

1 **Plant behaviour from human imprints and the cultivation of wild cereals in**  
2 **Holocene Sahara**

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5 **Depicting plant behaviour through human imprints: the ‘weediness’ of wild**  
6 **cereals and their cultivation in Holocene Sahara**

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19

20 **Abstract**

21 **The human selection of food plants cannot always have been aimed exclusively at isolating the**  
22 **traits typical of domesticated species today. Each phase of global change must have obliged**  
23 **plants and humans to cope with and develop innovative adaptive strategies. Hundreds of**  
24 **thousands of wild cereal seeds from the Holocene “green Sahara” tell a story of cultural**  
25 **trajectories and environmental instability revealing that weediness was a trait preferred by**  
26 **both hunter-gatherers and pastoralists. The archaeobotanical record of Takarkori rockshelter**

27 **in SW Libya covering four millennia of human occupation in the central Sahara gives us a**  
28 **unique insight into long-term plant manipulation and cultivation without domestication. The**  
29 **success of a number of millets was rooted in their invasive-opportunistic behaviour, rewarded**  
30 **during their coexistence with people in Africa. These wild plants were selected for features**  
31 **that were precious in the past but pernicious for agriculture today. Reconnecting past**  
32 **practices with modern farming strategies can help us to seek out the best resources for the**  
33 **future.**

34 Understanding the long-lasting relationship between plants and humans is of crucial importance to  
35 sustainable development, and food is a key determinant of this multifaceted ‘alliance’. Food plants  
36 are a central focus for various disciplines that often postulate a marked dichotomy between wild and  
37 domesticated species as playing different roles in cultural evolution. From this perspective, plant  
38 diversity decreases along an ideal, unilinear, human-controlled axis from resource exploitation to  
39 agricultural management<sup>1 2</sup>. The culmination of this process is the farming of the small number of  
40 domesticated species on which people largely rely for food today<sup>3</sup>. Such crops developed through  
41 human selection of desirable traits; by contrast, most wild plants are thought to have grown  
42 independently of human intentions and aims. Nevertheless, food plants include some minor wild  
43 cereals that, interestingly, present what is known as high ‘weediness’: the ability to thrive in human  
44 environments due to their preference for disturbed soils<sup>4</sup>. Weediness is known to be associated with  
45 a broad set of traits as weedy plants are prolific and the high rates of phenotypic plasticity and  
46 adaptation to agricultural systems, alongside the capacity to act as invaders in natural habitats, often  
47 lead to these plants being relegated to the undesirable ‘weed’ category (but for the definition in this  
48 paper see below, the Methods)<sup>5 6</sup>. Here, based on archaeological data from Saharan Africa, we  
49 present the first evidence that non-agricultural societies actually selected plants for their weediness.  
50 As known by rural and popular traditions, we noted that several wild plants others call ‘weeds’  
51 possess key adaptive characteristics that were strategic during past environmental changes. The  
52 sharp distinction between ‘unusefulness and usefulness’, typically made on ‘crop and non-crop’  
53 organisms by agri-food actors, has no sense by looking at the long-term  
54 archaeological/environmental records. We suggest that these modern concepts are no longer able (or  
55 sufficient) to explain complex or intermediate conditions of the human cultural history such as the

56 *middle ground*<sup>7</sup> between foraging and farming. Yet understanding the plant management of early  
57 foraging societies, when no agricultural system was known or potentially imitable, and when links  
58 between climate, environment and resources were deeply embedded in socio-cultural systems, is  
59 crucial to our knowledge of what happened when no domesticated species were obtained at the end  
60 of the cultivation process. Our archaeobotanical data provides direct evidence of long-lasting plant  
61 management, with wild cereals persistently adapting to both human desires and environmental  
62 changes. The setting is the Holocene “green” Sahara and the period the four millennia from  
63 approximately 7500 to 3500 calBC.

64

65 Numerous plant species have been gathered and manipulated but this has not always resulted in  
66 domestication<sup>8 9</sup>, a fact often explained as a consequence of the environment being sufficiently  
67 starch-protein productive<sup>10</sup> or of plant genetics impeding the isolation of ‘domestic’ traits<sup>3</sup>. Many  
68 partial or abandoned trajectories towards domestication that demonstrate that domestication did not  
69 have a single cause or pattern but was a process with different pathways and species were found<sup>11</sup>.  
70 We can now add that, even when involuntary, selection was not ‘only and always’ directed at  
71 isolating the features now considered typical of domesticated species. In the case of cereals, two  
72 main phenotypic changes occurring with domestication are considered: the large seed size and the  
73 non-shattering rachis<sup>12 13 14</sup>. The selection for these characters is known to have had effects on loss  
74 of seed dormancy, reduced vegetative dispersal by rhizomes and changes in reproductive shoot  
75 architecture<sup>15</sup> but classically these morpho-physiological traits are not detectable in the  
76 archaeological record. We present, therefore, the first diachronic archaeobotanical evidence showing  
77 that the primary quality that attracted hunter-gatherers in Africa seeking the benefits of cultivation –  
78 implying a shift of labour investment to just a few food plant species<sup>16</sup> – must have been the  
79 invasive and opportunistic behaviour of some wild grasses.

80

81 The plant remains discovered at various archaeological sites worldwide testify to millennia  
82 of systematic gathering, previously the early non-domestication cultivation of wild cereals for food  
83 and fodder had been suggested in the Near East<sup>17 18</sup>. Here, we provide evidence for the systematic  
84 gathering, processing and cultivation of wild cereals at a time when the Sahara hosted extensive wet

85 habitats and was covered by a savanna-like vegetation. Highly sophisticated relationships with the  
86 environment are apparent in many sites of the mountainous central Saharan regions<sup>19</sup>. Takarkori  
87 rockshelter lies on the first terrace of the Wadi Takarkori in the southern Tadrart Acacus (Libya),  
88 about 100m above the wadi bed (**Figure 1a**). Hence, wild cereal stands were not available in the  
89 immediate vicinity of the site but in the river plain, which also offered other plant foods besides  
90 game and fish. The first occupation of Takarkori by Late Acacus hunter-gatherers started at c. 8200  
91 calBC lasting until 6400 calBC. Later, Saharan Pastoral Neolithic groups introduced domestic  
92 animals and used the site until c. 3000 calBC<sup>20 21</sup>. The deposit comprises an impressive quantity of  
93 plant remains with excellent and prevalently dried preservation indicative of limited microbial  
94 degradation activity. This exceptional feature also characterizes other sites in the area<sup>22</sup> and in the  
95 Sahara more generally. Human groups at Takarkori had sophisticated subsistence strategies,  
96 corralling Barbary sheep<sup>23</sup>, exploiting dairy products and cooking vegetables and the site also offers  
97 astounding evidence of the human ability to make art and weave fibres<sup>24 25 26 27</sup>. We now report the  
98 unique evidence of plant accumulations from the site, where loose wild cereals were clearly visible  
99 on the archaeological surfaces. These accumulations consist of thousands of grass florets/spikelets  
100 concentrated on top of the organic sand layers, and distributed around a few different sectors of the  
101 site (**Figure 1b,c,d**). The accumulations are evidence of different episodes of plant processing and  
102 food plant storage during the period c. 7500-3500 calBC (**Figure 2**). They attest the presence of a  
103 good diversity of wild cereals in the past, though most of these species are now locally extinct in the  
104 central Sahara<sup>28 29</sup>.

105

106

## 107 **Results**

108

109 *Wild cereals accumulated in the site* - We identified 30 accumulations of dried seeds clearly visible  
110 on the organic sand layers uncovered during fieldwork (**Table 1**). As this record consists largely of  
111 wild cereals, the Takarkori seed accumulations are consistent with direct evidence of food at the site,  
112 though their use for fodder, and possibly bedding, cannot be discounted.

