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7 **Origins and evolution of oasis agriculture in the Sahara: Evidence from**
8 **morphometric analyses of archaeological date palm seeds**

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25

26 **Abstract**

27 Oasis agriculture has been a critical means of sustenance for humans in arid regions in North
28 Africa and West Asia. The date palm (*Phoenix dactylifera* L.) holds immense significance as
29 one of the most vital species in these agroecosystems. It was domesticated in the Gulf region
30 over 6,000 years ago and later spread to other regions. In the Sahara, the origins of the
31 germplasm and the diffusion history in terms of dating and routes remain largely unknown. To
32 explore these questions, we employed traditional and geometric morphometric methods to
33 analyze 312 well-preserved *Phoenix* seeds from three Libyan sites, dating from the 1st
34 millennium BCE to the modern period. We compared them with a large modern reference
35 collection and Egyptian archaeological seeds from a previous study. The identification of
36 domesticated morphotypes in the oldest site, Zinkekra, confirms that the date palm was already
37 cultivated in the Central Sahara during the 1st millennium BCE, probably through an
38 introduction from Egypt. The large proportion of wild morphotypes however indicates that they
39 represent early domesticates. By comparing seeds at sites in Libya and Egypt dating from
40 different periods, evidence was found of a decrease in unclassified seeds and wild morphotypes
41 over time, along with a simultaneous increase in seed elongation. These results likely reflect
42 the intensification of date palm cultivation, coinciding with the growing prevalence of human
43 selection and vegetative propagation. Our study highlights the potential of seed morphometric
44 analyses in uncovering the domestication and diffusion history of crops, shedding light on how
45 humans have adapted to challenging environments.

46 **Keywords:** Crop diffusion, Date palm (*Phoenix dactylifera* L.), Seed morphometrics,
47 Agrobiodiversity, Chronological and geographical dynamics, Sahara

48 **Introduction**

49 The emergence of oasis agriculture represents a milestone in the history of human life in the
50 arid deserts of North Africa and West Asia. Oases are unique anthropogenic agroecosystems
51 that were established in response to the shift towards a drier climate that began approximately
52 5,000 years ago (Kuper and Kröpelin, 2006; Purdue et al., 2018; Sterry and Mattingly 2020).
53 Since then, the Saharan and Arabian oases provide a crucial lifeline in an otherwise inhospitable
54 environment: they have evolved into densely populated settlements and centers for food
55 production. Situated at the intersections of desert pathways, they play a strategic role in both
56 trade and pilgrimage, as a result of and reason for their positioning.

57 The oasis agroecosystems of North Africa and West Asia are organized around the date palm
58 (*Phoenix dactylifera* L.). This emblematic species produces sweet fruits, dates, which are
59 consumed fresh, dried, or processed into products such as syrup or paste. Dates have long been
60 the main staple for oasis inhabitants and part of the goods exchanged through the caravan trade
61 (Mattingly, 2017). At present, their annual production has surpassed nine million tons and
62 continues to increase steadily (FAOSTAT, 2022). All parts of the plants are used, e.g. timber
63 for construction, leaves for basketry or livestock feed. Foremost, the cultivation of this
64 emblematic species fosters a microclimate that is favorable to the cultivation of other crops
65 (Potchter et al., 2008). The study of the history of date palm cultivation is therefore a good
66 proxy for understanding the emergence and intensification of agriculture in oasis communities.

67 The cultivation of date palm – also known as phoeniculture – is thought to have emerged in
68 the Gulf region, before spreading eastward toward Pakistan and westward throughout the
69 Sahara (Tengberg, 2012). Based on archaeological evidence, its cultivation in oasis
70 agroecosystems appears to have developed from the late 4th mill. BCE in Mesopotamia,
71 southeastern Iran, and eastern Arabia (Tengberg, 2012). In North Africa, local oral tradition
72 evokes an introduction of date palms during the Arab conquest (7th c. CE), but it is now clear
73 that they were present much earlier in the region (Sterry and Mattingly, 2020; Tengberg, 2003).
74 In Nilotic Egypt, date palms have been exploited or cultivated sporadically since the 3rd mill.
75 BCE, and phoeniculture was established by the second half of the 2nd mill. BCE (Gros-
76 Balthazard et al., 2020; Tengberg and Newton, 2016; Terral et al., 2012). Outside the Nile
77 Valley, date palm gardens developed at least since the 5th c. BCE as documented in the southern
78 region of the Kharga Depression (Newton, 2005).

79 Further west, the 5th c. BCE Greek historian Herodotus mentions date palms in the Central
80 Sahara (Histories, 4.182), and archaeological work has identified extensive ancient settlement

81 and agriculture in the Libyan Sahara (e.g. Daniels, 1973; Mattingly, 2022). The earliest
82 evidence for date palm cultivation here comes from Zinkekra, a Garamantian hilltop settlement,
83 where the numerous remains of *P. dactylifera* (fruits, seeds, male and female flowers,
84 associated with other crops such as emmer wheat, barley, fig and grape), dated to the first half
85 of the 1st mill. BCE, have been interpreted as likely evidence for an early form of oasis farming
86 (Van der Veen, 1992, 2010). There remain large gaps in our knowledge of the further spread of
87 the date palm. At the western edge of the Sahara, in Morocco, oasis cereal cultivation was
88 established by the 4th c. CE at the latest, but the date palm is, currently, not attested there until
89 the medieval period (Fenwick et al., 2021).

90 The posteriority of date palm archaeobotanical remains in the Sahara compared with West Asia
91 supports an emergence of oases agrosystems and date palm cultivation through step-by-step
92 westward diffusion from the Arabian Peninsula (Duckworth et al., 2020; Sterry and Mattingly,
93 2020). There are no known wild date palm populations (*Phoenix dactylifera* L.) in North Africa,
94 although wild relative species are present, such as the native species of the Canary Islands
95 (*Phoenix canariensis* Chabaud) and the sub-Saharan *Phoenix reclinata* Jacq. At present, the
96 sole substantiated wild populations (relictual populations) are located in the Omani mountains
97 (Gros-Balthazard et al., 2017) and the pre-domestic archaeobotanical records attributed to *P.*
98 *dactylifera* are from West Asian sites (reviewed by Gros-Balthazard and Flowers, 2021).
99 Nevertheless, genomic analyses have revealed that the diversity of North African date palms is
100 not solely derived from West Asian date palms (Hazzouri et al., 2015; Gros-Balthazard et al.,
101 2017). *Phoenix theophrasti* Greuter, currently growing in Greece and Turkey, has contributed
102 to this diversity as much as 20% (Flowers et al., 2019; Gros-Balthazard et al., 2021). The
103 chronology of this mixture remains unknown, although analyses of ancient genomes have
104 shown that it dates back at least 2,000 years (Gros-Balthazard et al., 2021; Pérez-Escobar et al.,
105 2021). Other, currently unknown sources of diversity must also be invoked to explain some of
106 the North African diversity (Flowers et al., 2019; Gros-Balthazard and Flowers, 2021; Gros-
107 Balthazard et al., 2020). Consequently, additional research is necessary to comprehend how
108 phoeniculture originated and developed in the Sahara. What are the origins of the germplasm?
109 When and from where it was imported? How has agrobiodiversity evolved over time?

110 Over the last decade, crop domestication studies have been transformed by the advent of
111 archaeophenomics, which allows large-scale quantification of phenotypes from archaeological
112 specimens and offers improved insights into past agrobiodiversity (Evin et al., 2020).
113 Traditional morphometrics is based on the measurement of traits such as length and width, to
114 characterize the size of an object, whereas geometric morphometrics focuses on shapes, which

115 can be defined as “the total of all information invariant under translations, rotations and
116 isotropic rescaling” (Kendall, 1989; Small, 1996). In perennial fruit crops, the comparative
117 study of ancient and modern seeds by morphometric methods has offered insights into the
118 signatures of domestication, the variation of agrobiodiversity through space and time, and the
119 changes in cultivation practices (Bouby et al., 2013, 2021; Fuller, 2018; Newton et al., 2014;
120 Terral et al., 2004). Domesticated phenotypes may be identified through morphological
121 divergences of forms from the ancestral wild type: domesticated plants have longer and
122 elongated seeds (e.g. in date: Gros-Balthazard et al., 2016; Rivera et al., 2014; Terral et al.,
123 2012, in cherry: Burger et al., 2011, or in grape: Bouby et al., 2013; Terral et al., 2010). This
124 dissimilarity is the result of human selection for larger fruits, and further diversification in
125 multiple varieties (Fuller, 2012; Terral et al., 2010, 2021). Increasing the length of fruits, rather
126 than their width, may indeed allow for larger fruit size without requiring a higher physiological
127 investment in seed content (Fuller, 2018). Further, it has been interpreted as evidence for
128 increased use of vegetative over sexual reproduction, a diminishment/halt of mixing with wild
129 populations and an intensification of production (Fuller, 2018). That wild and domesticated
130 seed shape and size tend to occupy opposite ends of a spectrum enables the tracking of the
131 domestication episode. As an example, the date seeds excavated from as-Sabiyah in modern
132 Kuwait, dating back approximately to 5,000 BCE and documented by Carter and Crawford
133 (2010), exhibited a wild morphotype, leading to the interpretation that they were either
134 harvested from the wild or represent early domesticated varieties (Gros-Balthazard et al., 2017).
135 Further, seed morphometrics provides a tool to track the geographical and chronological
136 dynamics of crop diversity. The study of 151 date palm seeds from seven Egyptian sites
137 revealed the presence of domesticated West Asian forms since at least the 14th c. BCE, and,
138 over the course of the 1st mill. BCE, the gradual elongation of seed shape coupled with the
139 decrease in wild morphotype frequency together substantiate an intensification of
140 phoeniculture (Terral et al., 2012).

