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Unlocking the Past: Exploring Moroccan Lake Sediments Through Ancient DNA and Palynology for Insights into Paleoenvironment, Land Use, and Practices

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1 **Unlocking the Past: Exploring Moroccan Lake Sediments through Ancient DNA and**
2 **Palynology for Insights into Paleoenvironment, Land Use, and Practices**

3
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7
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28 Original draft preparation, funding acquisition; **Frédérique Barloy-Hubler:** formal analysis,
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30 investigation, Writing- Original draft preparation; **José Antonio López-Sáez:** investigation;
31 **Régis Debruyne, Jose Utge-Buil, Françoise Dessarp:** investigation (experimental lab work);
32 **Dominique Marguerie, Philippe Lanos:** formal analysis; **Jean-François Berger:**
33 Conceptualization, resources, investigation, Writing- Original draft preparation. **All authors:**
34 Writing- Review and editing.

35 **Abstract:**

36 Over the last 12,000 years, the adoption of an agro-pastoral lifestyle has become prevalent,
37 leading to gradual change in landscapes. In northwestern Morocco, typical elements of an agro-
38 pastoral economy emerged around 7,400 cal BP in the Tingitana Peninsula. This was associated
39 with Cardial ceramic style and the presence of key cultivated plant species and domestic
40 mammals. However, in this region, the archaeological record of the last five millennia remains
41 fragmented, with significant regional variations that challenge our understanding of the
42 neolithization processes. This study introduces a new five-meter-long core from Lake Iffer in
43 the North African Middle Atlas. Our objective is to assess the site's potential to reveal insights
44 into the impacts of climate and human activities on the ecosystems and the landscape of the
45 Middle Atlas during the Holocene. Employing a pluridisciplinary approach, we combined
46 paleolimnology and palynology with, for the first time in this context, ancient DNA analysis
47 focusing on sedimentary samples spanning from Late Neolithic to Bronze Age.

48 Our findings reveal an environmental opening between 4.1-3.9 ka BP likely triggered by a
49 drought episode, possibly associated with the so-called "4.2 ka cal. BP event". During the same
50 period, we present evidence of increased anthropic pressure, reflected by the presence of ruderal
51 taxa and Bovidae, despite the absence of archaeozoological material. It attests of pastoral
52 activities at least 4,371 years ago at Iffer lake site while no evidence of cultivated plant taxa
53 was found. Moreover, our study demonstrates that both climatic fluctuations and human
54 activities contributed to the local decline of Elephantidae, as indicated by ancient sedimentary
55 DNA Our findings offer new perspectives for exploring and studying Mediterranean sites with
56 limited material evidence.

57

58 **Key-words:** pastoralism, Late Neolithic, Bronze Age, Morocco, Middle Atlas Lake, ancient
59 sedimentary DNA, Palynology

60

61 **Highligths:**

- 62 • Drought episode between 4,133-3,992 cal. BP, possibly linked to the "4.2 ka cal. BP event."
- 63 • Evidence of pastoralism demonstrated by Bovidae aDNA detection
- 64 • Presence of Elephantidae in the anthropological system since the late Neolithic.
- 65 • Anthropization and climate variations influence land use and wildlife variations.
- 66 • Multidisciplinary approach unveils new perspectives for exploring limited Mediterranean material.

67

68 **1. Introduction**

69

70 Over the past 12,000 years, human has seen his way of life change drastically. From nomadic
71 he gradually became sedentary and the adoption of an agro-pastoral regime became widespread.
72 This transition was possible from the end of the Late glacial in Near East in parallel with climate
73 changes (Bar-Yosef and Belfer-Cohen, 1989), and spreads across the Mediterranean from the
74 9th millennium BP onwards (Berger and Guilaine, 2009; Weninger et al., 2006). Intensification
75 of the economy of production and increasing anthropization have gradually evolved over the
76 last millennia, resulting in a gradual change in landscapes.

77 The Mediterranean region, situated between 30 and 40°N, is one of the most sensitive zones to
78 climatic fluctuations which contributed to shape the ecosystems. Its geographical situation lies
79 in a zone of influence of the North Atlantic oceanic circulation (Ait Brahim et al., 2019). In the
80 Mediterranean basin, past environmental changes have resulted from critical climate
81 oscillations and growing ecosystem instability exacerbated by human activities over the past
82 9,000 years (Cheddadi et al., 2016; Fletcher and Zielhofer, 2013; Mercuri et al., 2012; Sadori
83 et al., 2013).

84 In northwestern Morocco, typical elements of an agro-pastoral economy appeared in the
85 Tingitana Peninsula around 7,400 cal BP (Gibaja et al., 2012; Linstädter et al., 2018; Marinval
86 and Ballouche, 2003; Morales et al., 2016, Simoes et al. 2023), associated with Cardial ceramic
87 style similar to that of the eastern coast of the Iberian Peninsula. This event is accompanied by
88 the appearance of the main cultivated species of cereals and legumes, as well as domestic
89 mammals common to the early Iberian Neolithic, (Manen et al., 2007; Martínez-Sánchez et al.,
90 2018), suggesting that the Neolithic wave diffused from the southern coast of the Iberian
91 Peninsula via sea crossing following a north to south axis (Martínez-Sánchez et al., 2018).
92 However, the archaeological record of the last five millennia in northwestern Morocco remains
93 very fragmented and poorly studied, with great regional contrasts that complicate the
94 understanding of the chronology of the neolithization processes (Lucarini et al., 2021; Martínez-
95 Sánchez et al., 2018).

96 Lake sediment changes and variations in sedimentation rate offer valuable information about
97 past climate influences, water depth, and paleoenvironments (Damnati et al., 2016; Magny et
98 al., 2007). These elements associated with the study of ancient remains and chrono-cultural
99 frameworks helps understand biodiversity fluctuations and past land use impacts (Cheddadi et
100 al., 2015; Simonneau et al., 2013). Over the last two decades, lake sedimentary DNA has

101 complemented pollen and macro-remains, proving valuable for studying past community-level
102 changes (Capo et al., 2021). It enables direct identification of organisms in sedimentary archives
103 and helps understand changes in their representation over time. To date, such studies have never
104 been performed in northwestern Maghreb contexts.

105 In Morocco, valuable information on ecosystem changes and species dynamics has primarily
106 come from studies focused on the northern coasts, the Tingitane peninsula, and the Middle and
107 High Atlas Mountains. Several multi-proxy studies of Middle Atlas lakes (such as
108 Tigalmamine, Sidi Ali, Iffrah, Afourgagh) have documented the main hydroclimatic variations
109 and the evolutionary trend of regional climate during the Holocene (Lamb and van der Kaars,
110 1995; Rhoujjati et al., 2010; Zielhofer et al., 2019). Despite pioneering paleolimnological and
111 pluridisciplinary works in the Middle Atlas lakes since the 1990s (Cheddadi et al., 1998; Lamb
112 and van der Kaars, 1995), continuous and long Holocene records with robust absolute
113 chronologies in Mediterranean North Africa remain incomplete, despite recent
114 paleoenvironmental studies and anthropogenic impacts identification has been performed
115 (Cheddadi et al., 2019, 2015; López-Sáez et al., 2023; Nourelbait et al., 2016). Recently, a
116 continuous study from Lake Sidi Ali archive reconstructs Western Mediterranean hydro-
117 climatic variability, seasonality and forcing mechanisms. The study reveals low lake levels at
118 6.6-5.4 ka and from 3 ka, a multi-centennial-scale NAO-type pattern and Western
119 Mediterranean, and a winter rain maximum generally associated with solar minima (Zielhofer
120 et al., 2019, 2017).

121 Due to the scarcity of well-dated fossil records, the absence of reliable absolute chronologies,
122 and incomplete archaeological studies in Mediterranean North Africa, a comprehensive
123 analysis of spatial and temporal patterns of environmental variations and species dynamics,
124 which could provide insights into land use and practices, remains challenging. In consequence,
125 the process of progressive anthropization and the development of agro-pastoral practices which,
126 in parallel with the climate, have shaped the environment in northwestern Morocco over the
127 past 7,000 years, remain not fully understood. Therefore, these processes cannot be
128 contextualized and integrated into the known patterns in southern Europe and the Near East
129 edges of the Mediterranean.

130 In this study, we present a newly recovered five meters long core from Lake Iffer in the North
131 African Middle Atlas. Our objective is to assess the site's capability in providing insights into
132 the impacts of climate and human-induced changes on the Holocene ecosystems and landscape
133 of the Middle Atlas. To achieve this, we employed a pluridisciplinary approach combining
134 paleolimnology, palynology and, for the first time in this context, ancient sedimentary DNA

135 (sedaDNA) analysis on a few samples to explore the potential of paleogenomic methods on
136 such Mediterranean sites.