113 Based on their morphological features, these plant remains are attributed to *Brachiaria* (including *B.*

114 cf. *leersioides*-Blue signal grass), *Bromus* cf., *Cenchrus* (including *C.biflorus*-Kram kram, and  
115 *C.ciliaris*-African foxtail grass), *Dactyloctenium* (*D. aegyptium*-Crowfoot grass), *Digitaria*,  
116 *Echinochloa*, *Panicum*, *Pennisetum* (*P. cf. purpureum*-Elephant grass), *Setaria*, *Sorghum*, *Tragus*  
117 cf., *Urochloa* (*U. cf. panicoides*-Liverseed), and to undifferentiated Andropogoneae. Combined  
118 morphological analysis and ancient DNA extraction made it possible to identify *Panicum laetum*  
119 (Wild fonio, or desert panic), *Echinochloa colona* (Awnless barnyard grass, or Jungle rice) and  
120 *Sorghum bicolor* subsp. *verticilliflorum* (Wild Sudan grass) (for identification see Methods).  
121 Whole spikelets (grain enclosed by lemma and palea) are the most common records; spikelets  
122 consisting of the persistent papery tissues of external glumes (upper and lower glumes) and the  
123 smooth to verrucate inner glumes (lemma and palea) are found in some accumulations. Since  
124 *Brachiaria* and *Urochloa* inter-hybridize, the boundary between the two genera is sometimes  
125 unclear and a variable number of intermediate phenotypic stages (from *quasi*-awnless to mucronate  
126 tip spikelets) were observed, suggesting that large stands hosted mixed populations.  
127 In the accumulations studied here, *Pennisetum* mainly takes the form of involucre of soft and  
128 plumose sessile bristles, and *Cenchrus* of the spiny involucre fused at the base. Alongside the  
129 fertile spikelets we observed sterile or immature spikelets of *Pennisetum* and *Sorghum*, both  
130 presenting the typical morphology of the wild species. The sorghum has hulled spikelets with the  
131 shattering wild type of spikelet basis, and its immature florets/spikelets are flattened and sometimes  
132 with persistent rachillae, probably reflecting the ripening variability of the panicle (see SEM images  
133 in **Supplementary Material 1**).

134 Variable amounts of non-grass fruits/seeds include *Ficus*, *Ziziphus* cf., Cyperaceae, *Persicaria* and a  
135 few others (Asteraceae, Amaranthaceae, Apiaceae, and *Colocynthis*). Given the nature of the  
136 archaeological deposit, mostly organic sands<sup>19</sup>, the seed accumulations also comprise small  
137 amounts of stems (grasses and sedges), leaves and charcoal fragments, a few undetermined flowers  
138 and charred plant remains.

139

140 *The 'spot' vs 'mix' wild cereal accumulations* - The ratio of whole to fragmented plant remains  
141 allowed us to statistically distinguish between 'spot' (>5; **Figure 1c**) and 'mix' (<2; **Figure 1d**)  
142 accumulations (see Methods, and **Table 1**).

143 'Spot' accumulations prevalently consist of whole spikelets without external glumes of the  
144 millets listed above. This may result from threshing and winnowing, which removed a number of  
145 by-products after millet harvesting<sup>30</sup>. By-products such as unripe grains, de-grained ears, plant stalks  
146 and rachis, leaves, spike parts and isolated glumes are fairly insignificant in 'spot' accumulations.  
147 Winnowing by shaking, possibly with the help of baskets<sup>25</sup>, is the most plausible method given the  
148 limited space of the rockshelter terrace. The spikelets are unusually uniform in size (*Panicum* and  
149 *Echinochloa*:  $\sim 2.1 \pm 0.1$  mm length; *Sorghum*:  $\sim 6.4 \pm 0.4$  mm; see plots in **Supplementary Material**  
150 **2**), probably as an effect of sieving, a common procedure in the processing of millets<sup>31</sup>. The cleaned  
151 spikelets were stored for consumption. Overall, this evidence is insufficient to tell us whether these  
152 seeds were eaten directly in the form of porridge<sup>27</sup>, stored without further processing for later  
153 consumption or kept until the next season for seeding.

154 'Spots' were found both in a Late Acacus stone hut dated to approximately 7000 calBC (ID 8 and  
155 10, respectively *Sorghum*/Cyperaceae and *Urochloa/Brachiaria*) and in a cluster of the Middle  
156 Pastoral period (ID 13-18 and 20-22). Spatial analysis (**Figure 1b**) and study of the radiocarbon  
157 dates of these specimens suggest that almost all the MP 'spots' may belong to a single storage  
158 facility dated to c. 4500 calBC (4546 <95.4%> 4463 calBC; **Figure 2**). Furthermore, the absence  
159 among the spot materials of remains of ants, which are capable of moving seeds, allows us to rule  
160 out the idea that these insects were responsible for these seed accumulations. Considering all the  
161 data, this type of accumulation can be interpreted as a residual form of *low-level storage*. This term  
162 was used for purpose-built granaries in an early Holocene pre-domestication context of the Jordan  
163 Valley, which support the idea of a deliberate cultivation of wild cereals<sup>32</sup>. In our case, probably,  
164 this storage was made possible by the fact that most of these wild cereals exhibit strong seed  
165 dormancy, and would thus not have germinated until the following season (late spring and summer  
166 in the case of Liverseed and Jungle rice).

167

168 The 'mix' accumulations consist substantially or prevalently of plant fragments and glumes,  
169 and are more ambiguous: depending on the archaeology and chronology, they may be *food-*  
170 *processing waste* or *fodder residues* (as in the case of stable floors). The morphology and  
171 fragmentation of the soft parts, and the general archaeological context, provide a better

172 understanding of the nature of ‘mix’ accumulations. For example, the most recent samples are richer  
173 of isolated glumes (e.g., *Dactyloctenium*), accompanied by other cereal chaff and straw, and may be  
174 remains of fodder. Focusing specifically on the ‘mix’ with food processing residues, as the hulled  
175 cereals need dehusking, we found in our record numerous split spikelets with opened external and  
176 inner glumes, a number of glumes representing plant processing by-products<sup>30 31</sup>, and some charred  
177 seeds as refuse from burning activities at the site (**Figure 3**).

178 In total, the ‘spots’ contained ~150,000 seeds, almost all attributable to the MP1 pastoralists  
179 and LA3 hunter-gatherers (71% and 16% of the total seeds in the ‘spots’, respectively), while the  
180 ‘mix’ accumulations with ~80,000 seeds belonged to the MP2-MP2/LP1 pastoralists (85% of the  
181 total seeds in the ‘mix’) and to the LA2 hunter-gatherers (5%) (**Table 1**). ‘Spot’ accumulations  
182 suggest the excess from a prevalent gathering activity while the ‘mix’ type seems to originate from  
183 the mixed refuse produced by plant processing and animal breeding.

184

185 *Late Acacus vs Pastoral wild cereal accumulations* - In a diachronic perspective (**Figure 4**), the data  
186 indicates a major botanical change in the passage from the hunting-gathering Late Acacus phases  
187 (12 items from c. 7300 to c. 6400 calBC) to the Middle and Late Pastoral phases (11 items from c.  
188 4850 to c. 3970 calBC; 7 items from c. 3970 to c. 3500 calBC). No accumulation of seeds is  
189 recorded from the Early Pastoral phase, probably for taphonomic reasons since these layers suffered  
190 heavy erosion in the site<sup>19</sup>.

191 Within the Late Acacus, about ~ 800-1600 cereal seeds, with some remains of woody fruit  
192 plants such as *Ficus* and *Ziziphus* cf., and one ‘spot’ of ~ 17,000 *Setaria* seeds were found in the  
193 earliest five LA2 accumulations, dated c. 7500-7100 calBC. Concentrations generally increase (up  
194 to ~10,000 cereal seeds) in the seven LA3 accumulations, dated c. 7100-6400 calBC. At this point,  
195 the focus of hunter-gatherers seems to have shifted from the earlier group of cereals (*Pennisetum*,  
196 *Sorghum* and other Andropogoneae, and to a lesser extent *Panicum* and *Cenchrus*) towards the  
197 tufted annual *Urochloa*-Liverseed, perhaps for a combination of cultural and ecological reasons (see  
198 below).

