 du Mas des Caves | Lunel-Viel, Hérault, France | 550,000–400,000 BP (Mindel–Riss Interglacial, MIS 11) | Middle Acheulean | *Celtis* sp. | E | | [67] |
| 18 | Ceprano | Ceprano, Italy | 530,000–380,000 BP (MIS 13) | | *Celtis* sp. | P | <5% | [68] |
| 19 | Kleszczów Graben | Kleszczów, Poland | Ferdynandovian and Holsteinian interglacial | | *Celtis* sp. | P | <1% | [69] |
| 20 | Terra Amata * | Nice, France | 380,000 BP (MIS 11) | Acheulean | *Celtis australis* | E | | De Lumley in Refs [60,61] |
| 21 | Kärlich | Mülheim-Kärlich, Germany | Interglacial, MIS 11 | Early Palaeolithic | *Celtis* sp. | E<br>C and W<br>P | 1<br>27<br>1.4% | [58,70] |
| 22 | Munster/ Breloh | Niedersachsen, Lüneburger Heide, Germany | Holsteinian interglacial | | *Celtis* sp. | E<br>P | <5% | Müller 1974 cited in Refs [70,71] |
| 23 | Southwestern Mecklenburg | Hagenow, Germany | Middle Pleistocene | | *Celtis* sp. | E | | Erd cited in Ref [70] |
| 24 | Dethlingen | Lüneburger Heide, Germany | Holsteinian interglacial | | *Celtis* sp. | P | <5% | [72] |
| 25 | Döttingen | Rheinland-Pfalz, Eifel, Germany | Holsteinian interglacial | | *Celtis* sp. | P | <5% | [71] |
| 26 | Bilzingsleben | Bilzingsleben, Germany | Holsteinian interglacial | | *Celtis* sp. | P | | [73] |
| 27 | Kreftenheye Formation | Raalte, The Netherlands | >MIS 5 (reworked, remains from older interglacials) | | *Celtis* sp. | W | 1 | [74] |
| 28 | La Celle-sur-Seine | Vernou-La Celle-sur-Seine, France | 425,000 ± 46,000 BP (MIS 11) | | *Celtis australis* | L (impressions) | | [75] |
| 29 | Caune de l'Arago | Tautavel, France | 320,000–220,000 BP | Acheulean | *Celtis australis* | E | | De Lumley in Ref [60] |
| 30 | Grotte du Lazaret | Nice, France | Late Middle Pleistocene (Riss I, II and III) | Acheulean | *Celtis australis* | E | | De Lumley in Refs [60,61] |
| 31 | La Rouquette | Millau, France | 273,000 ± 23,000 BP (MIS 7) | | *Celtis australis* | E | 1 | [76] |
| 32 | Coudoulous I | Tour-de-Faure, Lot, France | 300,000–200,000 BP | | *Celtis australis* | E | | Bonifay and Clottes 1981 in Ref [76] |
| 33 | Cova del Bolomor | Tavernes de la Valldigna, Spain | >350,000 BP (MIS 8-9)<br>233,000–152,000 (MIS 7) | Mousterian | *Celtis australis* | P<br>E | <3% | [62] |
| 34 | Cova Negra | Xàtiva, Spain | 303,000–148,000 BP (MIS 6–8) | Mousterian | *Celtis* sp. | E | 25 | Unpublished |
| 35 | Meyrargues | Meyrargues, France | 170,000 and 145,000 BP | | *Celtis australis* | L | | [77] |
| 36 | Aygalades | Marsella, France | Middle Pleistocene | | *Celtis australis* | L | | [77,78] |
| 37 | Padul | Padul, Spain | 180,000 cal BP (MIS 6e) | | *Celtis* sp. | P | <5% | [79] |

* The presence of *Celtis australis* is not stated in Ref [61].

During the Upper Pleistocene, the distribution of *Celtis australis* suffered a profound modification. Between MIS 5 and MIS 3, hackberry remains were present in different archaeological sites of the western Mediterranean Basin, such as Cova del Bolomor, Abrigo de la Quebrada or Cova Negra [62,80]. On the other side of the Mediterranean, *C. australis* is documented in Douara Cave (Syria) [81], together with *C. tournefortii*, a species reported in Theopetra (Greece) [82]. On the contrary, *Celtis australis* is completely absent in the western part of the Mediterranean Basin beyond 35,000 BP, not being present in MIS 2 deposits, except for the pollen grains detected in Teixoneres [83], Cova del Toll [84] and Padul [79]. In the eastern part of the basin, *Celtis* sp. endocarps were recovered in Karain B and Oküzini [85], whereas *Celtis tournefortii* was reported in the palaeobotanical site of Ezero wetland (Bulgaria) [86] and again in Theopetra [82] (Table 3, Figures 5 and 6).

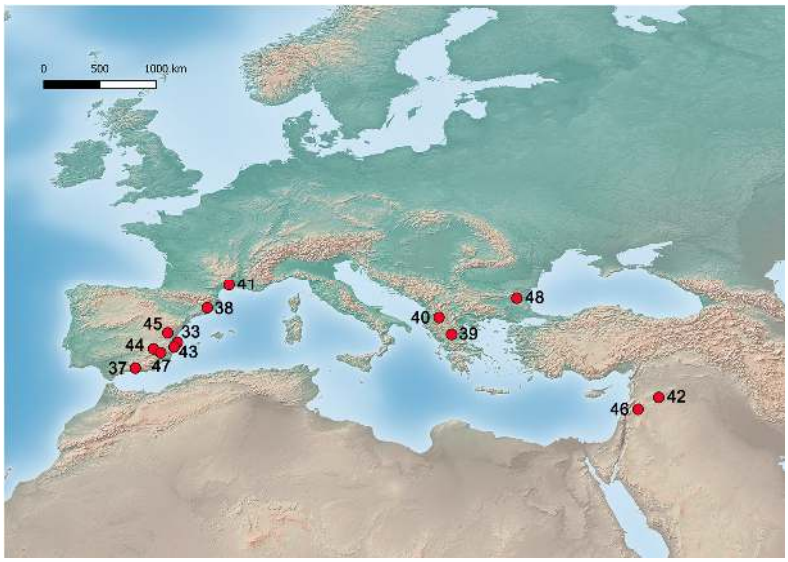



**Figure 5.** Early Upper Pleistocene (MIS 5, 4 and 3) sites where *Celtis* remains were reported (numbers in the figure correspond to ID numbers in Table 3) (map generated using QGIS version 3.4.13; Source: Natural Earth Data).