141 In this study, we applied morphometric methods to a set of 312 well-preserved seeds excavated
142 from three Libyan archaeological sites in order to unravel the origins and evolution of date palm
143 agrobiodiversity in the Central Sahara and the Libyan pre-desert zone. The first site, Zinkekra
144 (900-400 cal. BCE), is a settlement of the Garamantes, a people living in the Sahara and
145 mentioned by classical authors like Herodotus and Ptolemy (Herodotus, Histories IV,4. 183 and
146 Ptolemy, Geography, 4.6.12.). Analysis of the plant remains from this hilltop site has identified
147 the existence of a well-developed agricultural regime despite the harsh climatic conditions (Van
148 der Veen, 1992, 2010). Subsequent survey and excavation in this region have revealed the

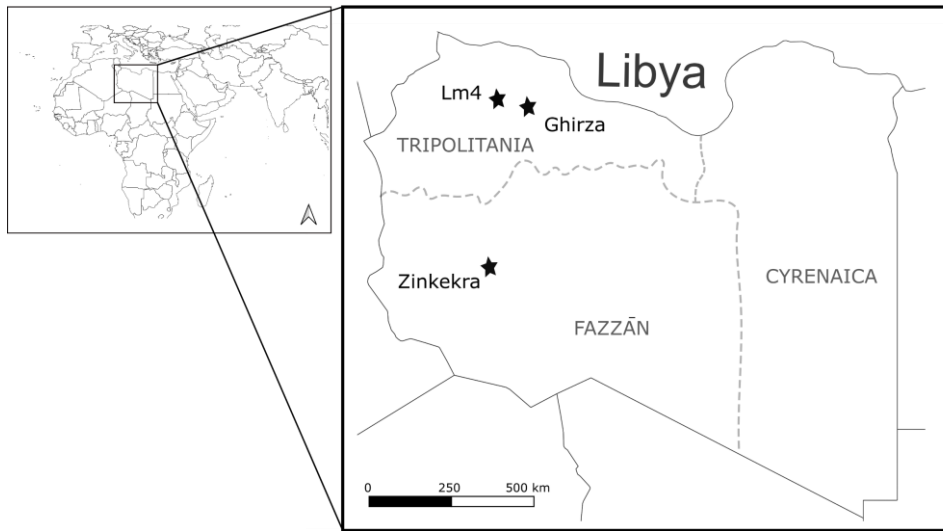
149 impressive scale and distribution of Garamantian settlement and agriculture (Mattingly, 2022;
150 Pelling, 2013; Sterry and Mattingly, 2020, 53-111). The two other sites, Lm4 and Ghirza, are
151 located in the Tripolitanian pre-desert to the north of the Garamantes and were dated to Roman
152 and Medieval periods, respectively (Dore and Van der Veen, 1986; Van der Veen, 1984; Van
153 der Veen et al., 1996), though the date seeds from Lm4 turned out to be recent, see below. Here
154 too extensive settlement and agriculture was recorded, especially during the Roman period
155 (Barker et al., 1996).

156 We analyzed these seeds along with a modern reference collection composed of more than
157 6,000 seeds from domesticated and wild date palms, and other *Phoenix* species. The objectives
158 were (1) to assess whether the Libyan seeds do indeed belong to *Phoenix dactylifera*, (2) to
159 establish whether they are wild or cultivated, (3) if cultivated, to identify their morphotypes and
160 possible region of origin, and (4) to determine how seed morphology has changed over time.
161 Finally, we incorporated 151 ancient Egyptian seeds previously analyzed by Terral et al. (2012)
162 into our study, to increase our sampling of ancient North African seeds and explore the onset
163 of date palm cultivation in the region, and the chronological dynamics of its agrobiodiversity,
164 both of which will contribute to our understanding of the history of oasis agroecosystems.

165 **Materials and methods**

166 **Archaeological material and radiocarbon dating**

167 A total of 312 desiccated archaeological seeds (stones) of *Phoenix* spp. from three
168 archaeological sites in Libya form the focus of this study (Figure 1, Table 1, Table S1). No
169 charred date seeds were used in this study because most were badly fragmented, and research
170 into the effects of charring on possible distortion of the date seeds is currently in progress. Table
171 1 lists the Libyan material and dating evidence used in this study and Table S1 provides the full
172 range of radiocarbon dates for the three sites. This material covers almost three millennia, from
173 the first half of the 1st mill. BCE (c. 900-400 BCE, Zinkekra, 127 seeds), through the medieval
174 period (c. 600-800 AD, Ghirza, nine seeds) to the modern period (Lm4, 176 seeds). Combined
175 with the 151 archaeological seeds from Egypt (from c. 14th c. BCE to c. 8th c. CE; Table 2;
176 Terral et al., 2012), our dataset provides the opportunity to study the dynamics of date palm
177 diversity in North Africa since the end of the 2nd mill. BCE (cf. also Sterry and Mattingly, 2020,
178 for a compilation of >1,000 Saharan radiocarbon dates on varied material covering this period).



179

180 **Figure 1.** Map of modern-day Libya with the location of the three archaeological sites from
 181 which the *Phoenix* seeds were analyzed.

182 Zinkekra represents an ancient hilltop settlement of the Garamantes, previously dated by 11
 183 radiocarbon dates to c. 900-400 cal. BCE (Figure 1, Table 1, Table S1). It is located on a spur
 184 overlooking the Wadi al-Ajal, in the desert region of Fazzān. The site was excavated between
 185 1965 and 1973 (Daniels, 1968, 1973), and posthumously published in full (Mattingly, 2010,
 186 site ZIN001-003). Occupation consisted of a series of huts built in dry-stone and mud walling
 187 and timber, with rooms, yards or animal pens, and hearths, mostly located on the top of the
 188 escarpment, with more limited occupation on the northern and southern slopes. Many of the
 189 rooms were filled with thick layers of organic debris: collapsed roofing material (palm fronds),
 190 dung, straw, and domestic refuse. While no systematic sampling of botanical remains had been
 191 carried out, seeds and small samples of the organic deposits had been collected. Analysis of this
 192 material in the early 1990s identified numerous remains of *Phoenix dactylifera*, including fruit
 193 stones (seeds), some entire fruits, perianths, rachillae, female and male flowers, detached
 194 anthers and embryos (Figure S1; Van der Veen 1992, republished in Van der Veen 2010). Also
 195 common were grains and chaff of emmer wheat and barley, seeds of figs and grapes, and a
 196 range of wild plants. The presence of rachillae, flowers, fronds and wood of the date palm
 197 demonstrates that date palms were growing locally and were likely cultivated. The crops were
 198 probably grown on the nearby wadi floor, where there is artesian water close to the surface, as
 199 well as a perennial spring. Most of the remains were preserved in desiccated form, though some
 200 were charred. The combination of cereals, fruits, herbs and date palm remains was interpreted
 201 as likely evidence for an early form of oasis cultivation in the Central Sahara (Van der Veen,
 202 1992). Most of the c. 1,000 date seeds were fragmented and/or badly preserved (some are
 203 thought to have passed through the digestive tracts of animals), but 127 were entire, well-

204 preserved, desiccated and from securely dated contexts and were thus selected for
205 morphometric analysis. We further selected four seeds that were radiocarbon dated, yielding
206 dates from the 8th to 5th c. BCE, supporting previous radiocarbon dates from charred and
207 desiccated cereals, dates, and charcoal (Table 1, Table S1, Figure S2).

208 Ghirza is a large Romano-Libyan settlement located in the pre-desert of Tripolitania, with a
209 main phase of occupation from the 2nd-4th/5th centuries CE and partial reoccupation in the early
210 medieval period (Figure 1, Table 1, Table S1). The site was excavated in 1957 by Brogan and
211 Smith (1984), see also Barker et al. (1996, site Gh127). It consists of fortified farms, a temple,
212 and two burial grounds with mausolea. The early medieval reoccupation included a large
213 merchant's house. While no systematic sampling for botanical remains was carried out, small
214 amounts of material were collected. The medieval material from the merchant's house included
215 barley grain and chaff, fig achenes and syconia, one fragment of almond, as well as 14 seeds of
216 *Phoenix dactylifera* (Van der Veen, 1984). Nine of these were well enough preserved to be used
217 in this analysis. As only seeds were found, local cultivation cannot be assumed (though date
218 palms and date harvesting are illustrated on the Roman period tomb relief carvings at the site).
219 The few Roman-period seeds were not well enough preserved to be included. One of the nine
220 medieval seeds was radiocarbon dated and gave an early medieval date: 6th-8th c. CE (Table 1,
221 Table S1, Figure S2), slightly earlier than the archaeological date given to the deposits.