199 Within the Pastoral Neolithic, relatively higher seed concentrations (~1500-45,000 seeds) are  
200 evident in the ‘spots’ of the earliest ten MP1 accumulations, dated c. 4800-4300 calBC. A new

201 cereal, *Echinochloa*, appears and immediately becomes abundant and recurrent in the record.  
202 Meanwhile, *Urochloa* continues to be common and sometimes prevalent (65-85% in 4 spots; **Table**  
203 **1**); *Panicum* and *Setaria* also seem to have been intensively exploited at this time. Although about  
204 two thousand years of cultural developments and critical environmental changes<sup>33 34</sup> separate these  
205 MP1 samples from those of the LA3 phase, the long-term continuity of the botanical discoveries  
206 made by previous hunting-gathering inhabitants is apparent. This can only be explained by the  
207 synergy between the adaptive behaviour of some wild cereals and perhaps by cultural transmission  
208 from generation to generation. Jungle rice, which probably did not grow in the area before, is a new  
209 arrival among the previous cereals. The archaeobotanical diagram (**Figure 4**) suggests that  
210 pastoralists brought Jungle rice with them and managed this plant alongside the various other millets  
211 already living in the area. The attention to this plant increased while the importance of Liverseed  
212 decreased and the plant almost disappeared from the MP2 and MP2/LP1 records.  
213

214

## 215 **Discussion**

216

### 217 *Plant processing at the site*

218 The whole spikelets and variable amounts of by-products in ‘spot’ and ‘mix’ accumulations reflect  
219 the different plant management and processing activities taking place at the site. Consistency  
220 between the botanical evidence and the archaeological contexts – mostly spatial and chronological  
221 data – supports the idea that this type of archaeobotanical record is a strong cultural marker for  
222 Saharan societies.

223 According to ethnographic information<sup>18 31</sup>, dispersed fruits fallen from wild plants such as  
224 *Pennisetum*, *Cenchrus* and *Echinochloa* may have been collected from the ground. Open baskets  
225 might have been used to gather seeds, as suggested by the large quantity of basketry fragments,  
226 including some that preserve trapped grains (*Pennisetum*, *Brachiaria*, *Dactyloctenium*), unearthed at  
227 Takarkori<sup>25</sup> and other sites in the region<sup>35 36</sup>. Thanks to the plant accumulations we now know that  
228 cereals were processed at the site, and that selected seeds were probably stored after threshing,  
229 winnowing and sieving. The preferential location of ‘spot’ accumulations in stone huts as can be



230 seen in the northern sector of the site (**Figure 1b**), indicates a long occupation by the last Late  
231 Acacus hunter-gatherers focusing on abundant and predictable - albeit seasonal - plant resources.  
232 Our data show that they particularly harvested and transported Andropogoneae to be processed at  
233 the site for about 500 years.

234 *A low-level storage phase is evidenced by the spots accumulated after c. 7200-6700 calBC*  
235 *(from ID 7, Panicoideae 57% with predominance of whole spikelets). This early storage seems to*  
236 *anticipate the ‘change’ from Andropogoneae (*Pennisetum*, *Sorghum*) to Paniceae (*Urochloa*), with a*  
237 *transition dating, in our record, to c. 7000-6600 calBC (from ID 8 to 9). The *Sorghum bicolor**  
238 *species includes the cultivated tropical grasses with the most ancient history of plant management in*  
239 *Saharan Africa<sup>37 38</sup>. Based on our record, we argue that sorghum was present but not widespread in*  
240 *the area, or alternatively that it grew far from the site, probably in mixed plots (e.g. with fonios<sup>39</sup>),*  
241 *and that the species was vulnerable to environmental instability. The spot of sorghum (72%, ID 8)*  
242 *also contains a significant amount of small-seed Cyperaceae (11%), perhaps an unwanted weed*  
243 *collected with the food plant when the stem was cut. This special ‘spot’ suggests that gatherers not*  
244 *only stored sorghum seeds for consumption but also for possible seeding in the subsequent season.*  
245 *If this was for cultivation it appears to have failed, because sorghum did not spread so much to be*  
246 *recorded in other subsequent spots (**Figure 4**). Today, *S. bicolor* (subsp. *bicolor*) is considered a*  
247 *competitive crop but the species is actually less invasive than weeds like Johnson grass (*Sorghum**  
248 **halepense* (L.) Pers.) and several millets. The presence of the prolific weed *Urochloa panicoides*, for*  
249 *example, was found to reduce sorghum yields by 25-40% in modern uncontrolled farms<sup>40</sup>. In the*  
250 *early Holocene Sahara, although sorghum produced larger seeds than other wild cereals, the weedy*  
251 *Liverseed, with its high seed productivity, clearly offered greater advantages to people. Humans*  
252 *therefore shifted from preferable cereals with larger seeds (sorghum, **Figure 3**) to the most invasive*  
253 *species (Liverseed), which in turn benefitted from anthropochory, or human dissemination.*

254

#### 255 *The adaptive behaviour of Jungle rice*

256 Archaeobotany suggests that a new influx of useful plants arrived at the site with Neolithic  
257 Pastoralists at around 4800 calBC (**Figure 4**). Less drought-tolerant than the sorghum of the Late  
258 Acacus phases, *Echinochloa* expanded in the area probably also favoured by a middle Holocene wet

259 and warm phase. At this time, the Sahara saw the development of wadi vegetation and semi-arid  
260 seasonal savanna with fragmented habitats and high lake levels in this area<sup>20 29</sup>. After a Neolithic  
261 MP1 phase of coexistence with *Urochloa* (*U. panicoides*), Jungle rice prevailed over the resident  
262 Liverseed during the MP2 (c. 4200-3900 calBC) and MP2/LP1 transition (c. 3970-3760 calBC), a  
263 time of great environmental instability in the central Sahara<sup>41</sup>.  
264 *Echinochloa colona* adapts easily to changing habitats in terms of soil water status<sup>42</sup> and  
265 competitiveness, and forms monotypic stands. These cause a decrease of plant species richness with  
266 the increase of river distance and grazing intensity<sup>43</sup>. The rise of records like *Dactyloctenium* during  
267 the Pastoral phases may represent an indicator of an early phase of overgrazing already suggested by  
268 pollen analyses<sup>20</sup>. Specifically, the intensive removal of plant biomass and trampling by small  
269 livestock – mostly ovicaprines – led to the establishment of fast-growing opportunistic species that  
270 expanded rapidly into native plant communities and vulnerable wetlands<sup>44</sup>. In this sense, these wild  
271 plants reacted as the *dump-heap* weeds associated with human-disturbed habitats that are thought to  
272 have thrived close to pre-agricultural dwellings<sup>45</sup> (but the weedy origin of the domesticated major  
273 crops in the Near East is debated<sup>46</sup>). In our record, where we have weeds without domesticate  
274 species, the behaviour of Jungle rice may be only partly explained by its opportunistic-invasive  
275 nature. Our data suggest that in the competition between two weedy and very similar plants  
276 (*Echinochloa* vs. *Urochloa*), Jungle rice was also favoured by human cultivation.

277

#### 278 *Cultivation without domestication in the central Sahara*

279 The evidence for the long-term manipulation of wild cereals raises the question of which  
280 traits were attractive to both gatherers and pastoralists, and how people continued to ensure good  
281 yields across the early to middle Holocene environmental changes. Despite differences in the  
282 subsistence basis of these peoples, our archaeobotanical record is evidence that some wild cereals  
283 (*Urochloa*, but also *Panicum* and *Cenchrus*) were continuously managed for four millennia, with  
284 systematic gathering and processing, possibly shifting towards some forms of cultivation more than  
285 once.  
286 Cultivation before domestication has been inferred from the presence of species outside their current  
287 natural habitats, the distance of natural plots from sites, overexploitation, the import of seeds and

288 climate changes (see <sup>9</sup> for example the Middle Euphrates). Many of these elements are in agreement  
289 with our story of wild cereals managed for millennia in the Sahara. But the Takarkori record  
290 includes all wild plants and thus points to *cultivation without domestication* with anthropic pressure  
291 forcing slight modifications in the seed morphology of *Panicum*, which became plumper, and  
292 *Echinochloa*, which became more elongate (**Figure 5**). The shape changes in our record can be  
293 regarded as “a directional change under selection by early cultivation practices”<sup>15</sup>. In Syria, minimal  
294 changes in seed size suggested the use of plump-grained wild cereals (e.g. wild einkorn), favoured  
295 by cultivation without domestication<sup>9</sup>. Such changes are thought to precede the increase in seed size  
296 during the domestication process<sup>47 48</sup>. However, the Saharan pathway seems to have been quite  
297 different from that taken by the ancestors of major crops in the Near East and elsewhere. For  
298 example, in eastern China, c. 4000calBC, plumper and longer grains were found which reflect  
299 significant morphological shifts likely due “towards harvesting of mature panicles as opposed to  
300 immature panicles”<sup>38</sup>. In Africa, the wild progenitors of pearl millet<sup>47</sup>, t’ef<sup>48</sup> and African rice<sup>49</sup> have  
301 smaller grains than the domesticated species, and selection for higher grain numbers (a feature  
302 common in wild species having more seeds in individual spikes) seems to have been one major trait  
303 isolated in the domestication of pearl millet and t’ef. However, our data show a path of four  
304 millennia that did not end with domestication as the species we identified are still largely reported as  
305 no-crop and weedy plants today (see **Supplementary Material 3** for a list of citations in the  
306 scientific literature).