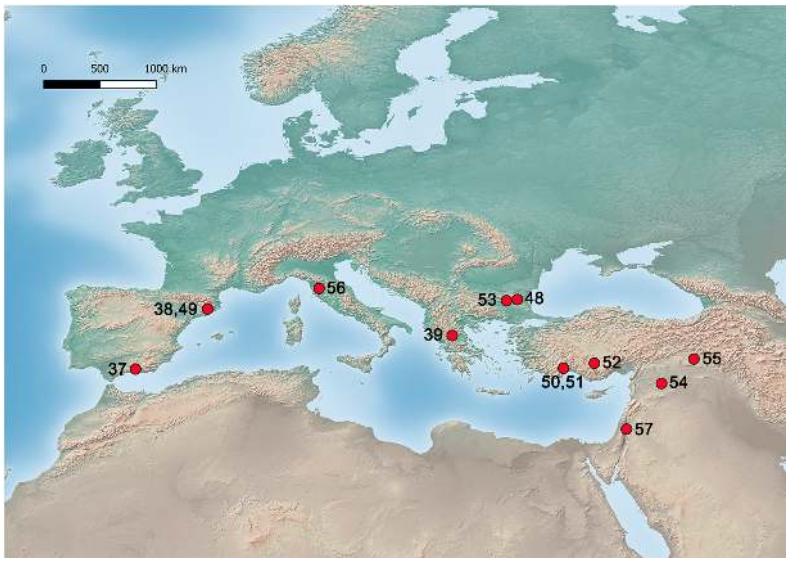



**Figure 6.** Late Upper Pleistocene (MIS 2) sites where *Celtis* remains were reported (numbers in the figure correspond to ID numbers in Table 3) (map generated using QGIS version 3.4.13; Source: Natural Earth Data).

**Table 3.** Upper Pleistocene sites where *Celtis* remains were reported (types of remains: wood charcoal (C), endocarp (E), leaves (L), pollen (P), phytoliths (Ph), wood (W)).

| ID | Site | Location | Chronology | Cultural Adscription | Taxa | Type | NR | Reference |
|---|---|---|---|---|---|---|---|---|
| 38 | Cova del Toll | Moià, Spain | MIS 5–6? | Middle Palaeolithic | *Celtis* sp. | P | <3% | [84] |
| 33 | Cova del Bolomor | Tavernes de la Valldigna, Spain | <121,000 BP (MIS 5e) | Mousterian | *Celtis* sp. | P<br>E | <3% | [83] |
| 39 | Theopetra | Kalambaka, Greece | 129,000 ± 13,000 BP–57,000 ± 6000 BP (MIS 5-4) | Middle Palaeolithic | *Celtis* cf. *tournefortii* | E<br>Ph | 1<br><6% | [82,87] |
| 37 | Padul | Padul, Spain | 107,000–92,000 cal BP (MIS 5c and MIS 5b) | | *Celtis* sp. | P | <5% | [79] |
| 40 | Lake Ohrid | FYROM | 131,000–69,900 BP (MIS 5 and early MIS 4) | | *Celtis* sp. | P | | [88] |
| 41 | Castelnau le Lez | Castelnau le Lez, France | 113,700 (+7200/−6700)–44,700 (+2100/−2000) BP (MIS 5-3) | | *Celtis australis* | L | | [78,89,90] |
| 42 | Douara Cave | Palmyra Basin, Syria | 52,000 (+5000/−3000) BP (MIS 3) * | Mousterian | *Celtis* cf. *australis* and *C.* cf. *tournefortii* | E | >127 | [81,91,92] |
| 43 | Abric de El Salt | Alcoi, Spain | 52,300 ± 4600 BP (MIS 3) | Mousterian | *Celtis australis* | E<br>Ph | 1 | [93,94] |
| 44 | Cueva del Niño | Ayna, Spain | 55,550 BP (MIS 3) | Mousterian | *Celtis* sp. | E | 17 | [95] |
| 45 | Abrigo de la Quebrada | Chelva, Spain | 40,243–39,075 cal BP (MIS 3) * | Mousterian | *Celtis* sp. | E | 7 | [80] |
| 46 | Baaz | Damascus, Syria | 39,565–36,169 cal BP (MIS 3) | Upper Palaeolithic | *Celtis* sp. | P | <5% | [96] |
| 47 | Cueva del Arco | Cieza, Spain | 36,091–35,203 cal BP (MIS 3) * | Mousterian | *Celtis* sp. | E | 10 | Unpublished |
| 48 | Straldzha Mire | Bulgaria | 37,500–17,900 cal BP (MIS 3-2) | | *Celtis* sp. | P | <5% | [97] |
| 37 | Padul | Padul, Spain | 27,000–15,000 cal BP (MIS 2) | | *Celtis* sp. | P | <5% | [79] |
| 49 | Teixoneres | Barcelona, Spain | 20,000–16,000 cal BP (MIS 2) | Upper Palaeolithic | *Celtis* sp. | P | <3% | [98] |
| 39 | Theopetra | Kalambaka, Greece | 20,000–12,000 cal BP (MIS 2) | Upper Palaeolithic | *Celtis* cf. *tournefortii* | E<br>Ph | 50<br><3% | [82,87] |
| 50 | Karain B | Antalya, Turkey | 19,899–18,991 cal BP (MIS 2) | Epipalaeolithic | *Celtis* sp. | E | 6 | [85] |
| 51 | Öküzini | Antalya, Turkey | 19,080–13,747 cal BP (MIS 2) | Epipalaeolithic | *Celtis* sp. | E | 380 | [85] |
| 52 | Pınarbaşı | Konya Plain, Turkey | 16,000–14,000 cal BP (MIS 2) | Epipalaeolithic | *Celtis* sp. | C | 1.09% | [99] |
| 53 | Ezero wetland | Nova Zagora, Bulgaria | 15,550–14,950 cal BP (MIS 2) * | | *Celtis* sp.<br>*Celtis tournefortii* tp.<br>*Celtis* sp. | P<br>E<br>W | 20%<br>3 per 45 $cm^3$<br>4 per 45 $cm^3$ | [86] |
| 38 | Cova del Toll | Moià, Spain | <13,000 cal BP (probably MIS 1, but perhaps covers part of MIS 2) | | *Celtis* sp. | P | <3% | [84] |
| 54 | Tell Abu Hureyra | Euphrates Valley, Syria | 13,111 ± 94–11,981 ± 217 cal BP (MIS 2) | Epipalaeolithic | *Celtis tournefortii* | E | | [100,101] |
| 55 | Körtik Tepe | Diyarbakir/Batman, Turkey | 12,479–11,388 (MIS 2) | Epipalaeolithic | *Celtis* sp. | C | 1 (0.01%) | [102] |
| 56 | Bagnoli | San Gimignano, Italy | GI 1e and GI 1c (MIS 2) | | *Celtis* sp. | P | <5% | [103] |
| 57 | Pella | Ṭabaqat Faḥl, Jordan | MIS 2 | Kebarian | *Celtis* sp. | C | | [104] |

* Direct dating of *Celtis* remains.