222 Lm4 is located c. 115 km west of Ghirza (Figure 1, Table 1, Table S1), and was excavated in
223 1984, as part of the UNESCO Libyan Valleys Survey project (Barker et al., 1996). It represents
224 a large Romano-Libyan open courtyard farm, in the Wadi el-Amud, and comprises farm
225 buildings and an olive press. While the site was occupied during the 1st-4th centuries CE, there
226 is evidence of medieval activity, as well as modern disturbance. The botanical remains include
227 wheat, barley, pulses, fig, grape, almond, and some date seeds (Dore and Van der Veen, 1986;
228 Van der Veen, 1985; Van der Veen et al., 1996). Most of the *Phoenix* remains were charred and
229 badly fragmented, and could not be included in this study. But a large cache of 206 desiccated
230 well-preserved seeds was recovered in building A, plus some in building E. Out of these, 176
231 seeds were well enough preserved to be analyzed. Radiocarbon dating of two of these seeds
232 however highlighted that they represent recent intrusive material, quite probably remains of
233 snack foods left by modern visitors to the site (Table 1, Table S1, Figure S2).

234

235

236 **Table 1.** Archaeological context, dating and number of seeds analyzed for each of the three
 237 Libyan archaeological sites. Calibrated ages were obtained using OxCal v4.4.2
 238 (<https://c14.arch.ox.ac.uk/oxcal.html>) and the IntCal20 Northern Hemisphere radiocarbon age
 239 calibration curve (Reimer et al., 2020). One seed was dated per context unless otherwise
 240 indicated. See Table S1 for further details and dating evidence.

Site	Archaeological dating	Context	No. of seeds analyzed	Lab code	14C age BP	Calibrated Age (95.4%)	
Zinkekra ZIN001-003 (127 seeds)	Early Garamantian (c. 900 - 400 BCE)	ZIN001.034 [3]	5	Poz-137604	2440 ± 30	751-684 BCE (22.3%) 668-634 BCE (9.8%) 622-613 BCE (1.1%) 591-408 BCE (62.3%)	
				Poz-137606	2500 ± 35	781-513 BCE (94.1%) 502-485 BCE (1.4%)	
		ZIN001.037 [1]	1				
		ZIN001.039E [1]	2				
		ZIN001.060 [1]	1				
		ZIN001.062 [9]	19				
		ZIN001.71 [6]	91	Poz-137603	2435 ± 35	751-684 BCE (20.7%) 668-634 BCE (9.3%) 622-613 BCE (1.2%) 591-406 BCE (64.3%)	
				Poz-137602	2460 ± 35	758-678 BCE (27.8%) 672-416 BCE (67.7%)	
		ZIN003.105 [3/3]	4				
		ZIN003.105 [4/4]	1				
ZIN003.105 [1/4]	3						
Ghirza (9 seeds)	Early Medieval	Building 32, Room 2	2				
		Building 32, Room 3	7	Poz-137709	1270 ± 30	664-778 CE (84.8%) 788-827 CE (10.7%)	
Lm4 (176 seeds)	Recent. 18 th /19 th century CE, or more recent	Lm4-A - Room III (25)	175	Poz-137600	125 ± 30 (1)	1675-1744 CE (26.6%) 1750-1765 CE (3.4%) 1799-1942 CE (65.4%)	
				Poz-137601	140 ± 30 (1)	1672-1778 CE (37.2%) 1798-1944 CE (58.3%)	
		Lm4-E - (6A) c	1				

241 In addition to the set of Libyan seeds, we have included 151 archaeological seeds from seven
 242 Egyptian sites previously described and analyzed by Terral et al. (2012) (Table 2). Among
 243 these, the earliest seeds were found in Tutankhamun's tomb in the Nile Valley dating back to
 244 the 14th c. BCE, followed by seeds from ‘Ayn-Ziyâda in the Kharga Oasis dating back to the
 245 5th c. BCE. The collection also includes seeds from a 1st c. BCE Graeco-Roman tomb at Hawara
 246 in the Fayum and from three Roman period sites. The most recent samples are from an 8th c.
 247 CE midden in Thebes, Nile Valley.

248 **Table 2.** Archaeological context, dating and number of seeds from the Egyptian sites*
 249 previously analyzed by Terral et al. (2012).

Site	Location	Context/ Archaeological unit	Cultural context/age	No. of Seeds
Thebes	Nile Valley	Tutankhamun's tomb (KV62)/TutanC55–C91	18 th dynasty/14 th century BCE	3
‘Ayn-Ziyâda	Kharga Oasis	Midden/ZMA007	Persian/c. 5 th century BCE	15
Hawara	Fayum	Tomb/Kcat26729 (F.N. Hepper 19.1978.12)	Graeco-Roman (c. 1 st century BCE)	24
Umm Balad	Eastern Desert	Midden/ UB3304–UB2221	Early Roman Empire (1 st –2 nd century CE)	50
‘Ayn-Manâwir	Kharga Oasis	Settlement/MMS23	Early Roman Empire (1 st –2 nd century CE)	30
‘Ayn-Manâwir	Kharga Oasis	Tomb/MQ10T1H	Roman period 3 rd century CE	2
Thebes	Nile Valley	Midden/C3	c. 8 th century CE	27

250 *At Ayn-Ziyâda and the two ‘Ayn-Manâwir sites the archaeobotanical data suggest local cultivation of
 251 the date palm (presence of vegetative remains). At the two Thebes sites and at Hawara in the Fayum
 252 local cultivation is likely as date palms were cultivated in those areas in those periods. The dates
 253 recovered at Umm Balad will most likely have been imported from the Nile Valley (Terral et al., 2012).

254 **Modern reference collection**

255 The modern dataset consists of 6,541 present-day *Phoenix* seeds from 328 *Phoenix* individuals
 256 (Table 3, Table S2, Figure S3). The term “individual” refers to the modern date palm specimen
 257 whose fruits and seeds have been collected. The majority ($N=264$) belongs to *Phoenix*
 258 *dactylifera*, the only domesticated *Phoenix* species, while the remaining are from *Phoenix* wild
 259 relative species ($N=64$; Table 3). For most, 20 seeds were analyzed to optimize the evaluation
 260 of intra-individual shape and size variation (Gros-Balthazard et al., 2016; Terral et al., 2012).
 261 However, two *Phoenix reclinata* and five *P. dactylifera* individuals, having solely 15 to 19
 262 seeds, were included as they represent poorly sampled species/regions (Table S2).

263 The 264 *P. dactylifera* modern reference collection is composed of both cultivated and
 264 uncultivated individuals originating from 14 countries covering the entire distribution range of
 265 the date palm, from Morocco to Northwestern India (Figure S3, Table 3, Table S2). The
 266 cultivated group refers to date palms grown in palm orchards and comprises both

267 cultivars/varieties, that are presumably cultivated under clonal propagation, and accessions
 268 grown from seeds. The uncultivated group is composed of both feral and wild date palms
 269 (Figure S3, Table 3, Table S2). Feral individuals ($N=13$) are date palms growing in a wild
 270 environment, without human intervention, but originating from previously cultivated palm,
 271 either in abandoned palm groves or spontaneously growing following dumping of a seed in a
 272 favorable environment. These were sampled in abandoned oases near the Egyptian oasis of
 273 Siwa, abandoned since at least the 9th or 10th c. CE (Battesti, 2013) and in Oman, in remote
 274 populations growing along wadis (Gros-Balthazard et al., 2017). Wild *P. dactylifera* individuals
 275 ($N=35$) likely represent the descendants of the ancestors of cultivated date palms growing as
 276 relictual populations in Oman, as described by Gros-Balthazard et al. (2017).

277 The 64 *Phoenix* wild relative individuals belong to five species (Table 3, Table S2) with
 278 distributions close or overlapping that of the date palm (Figure S3). They were included to test
 279 the presence of other *Phoenix* species in the ancient samples.

280 **Table 3.** Summary of the modern *Phoenix* seed reference collection. The full list may be found
 281 in Table S2.

Species	Condition	Status	# ind.
<i>P. dactylifera</i>	Cultivated	Cultivar	156
		Seedling	60
	Uncultivated	Feral	13
		Wild	35
<i>P. caespitosa</i>	Uncultivated	Wild	3
<i>P. canariensis</i>			6
<i>P. reclinata</i>			11
<i>P. sylvestris</i>			38
<i>P. theophrasti</i>			6

282

283 **Morphometric data acquisition**

284 Each seed, whether modern or ancient, was photographed according to two orthogonal views
 285 (dorsal and lateral). We used Adobe Photoshop CS6 v.13.0 for processing the images and
 286 obtaining a black silhouette in white background necessary for the geometric morphometric
 287 (Figure S4a).

288 For traditional morphometric data, we measured seed length and width of the dorsal view
 289 following the protocol of Gros-Balthazard et al. (2016) using ImageJ v.1.53e (Figure S4b).
 290 These measurements were obtained semi-automatically with seed outlines after scale
 291 calibration. Further measurements, namely thickness and surface of dorsal or lateral views,

292 were not included in this study as they were previously shown to be correlated with length and
293 width (Gros-Balthazard et al., 2016).