307         Aside from the aforementioned spot of *Sorghum* (ID8), the involuntary harvesting of ‘weeds’  
308 among gathered food plants – found in cultivation practices in the Near East - is difficult to detect in  
309 our record. Moreover, the small gathered seeds like Cyperaceae and wild grasses (Poaceae indiff. in  
310 the **Figure 4**) do not present a clear trend in the diagram. This again points to a selection of ‘special  
311 traits’ in these African plants. First, it may have been the weediness of the wild grasses growing in  
312 the area (the ID1 to 12 accumulated by the LA2 and LA3), and then the increasing attention towards  
313 the collection of mature seeds (*Panicum laetum*) and panicles richer of seeds (*Echinochloa colona*),  
314 which slowly directed some of the wild cereals towards a pre-domesticate form under cultivation. In  
315 this area of central Sahara, the long process from gathering to cultivation prepared these two species

316 in a pre-domesticate state, but the route seems to have continued (or was paralleled) elsewhere only  
317 for *E. colona*.

318

319

### 320 *The dual nature of wild cereals*

321 With few exceptions, the grasses we found in the Takarkori record are often described as  
322 aggressive colonizers, invaders, segetal, ruderal, sometimes mimic, weeds, and generalists growing  
323 wild in a broad range of habitats from swamps to open grasslands to semi-desert habitats. Many are  
324 annual species producing more seeds than perennials, and summer crops. Since they are drought-  
325 tolerant and withstand heavy grazing, they are currently widely cultivated as food or forage grasses  
326 in tropical areas (e.g. *Brachiaria* and *Urochloa*<sup>50</sup>, and **Supplementary Material 3**).

327 Our plant accumulations demonstrate that some Panicoideae (first *Pennisetum*, *Setaria* and  
328 *Sorghum*, then *Brachiaria/Urochloa* with *Panicum*, and *Echinochloa*) were continuously gathered  
329 as food for millennia. They were managed, and even actively propagated by seeding, so many of  
330 them survived environmental changes and lived in the area until desertification and water loss  
331 definitively limited their growth starting from c. 3500 calBC<sup>22</sup>.

332 Interestingly, in Eastern China, wild *Echinochloa* was gathered and processed with grinding stones,  
333 and it is thought that in this way it came to be an agricultural weed of cultivated rice meanwhile  
334 Asian rice begun its history of domesticated cereal<sup>51</sup>. In absence of any domesticated crop, our  
335 African records show that *Echinochloa colona* was cultivated in association with *Panicum laetum*  
336 among the others. Therefore, early cultivation may have comprised a varied mixture of small-  
337 grained seeds of millets that played an important role in human dietary starch-protein intake. They  
338 are plants with high nutritional value that guaranteed the food supply thanks to both their natural  
339 reproductive cycles and adaptation to human management/pressure. High-value Panicoideae species  
340 seem to have spread easily by moving into newly-created human environments<sup>14</sup>. Abundance and  
341 predictability were important factors in their evolutionary success, as the weedy traits were selected  
342 and appreciated first by early Holocene foragers for their food security and culinary practices, and  
343 later by Neolithic herders<sup>27</sup>.

344

345

346 *The selection of weediness*

347           The Late Acacus hunter-gatherers settled near the large stands to obtain large amount of  
348 seeds with low costs; the pastoralists continued this tradition, harvested larger quantities of mature  
349 grains and did not select only the 'large and non-shattering' seeds. Speaking about a 'process' and not  
350 'an event'<sup>15</sup>, our data show that the selection of weediness has continued during the transition from  
351 gathering to farming (**Figure 4**), and did not result in the domestication of all the  
352 plants cultivated for millennia. Humans selected invasive and opportunistic behaviours before  
353 morphological traits of some grasses. This is evident in the archaeobotanical record that shows, with  
354 overlapping, the trend from gathering under prevalently natural selection to the cultivation under  
355 both human and natural selections<sup>52</sup> (from ID 1-12 to ID 13-30, respectively). The selection of rapid  
356 growth and resilience (mainly *Urochloa* in our record) seems to have been a more conscious early  
357 action than the subsequent involuntary selection for the richest panicles searching for abundant  
358 grains (that caused the elongation of our *Echinochloa* spikelets). People selected weediness because  
359 it was an easier way to grow plants – and we suggest that this might be seen as a cultural decision.  
360 By this process the selected plants were rewarded as they improved fitness, and we argue that  
361 humans as any stressor elicited the biological reply of these weeds.

362           Efficient dispersal mechanisms, seed dormancy, and phenotypically plastic genotypes are  
363 common traits in the weed syndrome rooted in their capacity for rapid adaptation to environmental  
364 changes<sup>53</sup>. Interestingly, some wild cereals such as fonios are considered semi-domesticated species  
365 that have lost their efficient natural seed dispersal, an essential step towards domestication. These  
366 plants present advantageous adaptations for cultivation, as they are able to grow with other crops  
367 and also highly competitive with weeds<sup>39</sup> in subsistence agro-ecosystems. Although each weed  
368 species may have a diverse and unique history, our data suggest revising some common opinions on  
369 these invasive field weeds. Specifically, we argue that: a) the selection of large natural stands should  
370 not have been a form of low-skilled pre-cultivation but a genuine human strategy based on the  
371 presence of opportunistic-invasive behaviour of some grasses; b) these species were the direct object  
372 of long-term human manipulation and not ancillary plants that spread *after* crops; and c) weedy  
373 millets have sometimes had some behaviours (including the aptitude to mimicry) that, according to  
374 our data, make them pre-adapted in order to spread with domestic crops and this may have been  
375 effect of long-time human pressure on wild species. From a co-evolutionary perspective<sup>1</sup>, people  
376 selected for weediness - including abundance and predictability - as the most important feature of  
377 these wild cereals, thus ensuring that both plants and humans adapted successfully to environmental

378 crises. The cultivation system, often regarded as beneficial only to humans, also proved highly  
379 advantageous to some ‘special’ wild plants.

380

381 *Reconnecting past and future*

382 Weediness must have been a desirable trait in ancient times, and wild cereals actually present  
383 both wild (weed) and cultivated (crop) behaviours and characteristics. Our genera of millets include  
384 species that have been domesticated in parallel numerous times. We argue that their tendency to  
385 evolve as crops is probably rooted in the very long history of manipulation and management the  
386 record of Takarkori shows for the African route. We agree with Viguera et alii<sup>53</sup> that our weeds  
387 “*compose a unique evolutionary state, neither wild nor domesticated, that has developed in parallel*  
388 *to crop domestication*”. Signs of selection for lost-value traits are hard to be recognized today but it  
389 is probable that there were not ‘aborted trajectories’ as millennia of sophisticated plant management  
390 should have had consequences on plants as well as on humans. The opportunistic behaviour of these  
391 wild cereals favoured their development in unstable environments while the human pressure did not  
392 cause severe limits<sup>11</sup> on the chances of their autonomous survival. Today, as wild cereals are  
393 typically adapted to exploit the newly available (disturbed) habitats offered by humans<sup>54</sup>, we should  
394 change our view of such weeds. The same behaviour that allowed these plants to survive in a  
395 changing environment in a remote past makes them some of the most interesting staple resources for  
396 a future of global warming. They continue to be successfully exploited and cultivated in Africa  
397 today and are attracting the interest of scientists searching for new food resources. Our research  
398 suggests that, like modern gatherers, we should pay renewed attention to these plants in the hope of  
399 finding innovative responses to tackle desertification and biodiversity loss.