*Celtis* remains were reported in 18 archaeological sites and 3 palaeobotanical sites for the Lower Holocene (Table 4, Figure 7). *Celtis tournefortii* endocarps are extensively documented in different sites of the eastern Mediterranean, such as Theopetra, Çayönü or Tell Abu Hureyra [82,101,105]. On the contrary, *Celtis australis* is hardly reported, only in Hacilar (Turkey) [106], together with grain pollen in Lago dell'Accesa [107] and Gorgo

Basso [108]. However, most of the remains of this period are identified at the genus level, hindering a precise reconstruction of the impact of climatic change on the Mediterranean hackberry distribution; still, the absence in the Western Mediterranean is evident.

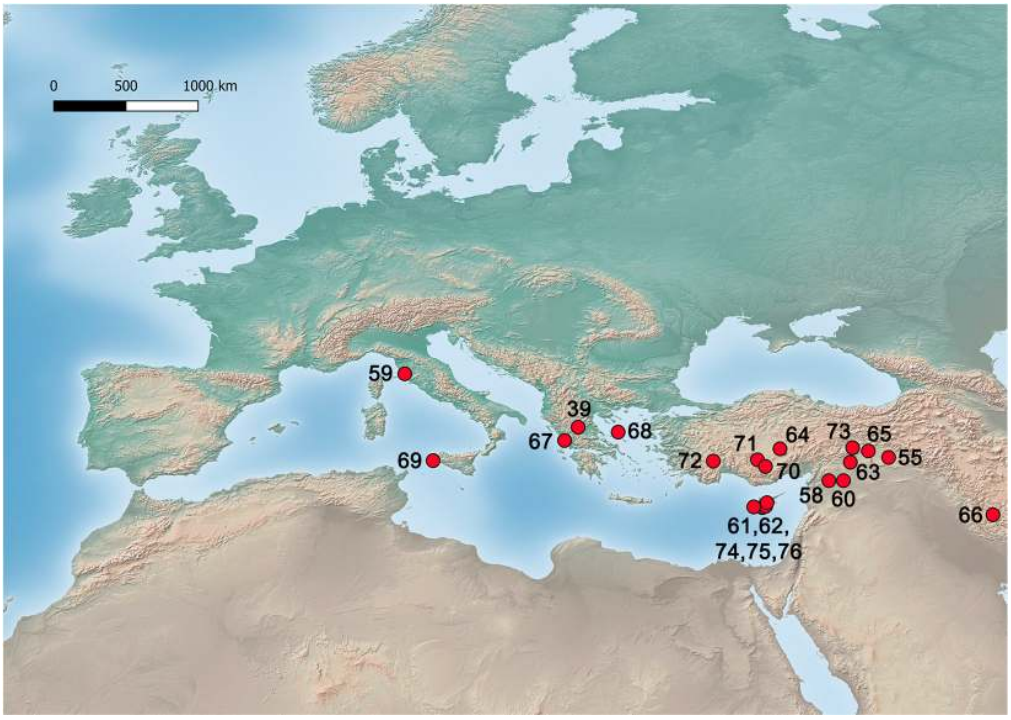



**Figure 7.** Lower Holocene sites where *Celtis* remains were reported (numbers in the figure correspond to ID numbers in Table 4) (map generated using QGIS version 3.4.13; Source: Natural Earth Data).

**Table 4.** Lower Holocene sites where *Celtis* remains were reported (types of remains: wood charcoal (C), endocarp (E), pollen (P), phytoliths (Ph)).

| ID | Site | Location | Chronology | Cultural Adscription | Taxa | Type | NR | Reference |
|---|---|---|---|---|---|---|---|---|
| 58 | Tell Qaramel | Aleppo, Syria | 12,193–11,250 cal BP | Khiamian | *Celtis* sp. | E | 400 | [109] |
| 59 | Lago dell'Accesa | Massa Marittima, Italy | Ca. 11,650–11,350 cal BP | | *Celtis australis* | P | | [107] |
| 55 | Körtik Tepe | Diyarbakir/Batman, Turkey | 11,600–11,350 cal BP | Pre-Pottery Neolithic | *Celtis* sp. | C | 15 (0.8%) | [102] |
| 60 | Jerf el Ahmar | Middle, Euphrates, Syria | 11,400–10,255 cal BP | Pre-Pottery Neolithic | *Celtis* sp. | E | 1 | [109] |
| 39 | Theopetra | Kalambaka, Greece | 11,200–9200 cal BP | Mesolithic | *Celtis* cf. *tournefortii* | E<br>Ph | 35<br><5% | [82,87] |
| 61 | Shillourokambos | Parekklisha, Cyprus | 10,700–9529 cal BP | Pre-Pottery Neolithic | *Celtis* sp. | E | 2 | [110] |
| 62 | Klimonas | Ayios Tychonas, Cyprus | Late 11th–middle 10th millennium cal BP | PPNA | *Celtis* sp. | E | | [111] |
| 63 | Nevali Çori | Sanliurfa, Turkey | 10,350 cal BP | PPNB, PN | *Celtis* sp. | E | 1 | [112] |
| 64 | Asikli Höyük | Aksaray, Turkey | 10,220–9468 cal BP | Pre-Pottery Neolithic | *Celtis* cf. *tournefortii* | E | 17,885 | [113] |
| 65 | Çayönü | Diyarbakır, Turkey | 10,200–9700 cal BP | Pre-Pottery Neolithic | *Celtis* cf. *tournefortii* | E | 2 | [105] |
| 66 | Ganj Dareh | Kermanshah, Iran | 10,200–9560 cal BP | PPNB | *Celtis* sp. | C | | [114] |
| 67 | Lake Voulkaria | Acarnania, Greece | 9966–8171 cal BP | | *Celtis* sp. | P | 5% | [115] |
| 68 | Cave of Cyclops | Gioura, Greece | 9700–6700 cal BP | Late Mesolithic | cf. *Celtis* sp. | E | 1 | [116] |
| 69 | Lake Gorgo Basso | Sicily, Italy | 9785–9010 cal BP | | *Celtis australis* | P | 5% | [108] |
| 70 | Can Hasan III | Konya plain, Turkey | 9600–8400 cal BP | Aceramic Neolithic | *Celtis* cf. *tournefortii*<br>*Celtis* sp. | E<br>C | 978<br>0.31% | [99,117,118] |

**Table 4.** *Cont.*

| ID | Site | Location | Chronology | Cultural Adscription | Taxa | Type | NR | Reference |
|---|---|---|---|---|---|---|---|---|
| 71 | Çatalhöyük | Konya plain, Turkey | 9327–8171 cal BP | Early Neolithic | *Celtis* sp.<br>(cf. *C. tournefortii*) | E<br>C | 1498<br>9.81%–5.44% | [119] |
| 72 | Hacilar | Burdur, Turkey | 9027–7780 cal BP | Late Neolithic | *Celtis australis* | E<br>(charred) | 125 | [106] |
| 73 | Cafer Höyük | Malatya, Turkey | 8990–8150 cal BP | Early, Middle and Late PPNB | *Celtis* sp.<br>*Celtis* sp.<br>*Pistacia*/*Celtis* sp. | C<br>E<br>E | <br>4<br>1 | [104,120] |
| 74 | Khirokitia | Larnaka, Cyprus | 9th–8th millennium cal BP | Late Aceramic Neolithic (Khirokitian) | *Celtis* sp. | E | 1 | [121,122] |
| 75 | Dhali-Agridhi (Idalion) | Dhali, Cyprus | c. 9th millennium cal BP | Late Aceramic Neolithic (Khirokitian) | *Celtis* sp. | E | 1 | [123] |
| 76 | Kholetria-Ortos | Paphos, Cyprus | 8550–7750 cal BP | Late Aceramic Neolithic (Khirokitian) | *Celtis* sp. | E | | [124] |