294 For geometric morphometrics, i.e. the measure of seed shape, we used Momocs v. 1.3.2 *R*
295 package (Bonhomme et al., 2014). Seed shape was quantified using outline analyses based on
296 Fourier transformations whose principle is to decompose a periodic function into a sum of more
297 simple trigonometric functions such as sine and cosine (Figure S4c). These simple functions
298 have frequencies that are integer multiples (harmonics) of one another. The first harmonics
299 provide approximations for the coarse-scale while harmonics of higher ranks describe fine scale
300 variations. The Elliptic Fourier Transform (EFT) method consists of fitting separately the *x* and
301 *y* coordinates of an outline projected on a plane (Giardina and Kuhl, 1977; Kuhl and Giardina,
302 1982). We sampled 130 equidistant points and seeds were centered and scaled with their
303 centroid to retain shape information only. They were aligned and normalized using the position
304 of their first points. Coordinates of seed outlines (130 points) were transformed into periodic
305 functions (harmonics) by the EFT. Each harmonic is characterized by four coefficients (two for
306 *x* and two for *y*) that provide a reconstruction of the seed outline. The higher the rank of the
307 harmonic, the more accurate the shape information. To determine the optimal number of
308 harmonics to use, we computed the harmonic power independently for both dorsal and lateral
309 views and further retained a number of harmonics corresponding to at least 99% of the harmonic
310 power, *i.e.* seven harmonics for each view (Supplementary Text S1). We assessed measurement
311 errors arising from data acquisition to ensure that these errors were insignificant compared to
312 the true differences among seeds (Supplementary Text S1). All statistical analyses were done
313 with *R* software v.4.0.3 (R Core Team 2020).

314 **Statistical analyses of seed size**

315 We constructed a reference dataset by measuring the length and width of 6,541 seeds from 328
316 modern *Phoenix* spp. individuals. We tested the differences in length and width among groups
317 of modern seeds and ancient Libyan seeds with Welch's Anova tests from *rstatix R* v.0.7.0
318 package (Kassambara, 2021). All possible combinations of group differences were assayed
319 using Games-Howell tests from the same package. We used three groups for *P. dactylifera*
320 (cultivated, feral, wild), one group of wild relative species and three other groups corresponding
321 to the three Libyan archaeological sites.

322 **Statistical analyses of seed shape**

323 **Modern reference collection**

324 We first explored the variability of seed shape in the modern collection (328 individuals, 6,541
325 seeds). Because there are 15 to 20 seeds per individual, individual centroids of the Elliptic
326 Fourier Transform (EFT) coefficients were calculated for each individual prior to downstream
327 analyses. We performed a principal component analysis (PCA) of the EFT coefficients using
328 Momocs *R* package v.1.3.2. We tested the morphological discrimination between date palms
329 and other *Phoenix* species, and between domesticated date palms, wild date palms and other
330 *Phoenix species*, with multivariate analyses of variance (MANOVA) on the PCA coordinates.
331 We calculated the discrimination rate of each group/species as the percentage of correctly
332 allocated seeds based on seed shape and averaged over each individual of a given group/species.
333 For this purpose, we performed linear discriminant analyses (LDA) with leave-one-out cross
334 validation using MASS *R* package v.7.3.51.6 (Venables and Ripley, 2002). To account for
335 unbalanced sample size among groups, we used a rarefaction method that consisted of 1,000
336 iterations randomly sampling n individuals (n = sample size of the smallest group) in each group
337 and averaged the allocation rate over iterations. To further explore the diversity of seed shape
338 within the date palm and highlight specific morphotypes of seed shape, an additional LDA was
339 carried out on this species alone. We then conducted a hierarchical ascendant classification
340 analysis with the upgma function from *R* package phangorn v.2.5.5 (Schliep, 2011), using the
341 Ward's D2 method implemented on the Mahalanobis distance matrix (matrix of morphological
342 disparity between individuals' centroids) obtained from this LDA. The resulting tree was
343 displayed with *R* package ggtree v.2.2.4 (Yu et al., 2017). Classification accuracy of the
344 morphotypes was recalculated using the LDA as explained above.

345 **Ancient samples**

346 Focusing on the archaeological Libyan *Phoenix* seeds, we first performed a PCA to explore the
347 diversity of seed shape in this material alone. We then compared those seeds to the modern
348 reference collection by adding them as supplementary individuals into the PCA space defined
349 by the modern collection. In order to classify them into species and groups, we performed
350 nested LDAs, where the variation space is defined by modern accessions, and seeds from
351 archaeological sites are predicted individuals. They were first assigned to either date palm or
352 wild relative species, considering probabilities >0.90 as a threshold for assignment. Seeds
353 allocated to *P. dactylifera* were then included in a second LDA in order to assign them to a
354 specific morphotype (again with a threshold of 0.90), with the aim of identifying ancient forms

355 exploited by past human societies. We applied the same morphometric procedure of
356 classification on the Egyptian archaeological seeds (Terral et al., 2012). Finally, we performed
357 a correspondence analysis with the CA function from FactoMineR v.2.4 R package (Lê et al.,
358 2008), using the frequencies of allocation to the distinct morphotypes for both the Libyan and
359 Egyptian seeds in order to determine the dynamics of agrobiodiversity through space and time.

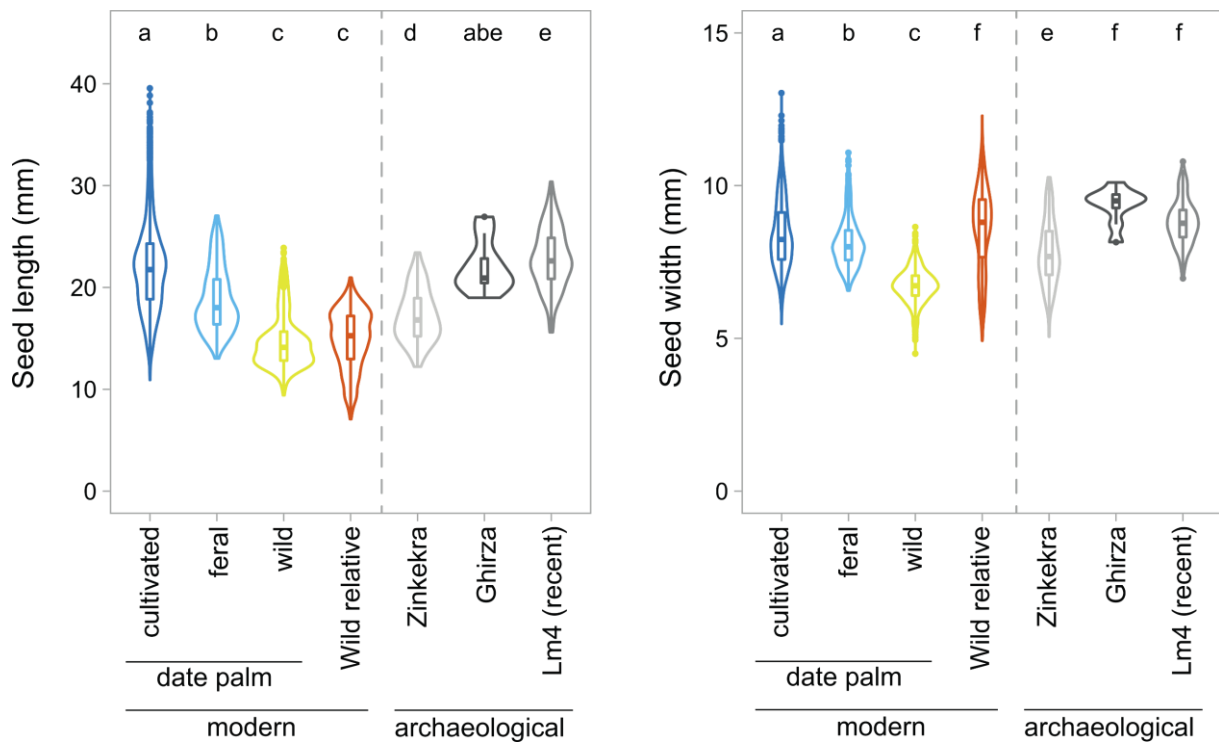
360 **Results**

361 **Seed size of the modern and Libyan seeds**

362 Length appeared as a distinguishing feature among the different types of date palms (cultivated,
363 feral, wild) and wild relative species (Figure 2). Seed length was significantly greater in
364 cultivated date palms (average = 21.9 mm) than in both wild date palms (average = 14.7 mm)
365 and wild relative species (average = 14.9 mm) (Welch's t-tests = 58.9 and 65.9, respectively,
366 *p-values* < 0.001). On the other hand, seed length was not significantly different between wild
367 date palms and wild relative species (Welch's t-test = 1.51, *p-value* = 0.66). Within date palms,
368 feral accessions display an intermediate seed size between cultivated and wild accessions. On
369 average, seed width also appeared different among the groups, although the ranges largely
370 overlapped for all groups (Welch ANOVA test, *p-value* < 0.001; Figure 2).

371 Of the Libyan seeds, those from Zinkekra measured on average 17.2 mm, significantly shorter
372 than seeds from both medieval Ghirza (average = 22.1 mm) and modern Lm4 (average = 22.8
373 mm; Welch's t-tests = 5.4 and 17.6, respectively, *p-values* < 0.005; Figure 2). Seed lengths from
374 the two latter sites were not significantly different (Welch's t-test = 1.51, *p-value* = 0.94).

375 When compared to the modern reference dataset, seeds from Zinkekra appeared significantly
376 shorter than the domesticated type (cultivated and feral) (mean differences = -4.53 mm, Welch's
377 t-tests = 19.1, *p-value* < 0.001). The Ghirza seeds had on average a similar length to modern
378 cultivated date palm (mean difference = 0.29, Welch's t-test = 0.337, *p-value* = 0.99) (Figure
379 2) and Lm4 seeds were on average slightly longer than those from the entire modern collection
380 of date palm seeds (mean difference = 1.08 mm, Welch's t-test = 4.63, *p-value* < 0.001). Seed
381 length has thus increased since the first mill. BCE, but has stabilized by the Medieval period,
382 although in our reference collection, it reached 40 mm, which was not the case for either Ghirza
383 or Lm4 seeds (Figure 2).