400

## 401 **Methods**

402

### 403 **Definition of the term ‘weediness’ and main traits of our weeds**

404 The term “weed” has been variously defined, depending on the different perspectives of ecologists,  
405 agronomists, archaeobotanists and the public, and we do not know a definition that has met a  
406 universal agreement<sup>55</sup> (see **Supplementary Material 3**).

407 The ‘weediness’ described in this research on the Saharan prehistoric landscape, at times of wild  
408 plants, requires a definition of the term in an ecological perspective. Weeds possess many adaptive  
409 strategies to survive such as the phenotypic plasticity (i.e., the ability of an organism to express  
410 different phenotypes depending on the biotic or abiotic environment<sup>56</sup>), the abundant seed  
411 production, the prolonged viability of propagules with dormancy (so as to survive under  
412 unfavourable conditions), the ability to a fast reproduction and to growth after seedling, the spread at  
413 a high rate, the high tolerance to environmental heterogeneity and to changes in environmental  
414 conditions, the strong interspecific competition and resilience. Weeds are part of a dynamic  
415 ecosystem<sup>57</sup> and all these traits make these weeds ideal for easy proliferation. Our weeds include  
416 invasive and opportunistic species.

417 The term ‘invasive’ is often used to indicate these plants (problematic today) as “they can  
418 successfully establish and spread following introduction into novel, often non-managed areas”<sup>55</sup>.

419 The authors of the previous definition reported also that “invasives are considered weeds in the  
420 broadest sense of the term; some authors prefer to use the designation ‘weed’ only for problematic  
421 plants in agriculture, and reserve the term ‘invasive’ to indicate problematic plants growing in non-  
422 managed or wild areas”<sup>55</sup>. Moreover, the species we identified in our archaeobotanical record are  
423 characterised by “opportunistic behaviour”. In ecology, an opportunistic plant can thrive in different  
424 conditions, and rapidly takes advantage of environmental changes because the species is  
425 behaviourally flexible.

426

### 427 **Excavation and sampling**

428 Takarkori was excavated entirely by hand, using small trowels. The plant accumulations were  
429 identified by sight, mapped using an Electronic Total Station (ETS) and removed. The samples were  
430 then gently dry-sieved with a 0.6 mm screen in the laboratory, and the residue was examined to  
431 check for smaller parts (seeds were not found). Direct radiocarbon datings of each plant  
432 accumulation placed them in a chronological trend from the hunter-gatherer (Late Acacus: LA2,

433 LA3) to Pastoral Neolithic phases (Middle and Late Pastoral: MP1, MP2, MP2/LP1), known for the  
434 stratigraphy of the site and the Tadrart Acacus region<sup>19 58</sup> (see Table 1, with archaeological phases  
435 and calibrated ages<sup>59</sup>; Figure 2). Stereomicroscope examination showed that the plant accumulations  
436 consisted largely of dried yellow to brown spikelets of Panicoideae with a few other plant taxa  
437 dispersed in the residual sand. These accumulations are consistent with one or a few plants entering  
438 the archaeological deposit contemporaneously.

439 Entomological analyses demonstrated that insects played no role in transporting plant parts into the  
440 site. Insect search was carried out on 13 samples: seven spots (ID 2, 9, 10, 12, 17, 20, 25), one mix  
441 (ID 30), and five samples of soils external to the plant accumulations but belonging to the same  
442 stratigraphic unit and used as controls. The search was performed using a stereomicroscope and  
443 every arthropod fragment was isolated using micro-paintbrushes and identify at the lowest  
444 taxonomic level. In all the samples fragments of spider beetles (Coleoptera, Ptinidae) and of  
445 migratory locusts (Orthoptera, Acrididae) were detected. Few fragments (mainly heads) of ants  
446 (Hymenoptera, Formicidae) were found only in the control samples, whereas among the plant  
447 accumulation material no ant fragments were identified.

448

#### 449 **Taxa identification and morphometry**

450 The botanical finds were hand-sorted and morphologically identified by observation under an  
451 Olympus SZ60 stereomicroscope at 40x-80x magnification, with the help of the specialized  
452 literature<sup>60 61 62 63 64 65 66</sup>. From each plant accumulation, whole spikelets of *Panicum laetum* Kunth,  
453 *Echinochloa colona* (L.) Link. and *Sorghum bicolor* (L.) Moench subsp. *verticilliflorum* (Steud.) de  
454 Wet ex Wiersema & J. Dahlb. - syn. *S. arundinaceum* (Desv.) Stapf - were extracted under the  
455 stereomicroscope. The main morphological and morphometrical characters, on fertile, mature and  
456 intact spikelets, are:

457

458 *P. laetum*: elliptic shape with pointed ends; bright spikelets, brown to reddish, with nuances of  
459 orange; fine longitudinal linear striations on lemma and palea; lemma: concave, lateral edges folded  
460 on the palea, 5-7 longitudinal veins are clearer than others; palea: almost flat, with two longitudinal  
461 veins more clear. The species is native to tropical Africa, and it has considerable importance in areas



462 of marginal subsistence where it is often consumed as a famine food. Measurements on 690  
463 specimens:  $2.01 \pm 0.09$  mm (length) x  $1.23 \pm 0.10$  mm (width) x  $0.90 \pm 0.08$  mm (thickness).  
464 *E. colona*: elliptic to oblong shape; notched apex (three points, the central one is thicker and longer  
465 than the others), curved downwards; awnless, shiny spikelets, yellow to light brown; fine  
466 longitudinal linear striations on lemma and palea; lemma: concave, lateral edges folded on the palea,  
467 five longitudinal veins with three veins more evident than the others, and the middle one slightly  
468 larger; palea: flat. The species is hexaploid, native to several regions including Africa<sup>67</sup>, and the wild  
469 progenitor of *Echinochloa frumentacea* Link (syn. *E. colona* var. *frumentacea* (Link.) Ridl; sawa  
470 millet or Indian barnyard millet)<sup>68 69</sup>. The close DNA affinity between the two species is supported  
471 by their cross-compatibility<sup>70</sup>. Although, phylogenetic relationships within *Echinochloa* species are  
472 not fully understood, the ploidy differences between wild and crop species suggest that gene flow  
473 from cultivars have not a role in the weed's evolution<sup>53</sup>. Measurements on 750 specimens:  $2.11 \pm$   
474  $0.13$  mm (length) x  $1.32 \pm 0.09$  mm (width) x  $0.88 \pm 0.10$  mm (thickness).

475 *S. bicolor* subsp. *verticilliflorum*: lanceolate shape; pointed apex (often covered with fine hairs,  
476 especially on the rachilla attachment point); shiny spikelets, dark brown with reddish hues; lemma:  
477 widely convex, without streaks, lateral edges folded on the palea; palea: convex; without streaks.  
478 The species is diploid, or tetraploid, native to Africa, and is the wild progenitor of *S. bicolor* subsp.  
479 *bicolor* (domesticated grain sorghum)<sup>71</sup>. Measurements on 100 specimens:  $6.41 \pm 0.35$  mm (length)  
480 x  $2.33 \pm 0.14$  mm (width) x  $2.35 \pm 0.17$  mm (thickness).

481

482 Photos of the spikelets in dorsal and lateral view were taken using the Leica MC170 HD camera  
483 connected to the stereomicroscope, maintaining constant parameters (default options for white  
484 background), and the magnification of the stereoscope (9.0x) (Figure 3). The length, width and  
485 thickness of each spikelet were measured using the software package Leica Application Suite - LAS  
486 EZ version 3.0.0 (Leica Microsystems).