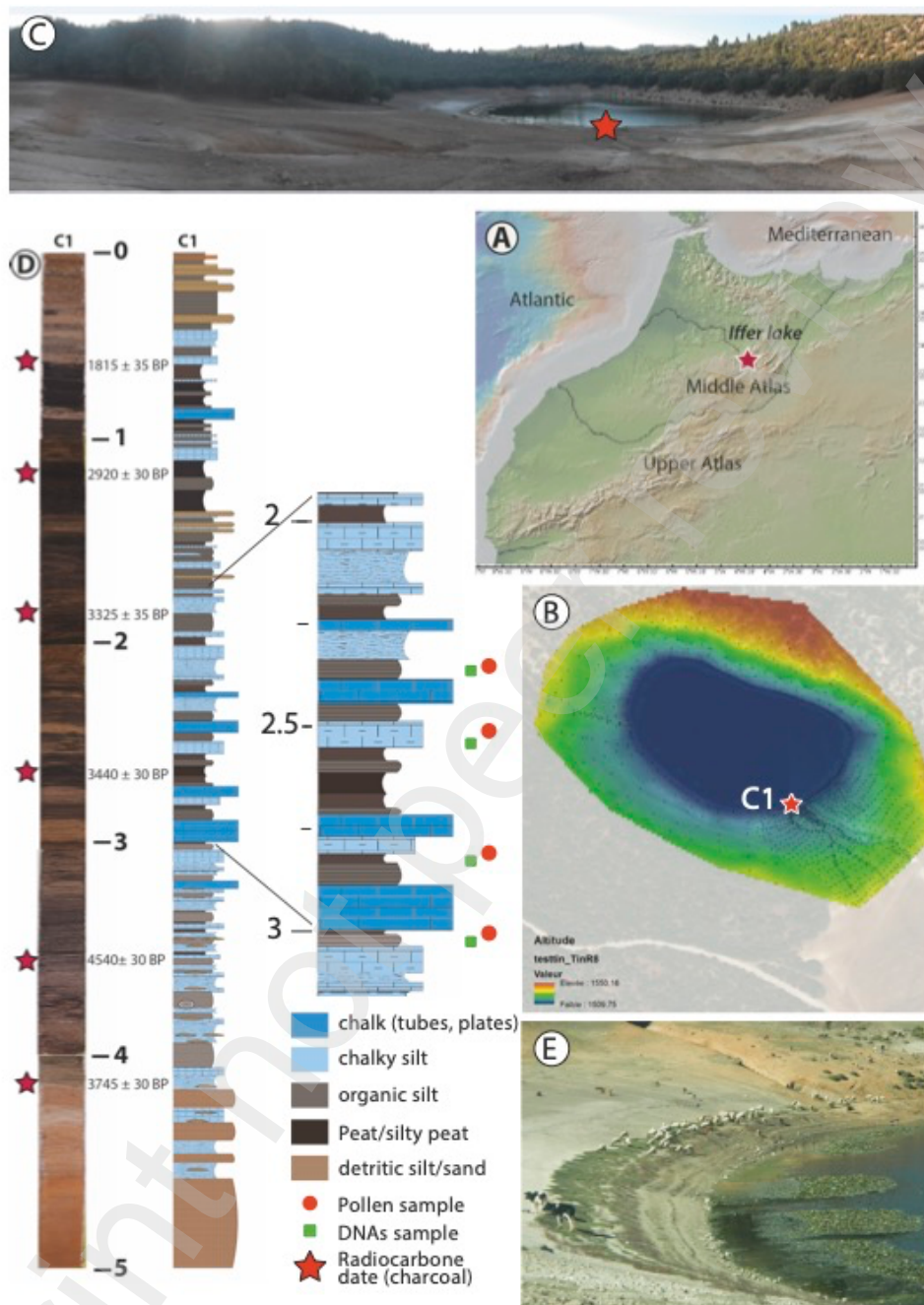
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139 **2. Study area**

140

141 Lake Iffer (33°36'30"N, 4°54'30"W), located in northeastern Morocco (Figure 1A), is one of
142 several lake systems in the tabular Middle Atlas Mountains at the boundary of the Imouzzère
143 and Amekla causses (Rhoujjati et al., 2012). Of moderate size (3.5 ha), it is located in a tectono-
144 karstic zone of middle altitude (Baali, 1998), and occupies the center of a watershed of endoreic
145 type whose surface of 4.5 km² extends between 1500 to 1846 m of altitude (Figure 1B). The
146 bein of the lake is composed of a calcic bicarbonate facies (Benkaddour et al., 2008; Damnati
147 and Taieb, 2003), associated with the intense karstification of the liasic dolomites lying on an
148 impermeable substratum formed by the Trias argillites (Baali, 1998). The lake is supplied by a
149 network of gullies that function periodically during the rainy season, particularly well-marked
150 on its eastern shore, connected to a vast lacustrine terrace. Its level fluctuates according to the
151 seasons and the annual rainfall. The climate is Mediterranean sub-humid with cold winters.
152 Remnants of ancient red Mediterranean soils (terra rossa) are observed on the slopes, more or
153 less heavily colluviated and brunified (rendziform) by Holocene pedogenesis (Alaoui et al.,
154 2020). The surrounding forest vegetation is composed of holm oaks (*Quercus ilex*) with a few
155 feet of Aleppo and maritime pines (*Pinus halepensis* and *P. maritimus*). The matorrals are
156 dominated by *Thymeleae tartonraira* and *Adenocarpus* (Lecompte, 1986). The lake has
157 significant water deficits because of recurring drought and human pastoral pressure since the
158 1980s, leading to the decrease in water level and increasing salinity, with relatively alkaline
159 water (Damnati et al., 2016). The aquatic flora of the lake is dominated by cattail (*Typha*
160 *latifolia*), white water lily (*Nymphaea alba*), pondweed (*Potamogeton pectinatus*) and Eurasian
161 watermilfoil (*Myriophyllum spicatum*), which are very dense near the shores (Chillasse et al.,
162 2001).



163
 164 **Figure 1: Geographic, topographic and lithostratigraphic data of the studied samples at Iffer lake**
 165 **(Morocco).** A. Location of the study site in the Moroccan Middle Atlas mountains; B. Topographic
 166 restitution of the lake perimeter with position of the studied core; C. Panoramic view of the eastern shore
 167 of the lake with the position of the core (red star) and the steep western and northern wooded slopes; D.
 168 Photograph and lithostratigraphy of core-C1 with position of radiocarbon dates, ancient sedimentary
 169 DNA and pollen samples; E. Photograph of the lake's western shoreline during a low-water event in
 170 autumn 2022, with flocks of sheep and cattle.

171 Morpho-stratigraphic analysis of the catchment was performed by Alaoui et al., (2020), who
172 confirmed an upper Pleistocene age at the base of the upper terrace lacustrine chalk formations
173 to the east (29,360+/-490 BP). Traces of nesting of highly oxidized and pedogenized peaty
174 lacustrine formations, rich in Neolithic flints and shards, are identified in the middle part of the
175 beine.

176 First geochemical and magnetic analyses of detrital formations stored in the lake reflect the
177 nature of the dolomite bedrock and from forest developed soils (Rhoujati et al. 2012, Damnati
178 et al. 2015). These preliminary studies describe warm and dry climate (6500-4600 cal. BP),
179 wetter climatic conditions with high lake level (4600-2000 cal. BP), increasing pastoral and
180 agricultural activities (e.g. Figure 1E) caused the decline of forest linked to increased soil
181 erosion from 2,000 years.

182

183

184 **3. Material and methods**

185

186 ***3.1 Archeological context and Geomorphology of the site***

187

188 The new field study conducted at Lake Iffer combined surveys of natural sections (from
189 regressive erosion gullies) and a transect of six cores (from 3 to 6m), carried out with a "Cobra"
190 thermic corer, which complete a series of three deep cores (10m) located in the middle of the
191 lake, which have been the subject of sedimentological analyses and a palynological study
192 (Damnati et al., 2016; Rhoujati et al., 2012). The 500-cm-long sediment core IF-C1 was
193 extracted from the eastern shore of the lake (Figure 1C).

194 On IF-C1, six accelerator mass spectrometry radiocarbon dates were measured on charcoals at
195 the Artemis-Lyon/Saclay and Poznan Radiocarbon Laboratory (Table S1). We used a Bayesian
196 approach implemented in the new version of ChronoModel (Lanos & Dufresne, 2022) and the
197 calibration data set IntCal20 (Reimer et al, 2020) to estimate an average age-depth curve
198 (MCMC; 3,000,000 iterations, SI, Figure S1). From the age-depth curve obtained by
199 ChronoModel 3.2.2, the sediment accumulation rate was estimated. The estimated curve with a
200 confidence interval allows to calculate a date interval whatever the depth (posterior probability
201 density region HPD at a given confidence level (95%)) and an age (Mode A Posteriori) was
202 assigned for each sample (Table S2).