We have to wait until the Middle Holocene to witness the beginning of the recovery of *Celtis* populations in the Western Mediterranean. In the Iberian Peninsula, the ancient references from the Holocene come from Poças de São Bento (Portugal), dated to ca. 4600 cal BC [125], and its presence did not consolidate until the Bronze Age. The reduction in evidence in the whole basin is noteworthy: only nine archaeological sites and two palaeobotanical sites report *Celtis* remains (Table 5, Figure 8). This situation, concerning the archaeological sites, could be related to a loss of human interest in this plant.

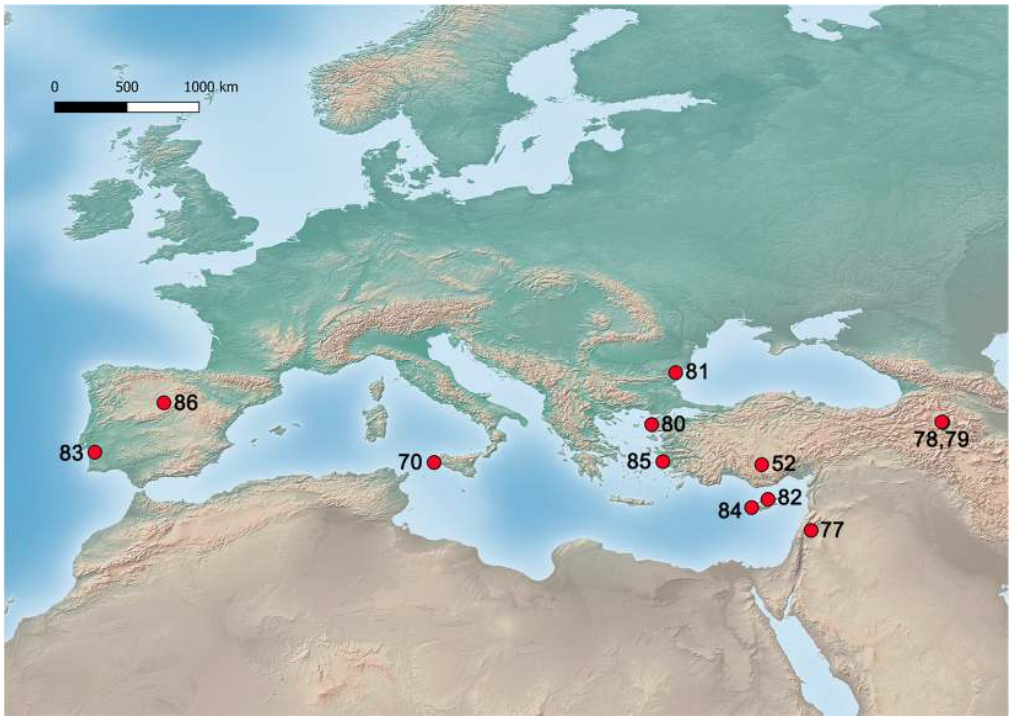



**Figure 8.** Middle Holocene sites where *Celtis* remains were reported (numbers in the figure correspond to ID numbers in Table 5) (map generated using QGIS version 3.4.13; Source: Natural Earth Data).

**Table 5.** Middle Holocene sites where *Celtis* remains were reported (types of remains: wood charcoal (C), endocarp (E), pollen (P)).

| ID | Site | Location | Chronology | Cultural Adscription | Taxa | Type | NR | Reference |
|---|---|---|---|---|---|---|---|---|
| 52 | Pınarbaşı | Konya plain, Turkey | 8395–6392 cal BP | Final Neolithic Chalcolithic | *Celtis* sp. | C | 2.34% 1.12% | [99,126] |
| 77 | Ramad | Damasco, Syria | 8250–7950 cal BP | PPNB | *Celtis*/*Ulmus* sp. | C | | [118,127] |
| 70 | Lake Gorgo Basso | Sicily, Italy | 8213–4402 cal BP | | *Celtis australis* | P | <5% | [108] |
| 78 | Aknashen | Ararat valley, Armenia | 7975–7157 cal BP | Neolithic | *Celtis* sp. | E | 5 | [128] |
| 79 | Aratashen | Ararat valley, Armenia | 7861–7428 cal BP | Neolithic | *Celtis* sp. | E | 1 | [128] |
| 80 | Kumtepe A | Troas, Turkey | 7435–6550 cal BP 4950–4400 cal BP | Late Neolithic Early Bronze Age | *Celtis* sp. | C | 1.17% 0.82% | [129] |
| 81 | Lake Beloslav | Varna, Bulgaria | 6796–3874 cal BP | | *Celtis* sp. | P | >1% | [130] |
| 82 | Ayios Epiktitos-Vrysi | Kirenia, Cyprus | 6750–5750 cal BP | Late Aceramic Neolithic (Khirokitian) | *Celtis australis* | E | | [124] |
| 83 | Poças de São Bento | Torrão, Portugal | ca. 6550 cal BP | Early Neolithic | *Celtis australis* | E (charred) | 12 | [125] |
| 84 | Kissonerga-*Mosphilia* | Kissonerga, Cyprus | 6550–4150 cal BP | Chalcolithic (Early, Middle and Late) | *Celtis* sp. | E | 7 | [124,131] |
| 85 | Heraion of Samos | Kastro-Tigani, Samos, Greece | 5050–3950 cal BP | Early Bronze Age | *Ulmus*/*Celtis* sp. | C | <1% | [132] |
| 86 | El Carrizal de Cuéllar | Lastras de Cuéllar, Spain | 4576–4346 cal BP | | *Celtis* sp. | P | <10% | [133] |

### 3.2. New Direct Radiocarbon Dating of Celtis Remains

The only way to settle the discussion regarding the antiquity of *Celtis* remains is through their radiocarbon dating. Radiocarbon dating is a method, which provides objective estimates of the age of carbon-based materials that originated from living organisms [134,135]. However, the direct chronological dating of *Celtis* sp. endocarps is really scarce (in Tables 1–5, we present the chronology of the level where the remains were recovered, obtained on other types of samples). Moreover, most of the deposits where they were found are beyond the range covered by this dating method. As far as we know, for the Middle Palaeolithic, only *Celtis* endocarps from Douara cave were directly dated, yielding a date of 52,000 (+5000/−3000) BP [136]. In addition, in the palaeobotanical site of Ezero wetland, *Celtis* endocarps were directly dated at 12,900 ± 60 BP [86]. For this work, two endocarps from Middle Palaeolithic Iberian sites (Abrigo de la Quebrada and Cueva del Arco) were dated (Figure 9). The radiocarbon dating results and the specifics of the analysis are presented in Table 6.