487 These identifications were supported by molecular analyses. Ancient DNA was successfully  
488 recovered from the spikelets of *Panicum*, *Echinochloa* and *Sorghum*, allowing for the Polymerase  
489 Chain Reaction (PCR) amplification and sequencing of the barcode regions used for the taxonomic  
490 determination. Chloroplast marker *rbcL* provided the identification of the three genera. The DNA

491 barcode sequence obtained from *Echinochloa* matched with maximum identity value (99%) seven  
492 samples in GenBank: the five accessions identified as *E. colona*, one accession of *E. frumentacea*  
493 [(Roxb.) Link] and one accession of *E. ugandensis* (Snowden & Hubbard). Moreover, the multi-  
494 locus approach (*rbcL*, *matK*, *trnH-psbA* and *trnL* markers) allowed for the species identification of  
495 *Panicum laetum*<sup>72 73</sup>.

496

### 497 **Spikelet number estimations**

498 All the specimens in the accumulations of  $\leq 15$  ml were counted (ID 5, 9, 11, 13, 14, 15, 16, 20, 23,  
499 24, 25, 27, and 28). To estimate the total number of macroremains in the other twenty-one  
500 accumulations, three separate 2, 4, 10 ml sub-samples were taken from each accumulation. The  
501 number of specimens in each sub-sample was used to compute the average number providing  
502 estimates according to the total volume. To account for differences in the counts, the weighted  
503 average and the absolute error were calculated for the final estimate in the total volume as shown in  
504 Table 1. The number of seeds in the 30 plant accumulations was used to calculate the total number  
505 of seeds in each cultural phase and in the archaeobotanical record.

506

507 The number of broken spikelets was recovered by a visual validation according to the known size  
508 and morphology of the whole spikelet<sup>74</sup>. A spikelet was determined by a lemma-palea association, or  
509 by 3-8 fragments depending on their size. The amount of spikelets recovered by inspecting the  
510 broken parts of *Brachiaria*, *Urochloa*, *Panicum*, *Echinochloa*, *Digitaria*, *Dactyloctenium* and  
511 *Setaria* was used to calculate the percentage ratio of whole to fragmented spikelets in each plant  
512 accumulation. This ratio was helpful in describing what was evident on visual examination, i.e. the  
513 different status of plant accumulations with prevalent whole spikelets ('spots') and those with  
514 prevalent chaff and processing by-products ('mix').

515

### 516 **References**

517

518 1. Zeder, M.A. Core questions in domestication research. *P. Natl. Acad. Sci. USA* **112**, 3191–3198  
519 (2015).

- 520 2. García-Granero, J.J., Urem-Kotsou, D., Bogaard, A. & Kotsos, S. Cooking plant foods in the  
521 northern Aegean: Microbotanical evidence from Neolithic Stavroupoli (Thessaloniki, Greece).  
522 *Quatern. Int.* doi.org/10.1016/j.quaint.2017.04.007 (2017).
- 523 3. Diamond, J. Evolution, consequences and future of plant and animal domestication. *Nature* **418**,  
524 **700–707** (2002).
- 525 4. Cox, S. in *Plant Breeding and Farmer Participation* (eds Ceccarelli, E. P. G. S. & Weltzien, E.)  
526 **1–26** (Rome, Italy: FAO, 2009).
- 527 5. Baucom, R. S. & Holt, J. S. Weeds of agricultural importance: bridging the gap between  
528 evolutionary ecology and crop and weed science. *New Phytol.* **184**, **741–743** (2009).
- 529 6. Kuester, A., Conner, J. K., Culley, T., & Baucom, R. S. How weeds emerge: A taxonomic and  
530 trait-based examination using United States data. *New Phytol.* **202**, **1055–1068** (2014).
- 531 7. Smith, B. D. Low-level food production. *J. Archaeol. Res.* **9(1)**, **1–43** (2001).
- 532 8. Weiss, E., Kisley, M. & Hartmann, A. Autonomous cultivation before domestication. *Science*  
533 **312**, **1608–1610** (2006).
- 534 9. Willcox, G., Fornite, S. & Herveux, L. Early Holocene cultivation before domestication in  
535 northern Syria. *Veg. Hist. Archaeobot.* **17(3)**, **313–325** (2008).
- 536 10. Murphy, D. J. *People, Plants & Genes: The Story Of Crops And Humanity* (Oxford Univ.  
537 Press, 2007).
- 538 11. Fuller, D. Q., et al. Convergent evolution and parallelism in plant domestication revealed by  
539 an expanding archaeological record. *P. Natl.l Acad. Sci. USA.* **111(17)**, **6147–6152** (2014).
- 540 12. Meyer, R. S. & Purugganan, M. D. Evolution of crop species: genetics of domestication and  
541 diversification. *Nat. Genet.* **14**, **840–852** (2013).
- 542 13. White, C. E. & Makarewicz, C. A. Harvesting practices and early Neolithic barley  
543 cultivation at el-Hemmeh, Jordan. *Veg. Hist. Archaeobot.* **21(2)**, **85–94** (2012).
- 544 14. Fuller, D. Q. & Allaby, R. G. Seed dispersal and crop domestication: shattering,  
545 germination, and seasonality in evolution under cultivation. *Annu. Plant Rev.* **38**, **238–295** (2009).
- 546 15. Fuller, D. Q., Allaby, R. G., & Stevens, C. Domestication as innovation: the entanglement of  
547 techniques, technology and chance in the domestication of cereal crops. *World Archaeol.* **42(1)**, **13–**  
548 **28** (2010).
- 549 16. Purugganan, M. D. & Fuller D. Q. The nature of selection during domestication. *Nature*  
550 **457**, **843–848** (2009).
- 551 17. Willcox, G., Nesbitt, M. & Bittmann, F. From collecting to cultivation: transitions to a  
552 production economy in the Near East. *Veget. Hist. Archaeobot.* **21**, **81–83** (2012).

- 553 18. Kislev, M.E., Weiss, E. & Hartmann, A. Impetus for sowing and the beginning of  
554 agriculture: ground collecting of wild cereals. *P. Natl. Acad. Sci USA* **101(9)**, 2692–2695 (2004).
- 555 19. Biagetti, S. & di Lernia, S. Holocene deposits of Saharan rock shelters: the case of  
556 Takarkori and other sites from the Tadrart Acacus Mountains (Southwest Libya). *Afr. Archaeol.*  
557 *Rev.* **30(3)**, 305–338 (2013).
- 558 20. Cremaschi, M. et al. Takarkori rock shelter (SW Libya): an archive of Holocene climate and  
559 environmental changes in the central Sahara. *Quaternary Sci. Rev.* **101**, 36–60 (2014).
- 560 21. di Lernia, S. & Tafuri, M. A. Persistent deathplaces and mobile landmarks: The Holocene  
561 mortuary and isotopic record from Wadi Takarkori (SW Libya). *J. Anthropol. Archaeol.* **32(1)**, 1–15  
562 (2013).
- 563 22. Mercuri, A. M. Plant exploitation and ethnopalynological evidence from the Wadi Teshuinat  
564 area (Tadrart Acacus, Libyan Sahara). *J. Archaeol. Sci.* **35(6)**, 1619–1642 (2008).
- 565 23. di Lernia, S. Dismantling Dung: Delayed Use of Food Resources among Early Holocene  
566 Foragers of the Libyan Sahara. *J. Anthropol. Archaeol.* **20**, 408–441 (2001).
- 567 24. di Lernia, S. et al. Colour in context. Pigments and other coloured residues from the Early-  
568 Middle Holocene site of Takarkori (SW Libya). *Archaeol. Anthropol. Sci.* **8(2)**, 381–402(2016).
- 569 25. di Lernia, S., N'siala, I. M. & Mercuri, A. M. Saharan prehistoric basketry. Archaeological  
570 and archaeobotanical analysis of the early-middle Holocene assemblage from Takarkori (Acacus  
571 Mts., SW Libya). *J. Archaeol. Sci.* **39(6)**, 1837–1853 (2012).
- 572 26. Dunne, J. et al. First dairying in green Saharan Africa in the fifth millennium BC. *Nature*  
573 **486(7403)**, 390–394 (2012).
- 574 27. Dunne, J., Mercuri, A. M., Evershed, R. P., Bruni, S. & di Lernia, S. Earliest direct evidence  
575 of plant processing in prehistoric Saharan pottery. *Nat. Plants* **3**, 16194 (2016).
- 576 28. Ozenda, P. *Flore Et Végétation Du Sahara* (Centre National de la Recherche Scientifique,  
577 2000).
- 578 29. Mercuri, A.M. Human influence, plant landscape evolution and climate inferences from the  
579 archaeobotanical records of the Wadi Teshuinat area (Libyan Sahara). *J. Arid Environ.* **72(10)**,  
580 **1950–1967** (2008).
- 581 30. Song, J., Zhao, Z. & Fuller, D. Q. The archaeobotanical significance of immature millet  
582 grains: an experimental case study of Chinese millet crop processing. *Veg. Hist. Archaeobot.* **22(2)**,  
583 **141–152** (2013).