384

385 **Figure 2.** Comparison of seed length and width between three groups of *Phoenix dactylifera*,
 386 the other wild relative species and the 312 archaeological seeds from Libya. Letters above the
 387 violin plots correspond to the Games-Howell test statistics: different letters indicate significant
 388 differences among groups.

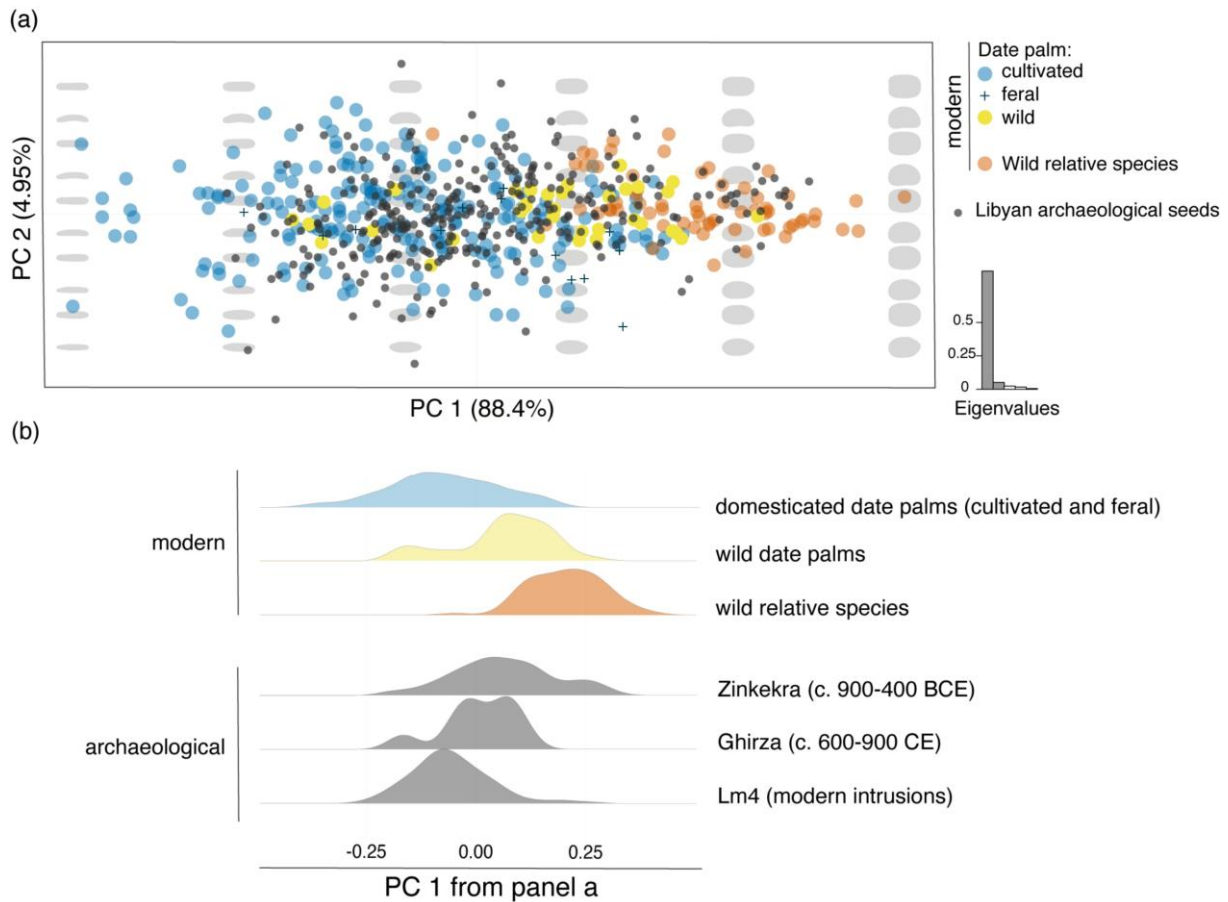
389 Seed shape of modern and ancient *Phoenix* spp.

390 Seed shape of 6,541 modern seeds and 312 and 151 archaeological seeds from Libya and Egypt
 391 was appraised by the Elliptic Fourier Transform (EFT) methods (Supplementary Data, available
 392 online).

393 Seed shape diversity in the modern reference collection

394 Seed shape appeared as a reliable marker to differentiate domesticated (cultivated and feral)
 395 date palms from wild date palms and wild relative species (MANOVA on 56 principal
 396 components, $F = 58.17$, $P < 0.001$; Figure 3). The distinction is explained by a difference in
 397 seed elongation, as seen in the first component of a Principal Component Analysis (PCA)
 398 carried out on the EFT coefficients (88.4% of variance explained). Indeed, cultivated date palms
 399 display elongated seeds and pointed apices in comparison with both wild date palms and wild
 400 relative species (Figure 3a). Further, seed shape of wild date palms was on average significantly
 401 different from both that of domesticated date palms (whether cultivated or ferals) and from
 402 those of wild relative species (MANOVA, $F = 24.61$, $P < 0.001$ and MANOVA, $F = 18.91$, P
 403 < 0.001 , respectively). The majority had an intermediate morphotype, converging toward the
 404 uncultivated wild *Phoenix* relative species (subspherical seeds). Feral date palms were found

405 within the diversity of cultivated forms, including where the cultivated forms overlapped the
406 wild ones (Figure 3a).



407

408 **Figure 3.** Seed shape analysis. (a) Principal Component Analysis (PCA) carried out on Elliptic
409 Fourier Transform (EFT) coefficients of the 328 individuals from modern reference collection.
410 One colored point corresponds to one individual (mean coefficients of its seeds). The 312
411 Libyan seeds from Zinkekra, Ghirza and Lm4 were added as supplementary individuals to the
412 analysis. The gray shapes in the background illustrate the morphological space, i.e. the main
413 synthetic axes of shape variation captured by principal components. On each point of the
414 PC1xPC2 plane, one can calculate the corresponding Fourier coefficients values and then the
415 two (dorsal and lateral) corresponding shapes using the inverse EFT transform. (b) Ridgeline
416 plot representing the distribution of the PC1 coordinate for the three groups of the modern
417 reference collection and the three archaeological sites from Libya.

418 In view of classifying the excavated Libyan and Egyptian seeds into groups identified in the
419 modern reference collection, we assessed the discrimination power of seed shape for
420 differentiating domesticated date palms, wild date palms and other wild relatives. A Linear
421 Discriminant Analysis (LDA) with leave-one-out cross-validation on a balanced sample size
422 led to an average of 74.47% seeds correctly allocated (Table S5). Of the 229 domesticated date
423 palms, 73.75% were correctly allocated, while most of the remaining ones were assigned to
424 wild date palms (15.12%). For wild date palms, 74.82% are correctly allocated; the remaining

425 ones are assigned to both domesticated date palms and other wild relatives (12.01% and
426 13.16%, respectively), corroborating their intermediate position in the PCA (Figure 3a).
427 Finally, 71.11% of wild relative species were positively assigned to this group, with incorrect
428 allocations mostly assigned to wild date palms (20.63%). When using the full dataset rather
429 than the rarefaction method, and thus unbalanced sample size among the three groups, the
430 positive allocation rate reached an average of 90.9% among the three groups (Table S5). This
431 higher positive rate may be explained by the large variability of the domesticated group which
432 may not be properly represented with a randomly sampled fraction. Finally, we pooled both
433 domesticated and wild date palms to test the discrimination between date palms and other wild
434 relatives. The discrimination appeared high, with 89% and 93.3% of individuals correctly
435 assigned when using balanced and unbalanced sample size, respectively (Table S6).

436 The neighbor-joining tree based on the Mahalanobis distance revealed 12 morphotypes (MT1
437 to MT12; Figure 4a, Tables S7-S8). The classification rate (representing the percentage of seeds
438 correctly allocated to its morphotype) ranged from 57.1% (MT7) to 90.9% (MT1). Of the 264
439 modern *P. dactylifera* individuals, 233 (88.26%) were assigned to one of these morphotypes
440 with a probability >0.90. Two morphotypes (MT1 and MT2) were mostly composed of
441 uncultivated forms or seedlings, displaying rounded seeds, further referred to as wild
442 morphotypes. MT1 comprised solely wild date palms, while MT2 included mostly wild date
443 palms, and also feral accessions, cultivated seedlings and a single cultivar. Two other
444 morphotypes (MT3 and MT4) grouped individuals of sub-rounded seeds, mostly cultivated
445 accessions (both seedlings and varieties), feral and wild date palms. The other eight
446 morphotypes (MT5 to MT12) grouped seeds with a more elongated shape. They were mostly
447 composed of domesticated accessions, whether cultivated or feral (223 accessions, 94.89%).
448 MT5 and MT6 were particularly elongated. Overall, those morphotypes appeared poorly
449 geographically structured: they were mostly composed of individuals from different geographic
450 origins (Figure 4a, Table S8). Only morphotype MT5 contained date palms exclusively
451 originating from North Africa, including Egypt. Even so, palms from this region made up the
452 majority of MT6 (80.0 %) and MT10 (85.0 %). None of the morphotypes comprised only West
453 Asian domesticated date palms, though they made up the majority of MT4 (79.5 %) and MT7
454 (85.7 %; Table S8).