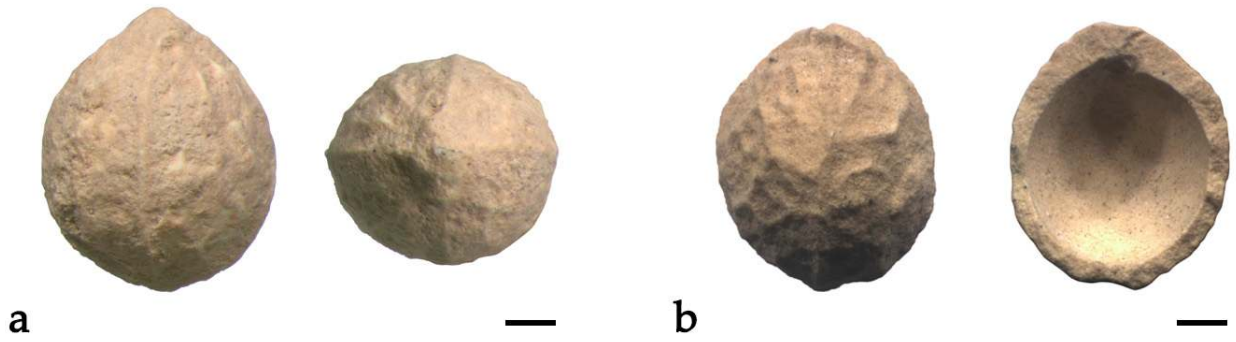



**Figure 9.** *Celtis* endocarps from Abrigo de la Quebrada (**a**) and Cueva del Arco (**b**) (scale bar: 1 mm).

**Table 6.** Radiocarbon dating results of *Celtis* endocarps.

| Site | Laboratory Number | Analysed Material | Radiocarbon Age (BP) | Cal BP (95.4%) | Stable Isotopes | Percent Modern Carbon | D14C | Δ14C |
|---|---|---|---|---|---|---|---|---|
| Abrigo de la Quebrada | Beta–506374 | Carbonate | 35,120 ± 220 | 40,243–39,075 | IRMS δ13C: −9.3 o/oo IRMS δ18O: +6.1 o/oo | 1.26 ± 0.03 pMC | −987.37 ± 0.35 o/oo | −987.48 ± 0.35 o/oo (1950:2018) |
| Cueva del Arco | Beta–627630 | Carbonate | 31,190 ± 190 | 36,091–35,203 | IRMS δ13C: −6.5 o/oo IRMS δ18O: +9.0 o/oo | 2.06 ± 0.05 pMC | −979.41 ± 0.49 o/oo | −979.58 ± 0.49 o/oo (1950:2022) |

Both *Celtis* endocarps provide results coherent with the archaeological deposits where they were found, so their intrusive character must be rejected, despite their uncharred preservation, and they demonstrate the undeniable presence of *Celtis* sp. in the Iberian Mediterranean Basin during MIS 3.

### 3.3. Chemical Composition of Celtis australis Fruits

Regarding the morphological analysis of hackberry fruits, the unit weight of hackberry fruits ranges between 0.400 and 0.587 g (Table 7). It is a small fruit, and the weight found in this study from the Valencian area is lower than that registered by Vidal-Cascales et al. [137] in fruits from wild trees growing in the forests of Moratalla (Murcia, Spain). These authors found an average unit weight of 0.77 g. The greater weight of the fruit is related to the greater dimensions of calibre (diameter and height). The calibre values of the fruits found in this study are similar to those reported by Demir et al. [138] in hackberries from Turkey, where more than 50% of the fruits had a diameter of 9.47 mm and a fruit height of 10.73 mm, a geometric mean diameter of 9.75 mm, a degree of sphericity of 0.9099 and a surface area of 283.25 $mm^2$. These authors indicate that the area and, consequently, the volume of hackberry fruits increased with the moisture content. This would explain the differences in the values of fruit volume.

**Table 7.** Morphological parameters of hackberry fruits (mean ± SD, minimum and maximum value, $n$ = 30).

| Parameter | Value (Mean ± SD) | Minimum Value | Maximum Value |
|---|---|---|---|
| Unit fruit weight (g) | 0.505 ± 0.051 | 0.400 | 0.587 |
| Fruit diameter (mm) | 9.20 ± 0.63 | 7.89 | 10.35 |
| Fruit height (mm) | 10.22 ± 0.84 | 8.49 | 11.67 |
| Fruit volume ($mm^3$) | 1742.60 ± 326.99 | 1067.82 | 2425.30 |
| Geometric mean diameter (mm) | 9.31 ± 0.57 | 7.92 | 10.4 |
| Degree of sphericity | 0.91 ± 0.05 | 0.79 | 1.01 |
| Surface area ($mm^2$) | 273.29 ± 33.34 | 196.86 | 339.56 |
| Pulp and peel weight (g) | 0.211 ± 0.005 | 0.207 | 0.217 |
| Seed weight (g) | 10.833 ± 0.472 | 10.200 | 11.300 |
| Pulp and peel (%) | 42.88 ± 0.48 | 42.35 | 43.50 |
| Seed (%) | 56.43 ± 0.23 | 56.12 | 56.67 |

The pulp and peel fraction represents 42.88% of the fruit's fresh weight, whereas the seed or stone is 56.43% (Table 7). Boudraa et al. [139] reported that the Algerian hackberry pulp represents 55.6% of the fruit's fresh weight, higher than the value obtained in this study.

The proximal nutritional composition and energy value of the fruits are presented in Table 8. The moisture content in the whole fruit is 21.9% lower than the exclusive moisture of the pulp and peel. The results of this study concerning dry matter are similar to those reported by Demir et al. [138] with Turkish hackberries (90.23%). In contrast, the moisture content is lower than that found by other authors: 43.9% of moisture content in the flesh and 39.7% in the peel reported by Vidal-Cascales et al. [137], 31% in fresh hackberries from Algeria according to Boudraa et al. [139], 30% in fresh Croatian hackberries reported

by Ota et al. [140]. Moisture content is inversely related to dry matter fraction, and its variations may be related to the contribution of rainwater or possible irrigation. Moreover, the difference in the moisture content could be due to different harvesting seasons and their impact on the loss of water. In our sample, harvesting took place well into the autumn, and the fruits may have lost moisture.