- 584 31. Moreno-Larrazabal, A., Teira-Brión, A., Sopelana-Salcedo, I., Arranz-Otaegui, A. &  
585 Zapata, L. Ethnobotany of millet cultivation in the north of the Iberian Peninsula. *Veg. Hist.*  
586 *Archaeobot.* **24(4)**, 541–554 (2015).
- 587 32. Kuijt, I. & Finlayson, B. Evidence for food storage and predomestication granaries 11,000  
588 years ago in the Jordan Valley. *P. Natl. Acad. Sci. USA* **106(27)**, 10966–10970 (2009).
- 589 33. Cremaschi, M. in *Droughts, Food and Culture* 65–81 (Springer US, 2002).
- 590 34. Kuper, R. & Kröpelin, S. Climate-controlled Holocene occupation in the Sahara: motor of  
591 Africa's evolution. *Science* **313(5788)**, 803–807 (2006).
- 592 35. Castelletti, L. et al. in *The Uan Afuda Cave Hunter-gatherer Societies of Central Sahara* (ed  
593 di Lernia, S.) 131–148 (AZA Monographs 1, All'Insegna del Giglio, Firenze, 1999).
- 594 36. Cremaschi, M. & Zerboni, A. in *Landscape and Societies, Selected Cases* (eds Martini, I. P.,  
595 Chesworth, W.) 67–89 (Springer Science, 2011).
- 596 37. Wasylikowa, K., & Dahlberg, J. in *The Exploitation of Plant Resources in Ancient Africa*  
597 11–31 (Springer US, 1999).
- 598 38. Fuller, D.Q. Contrasting patterns in crop domestication and domestication rates: recent  
599 archaeobotanical insights from the Old World. *Ann. Bot.* **100(5)**, 903–924 (2007).
- 500 39. De Wet, J. M. J. in *Advisory Group Meeting on the Possible Use of Mutation Breeding for*  
501 *Rapid Domestication of New Crop Plants* (Vienna, Austria, 1986).
- 502 40. Walker, S., Wu, H. & Bell, K. Emergence and Seed Persistence of *Echinochloa colona*,  
503 *Urochloa panicoides* and *Hibiscus trionum* in the Sub-tropical Environment of North-Eastern  
504 Australia. *Plant Prot. Q.* **25(3)**, 127 (2010).
- 505 41. Clarke, J. et al. Climatic changes and social transformations in the Near East and North  
506 Africa during the 'long' 4th millennium BC: A comparative study of environmental and  
507 archaeological evidence. *Quaternary Sci. Rev.* **136**, 96–121 (2016).
- 508 42. Khedr, A., Serag, M., Shaaban, H. & Abogadallah, G. Differential responses of aquatic and  
509 aerobic forms of *Echinochloa crus-galli* (L.) Beauv. and *E. colona* (L.) Link. by morpho-  
510 physiological and molecular analysis. *Environ. Earth Ecol.* **1(1)**, 81–93 (2017).
- 511 43. Andrew, S.M., Totland, Ø. & Moe, S.R. Invasion of the cosmopolitan species *Echinochloa*  
512 *colona* into herbaceous vegetation of a tropical wetland system. *Ecol. Res.* **29**, 969 (2014).
- 513 44. Zedler, J. B. & Kercher, S. Causes and consequences of invasive plants in wetlands:  
514 opportunities, opportunists, and outcomes. *Crit. Rev. Plant Sci.* **23(5)**, 431–452 (2004).

- 515 45. Smith, B. D. General patterns of niche construction and the management of 'wild' plant and  
516 animal resources by small-scale pre-industrial societies. *Philos. T. Roy. Soc. B.* **366(1566)**, 836–848  
517 (2011).
- 518 46. Abbo, S., Gopher, A., Rubin, B., & Lev-Yadun, S. On the origin of Near Eastern founder  
519 crops and the 'dump-heap hypothesis'. *Genet. Resour. Crop Ev.* **52(5)**, 491–495 (2005).
- 520 47. Fuller, D. Q. & Hildebrand, E. *Domesticating Plants in Africa* (eds Mitchell, P. & Lane, P.)  
521 **507–525** (Oxford Univ. Press, 2013).
- 522 48. D'Andrea, A.C., Klee, M. & Casey, J. Archaeobotanical evidence for pearl millet  
523 (*Pennisetum glaucum*) in sub-Saharan West Africa. *Antiquity* **75(288)**, 341–348 (2001).
- 524 49. Wu, W. et al. A single-nucleotide polymorphism causes smaller grain size and loss of seed  
525 shattering during African rice domestication. *Nat. Plants* **3**, 17064 (2017).
- 526 50. González, A.T. & Morton, C.M. Molecular and morphological phylogenetic analysis of  
527 *Brachiaria* and *Urochloa* (Poaceae). *Mol. Phylogenet. Evol.* **37(1)**, 36–44(2005).
- 528 51. Yang, X., et al. Barnyard grasses were processed with rice around 10000 years ago. *Sci. Rep-*  
529 *UK.* **5**, 16251 (2015).
- 530 52. Milla, R., Osborne, C.P., Turcotte, M.M. & Violle, C. Plant domestication through an  
531 ecological lens. *Trends Ecol. Evol.* **30(8)**, 463–469 (2015).
- 532 53. Vigueira, C.C., Olsen, K.M., & Caicedo, A.L. The red queen in the corn: agricultural weeds  
533 as models of rapid adaptive evolution. *Heredity* **110(4)**, 303–311 (2013).
- 534 54. Gurevitch, J., Scheiner, S.M. & Fox, G.A. *The Ecology of Plants* (A.D. Sinauer Associates,  
535 Inc.) **258–259** (Sunderland, Massachusetts, USA, 2002).

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### 538 **Methods section**

- 539 55. Kohli, R.K., Batish, D.R., & Singh, H.P. in *Handbook of sustainable weed management* (eds  
540 Singh, H.P. et al) **1–19** (Haworth Press Inc, New York, 2006).
- 541 56. Agrawal, A.A. Phenotypic plasticity in the interactions and evolution of  
542 species. *Science.* 294(**5541**), 321–326 (2001).
- 543 57. Aldrich, R.J. *Weed-crop ecology: principles in weed management* (New Breton Publ., North  
544 Scituate, Mass, 1984).
- 545 58. Cremaschi, M., & di Lernia, S. Holocene climatic changes and cultural dynamics in the  
546 Libyan Sahara. *Afr. Archaeol. Rev.* **16(4)**, 211–238 (1999).