203 This core was sampled every 10 cm for pollen analyses, and was passed through the core
204 scanner for XRF analysis every centimeter. Hydroclimatic fluctuations have succeeded one
205 another leading to the oscillation of lake levels for more than 6 millennia, visible on both sides
206 of the lake, by the alternation between silty-organic and chalky facies. The yellowish sandy or
207 silty facies, more or less rubefied, testify to more detritic phases, connecting the slopes and the
208 lake. The samples were collected between 2.3 and 3.03m depth, i.e. according to the age-depth
209 model between 4,600 and 3,900 BP (late Neolithic-early Bronze Age). This part of the core
210 corresponds globally to a period of higher water levels (positive water balance), associated with
211 lacustrine deposits containing numerous carbonate biomarkers (tubes and plates) (Figure 1D).
212 To document human occupation near the lake, fifteen windows of archaeological survey were
213 carried out over 1.5 to 2 ha with the support of a GPS on the eastern terrace of the lake, rich in
214 chipped flints, with scattered ceramics on the surface. Three sectors indicate an occupation of
215 the Epipaleolithic period (flakes with cut edges and bladelets also pointed by abrupt retouches).
216 Five other sectors indicate a debitage rather of Mesolithic age (with segments of circle,
217 unidirectional nuclei with negatives of narrow bladelets). Eight places show evidence of
218 Neolithic occupation *sensu lato*. The presence of larger flint pieces with more imposing
219 modules indicates productions attributable to a Late Neolithic, possibly corroborated by the
220 presence of some beige ceramic shards with incised decorations of the campaniform culture
221 type (study in progress R. Guilbert-Berger). Concentrations of more recent ceramics (non-
222 turned and turned) testify to proto-historic to antique human occupations (studies in progress).

223
224

225 **3.2 Palynological analysis**

226

227 A total of 48 samples have been studied in Iffer-C1 core sequence. The chemical
228 treatment of the samples has been carried out following the so-called classical method (Burjachs
229 and Renault-Miskovsky, 1992; Faegry and Iversen, 1975; Girard and Renault-Miskovsky,
230 1969; Goeury and De Beaulieu, 1979; Moore et al., 1999), resulting in a final portion of the
231 sediment preserved in glycerin gelatin (detailed in SI). An optical microscope (Nikon Eclipse
232 50i model), with 40X, 60X and 100X objectives, the latter with immersion oil, has been used
233 for the identification of the pollen and non-pollinic microfossils. The reference collection of the
234 Environmental Archaeology Research Group of the CSIC (Madrid), in addition to various
235 bibliographic sources on the morphometric characterization of palynomorphs have been used

236 for the identification of pollen morphotypes (Bonnefille, 1980; Moore et al., 1999, 1991; Moore
237 and Webb, 1978; Reille, 1995, 1992).

238 Non-pollen microfossils (algal spores, cyanobacteria, fungal spores and talus remains, fungal
239 bodies of fungi, fragments of bryophytes or pteridophytes, animal micro-species, microfossils
240 of unknown biological nature, etc.) were also identified based on abundant bibliographic
241 references (Bakker and Van Smeerdijk, 1982; Lopez-Saez et al., 1998; Pals et al., 1980;
242 Pantaleon-Cano et al., 1996; Sáez-López et al., 1999; van Geel, 1978; van Geel et al., 2003;
243 van Geel et al., 1989, 1980). For the elaboration of the pollen diagram, hydro-hygrophilic taxa,
244 non-pollen microfossils, as well as *Aster* type, Cardueae and Cichorioideae have been excluded
245 from the base sum, due to their zoophilic character being usually overrepresented (Bottema,
246 1975; López-Sáez et al., 2003; Sáez-López et al., 1999). The relative percentage of these
247 excluded palynomorphs has been calculated with respect to the total sum.

248 In this study we describe results (Table S3) of the four samples (at 300, 279, 250 and 236 cm
249 depth) that coincide with ancient DNA (aDNA) samples.

250

251

252 **3.3 Ancient DNA analysis**

253 The entire Iffer-C1 core was opened in a dedicated room in the Palgene platform (ENS
254 Lyon). DNA samples were taken each nine centimeters. We first scraped the sediment surface
255 using sterile scalpels (5-10mm), then sampled inner uncontaminated sediments with a new
256 sterile scalpel and transferred them to sterile tubes. Subsampled sediment was stored at -20°C
257 for subsequent extractions. For this study, four samples were chosen for analysis (Figure 1D,
258 Table S2). All the extractions were then conducted on the P2GM platform (MNHN Paris)
259 equipped with specialized facilities devoted to aDNA analysis.

260 The four extractions of *sedaDNA* were performed from 100 mg of sediment (+/- 10%), in one
261 batch, including one extraction blank following Dabney et al (2013) protocol (detailed in SI).
262 We prepared libraries following a slightly modified protocol from Meyer and Kircher (2010)
263 using the double indexing strategy of Kircher et al. (2012) (detailed in SI).

264 All samples underwent enrichment using custom probes (MyBaits custom design) designed to
265 target 19 mammal and 22 plant taxa (Table S4, SI). The enrichment utilized complete
266 mitogenome for mammals and *matk*, *rbcl*, and *trnl-trnt* chloroplast loci for plants. Libraries
267 were captured per batch of two following the MYbaits manual V3, with 48 hours hybridisation
268 at 56°C . The captures were amplified using KAPA Hi-Fi polymerase following the MyBaits

269 manual instructions. Captured libraries were all sequenced in paired-end on a partial Illumina
270 NovaSeq 6000 S4 XP lane (300 cycles, PE 150).

271 Reads were processed through the Paleomix pipeline (Schubert et al., 2014), (Table S5)
272 allowing 1) adapters removal, read pairing and merging, and sequence filtering using
273 AdapterRemoval (Lindgreen, 2012) (min length reads \geq 35bp, trimns: yes, triml qualities: yes,
274 mm: 5); 2) duplicates filtering and 3) reads mapping (Li and Durbin, 2009), (BWA aln; -l 1024;
275 -o 2; -n 0.01) against a database comprising one sequence per genus and targeted loci (retaining
276 the longest sequence) from available mammal and viridiplantae in the GenBank Database
277 (march 2020). Reads were secondary analyzed with Prinseq (Schmieder and Edwards, 2011) to
278 remove low complexity sequences (-lc_method dust -lc_threshold 7 -trim_tail_left 5 -
279 trim_tail_right 5). Bam files were filtered with samtools (Danecek et al., 2021) using tag "X0:i:"
280 to generate two sequence files, one with unique best hit and one with multiple best hit. All reads
281 with matches were identified through DNA homology searches using BLAST (Altschul et al.,
282 1990) against the nr database (08/2022) to validate or determine the best taxonomic assignment.
283 Significant homologies obtained by Blast (best query cover and e-value) that refer to a single
284 taxon are retained. If scores are equivalent for multiple taxa, the taxonomic rank is adjusted
285 until a clear result is obtained (from genus to family depending on the case). To achieve precise
286 and unambiguous taxonomic classification, biocurators performed this analysis manually. Taxa
287 present in the control (extraction blank: sample without DNA) were excluded from the study
288 and regarded as experimental contamination.

289 Mosses, ferns, algae and hornworts were not included in this study. We have selected taxa that
290 represent more than 1% of the total number of reads attributed to plant or mammal taxa in at
291 least one of the four samples studied (Table S6). However, taxa that do not fill the 1% criterion
292 but described in the pollen analysis (Table S6) were added in figure 2. Given the capture design
293 and the results obtained for both *seda*DNA and palynology, we have chosen the following four
294 categories: mammals, trees, aquatic plants and terrestrial plants. The relative evolution of the
295 proportion of each taxon ($>1\%$ of total reads assigned) is then considered intra-categories
296 (normalized in %, Figure 2). The results were illustrated as charts using R version 4.2.2 (2022-
297 10-31) via Rstudio version 2022.12.0+353 and ggplot2, hrbrthemes and dplyr packages.
298 Finally, *seda*DNA deamination pattern and fragment length distributions were inspected with
299 mapDamage2 (Jónsson et al., 2013) for taxa with sufficient read counts after mapping of the
300 reads against each reference genomes (Table S7, Figure S3).