**Table 8.** Proximal parameters for fresh weight of hackberry fruits (mean ± SD, minimum and maximum value, $n$ = 3).

| Parameter | Value (Mean ± SD) | Minimum Value | Maximum Value |
|---|---|---|---|
| Dry matter (%) whole fruit | 81.60 ± 0.22 | 81.30 | 81.80 |
| Dry matter (%) pulp and peel | 76.44 ± 0.40 | 75.90 | 76.81 |
| Moisture (%) whole fruit | 18.40 ± 0.22 | 18.20 | 18.70 |
| Moisture (%) pulp and peel | 23.56 ± 0.40 | 23.19 | 24.10 |
| Fat (%) | 0.489 ± 0.052 | 0.449 | 0.561 |
| Protein (%) | 2.49 ± 0.02 | 2.45 | 2.51 |
| Ashes (%) | 4.035 ± 0.118 | 3.934 | 4.198 |
| Fibre (%) | 7.34 ± 0.21 | 7.18 | 7.62 |
| Carbohydrates (%) | 62.10 ± 0.27 | 61.73 | 62.32 |
| Energy (kcal 100 $g^{-1}$) | 262.75 ± 0.56 | 13.849 | 15.064 |

The major nutrients of fresh fruits (pulp and peel) are carbohydrates (62.10%), followed by fibre (7.34%) and protein (2.49%). Fat is a minor component (0.489%), and the ashes, which include the total minerals' fraction, present a high value (4.035%) (Table 8). Ota et al. [140] found that hackberry fruits contained 10.2% of total dietary fibre when the moisture content was 30%. The work of Demir et al. [138] evidenced that fat and protein content is 6.7% and 19.32%, respectively, when the moisture of the fruits is 9.77% (equivalent to 0.625% fw in fat and 1.887% fw in protein), in line with the values found in this study of fruits from the Valencian area. This proximal composition provides an energy content of 262.75 kcal 100 $g^{-1}$, similar to that reported by other authors [138]. This energy content is approximately three times higher than that provided by the apple fruit [141] due to the lower water content and higher protein and carbohydrate content in hackberry fruits.

The high content of carbohydrates is positively related to the high soluble solids (sugars) content (Table 9). The soluble solids in fresh hackberry fruits (pulp and peel) present an extraordinarily high value (48.67 °Brix) compared to the values of commonly consumed fruits [142]. This result is in complete agreement with other works [137,140]. Vidal-Cascales et al. [137] relate this unusually high content in soluble solids to the high individual values of sucrose, glucose and fructose. Hackberry fruits are non-acidic (pH = 6.55) and have low total acidity, expressed in g citric acid 100 $g^{-1}$ (0.247). The acidity values are similar to those found by other authors [137,140].

**Table 9.** pH, titratable acidity, soluble solids content, total polyphenols and total antioxidant capacity parameters for fresh weight of hackberry fruits (mean ± SD, minimum and maximum value, $n$ = 3).

| Parameter | Value (Mean ± SD) | Minimum Value | Maximum Value |
|---|---|---|---|
| pH | 6.55 ± 0.05 | 6.49 | 6.59 |
| Titratable acidity (g citric acid 100 $g^{-1}$ fw) | 0.247 ± 0.029 | 0.210 | 0.280 |
| Soluble solids content (°Brix) | 48.67 ± 1.73 | 47.00 | 51.00 |
| Total polyphenols (mg EAG 100 $g^{-1}$ fw) | 192.19 ± 12.60 | 174.85 | 203.03 |
| Total antioxidant capacity (µmol Trolox 100 $g^{-1}$ fw) | 770.70 ± 97.85 | 650.43 | 885.92 |

Regarding the bioactive components (Table 9), the amount of total phenolic (192.19 mg equivalent gallic acid 100 $g^{-1}$) is slightly lower (249.1 mg equivalent gallic acid 100 $g^{-1}$) than that reported by Vidal-Cascales et al. [137] in fruits from wild trees of Moratalla (Spain) and that (239.1 mg gallic acid 100 $g^{-1}$) reported by Ota et al. [140] in Croatian hackberry

mesocarp but similar (172 mg gallic acid 100 $g^{-1}$) to that in edible fruits from the Indian Himalayan region [143]. Biotic and abiotic stress conditions are responsible for the greater accumulation of polyphenols in plants, and it is one of the factors, which can influence these differences. The antioxidant capacity of the fruits is high. It was not possible to compare it with other studies due to the different analysis methods and expression of the results. Nevertheless, the literature confirms that the high antioxidant capacity of hackberry fruits justifies their use in traditional medicine [144].

Among the minerals (Table 10), Mg was at the highest concentration in the pulp and peel of hackberry fruits, followed by K, Ca and P. This variation of macrominerals coincides with that shown by Ota et al. [140], except for magnesium, which does not provide values for this mineral. Boudraa et al. [139] found that Ca is the major mineral element, followed by Mg and K. For the microelements in the pulp and peel of hackberry fruits, B was the major microelement at 3.687 mg 100 $g^{-1}$ fw, followed by Fe (2.307 mg 100 $g^{-1}$ fw) and Cu (0.479 mg 100 $g^{-1}$ fw) and slightly lower concentrations for Zn, Mn and Se. The mineral element with the lowest concentration is Mo. Demır et al. [138] also found that boron concentrations are slightly higher than those of iron in hackberry fruits.

**Table 10.** Individual minerals for fresh weight of hackberry fruits (mean ± SD, minimum and maximum value, $n$ = 3).

| Parameter (mg 100 $g^{-1}$ fw) | Value (Mean ± SD) | Minimum Value | Maximum Value |
|---|---|---|---|
| Magnesium | 413.910 ± 1.020 | 412.550 | 414.940 |
| Potassium | 358.247 ± 1.822 | 356.35 | 360.65 |
| Calcium | 212.479 ± 1.148 | 211.601 | 214.073 |
| Phosphorus | 104.670 ± 0.022 | 104.640 | 104.690 |
| Sodium | 10.978 ± 0.493 | 10.353 | 11.534 |
| Boron | 3.687 ± 0.045 | 3.625 | 3.729 |
| Iron | 2.307 ± 0.108 | 2.188 | 2.447 |
| Copper | 0.479 ± 0.042 | 0.421 | 0.510 |
| Zinc | 0.203 ± 0.020 | 0.177 | 0.226 |
| Manganese | 0.144 ± 0.007 | 0.139 | 0.153 |
| Selenium | 0.143 ± 0.022 | 0.113 | 0.163 |
| Molybdenum | 0.013 ± 0.010 | 0.006 | 0.028 |

Ota et al. [140] found that hackberry fruits contained 1060 mg of K 100 $g^{-1}$ dw when the moisture content was 30% (equivalent to 315 mg of K 100 $g^{-1}$ fw). Demır et al. [138] found that hackberry fruits contained 344.26 mg of K 100 $g^{-1}$ fw. Both results align with the concentrations found for this element in the fruits from Valencia in this study.

The mineral contents of the fruit depend on genetic factors and edaphoclimatic conditions. The hackberry trees from which the fruit was harvested in the present study were growing wild, with no agricultural practices applied.