- 547 59. Bronk Ramsey, C. Bayesian analysis of radiocarbon dates. *Radiocarbon* **51(1)**, 337–  
548 360 (2009).
- 549 60. Wasylikowa, K. Holocene flora of the Tadrart Acacus area, SW Libya, based on plant  
550 macrofossils from Uan Muhuggiag and Ti-n-Torha/Two Caves archaeological sites. *Origini* **16**,  
551 125–159 (1992).
- 552 61. Wasylikowa, K. Exploitation of wild plants by prehistoric peoples in the Sahara.  
553 *Würzburger Geogr. Arbeiten* **84**, 247–262 (1992).
- 554 62. Mercuri, A. M. in *UanTabu in the Settlement History of the Libyan Sahara, Arid Zone*  
555 *Archaeology, Monographs 2* (ed Garcea, E. A. A.) **161–188** (All’Insegna del Giglio, Firenze, 2001).
- 556 63. Olmi, L. et al. Cereali selvatici nel Tadrart Acacus - Sahara Centrale, durante l'Olocene  
557 iniziale e l'Olocene medio. *Atti della Società dei Naturalisti e Matematici di Modena* **137**, 411–430  
558 (2007).
- 559 64. Clayton, W. D. & Renvoize, S. A. *Flora of Tropical East Africa: Gramineae (part 3)* **451–**  
560 **898** (Rotterdam, A. A. Balkema for the East African Governments, 1982).
- 561 65. Sheriff, A. S. & Siddiqi, M. A. in *Flora of Libya* (ed El-Gadi, A. A., Tripoli, 1988).
- 562 66. Boulos, L. *Flora of Egypt. Volume four. Monocotyledons (Alismataceae – Orchidiaceae)*  
563 (Al Hadara Publishing, Cairo, 2005).
- 564 67. Lansdown, R.V. *Echinochloa colona*. The IUCN Red List of Threatened Species 2013:  
565 e.T164380A1047208. <http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T164380A1047208.en>.  
566 Downloaded on 03 July 2017.
- 567 68. Hilu, K.W. Evidence for RAPD markers in the evolution of *Echinochloa* millets (Poaceae).  
568 *Plant Syst. Evol.* **189**, 247–257 (1994).
- 569 69. Sood, S., et al. Barnyard millet—a potential food and feed crop of future. *Plant*  
570 *Breeding*. **134(2)**, 135–147 (2015).
- 571 70. Yamaguchi, H., Utano, A. Y. A., Yasuda, K., Yano, A., & Soejima, A. A molecular  
572 phylogeny of wild and cultivated *Echinochloa* in East Asia inferred from non-coding region  
573 sequences of *trnT-L-F*. *Weed Biol. Manag.* **5(4)**, 210–218 (2005).
- 574 71. Carman, J.G., Jamison, M., Elliott, E., Dwivedi, K.K., Naumova, T.N. Apospory appears to  
575 accelerate onset of meiosis and sexual embryo sac formation in sorghum ovules. *BMC Plant Biol.*  
576 **11(1)**, 9 (2011).
- 577 72. Olmi, L. et al. in *Windows on the African Past: Contemporary Approaches to African*  
578 *Archaeobotany*. **175–184** (Africa Magna Verlag, Frankfurt, 2012).

- 579 73. Fornaciari, R., Fornaciari, S., Francia, E., Mercuri, A .M. & Arru, L. *Panicum* spikelets from  
580 the Early Holocene Takarkori rockshelter (SW Libya): Archaeo-molecular and-botanical  
581 investigations. *Plant Biosyst.* doi.org/10.1080/11263504.2016.1244117 (2016).  
582 74. Martinoli, D. & Nesbitt, M. Plant Stores at Pottery Neolithic Höyücek, Southwest Turkey.  
583 *Anatol. Stud.* **53**, 17–32 (2003).

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597

## 598 **Author contributions**

599 S.d.L. and A.M.M. conceived and planned the project. A.M.M. and S.d.L. wrote the paper. A.M.M.  
700 studied the archaeobotanical record and S.d.L. the stratigraphic and archaeological context. R.F.  
701 performed morphometry and data analysis. M.G. made GIS analysis. S.V. made the entomological  
702 study. S.d.L. designed and directed the excavations and field sampling. All authors read and



703 approved the final manuscript.

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706 **Legends**

707

708 Table 1 – The 30 plant accumulations from the archaeobotanical record of Takarkori rockshelter:  
709 archaeological context and archaeobotanical results.

710 Cultural phases (\*) = LA: Late Acacus; MP: Middle Pastoral; LP: Late Pastoral. From the oldest,

711 they are: LA2: 8500-7900 uncal bp; 7600-6650 calBC; LA3: 7900-7400 uncal bp; 7050-6100

712 calBC; MP1: 6100-5500 uncal bp; 5200-4250 calBC; MP2: 5500-5000 uncal bp; 4450-3700 calBC;

713 LP1: 5000-4000 uncal bp; 3950-2350 calBC.

714 Calibrated years BC (\*\*) = date calibration was carried out using OxCal Online v. 4.3 <sup>59</sup>

715

716 Figure 1 – Context of the archaeobotanical record of Takarkori rockshelter. a) The Tadrart Acacus

717 Mountains, SW Libya, and location of the site (red circle); b) GIS map of the excavation and

718 position of plant accumulations by type (mix, spot) and chronology (Late Acacus: yellow; Middle

719 Pastoral: blue; Middle/Late Pastoral: grey); c) ‘spot’ accumulation of the Middle Pastoral = MP1

720 phase (ID 17 in the map ‘b’); d) ‘mix’ accumulation of the Late Acacus = LA3 phase (ID 6 in the

721 map ‘b’).

722

723 Figure 2 – Multiplot of calibrated (calBC) radiocarbon dates of the 30 archaeobotanical samples

724 (Late Acacus: yellow; Middle Pastoral: blue; Middle/Late Pastoral: grey). See Table 1 for details of

725 dates (generated using OxCal Online ver. 4.3 <sup>59</sup>).

726

727 Figure 3 – “Spot” and “mix” plant accumulations.

728 ‘Spot’: a) overview (ID 15); dorsal and ventral view of the spikelets of: b) *Panicum laetum* (ID 15);

729 c) *Echinochloa colona* (ID 15); d) uncharred grain (ID 14); e) *Sorghum bicolor* subsp.

730 *verticilliflorum* (ID 8). ‘Mix’: f) overview (ID 24); g) split spikelets of *E. colona* (ID 24); h) charred

731 grains in dorsal and ventral view (ID 26); i) outer glumes of *E. colona* (ID 23).

732

733 Figure 4 – The archaeobotanical record of plant accumulations from Takarkori rockshelter **is unique**

734 **in showing so clearly and gradually the data on the long transitional process from gathering to**

735 **cultivation.** Histograms show the percentages of seeds/fruits identified and counted in the plant  
736 accumulations, and their total concentrations (in 10 ml); samples are plotted in chronological order  
737 from the oldest (bottom) to the youngest (top) accumulation.

738

739 Figure 5 - Morphometry of ellipticity.

740 The graphs show changes in the spikelet morphology of Wild fonio and Jungle rice during the  
741 occupation of the site. The ellipticity (the degree of deviation from sphericity) of Wild fonio  
742 decreases, with the spikelets tending towards an increasing roundness, especially visible when  
743 comparing length and thickness. The ellipticity of Jungle rice increases because the spikelets tend to  
744 lengthen. This is especially visible when comparing length and width (n = number of measured  
745 spikelets).

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#### 748 **Supplementary Material**

749

750 SM 1. – Scanning Electron Microscope image of *Sorghum bicolor* subsp. *verticilliflorum* spikelets  
751 (ID 12): a) ventral view, with two floret rachillae; b) dorsal view, with basal end presenting a wild  
752 type (smooth) abscission scar.

753

754 SM 2. - Scatter plot showing the length and width uniformity of the spikelets of Wild fonio, Jungle  
755 rice and Wild Sudan grass from the plant accumulations found at Takarkori (n: number of measured  
756 spikelets; S: *Sorghum*; P: *Panicum*; E: *Echinochloa*).

757

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The graphs show changes in the spikelet morphology of Wild fonio and Jungle rice during the occupation of the site. The ellipticity (the degree of deviation from sphericity) of Wild fonio decreases, with the spikelets tending towards an increasing roundness, especially visible when comparing length and thickness. The ellipticity of Jungle rice increases because the spikelets tend to lengthen. This is especially visible when comparing length and width (n = number of measured spikelets).

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341 **Depicting plant behaviour through human imprints: the weediness of wild cereals and their**  
342 **cultivation in Holocene Sahara**

343

344 Anna Maria Mercuri<sup>1,\*</sup>, Rita Fornaciari<sup>1</sup>, Marina Gallinaro<sup>2</sup>, Stefano Vanin<sup>3</sup>, Savino di Lernia<sup>2,4\*</sup>

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346 SUPPLEMENTARY MATERIAL

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350 Figure SM 1. – Scanning Electron Microscope image of *Sorghum bicolor* subsp. *verticilliflorum*  
351 spikelets (ID 12): a) ventral view, with two floret rachillae; b) dorsal view, with basal end presenting  
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