301

302

303 4. Results and Discussion

304

305 4.1 Landscape dynamics

306

307 At the molecular level, less than 1% of total sequences could be assigned (Table S5). In
308 sample SL383394 at 302cm depth, showed no identified mammals, and very low number of
309 plant reads (n=161) (Table S2, S6), reaching a maximum of four reads for taxa of interest. For
310 this reason, the relative proportions of plant families for this sample are biased and difficult to
311 interpret and we decided to not present and discuss *sedaDNA* results for this sample. This
312 period corresponds to one of the four arid abrupt events identified around 4.5-4.4 ka BP, in
313 Lake Tigalmamine (about 100 km from Lake Iffer, El Hamouti, 2014). The dates also mark the
314 end of Lake Iffer's initial filling and the existence of a shallow water body due to low water
315 inputs, with very high carbonate content (Rhoujjati et al, 2012). This high alkalinity, combined
316 with aridity, may have led to greater DNA degradation, as already reported in other studies
317 (Capo et al, 2021). This deficiency of DNA may explain the low sequencing yields for this
318 sample (approximately 4 to 30 times less sequences than the other three samples, Table S5) and
319 the difficulties in taxonomic identification. (Parducci et al, 2017). Sequenced DNA quantities
320 for the three other samples are adequate (Table S5). They indeed cover the 4.3-3.9 ka BP period,
321 that corresponds to declining carbonate contents and temperatures in Lake Iffer, due to rising
322 lake water levels linked to wetter conditions. Regional references also indicate episodes of low
323 lake levels with reduced precipitation/evaporation ratio during this time (Rhoujjati et al, 2012).

324

325 Three major genera of trees (*Pinus*, *Quercus* and *Arbutus*) can be clearly identified within
326 *sedaDNA* during the considered period (Figure 2A, Table S6). *Pinus* and *Quercus* are currently
327 present on the site and their DNA as well as pollen remains are present throughout the period
328 studied. *Arbutus* is only detected by *sedaDNA* analysis at 4,371 cal. BP (30% of the tree and
329 shrub population) before drastically decrease. Its presence is in accordance with a previous
330 study at Benzú Cave, located in the northernmost tip of the Tingitan Peninsula, 360 kilometers
331 north of Iffer Lake, where it was used as fuel together with *Quercus* sp., *Olea* sp., *Fraxinus* sp.
332 among others (Muñoz et al., 2013; Vijande-Vila et al., 2019). Its absence in the pollen register
333 could be explained by its entomophilous pollination, the fact that *Arbutus* is a poor pollen
334 producer since its mode of pollination is autogamy (Hagerup, 1957; Faida et al., 2023) and