455

456 **Comparison of excavated Libyan and Egyptian seeds with the modern reference dataset**

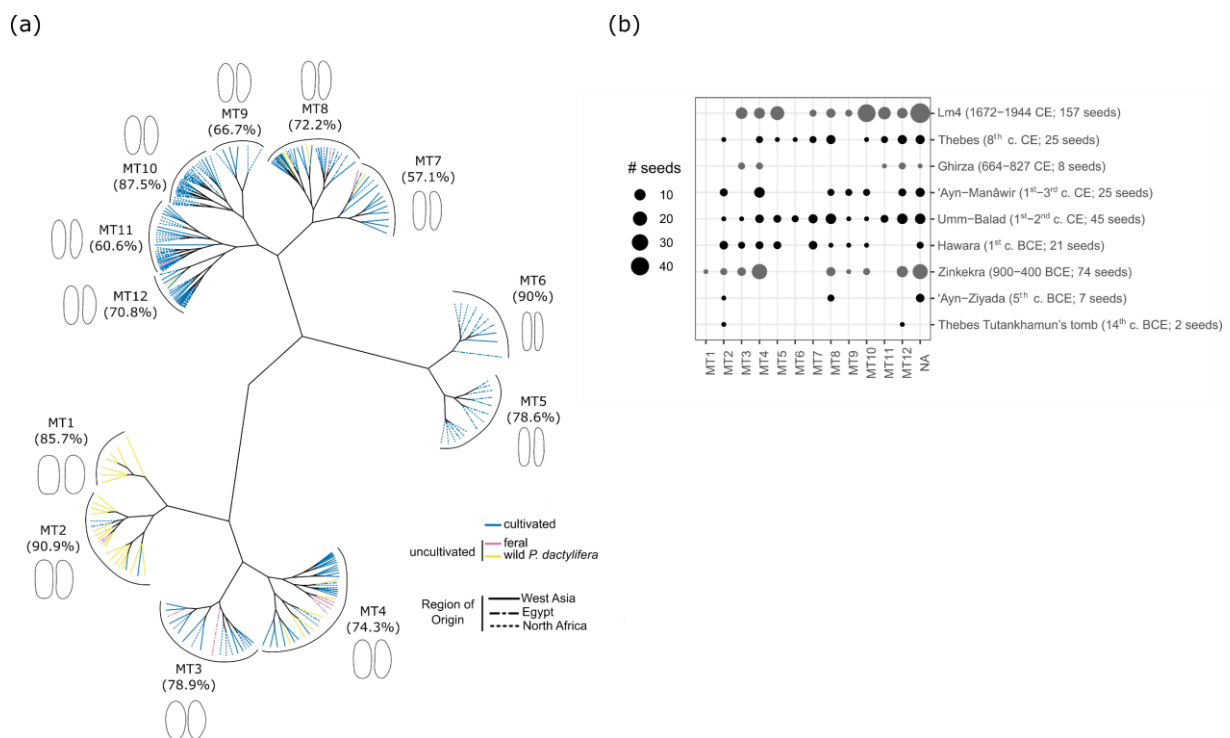
457 The Libyan seeds showed a large diversity of shapes, as evidenced by the principal component
458 analysis (PCA) of EFT coefficients (Figure S8). Seed shape from the 1st mill. BCE site of
459 Zinkekra ($N=127$) differed from that of the modern site of Lm4 ($N=176$), the former being
460 rounder than the latter (MANOVA, $F=60.73$, $p\text{-value} < 0.001$). The few seeds from medieval
461 Ghirza ($N=9$) were dispersed in the middle of the plot.

462 Most of these ancient seeds were found within the diversity of shape displayed by the modern
463 reference collection (Figure 3). However, on PC1, related to seed elongation, they reached
464 neither the left extremity (very elongated seeds of domesticated date palms), nor the right
465 extremity (rounded seeds of wild relative species). The 151 Egyptian archaeological seeds were
466 also found within the modern shape diversity. We evidenced a shift towards positive PC1
467 coordinates over time for both the Libyan and Egyptian seeds: the more recent the seeds, the
468 more elongated they are (Figure S9).

469 A first LDA was used to classify the archaeological seeds into either *P. dactylifera* or other
470 wild relative species. Most seeds from both the Libyan and the Egyptian archaeological sites
471 were assigned with probability >0.90 to *P. dactylifera* (76.60% and 82.78 %, respectively).
472 Focusing on the three Libyan sites, this represented 58.27% of Zinkekra seeds, all but one from
473 Ghirza (88.89%) and the vast majority of seeds from Lm4 (89.20%; Table S9). Some seeds
474 were assigned to other *Phoenix* species: 24.41% from Zinkekra, one seed from Ghirza
475 (11.11%), and 4.55% from Lm4. Unfortunately, since our modern reference dataset did not
476 permit a good discrimination of the various non-*dactylifera* species (discriminant power of
477 26.2% with a LDA comprising only those species), we could not allocate these seeds to a
478 specific species. Finally, a total of 33 seeds, mainly from Zinkekra (66.67%), were not assigned
479 to any of the two groups defined by our reference collection dataset using a probability >0.90 .
480 Splitting date palms in domesticated and wild populations did not improve the allocation rate
481 (Table S10).

482 The Libyan and Egyptian seeds allocated to *P. dactylifera* in the first LDA were incorporated
483 in a second LDA to identify their corresponding morphotype. Zinkekra was the only Libyan
484 site with seeds allocated to wild morphotypes MT1 and MT2 (Figure 4b, Table S11). However,
485 the majority of its seeds were assigned to MT4, a sub-rounded morphotype composed mostly
486 of domesticated accessions from West Asia, and a few North African cultivars, one of which
487 being the Libyan cultivar Tiswin (Figure 4b, Tables S7-S8-S11). Notably, some of the Zinkekra
488 seeds were allocated to elongated morphotypes (Figure 4b, Tables S7-S8-S11). The medieval

489 Ghirza seeds were allocated to MT3 and MT4 (sub-rounded), and MT11 and MT12 (elongated,
 490 Figure 4b, Table S11), composed of cultivated individuals originating from distinct
 491 geographical origins (Table S8). Finally, the site Lm4 with modern intrusions was mainly
 492 represented by MT10, followed by MT5 and MT11 (Figure 4b, Table S11), all three
 493 representing elongated morphotypes and mostly composed of Egyptian and western North
 494 African individuals (Table S8). In particular, MT10 comprised the cultivar Siwi, a famous
 495 cultivar from the Siwa oasis, in the Egyptian Libyan desert. We noted that 31.21% of Lm4 seeds
 496 were not allocated to one of the 12 morphotypes with probability > 0.90, a proportion
 497 comparable to what was found for Zinkekra (32.43%), but higher than what was observed in
 498 the reference collection (11.74%).



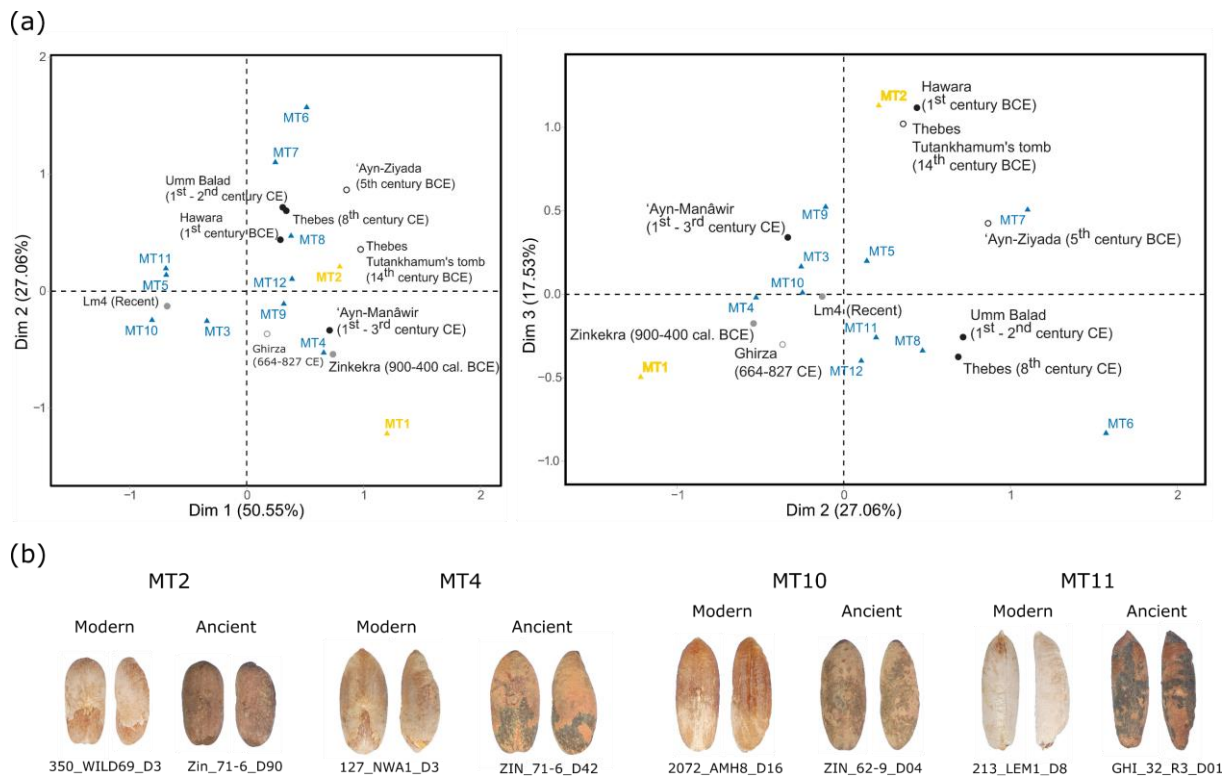
499

500 **Figure 4.** Date palm morphotypes and assignment of the Libyan and Egyptian seeds excavated.
 501 (a) UPGMA dendrogram based on the minimum Mahalanobis distance matrix among cultivated
 502 and uncultivated (feral and wild) individuals from the date palm *P. dactylifera*. Positive
 503 classification rate (%) and geographic origin of individuals are also presented for the twelve
 504 morphotypes. Mean seed outlines were reconstructed for the morphotypes. (b) Number of seeds
 505 from Libyan (grey) and Egyptian (black) archaeological sites assigned to each of the 12
 506 morphotypes highlighted in the UPGMA tree from panel (a).