## 4. Discussion

### *4.1. All That Is Uncharred Is Not Intrusive*

Given the data presented above, we can affirm that the documentation of *Celtis* sp. is abundant, even in ancient chronologies where the archaeobotanical data are usually scarce. However, why does its presence in the archaeological sites raise some doubts? The state of preservation of the remains is key.

The endocarps of *Celtis* sp. hardly ever appear charred (they have been documented in Cova Negra, Poças de São Bento and La Cisterne). They are frequently preserved uncharred or characterised in the bibliography as mineralised. This state of preservation can be explained because of the high mineral content of the woody endocarp walls [31,34,36]. This composition makes their preservation in archaeological sites possible without the action of other preservation agents, such as carbonisation. In fact, the practical absence of charred remains of *Celtis* sp. is used as an argument to affirm that the remains are intrusive.

We must point out here that, possibly, some documented remains are actually charred. However, their state of preservation could be misidentified, since the endocarps do not turn black when charred but grey or white, as pointed out by Miller [145], as is the case in other diaspores with high mineral content, such as the Boraginaceae nutlets [146].

Their antiquity is also questioned because this taxon is not usually documented in other macrobotanical assemblages, such as in the anthracological. The anatomy of *Celtis* spp. wood is well defined—although sometimes it cannot be differentiated from *Ulmus* spp.—so its absence in the Pleistocene archaeological deposits is striking; it has only been documented in the Middle Pleistocene deposits of Kärlich and Ezero and in the Upper Pleistocene sites of Pınarbaşı, Körtik Tepe and Pella. Nevertheless, we can propose two possible hypotheses to explain this absence: (A) the antiquity of the sites mentioned above, together with the fragility of the angiosperm wood charcoal fragments compared to gymnosperms charcoal pieces [147–149], could result in their remains being identified only at the group level as Angiosperm due to their state of preservation (in Holocene sites, *Celtis* wood charcoal is more ubiquitous); (B) the absence of charred wood of *Celtis* sp. could be explained by the possible protection of a tree which provides humans with food, as has been observed for *Pinus pinea* [150,151] and *Corema album* [152], and raw material for elaborate tools.

The only way to settle the discussion regarding the antiquity of *Celtis* sp. remains in archaeological sites is through their radiocarbon dating, as has been carried out with other species, such as *Olea europaea* [153]. However, most of the deposits where they were found are beyond the range covered by this dating method, and it is an expensive method. Nevertheless, Wang et al. [31] noted the interest in dating the endocarps of *Celtis* sp., since the biogenic carbonate reflects the $C^{14}$ atmospheric values of only one growing season. The radiocarbon data obtained for *Celtis* endocarps from Abrigo de la Quebrada and Cueva del Arco confirm the antiquity of these remains, as well as their presence during MIS 3 in the Mediterranean Iberian region. Jahren et al. also pointed out the interest in *Celtis* endocarps as a proxy for palaeoclimatic reconstructions through oxygen isotope analyses [154].

### 4.2. Variation in the Geographic Distribution of *Celtis* spp.

Climatic changes and anthropic action have modified the distribution of flora up to the current situation [155–159]. The native character of *Celtis australis* in the Mediterranean Basin is widely accepted. However, its geographic distribution extremely changed according to the climatic condition changes from the Pliocene, as shown by the palaeobotanical data gathered in this work.

The Pliocene was a warm and humid period. Therefore, subtropical climatic conditions prevailed in most of Europe, where the forests were dense and diversified. During Upper Pliocene, Quaternary vegetation was established in Europe, so the Mediterranean and temperate or subtropical species lived together. Nevertheless, the progressive worsening of the climatic conditions caused the migration of the subtropical taxa and the consolidation of the Eurosiberian and Mediterranean plants [5], such as *Celtis australis.*

An increase in aridity 2.6 million years ago favoured the spread of Mediterranean species. With the beginning of the glacial–interglacial cycles, the exotic elements of Tertiary flora gradually disappeared from Europe, such as *Carya*, *Tsuga* or *Pterocarya.* In contrast, Mediterranean species, such as *Quercus*, *Acer* or *Artemisia,* continued their spread [5]. During the Lower Pleistocene, *Celtis* was detected in the northwestern part of the Mediterranean Basin, basically during warm periods, such as along the Gelasian or at the end of the period during MIS 25 in Gran Dolina. During the Middle Pleistocene, *Celtis* spread to the north of Europe, at least during the warmest moments of the period [58,160]: most of the remains were reported at levels dated to the Holsteinian interglacial (MIS 11) or the Ferdynandovian interglacial (MIS 15-13). During these warm and humid periods, hackberry was documented in German or Polish sites with other exotic taxa, such as *Pterocarya* and *Juglans* [161]. The longer duration of the Holsteinian interglacial could allow the expansion of thermophilous species [162]. However, hackberry would not be an abundant species,

considering that its pollen curve is always under 5% of the assemblages. *Celtis* presence clearly placed during cold stages is restricted to southern Europe, such as in Grotte de l'Escale (Middle or Upper Mindel glaciation) or Padul (MIS 6e). MIS 10 represents one of the coldest moments in Europe, so this period must have been critical for *Celtis* populations in northern Europe, where they disappeared. In fact, after this stage, *Celtis* is only documented in the Mediterranean Basin, such as in Lazaret or Cova de Bolomor. Even in the later interglacials, such as MIS 9, when temperatures where higher than in MIS 11, *Celtis* is not documented in Europe outside this area. This could be related to their shorter duration [162,163].

During the Upper Pleistocene, climatic oscillations were more pronounced and faster. These new climatic conditions deeply affected the distribution of *Celtis* populations. Although during the interglacial of MIS 5, warm and temperate species were well represented in Europe [164–168], with the beginning of MIS 4, steppe elements were predominant, together with cryophilous trees [80,87,94]. Therefore, although *Celtis* is documented during the initial moments, from 30,000 cal BP onwards, it is only present in the Eastern Mediterranean, limited to the species *Celtis tournefortii*. The presence of *Celtis* during the cold periods of the Middle Pleistocene and part of the Upper Pleistocene in southern parts of Europe could be interpreted within the characterisation of the European Mediterranean Peninsulas as refugia [155,158,169,170], restricted to warmer areas, not being documented in the Atlantic watershed of the Iberian Peninsula [171–173]. From these refugia, some species could recolonise Europe after the ice retreat: for instance, Postigo Mijarra et al. [55] pointed out that *Juglans*, *Carpinus*, *Platanus*, *Fagus*, *Celtis* and *Castanea* survived in the Iberian Peninsula during the Upper Pleistocene. The rare presence of *Celtis* pollen in the western Mediterranean Basin in MIS 3 and MIS 2 in Teixoneres, Padul and Bagnoli could be evidence of the resistance of some small and isolated populations in the Iberian and Italic Peninsula. In fact, the late recolonisation of the western Mediterranean Basin by *Celtis australis* could be explained by the small size of the surviving populations or by their scattered and discontinuous distribution: *Celtis* pollen in these sites represents less than 5% of the assemblages. However, the contribution of long-distance transport should be considered, since no macrofossils have been reported.