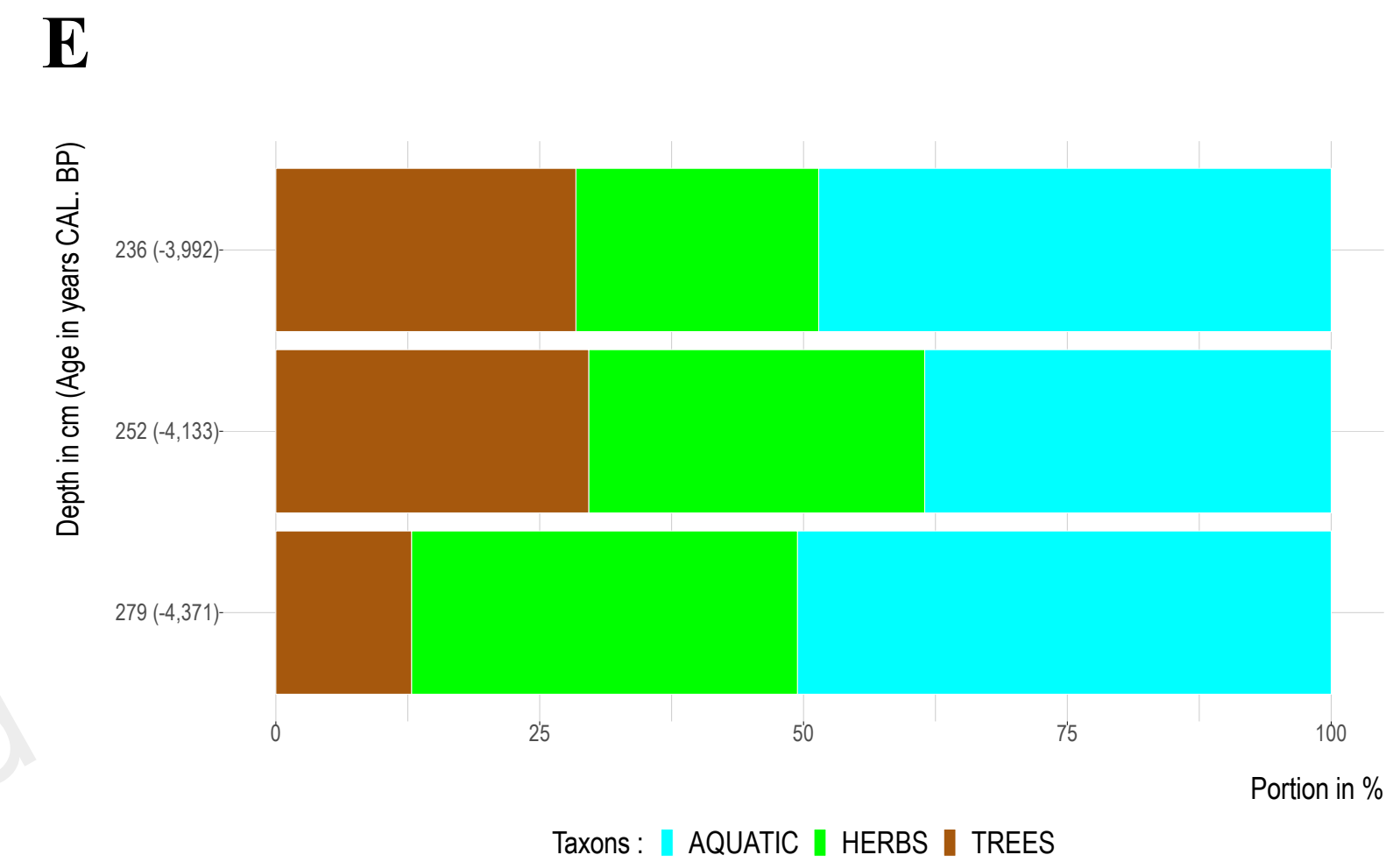
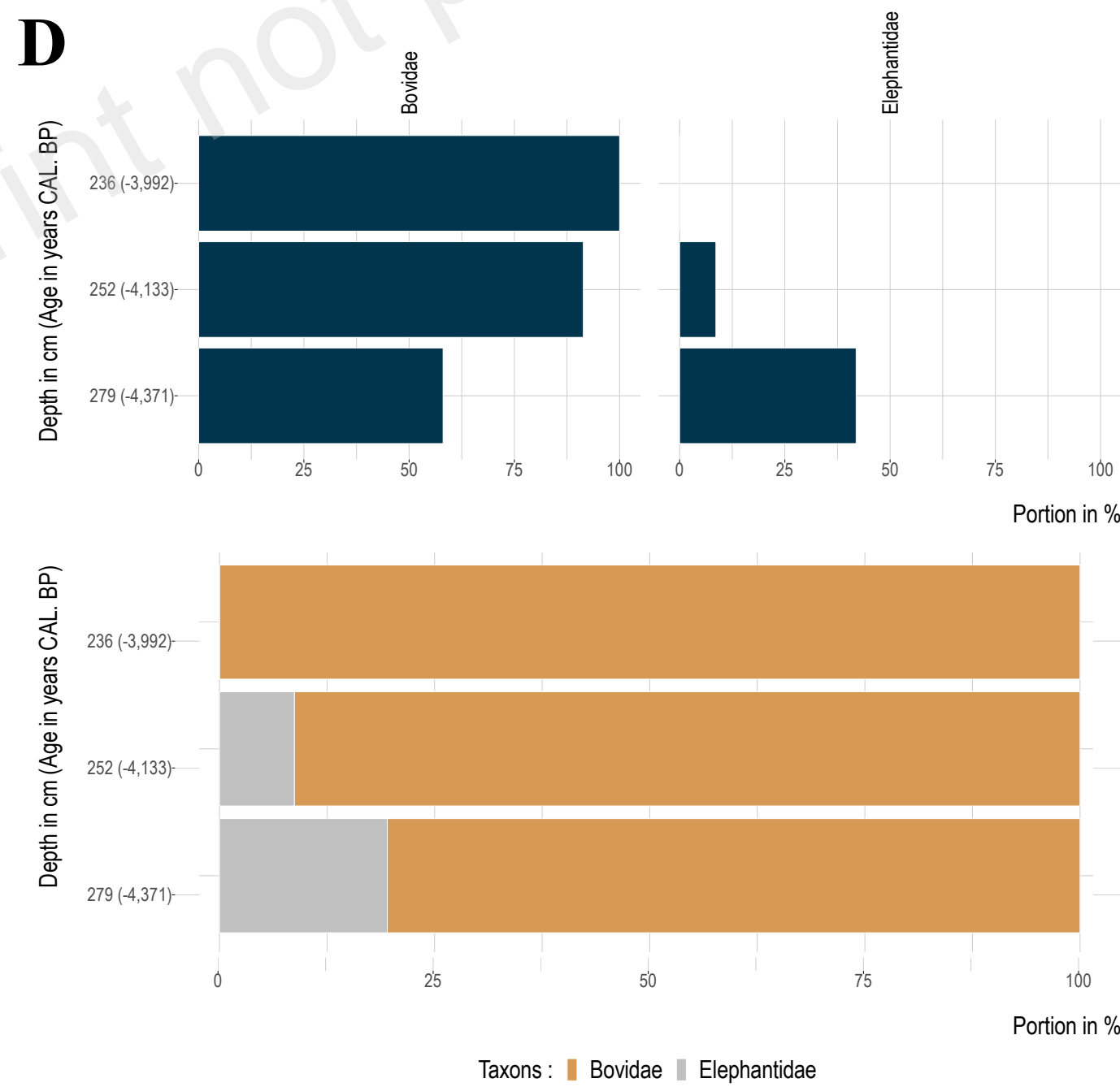
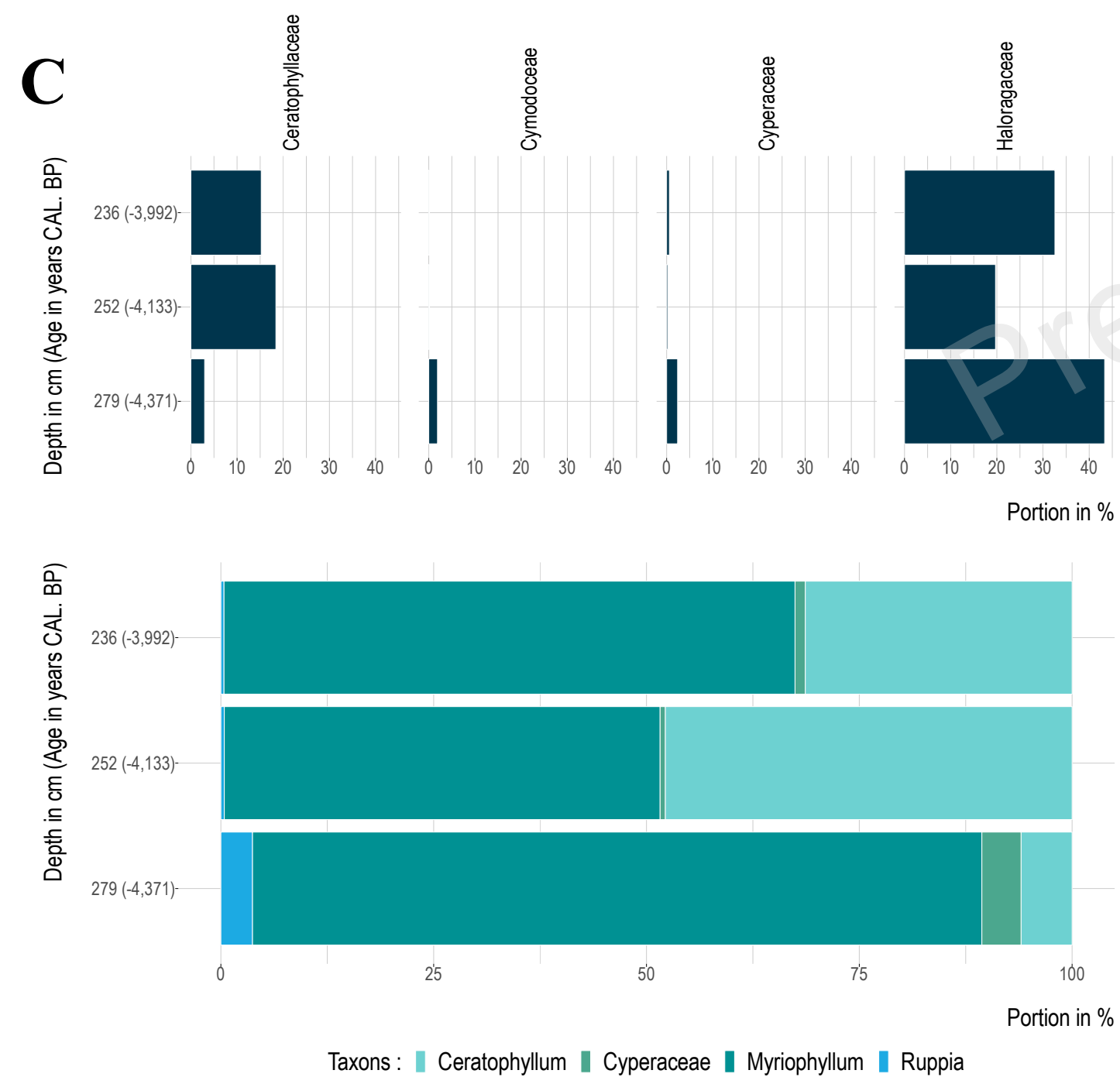
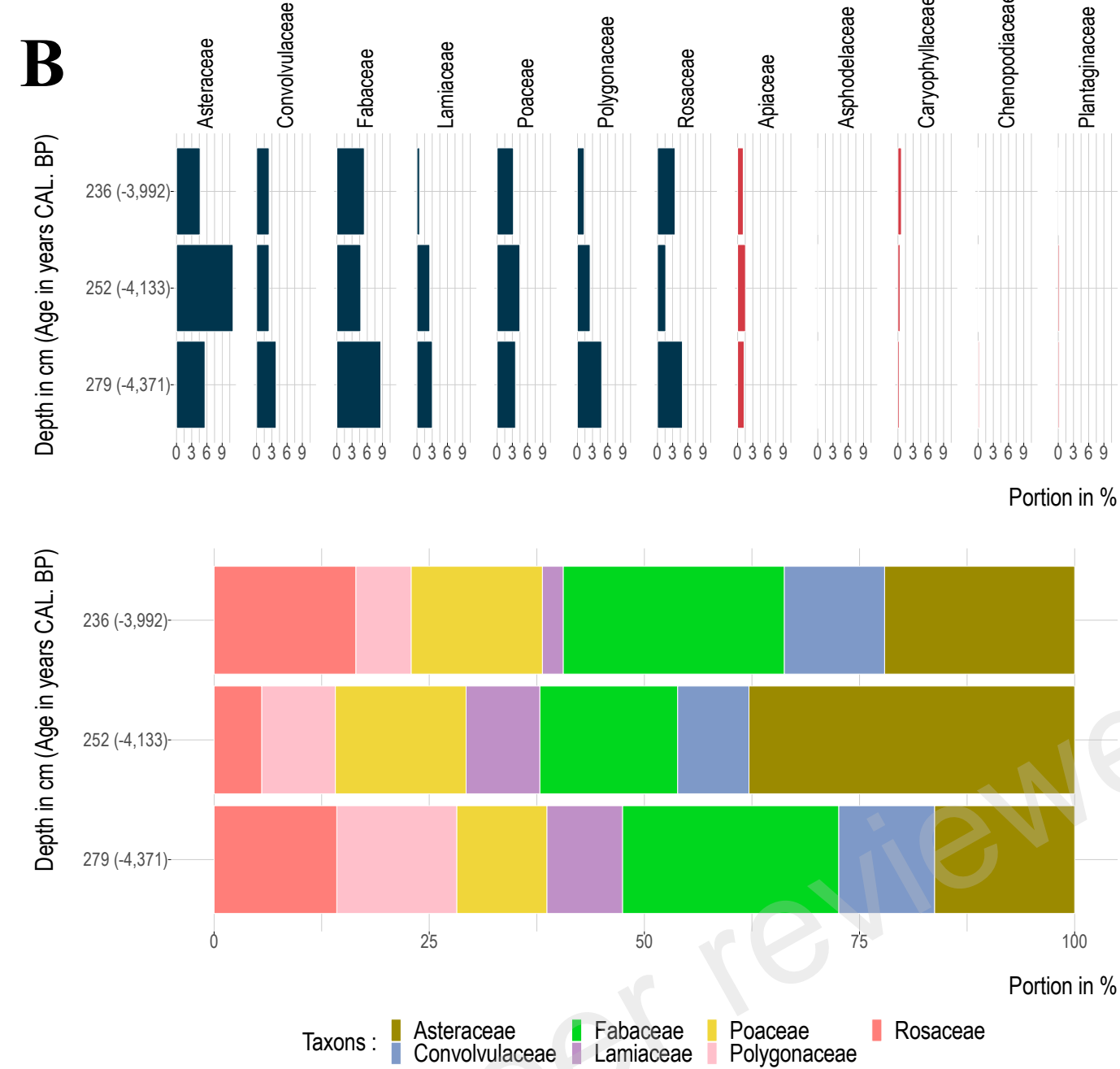
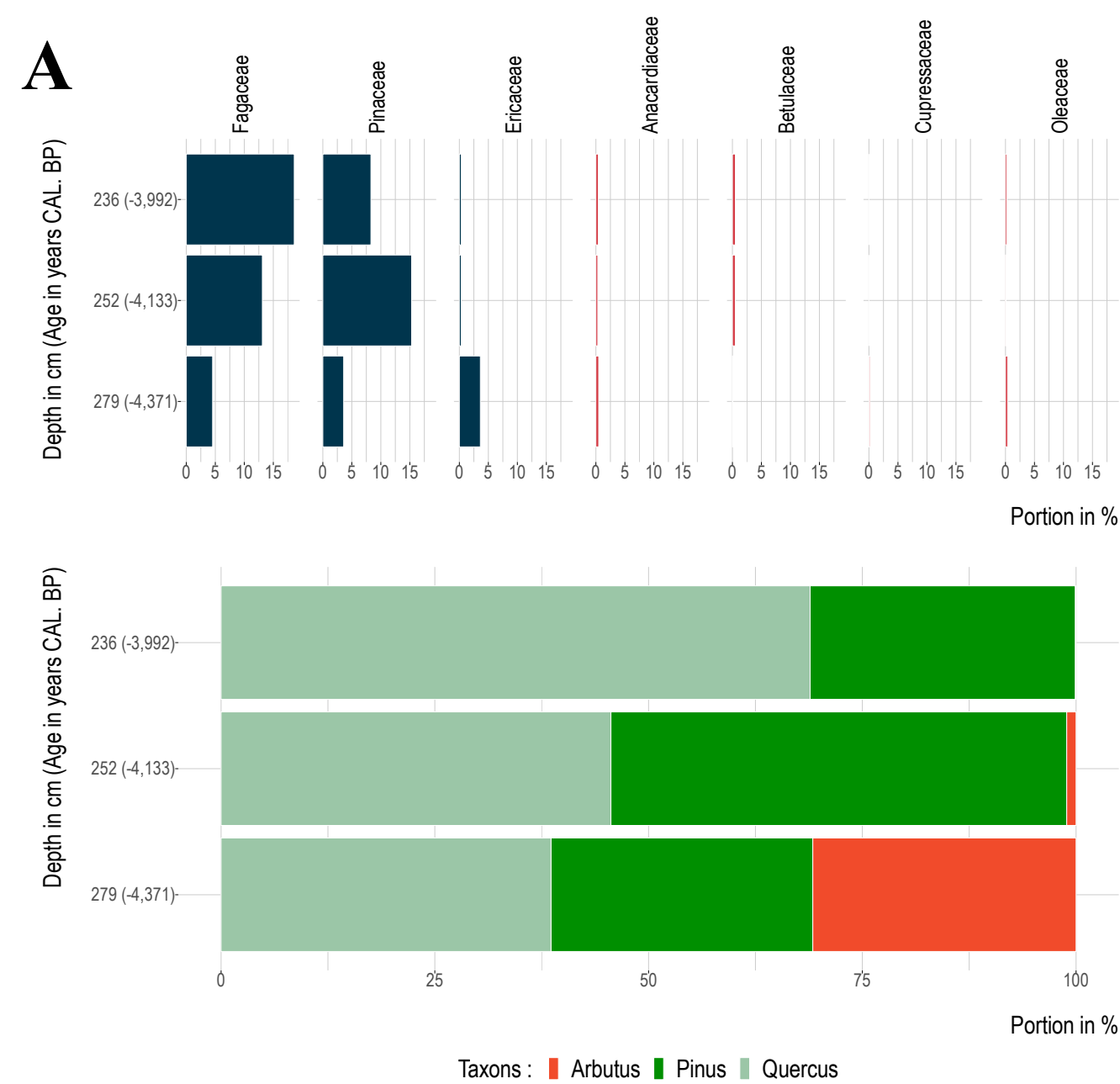