507 Concerning the Egyptian archaeological seeds, all the sites, especially the Graeco-Roman site
 508 of Hawara and the Roman site of ‘Ayn-Manâwir, included seeds assigned to the wild
 509 morphotype MT2 (Figure 4b, Table S12). Here, MT7, MT8 and MT12 were the most
 510 represented morphotypes, except at ‘Ayn-Manâwir, where the majority of seeds were assigned
 511 to MT4 (Figure 4b, Table S12), as at Zinkekra. Finally, MT6, a morphotype dominated by

512 Egyptian varieties (Table S8), was only present in Egypt; it was not evidenced in the Libyan
 513 seed assemblage (Figure 4b, Table S12).

514 The frequencies of seeds allocated to distinct morphotypes for each Libyan and Egyptian site
 515 were processed with a correspondence analysis (CA) to explore chronological and geographical
 516 relationships between archaeological sites and morphotypes (Figure 5a, Figure 5b, Tables S11-
 517 S12). The first axis separated Lm4 (modern intrusions) from all the archaeological sites (Figure
 518 5a). The second axis separated the Libyan sites from the Egyptian ones, except for the Roman
 519 period ‘Ayn-Manâwir site, located in the Western Desert of Egypt (Figure 5b). These sites had
 520 higher amounts of the sub-rounded morphotype MT4. The third axis split the Egyptian sites by
 521 chronological period, with the 1st mill. BCE sites composed of higher proportions of the wild
 522 MT2, and the 1st mill. CE sites characterized by higher amounts of MT6 and MT8.



523
 524 **Figure 5.** Chronological comparison of the shape of ancient date palm seeds from North Africa.
 525 (a) Correspondence analysis biplots (left: first and second dimension; right: second and third
 526 dimension) with Libyan and Egyptian ancient seeds allocated to distinct morphotypes (see the
 527 neighbor-joining tree in Figure 4a), showing chronological and geographical trends of date
 528 palm agrobiodiversity. Sites with less than ten seeds were added as supplementary individuals
 529 in the CA (empty circle points). (b) Examples of convergent modern and ancient seed
 530 morphotypes.

531 **Discussion**

532 Our study aimed to improve our understanding of the origins of date palm in North Africa and
533 the changes in its agrobiodiversity throughout the past three millennia. We focused on 312 seeds
534 excavated from three Libyan sites, some directly radiocarbon dated. They were compared to a
535 modern reference collection composed of >6,000 *Phoenix* seeds and 151 Egyptian
536 archaeological seeds from a previous study (Terral et al., 2012). We used morphometric
537 methods to quantitatively study both seed size and shape in order to determine which forms of
538 *Phoenix* were exploited or cultivated during the 1st mill. BCE and later.

539 **Diversity in modern *Phoenix* seeds**

540 **Size and shape discrimination between date palms and wild relatives**

541 The results of the morphometric analysis on the reference collection showed that domesticated
542 date palm seeds are on average a third longer than their wild counterparts, and their shape
543 appears more elongated, which supports earlier findings (Gros-Balthazard et al., 2016; Rivera
544 et al., 2014; Terral et al., 2012). This is the result of human selection for bigger fruits, which
545 promoted an elongation of the fruit and, inadvertently, that of the seed (Fuller 2018). Indeed,
546 for instance in *Vitis vinifera* L., the bigger the berry, the more elongated the pip (Bonhomme et
547 al., 2020). Seeds have an advantage over fruits in that they can survive in archaeological
548 deposits, making their phenotypes traceable over time. The elongation of the seeds has thus
549 been interpreted as a continuous domestication syndrome, where primitive varieties having
550 rounded (wild) morphotypes are overall less domesticated than those presenting elongated
551 morphotypes (e.g. in date palm, Gros-Balthazard et al., 2016; Terral et al., 2012; in olive, Terral
552 et al., 2021; Newton et al., 2014; in grape, Bouby et al., 2013; Terral et al., 2010).

553 As expressed in previous studies, size alone cannot be used to determine the wild or
554 domesticated status of date palms. Indeed, the size of the cultivated date palm seeds displays a
555 large variability (10.9 to 39.6 mm) that largely overlaps with that of wild date palms (9.4 to
556 23.9 mm). Further, although seed size is genetically inherited, it is also drastically affected by
557 the environment (Gros-Balthazard et al., 2016; Olejniczak et al., 2018). Cultivated date palms
558 grow in more favorable environments compared to wild ones, including water and manure
559 inputs, which probably boost fruit size and thus seed size. In fact, experiments have shown that
560 the pips of both wild grapevine and grape varieties were bigger when put in cultivation than
561 when growing in natural conditions (Bouby et al., 2005; 2013). In palm gardens specifically,
562 an additional cultivation practice known as date thinning may further promote the development

563 of bigger fruits: cultivators remove dates from the bunches precisely for this purpose. The size
564 of seed thus not only reflects the wild or cultivated status but also largely the environment where
565 the producing palms are growing.

566 Geometric measurements such as EFT coefficients were, on the other hand, shown to be only
567 slightly affected by environmental factors and are thus more reliable for distinguishing
568 populations or species living in contrasting environments (Gros-Balthazard et al., 2016; Terral
569 et al., 2010). As an illustration, wild individuals growing either in natural conditions or in
570 collections produce pips of the same shape, contrary to what has been described for size (Bouby
571 et al., 2013). This method also goes beyond the analysis of just seed elongation, by providing
572 finer quantification of the seed phenotype which can be classified into various morphotypes
573 providing a means to trace their region of origin (Terral et al., 2010).

574 Domesticated and wild date palm seeds were found at both extremes of a seed elongation
575 gradient, but the two types overlap: some domesticated date palms have more rounded seeds
576 and a few wild date palms display elongated seeds, leading to inaccurate allocations in the
577 discriminant analysis. This has also been observed in other crops (Pagnoux et al., 2015; Terral
578 et al., 2010, 2021) and can be attributed to several factors. First, other traits, unrelated to seed
579 shape, may have been selected such that date palms presenting interesting fruit traits in terms
580 of taste, color, etc. may be found in cultivated gardens even if presenting small and round fruits,
581 and by extension round seeds. This might be the case of the cultivar Qadi, the sole cultivar
582 being found in the rounded morphotype MT2 otherwise composed of wild and feral palms and
583 cultivated palms grown from seeds. Further, the reproduction technique (vegetative or sexual)
584 can have a significant impact on the average size and shape of seeds in a garden (Fuller 2018).
585 On the one hand, vegetative propagation allows farmers to target and reproduce palms
586 producing bigger fruits, hence longer seeds. On the other hand, the recourse to sexual
587 reproduction may have given rise to palms producing seeds with a wild morphotype (Fuller
588 2018). This has been shown for *Vitis vinifera* L., where progeny arising from seeds displays a
589 large variety of forms, including wild forms, even when produced by elite varieties (Bouby et
590 al., 2013). This has not been tested in date palms, but the combination of clonal and sexual
591 reproduction implemented by farmers could enable the co-existence of both rounded and
592 elongated morphotypes. As a matter of fact, among the six domesticated accessions in the
593 otherwise wild morphotype MT2, five were seedlings. Finally, gene flow from both wild date
594 palms and a wild relative species has been evidenced by genomic analyses (Gros-Balthazard et
595 al., 2017; 2021; Flowers et al., 2019) and likely contributed to maintaining rounded seeds in the
596 domesticated compartments.

597 **A large diversity in modern date palm seeds**

598 Our study revealed a larger variability in the domesticated date palms than in wild *Phoenix*,
599 consistent with an earlier study (Gros-Balthazard et al., 2016). Greater phenotypic variability
600 in cultivated taxa compared to their wild relatives is considered a consequence of varietal
601 diversification (Darwin, 1876; Glémin and Bataillon, 2009). It is made possible by the
602 relaxation of selective constraints in a cultivation context, which enables the selection of forms
603 that are unfit to natural environments. Conversely, the limited phenotypic variation observed in
604 wild populations has been interpreted as a tendency to resist changes resulting from natural
605 selection for optimal phenotypes (canalization process, Waddington, 1942). Therefore, it can
606 be expected that, over generations of natural selection, feral palm seeds would revert to a wild
607 morphotype. Here, they were found in the full range of shapes displayed by cultivated date
608 palms, but most of them display a sub-rounded morphotype.