The climatic change at the beginning of the Lower Holocene seemed to positively impact the spread of *Celtis* species, at least for *Celtis tournefortii* in Eastern Mediterranean and Near East, whose endocarps are frequently (and abundantly) found in Neolithic sites. On the contrary, *Celtis australis* is not frequently identified for this period. Its spread in the Western Mediterranean Basin only occurs during the Middle Holocene and is consolidated in the Bronze Age. Mateu-Andrés et al. [174], considering its low genetic diversity, point to a recent expansion of *Celtis australis* in the Mediterranean Basin from the Eastern Mediterranean following the Neolithic expansion routes, thanks to human action due to the economic interest in it. On the contrary, the presence of *Celtis* spp. in the Near East and Eastern Mediterranean decreased during the Middle Holocene.

### *4.3. Gathered during the Palaeolithic*

If we accept that the presence of *Celtis* remains in the Palaeolithic sites is not a consequence of post-depositional disturbances but contemporaneous to the formation of the archaeological level where they were recovered, we can question what their route of entry to the archaeological deposit was. In the archaeobotanical record, three types of routes of entry are distinguished: animal, physical and human. Birds propagate the seeds of *Celtis* sp. easily, so they can be considered a potential deposition agent. The growth of this tree near the site could cause its natural deposition in the deposit. Finally, humans can be considered potential depositional agents when gathering fruits for consumption, discarding the inedible part, the endocarp, in the habitat.

The economic interest in *Celtis* fruits is beyond doubt: they are edible and, as our composition analysis reveals, they are rich in carbohydrates, fibres, proteins and minerals, being an energetic source. Moreover, their sweetness and low acid flavour make them

attractive to humans. Their intentional gathering and consumption have been pointed out during the Neolithic in several sites, such as Çatalhöyük and Hacilar (Turkey), where the endocarps are extremely abundant [106,119]. In more recent chronologies, their use was documented in Lattes during the 1st century AD [175]. Even a ritual character has been attributed to hackberry fruits found in the Middle Bronze Age burial mound of Izvorovo (Bulgaria) [176,177].

It is not easy to define the deposition agent, since, in any case, the endocarps remain unaltered. In Gran Dolina, a spatial analysis of the *Celtis* remains was carried out to assess their possible intentional gathering [45]. These authors also considered other criteria, such as the absence of rodent gnaw marks, the absence of *Celtis* remains in hyena coprolites, their fragmentation degree and their association with univocal anthropic remains.

The ubiquity of *Celtis* endocarps in Lower and Middle Palaeolithic sites where carpological analysis was carried out must be stressed: they are present in 80% of the Lower Palaeolithic sites and 50% of the Middle Palaeolithic sites. The reduction in their presence in the Upper Palaeolithic (5%) could be related to the reduction in the *Celtis* populations in the Mediterranean Basin due to the increased aridity in the last glacial cycle (Figure 10). In most of the Palaeolithic sites included in this work, human gathering of *Celtis* fruits was suggested, as well as in other sites beyond the range of this paper, such as Zhoukoudian (China) [178,179]. Hackberry fruits can be gathered by different methods: (A) climbing up the trees to collect the fruits manually; (B) cutting the branches with fruits to collect them more easily on the floor, although this method is not sustainable because the crown of the tree is considerably reduced; or (C) knocking down the fruits, combined or not with the use of a net, but this is difficult considering the thorny and dense Mediterranean understorey and the resistance of the fruits to fall. Despite the complex and time-consuming gathering, rich in carbohydrates, tasty and sweet foodstuff is obtained.

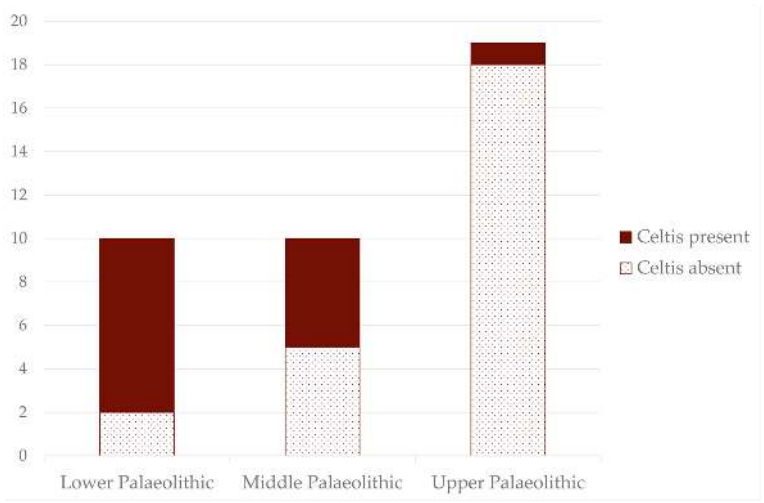



**Figure 10.** *Celtis* presence on the total of Palaeolithic sites with carpological analyses.

The analyses carried out on *Celtis australis* fruits in this paper showed that, despite being a small fruit, it offers a large amount of nutrients, such as carbohydrates, fibre and protein, and higher energy content than other fruits. Since fruit size can vary depending on the degree of moisture throughout the year (as well as the region in which it is found), it likely became a profitable seasonal resource in the Palaeolithic; the possible gathering of this fruit would be understood in a context of growing evidence of plant consumption in hunter–gatherer groups, which demonstrates an omnivorous and diversified diet [119,150,151,180–182], even more so if there is evidence of its collection in Neolithic contexts with consolidated agriculture, as in the case of Çatalhöyük [119].

## 5. Conclusions

This work shows different approaches to the presence of *Celtis* in Pleistocene and Holocene deposits.

- *Celtis* sp. is present in archaeological contexts even in ancient chronologies and despite its (usually) uncharred state. The dating of the remains of Abrigo de la Quebrada and Cueva del Arco joins that of Douara cave and confirms their antiquity, so we must not systematically doubt the uncharred remains.
- *Celtis australis* seems to be adapted to Mediterranean droughts but sensitive to cold periods, such as MIS 10 or MIS2, founding refugia, firstly in the Mediterranean Basin, and secondly being reduced in the Near East.
- During the Lower Pleistocene and the Middle Holocene, the distribution of *Celtis* populations matches up with their current distribution, whereas during the Middle Pleistocene, they exceed their current limits, reaching northern Europe, which is related to climatic phases that are more favourable to their spread.
- Its scarce presence in the southern peninsulas of Europe, traditionally considered refugia, during the Final Upper Pleistocene and Lower Holocene is noteworthy, but we cannot rule out that this is due to bias in the sampling or in data publication.
- The hypothesis of human gathering of *Celtis* fruits is based on (1) the absence of charred hackberry wood, perhaps linked to some vegetation management, which protects the foodstuffs, and (2) their high protein and carbohydrates input related to the presence of sucrose, glucose and fructose fits within a diet, which includes different types of resources, as documented in several Palaeolithic sites.

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