Figure 2: Taxa assigned via *sedaDNA* analysis at Iffer lake between Late Neolithic to Bronze Age among four groups: A) trees and shrubs, B) herbs, C) aquatic plants and D) mammals; and E) : relative proportions of tree/herbs/aquatic plants identified. In A, B, C and D panels: Up: Relative proportion of each plant family/genus among all assigned plant/mammal reads - for which the number of reads >1% of the total number of reads assigned to either plant or mammal taxa in at least one sample or present in the pollen records ; bottom: relative proportion of the main plant and mammal taxa assigned (>1%); red: Plant taxa for which the percentage is <1% and identified in pollen remains.

335 because its pollen is large and heavy and does not travel far from the tree and, moreover, it is
336 similar to other pollens of the Ericaceae family and difficult to distinguish (Almeida et al, 2022).
337 Nowadays in Morocco, *Arbutus* occurs in scrublands, oak forests, and dense maquis. Its density
338 depends on a gradient with densest populations where the climate is subhumid to humid as this
339 species prefers fresh, well-drained soils (Wahid et al, 2019). However, *Arbutus* shows strong
340 resistance to hard environmental conditions and has the ability to regenerate after forest fires
341 (El Haouari et al, 2021). The significant decline in its population, in proportion to that of
342 *Quercus* and *Pinus* after 4.2 ka BP could be explained by the so-called “4.2 cal. ka BP event”
343 corresponding to an interval of cooling and drying conditions (Bini et al, 2019). During this
344 period, the percentages of tree pollen show, in Morocco, a moderate increase in tree cover
345 between 4.5 and 4.2 ka BP followed by a decline, creating an opening of the forests between
346 4.2 and 3.9 ka BP (di Rita et al, 2022). As *Arbutus* is part of the understory vegetation and its
347 growth has been shown to be inversely related to the presence of holm oak (Badal et al, 1994),
348 we can hypothesize that the growth of the forest cover between 4.5 and 4.2 ka BP, followed by
349 its opening, also observed with our *sedaDNA* results, is one of the causes of the decline of this
350 species after 4.2 ka BP.

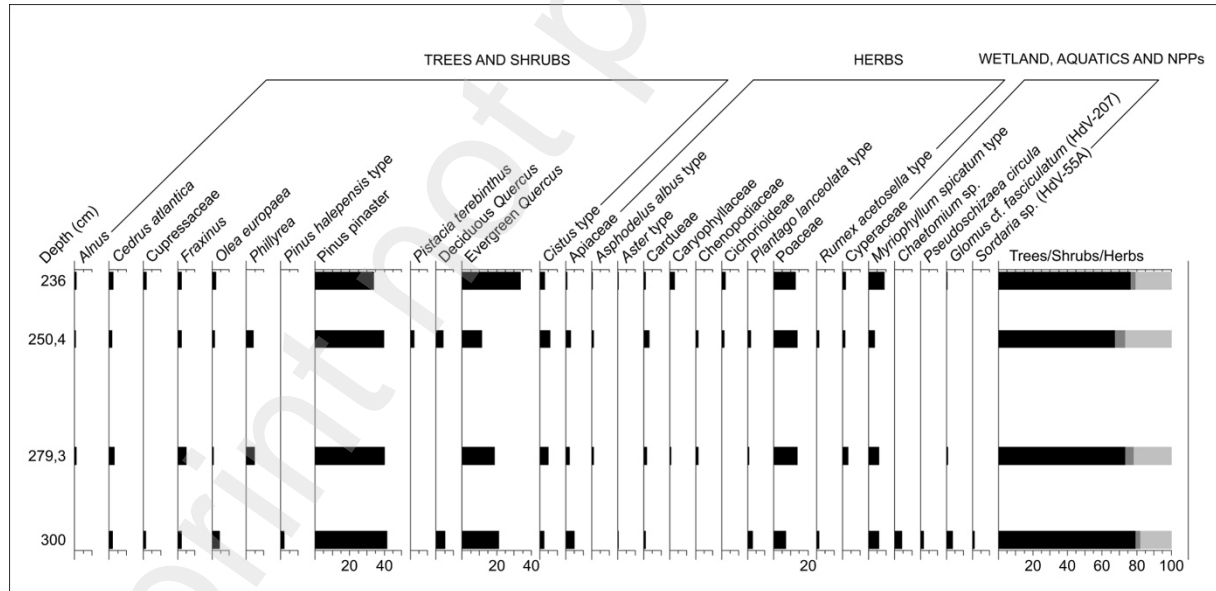
351 This forest development around the 4.2 ka BP event is clearly evidenced by our Iffer Lake
352 *sedaDNA* analysis. The proportion of tree DNA increases from 12% to 30% between 4.3 ka
353 and 4.1 ka BP and then stabilizes (Figure 2E). This dominant association of *Quercus* and *Pinus*
354 is also corroborated by palynological analyzes which confirm that this *Pinus-Quercus* mixed
355 forest ecosystem is well developed during this period (Table S3, Figure 3). They are associated
356 with *Olea europea* around 4.5 ka BP and then riparian taxa at 4.3 ka BP (*Alnus* and *Fraxinus*)
357 while *Cedrus* remains constant. We first observe a predominant presence of *Quercus*, that
358 decline together with *Cedrus* or *Olea europea*, indicating some deforestation around 4.1 ka BP.
359 This episode is followed by a re-expansion of oak forests at 3.9 ka BP and *Olea europaea* and
360 the progressive disappearance of riparian taxa, (Figure 2A, Figure 3).