609 Our in-depth analysis of date palm seed shapes revealed the complex agrobiodiversity of the
610 date palm with 12 distinct morphotypes, poorly structured geographically: most were composed
611 of date palms having different origins, although some included mainly individuals from one
612 defined area. Similar observations were made regarding domesticated olive cultivars, and this
613 was linked to the intensification of trade across the Mediterranean during the Roman period
614 (Terral et al., 2004, 2021).

615 **On the origins and evolution of phoeniculture in North Africa**

616 **The earliest evidence of local phoeniculture in the Central Sahara**

617 Archaeological date seeds from Zinkekra (c. 900-400 BCE) have previously been assigned to
618 the date palm (Van der Veen, 1992, 2010). The numerous remains recovered were interpreted
619 as evidence for local cultivation and a form of early oasis agriculture, due to the presence of all
620 parts of the palm, combined with other crops such as grapes, figs and cereals (Figure S1; Van
621 der Veen, 1992, 2010). A few date stones recovered from the Wadi Tanezzuft Valley in Libya
622 (c. 300 km from Zinkekra) date back further in time, radiocarbon dated to around 1,000 BCE,
623 but were interpreted as imported rather than locally produced given their scarcity and the
624 absence of vegetative parts among the archaeobotanical remains (Cottini and Rottoli, 2002).
625 Thus, Zinkekra represents one of the earliest sites in North Africa, outside Egypt, where local
626 date palm cultivation has been recorded.

627 Our analyses substantiated the conclusion that date palm cultivation already took place during
628 the Garamantian period in the Central Sahara: a large fraction of the seeds from Zinkekra
629 presented an elongated phenotype typical of domesticated date palms. Nonetheless, the mixed
630 presence of both wild and domesticated morphotypes may be interpreted as an early stage of
631 date palm cultivation, as previously suggested (Van der Veen, 1992; 2010). This may indeed
632 be related to two processes. First, the original germplasm brought to the region may have been
633 early domesticates that still had more or less rounded seeds. Second, sexual reproduction was
634 likely the main mode of propagation at the time, especially at the establishment of the
635 agroecosystem, maintaining a large proportion of wild phenotypes in cultivation, as seen in
636 grapes (Bouby et al., 2013) and other fruit trees (Fuller, 2018).

637 The limited geographic structure of the modern morphotypes posed a challenge for tracking the
638 origin of Libyan shapes, but notable observations can still be made. The most represented
639 morphotype at Zinkekra was the sub-rounded MT4, mostly composed of cultivars from West
640 Asia and Egypt. This may indicate that early cultivated forms originated from the East,
641 corroborating the hypothesis of a diffusion of date palm from the Gulf throughout Egypt and
642 the Sahara (Tengberg, 2012; Gros-Balthazard & Flowers, 2021; Duckworth et al., 2020). More
643 precisely, the diversity from Zinkekra most probably came from close-by Egyptian oases, where
644 phoeniculture was already developed at the time (Sterry and Mattingly, 2020; Tengberg and
645 Newton, 2016). This result is substantiated by the similar morphotype assemblage found at
646 ‘Ayn-Manâwir. In fact, the east-west route linking the Western desert of Egypt (where ‘Ayn-
647 Manâwir is located) and the Fazzan (where Zinkekra is situated) is dated to the late 2nd or early
648 1st mill. BCE (Mattingly, 2017).

649 **An intensification of phoeniculture through time**

650 Our morphometric analyses of seeds spanning three millennia revealed an intensification of
651 phoeniculture through time. This was evidenced by, first, a decrease in the frequency of
652 rounded morphotypes through time in both Libya and Egypt (as seen before, Terral et al., 2012).
653 At Zinkekra, rounded and sub-rounded morphotypes (MT1 to MT4) made up more than 40%
654 of the assemblage, a proportion never met in the other later sites, except at Ghirza but that data
655 set is very small (just eight seeds). It was also the only site with seeds allocated to MT1, a
656 morphotype only made up of wild accessions from the modern reference collection. On the
657 other hand, the medieval site of Thebes Midden/C3 had only 10% of rounded seeds (allocated
658 to MT1 to MT4). Secondly, we observed an elongation of seeds over time. As mentioned above,
659 this may be seen as the result of both increased human selection for bigger fruits and the gradual

660 adoption of elaborated cultivation practices: vegetative propagation over reproduction by seed,
661 and other agricultural techniques such as irrigation (a technology which appeared in the 4th-3rd
662 c. BCE in the region, Wilson et al., 2020). Further, even if the mean was similar, the length
663 distribution in modern varieties exceeded 30 mm which has barely been found in older sites
664 (but see the Judean date palms, Sallon et al., 2020). Also, MT5 and MT6 were absent from the
665 archaeological dataset before the Roman period. These morphotypes are made up of very
666 elongated seeds, such as that of the Tunisian variety Lagou. This probably resulted from a
667 continuous selection for even bigger fruits during the modern period. Finally, the diversification
668 of the morphotypes since the early 1st c. CE also illustrates phoeniculture intensification.
669 Indeed, the influence of the Roman empire may have contributed to an intensification of the
670 exchange across the Mediterranean basin, as shown in the Levantine region (Gros-Balthazard
671 et al., 2021). For example, MT6 and MT11, two morphotypes with a high proportion of North
672 African cultivars, especially Tunisian (e.g. the cultivar Deglet Noor), were absent in Libya and
673 Egypt before the Roman period.

674 **A probable loss of agrobiodiversity through time**

675 While our modern reference collection certainly presents an incomplete picture of the current
676 agrobiodiversity, several lines of evidence suggested a loss of agrobiodiversity over time. More
677 than 40% of Zinkekra seeds were not allocated to *Phoenix dactylifera*, with a quarter to the
678 group composed of wild relative species. We found similar results for the Egyptian site of ‘Ayn
679 Ziyâda, located in the Kharga oasis and dated to approximately the same period. The question
680 of the presence of *Phoenix* in the North of Africa, especially that of *Phoenix theophrasti* has
681 already been raised by Gros-Balthazard and Flowers (2021), although we could not test the
682 presence of the other species present in our reference collection as they could not be
683 discriminated with confidence. We noted that over 10% of modern date palm seeds were
684 mistakenly attributed to wild relative species. Thus, allocation of seeds to the non-*dactylifera*
685 group did not necessarily imply the presence of other *Phoenix* species, as this could also be due
686 to sampling bias, an imperfect modern reference collection and overlapping shapes. In any case,
687 a large portion of ancient seeds do not have modern analogues in our reference collection, which
688 may be due to sampling bias but also to a loss of diversity through time.

689 Even more surprisingly, out of the modern intrusion Lm4 seeds categorized as *P. dactylifera*,
690 only 61% were identified as belonging to a specific morphotype. This suggests that even in the
691 18th-20th c., a significant proportion of seeds do not have counterparts in our modern reference
692 collection. One possible explanation is that the seed morphologies in our collection, which are

693 more distinct and less variable, represent a recent development, indicating a decline in
694 biodiversity resulting from market intensification.

695 **Summary and Conclusion**

696 The use of morphometric methods, especially the Elliptic Fourier Transform, confirmed that
697 the Garamantes of Libya cultivated date palms as part of an oasis agroecosystem during the 1st
698 mill. BCE in the Central Sahara. Among the domesticated morphotypes identified in the Fazzān,
699 there was a prevalence of sub-rounded phenotypes originating from the East, as expected with
700 regards to the date palm diffusion route from its domestication center. The important number
701 of seeds converging towards a wild phenotype argues for an early stage of date palm cultivation
702 in this region. The addition of archaeological seeds from Egypt provided the opportunity to
703 study the dynamics of date palm diversity in North Africa since the end of the 2nd mill. BCE,
704 through a large diversity of historical periods including the Persian, Greco-Roman, Roman,
705 medieval and modern periods. We observe a shift towards elongated and longer seed
706 phenotypes. The oldest sites, Zinkekra and ‘Ayn-Ziyâda, have mainly rounded and sub-rounded
707 seeds, while the sites from the common era present elongated seeds. Over time, farmers may
708 have not only selected date palms producing bigger fruits, they also increasingly have mastered
709 cultivation practices such as vegetative clonal propagation that favor larger fruits, which
710 together may explain the trend. The late appearance of typical North African cultivars in
711 archaeological sites could be the result of the extensive trade connections that developed during
712 the Roman period that have enhanced the dispersion of cultivars east and west. Finally, we also
713 note how phoeniculture may have lost agrobiodiversity in the past few hundred years,
714 reflecting homogenization of date palm cultivars. Our results call for further morphometric
715 studies applied to archaeological material to better understand the date palm’s historical
716 biogeography and the emergence of oasis agriculture elsewhere in Saharan North Africa.

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726 **Author Contributions**

727 MGB and JFT designed the idea and the study; MGB, JFT, SI and TK collected modern
728 reference collection; MVDV identified the archaeological material from Libya, and TK
729 acquired the pictures; MVDV and DJM provided critical information on the Libyan
730 archaeological sites; TK and MGB performed the analyses; TK, MGB and MVDV wrote the
731 article; all the authors revised the manuscript.

732 **Data availability**

733 The data that support the findings of this study are openly available in DataSuds repository
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746 **Supplemental material**

747 Supplemental material for this article is available online.

748 **References**

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