361 This significant disturbance in the relative composition of mixed oak and pine forests between
362 4.1 and 3.9 ka BP could be attributed to drought but also probably to possible fires. In Ait Ichou,
363 70 km from Ifter lake, the number of micro-charcoals increased considerably after ~4.5 ka BP
364 with maximum values between ~3 and 1.5 ka BP (Tabel, 2015). As human activities in the
365 Middle Atlas were rather minor until ~2-1.5 ka BP (Cheddadi et al, 2015; Tabel, 2015), these
366 fires are likely of natural origin, given the more arid environment. A recent study, carried out
367 in the northeast of Spain, shows that, while these two species regenerate effectively after fire,
368 *Pinus* recolonizes disturbed areas via seedlings, whereas *Quercus* regrows vigorously after

369 disturbances. Therefore, in mixed forests, even small-scale fires can lead to significant
 370 probabilities of transitioning from mixed forests to monospecific forests, with *Quercus*
 371 dominating at higher altitudes and *Pinus* at lower altitudes, particularly in drier and warmer
 372 conditions (Broncano et al, 2005). We can therefore hypothesize that the relative deforestation
 373 and the decrease in Pine DNA in favor of oak DNA between 4.1- 3.9 ka BP would correspond
 374 to the consequence of fires, themselves linked to an episode of drought.

375 At Dayat Hachlaf, a few kilometers from lake Iffer, *Quercus* and *Pinus* forest contingencies
 376 have been recorded since 6 ka BP, with a noticeable change in forest composition around 3.5
 377 ka BP (Nourelbait, 2016). These *Quercus-Pinus* variations were not really recorded via the
 378 palynological study. *Pinus* is a well-known quantitatively and extensively dispersed pollen
 379 producer (Poska and Pidek, 2010; López-Sáez et al., 2013), dominating Iffer lake record and
 380 complicating the correlation between its presence on the site and its pollen abundance (Bell &
 381 Fletcher, 2016), well in less proportion. Other trees are detected by the pollen (Cupressaceae,
 382 *Cedrus*, *Olea europaea* and riparian taxa (*Fraxinus*), only found as traces for some of them
 383 among *seadDNA* data, indiscernible among other representatives of the same families (co-best
 384 hits and <2% of assigned reads).

385



386

387 **Figure 3:** Palynological diagram reconstituted from four samples at Iffer lake, covering a 380 years
 388 period (Late Neolithic to Bronze Age)

389

390 Among herbaceous, seven families could be determined among *seadDNA* sequences, each with
 391 a majority *genus* (Lamiaceae/*Salvia*, Convolvulaceae/*Convolvulus*, Fabaceae/*Medicago*,
 392 Polygonaceae/*Rumex*, Asteraceae/*Artemisia*, Poaceae/*Phragmites*, Rosaceae/*Potentilla*, Figure

393 2B). We noticed a slight variation in the proportion of these taxa over time where Fabaceae is
394 the most abundant around 4.3 ka BP whereas Asteraceae dominates at 4.1 ka BP in detriment
395 of other families, and in association with other ruderal taxa in the palynological record
396 (*Plantago lanceolata*, *Rumex*, *Medicago*; Figure 3). The palynological rests are dominated by
397 Poaceae, showing probably the presence of grasslands in the vicinity.

398 Finally, we could determine two major *genera* of aquatic plants among *sedaDNA* sequences
399 (Figure 2C, Table S6): *Myriophyllum* (Haloragaceae) and *Ceratophyllum* (Ceratophyllaceae),
400 along with low amount of *Ruppia* (Cymodoceae) and *Carex* (Cyperaceae). *Myriophyllum* and
401 *Carex* were also determined in palynological remains with the same relative evolution of their
402 proportion (Figure 3). As already demonstrated in previous studies, aquatic plants, which grow
403 in and around the lake, dominate the assemblage (Figure 2E) to the detriment of terrestrial plants
404 which are often under-represented (Birks, 2003, Alsos, et al 2018). *Myriophyllum* appears in
405 the pollen record of the four samples with constant values of 4-9% (Figure 3), indicating a stable
406 presence throughout this time, as well as shallow and somewhat eutrophic waters. *sedaDNA*
407 results (Figure 2C, Table S6) show a decrease of *Ruppia* and *Carex* over the time since these
408 two species, represent respectively 3.7% and 4.6% of aquatic plants at 4.3 ka BP then pass to
409 the state of traces.

410 *Myriophyllum* dominated in the lake during the whole studied period even if we observe, at
411 4,133 cal. BP, an increase of the proportion of *Ceratophyllum sp.* *Myriophyllum* and
412 *Ceratophyllum* are two species of submerged macrophytes with common characteristics (fast
413 growth, low preference for light). However, *Myriophyllum* is a rooted species, while
414 *Ceratophyllum* does not form roots and is found free-floating. Consequently, nutrient uptake by
415 *Ceratophyllum* is almost entirely foliar whereas *Myriophyllum* can absorb nutrients from
416 sediments and the water column, thereby limiting nutrients available to floating plants (Cao &
417 Wang, 2012). Although Noubail et al (2016) seems to denote that the proportion of aquatic
418 plants cannot be used as indicators of lake level variations but only presence of water in the
419 site, a paleoecological analysis of the macro-remains of Lake Iffer for 6000 years (Middle Atlas,
420 Morocco, Huillery, 2022) shows, between 4,350 and 3,320.5 cal. BP, a progressive installation
421 of relatively humid conditions. Same study pointed out abundance of microcharcoals between
422 4.1-3.9 ka BP that testifies local fires (which corroborates our hypothesis concerning the cause
423 of the *Quercus-Pinus* shift). We can hypothesize that *Ceratophyllum* benefited from favorable
424 conditions (light, dissolved nutrient) at 4.1 ka BP but that then, plant degradation following
425 fires and humidification of the environment favored *Myriophyllum*. This hypothesis
426 corresponds to the observations showing that, in Lake Iffer, between 4.6 and 3.6 ka BP, the

427 organic matter content marks a very significant return in terms of contribution compared to the
428 previous period (Rhoujjati et al, 2012).

429 In total, all taxa identified by pollen were retrieved in sedaDNA (sometimes as traces) but
430 *sedaDNA* identified seven taxa absent in pollen (Ericaceae, Convolvulaceae, Fabaceae,
431 Lamiaceae, Rosaceae Ceratophyllaceae and Cymodoceae), either because pollen diffusion
432 mode (anemogamy and entomogamy) or low quantity of pollen produced and/or detected. The
433 absence of total overlap between the two approaches as well as the relative differences between
434 trees/shrubs and herbaceous is not surprising. Pollen reflects local and regional landscape while
435 *sedaDNA* explain local vegetation variation (Capo et al., 2021, Parducci, 2013, 2019).

436
437 Altogether, results indicate an environment dominated by evergreen oak and Poaceae. Around
438 4.3 ka BP, increased environmental humidity is characterized by the rise of *Fraxinus* and
439 Cyperaceae. This precedes a relative opening of the environment, between 4.1- 3.9 ka BP, with
440 relative deforestation, the gradual disappearance of riparian taxa and the decrease in Pine in
441 favor of oak. This may have resulted from a drought episode, possibly linked to the "4.2 ka cal.
442 BP event." Additionally, we observe greater anthropic pressure during the same period, as
443 evidenced by the presence of ruderal taxa.

444
445

446 ***4.2 Evidence of increased anthropization and pastoralism***

447

448 Morocco, especially the Western Maghreb, is the most well-dated and documented
449 region of Mediterranean Africa (excluding Egypt) between 6,000-2,900 years BP. However,
450 information remains scarce, particularly about the ways of life that supported people in this area
451 during the preceding fourth and early third millennia BP (Lucarini et al., 2021).

452 Among *sedaDNA* sequences, the major part of mammal reads mapped on Elephantidae and
453 Bovidae mitogenomes. Two main genera identified within Bovidae are *Ovis* and *Bos*, but
454 differentiation between the two genera was not always possible due to the similarity of the
455 genomic regions mapped to the reads. In the palynological record, in sample 300, fungal
456 ascospores of coprophilic ecology (*Sordaria* sp., Figure 3), a fungi that develop in animal
457 excrement, have been identified (van Geel, 1978, López Sáez and López Merino, 2007). Its
458 scarce dispersion undoubtedly determines the existence of animals on a local scale.

459 Domesticated animals, mainly caprines and cattle (all already present during the eighth-seventh
460 millennia BP), remained widely attested throughout Mediterranean Africa. In Western

461 Maghreb, their presence is reported in coastal sites during the early to mid-sixth millennium BP
462 with evidence of cattle, caprines, and pigs (Linstädter et al., 2018; Morales et al., 2013;
463 Schmieder and Edwards, 2011). Later, the site of Oued Beh (late sixth millennium BP),
464 indicates a possible socially complex agricultural society (Rus et al., 2012). Evidence of
465 pastoral activity and crop cultivation remains diffuse for the first half of the fifth millennium
466 BP (Lucarini et al., 2021). Finally, during the fourth millennium BP until the start of the third
467 millennium BP only few remains attest of pastoral way of life with the presence of domestic
468 cattle and caprines (Wengler et al., 1994; Wengler and Vernet, 1992).

469 Here we evidence, for the first time, presence of Bovidae on the Iffer site, since 4,371 cal. BP
470 and continuously during at least 380 years. The site and the approach to the lake as an access
471 to the water could have constituted a favorable environment for grazing. We observe the
472 proportion of this taxa increasing since 4,133 cal. BP at the expense of the Elephantidae,
473 detected since 4,371 cal. BP before disappearing 140 years later (Figure 2D). This corresponds
474 to a slight landscape opening and increased human influence, marked by the presence of ruderal
475 taxa. However, there is no indication of cultivated plant taxa at this site. This is not unexpected
476 as it is well-established that agriculture was delayed in most of Mediterranean Africa, due to
477 pastoral groups that have traditionally exhibited robust and resilient lifestyles, influenced by
478 Saharan foraging and pastoral practices (Lucarini et al., 2021). Also, these populations probably
479 exploited wild plants such as acorns, pine nuts, and arbutus (Barker et al., 2010, 2009; Morales,
480 2018; Morales et al., 2015) that were crucial sources of food along the Saharan belt (Dunne et
481 al., 2016; Lucarini, 2014; Mercuri et al., 2018; Wasylikowa, 2001), and the Mediterranean coast
482 (Lucarini et al., 2016) even during Neolithic.

483

484

485 ***4.3 Presence of Elephantidae is impacted by anthropic pressure and climatic*** 486 ***variations***

487

488 The presence of elephants is attested by *sedaDNA* identified in two of the four samples,
489 spanning 140 years (from 4,371 to 4,133 cal BP, Figure 2D). This detection is noteworthy as
490 elephants was not a targeted taxon in the capture. Unlike plants, detecting animals through
491 *sedaDNA* is often challenging and incomplete, given the limited traces they leave. Thus, their
492 detection suggests a significant population on the site, sufficient for their DNA to be deposited
493 and later detected thousands of years later (Giguet-Covex et al., 2019).

494 In the Plio-Pleistocene, proboscidean species in Morocco include the genera *Anancus*,
495 *Mammuthus* (the species *M. africanavus*) and *Elephas*. In Morocco, *Elephas* taxa include the
496 species *Elephas recki* Dietrich 1915, a widespread Pleistocene African species that ranged from
497 Eritrea (Martínez-Navarro, 2010) to the Atlantic coast of Morocco (Arambourg, 1979) and the
498 species *Elephas iolensis* excavated from the mid-pleistocene Anchrif fossil site (Marinheiro et
499 al., 2014; Ouchaou et al., 2017). These specialized grazing species became extinct in the
500 Middle-Upper Pleistocene (Manthi et al., 2020), likely due to the intensity and increasing rate
501 of climatic fluctuations, which favored the generalist and mixed feeder *Loxodonta africana*.
502 The subspecies *Loxodonta africana pharaohensis*, also called Atlas elephant, was present in
503 North Africa and therefore in Morocco, until its extinction in Roman times. In particular, the
504 'African Humid phase' in North West Africa (c.10.5–5.5 ka cal BP) offered favorable
505 conditions permitting its far wide distribution (Schuhmacher, 2017).

506 The exact determination of the genus and the species of Elephantidae at Iffer site was impossible
507 due to the similarity of the genomic regions mapped to the reads in both *Elephas* and *Loxodonta*
508 genus. Although paleontological evidence suggests the absence of *Elephas* genus in this region
509 during that period, we could hypothesize they could belong to *Loxodonta* taxa. Moreover, none
510 of the reads attributed to Elephantidae matches 100% with the available sequences of current
511 representatives (mitogenomes available for seven different species). It suggests that these
512 sequences could be attributed to a species not represented in the current databases and therefore
513 possibly ancient, as it is the case for *Loxodonta africana pharaohensis*.

514 During the Neolithic and Bronze Age period, the presence of elephants in Morocco has been
515 documented through various archaeological artefacts and rock art (eg: petroglyph of an
516 elephant, cave site of Aït Ouazik, late Neolithic, engravings of Hassi Ghilan; (Boudouhou,
517 2020; Daugas, 2010; Schuhmacher, 2017). While these representations and archeological
518 elements could testify of their environment, of the richness of the fauna in the Atlas and of the
519 use of elephants (hunting, transportation, trade, ivory) (Daugas, 2010; Fregel et al., 2018;
520 Schuhmacher, 2017), the scarce number of objects and remains in Morocco do not allow to
521 fully understand their exploitation and incorporation in the human system and in this region
522 during Neolithic and Bronze Age. Here, we both show archeological and biological evidence
523 of human site occupation and of pastoralism 4,371 years ago, while elephants were present at
524 Iffer site. Although we cannot presume human-elephant interactions, we can assume that these
525 animals were indeed part of the anthropological system and could even be exploited. Their
526 importance is attested, for example, by the existence, since the Chalcolithic, of African ivory
527 exchange networks from the Maghreb to southwestern Spain and Portugal (Schuhmacher,

2017). Its disappearance from sample 236 at 3,992 cal. BP, for which the plant biodiversity as well as the number of DNA sequences attributed to each taxon is similar to samples 279 and 252, could more likely be linked to both anthropic pressure and climatic variations. Their disappearance followed a period of warmer and drier climate leading to a decline of the forest and an opening of the landscape. Together with a possible exploitation of this species, the relative intensification of pastoralism and a change in land use (even if no agricultural practice was detected), their preferred environment could have been modified affecting their ability to survive.

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537
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5. Conclusion

539

Here, for the first time in Northern Western Maghreb, we employed both palynological and paleogenomic to reveal climate changes and human presence at Iffer lake from late Neolithic to Bronze Age. Archeological and biological results demonstrate evidence of pastoralism 4.3 ka years ago on this site. The intensification of anthropic pressure in this region precedes the environment opening between 4.1-3.9 ka BP possibly triggered by a drought episode linked to the so-called "4.2 ka cal. BP event". Both factors likely contributed to the local decline of Elephantidae, whose presence is attested through ancient sedimentary DNA.

Our results hold significant importance for the archaeological community. They not only shed light on the processes of anthropization in this region, but also provide valuable evidence of pastoral practices for a period poorly documented. Particularly noteworthy is the detection, for the first time through *sedDNA*, of the presence of Bovidae and Elephantidae. It offers new perspectives for the exploration and study of these Mediterranean sites with scarce archeozoological material. An extensive analysis of the genomic data (including at the microbial level) is currently underway to gain a deeper understanding of the ecological changes of this site. This data will be complemented by a more comprehensive paleoclimatic study to facilitate a better interpretation of biodiversity changes.

Extending ancient sedimentary DNA analysis to more recent and arid periods, characterized by intensified anthropization and catchment detriticism, would be valuable in observing the evolution and response of DNA signatures and biodiversity. Additionally, a high-resolution coupled analysis between DNAs and pedosedimentary facies, as opposed to traditional sedimentology and geochemistry, could help discern the connection between the DNA signal and the stability/instability of slopes near Lake Iffer.

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574

575 **Data availability:** Raw genomic sequence data are available on request.

576

577 **Declarations of interest:** The authors declare that they have no known competing financial
578 interests or personal relationships that could have appeared to influence the work reported in
579 this paper.

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