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**Patterson, DB, Lehmann, SB, Matthews, T, Levin, NE, Stynder, D, Bishop, LC and Braun, DR**

**Stable isotope ecology of Cape dune mole-rats (*Bathyergus suillus*) from Elandsfontein, South Africa: implications for C<sub>4</sub> vegetation and hominin paleobiology in the Cape Floral Region**

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### Article

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1 **Stable isotope ecology of Cape dune mole-rats (*Bathyergus suillus*) from Elandsfontein,**  
2 **South Africa: implications for C<sub>4</sub> vegetation and hominin paleobiology in the Cape Floral**  
3 **Region**

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25 Keywords: *Bathyergus*, isotope ecology, C<sub>4</sub>, hominin, Elandsfontein, mid-Pleistocene

26

27 **Abstract**

28 The archaeological and paleontological records from the west coast of South Africa have  
29 potential to provide insights into ecosystem dynamics in the region during the mid-Pleistocene.  
30 Although the fossil record suggests an ecosystem quite different than that of the region today,  
31 we understand little about the ecological factors that contributed to this disparity. The site of  
32 Elandsfontein (EFT) dates to between 1.0 and 0.6 million years ago (Ma), preserves *in situ* lithic  
33 and faunal materials found in direct association with each other, and provides the rare  
34 opportunity to examine the relationship between hominin behavioral variability and landscape  
35 heterogeneity in a winter rainfall ecosystem. In this study, we examine the stable carbon  
36 isotopic composition of a large sample (n = 81) of Cape dune mole-rats (*Bathyergus suillus*) and  
37 contemporaneous large mammals (> 6 kg; n = 194) from EFT. We find that  $\delta^{13}\text{C}$  values of *B.*  
38 *suillus* are significantly different to those of contemporaneous large mammals from EFT  
39 indicating a significant presence of plants utilizing the C<sub>4</sub> photosynthetic pathway during the  
40 mid-Pleistocene, in contrast to present C<sub>3</sub> dominated ecosystems along the west coast of South  
41 Africa. Additionally, we find that artifact density at EFT localities is positively correlated with  $\delta^{13}\text{C}$   
42 values in *B. suillus* enamel suggesting that evidence of more intense hominin occupation may  
43 be associated with the presence of more C<sub>4</sub> vegetation. Lastly, we hypothesize that this unique  
44 distribution of vegetation 1) provided abundant resources for both hominin and non-hominin  
45 taxa and 2) may have concentrated hominin and animal behavior in certain places on the  
46 ancient landscape.

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## 53 **1. Introduction**

### 54 **1.1 Southern African Paleoecosystems**

55 Differing combinations of climatological factors influence ecosystem dynamics in eastern  
56 and southern Africa (Levin, 2015). As a result, placing the rich Quaternary fossil records of  
57 these two regions within a resolute ecological framework requires the integration of marine and  
58 terrestrial proxies reflective of a variety of spatial and temporal scales (deMenocal, 2004;  
59 Behrensmeyer, 2006; Behrensmeyer and Reed, 2013). The last 1 million years of the African  
60 fossil record is particularly interesting because it witnesses many important shifts in mammal  
61 clades (Vrba, 1995; Faith, 2011; Patterson et al., 2014), as well as the blossoming of what many  
62 consider the behavioral repertoire of modern humans (McBrearty and Brooks, 2000; Marean et  
63 al., 2007). Although the integration of high-resolution paleoecological data has proved  
64 successful at many eastern African localities (Potts et al., 1999; Tryon et al., 2014, 2015; Faith  
65 et al., 2015), much less is understood about ecosystems and faunal communities in southern  
66 Africa during a critical time period in mammalian evolution. As a result, extrapolating the  
67 paleoenvironmental conditions of eastern Africa to concurrent time periods in southern Africa  
68 has been especially challenging (Patterson et al., 2014).

69 In southern Africa, differences in the seasonal distribution of precipitation are largely  
70 responsible for the geographic distribution of vegetation (Chase and Meadows, 2007). In the  
71 summer rainfall zone (SRZ), the majority of precipitation falls between October and March. In  
72 contrast, the winter rainfall zone (WRZ), a narrow band incorporating the western and part of the  
73 southern coasts, receives the majority of its rainfall between April and September (Fig. 1).  
74 Between these two regions is the year-round rainfall zone (YRZ) that receives rainfall  
75 throughout the year. Although the extent of these zones are clearly discernable in contemporary  
76 southern Africa, their distribution over the past million years is far from understood. It is,  
77 however, becoming increasingly clear that oscillations in atmospheric and oceanic circulation as

78 well as glacial and interglacial cycles affected the location, duration and intensity of rainfall in  
79 these regions during the Quaternary (Chase and Meadows, 2007).

80 **INSERT FIGURE 1**

81 The relationship between precipitation and vegetation in southern Africa is most evident  
82 in the distribution of plants utilizing the C<sub>3</sub> and C<sub>4</sub> photosynthetic pathways. Globally, C<sub>4</sub> plants  
83 are adapted to low- to mid-elevation tropical systems with high temperatures and warm season  
84 precipitation, while C<sub>3</sub> plants are dominant in regions of higher elevation with lower  
85 temperatures and cool season precipitation (Tieszen et al., 1979; Ehleringer et al., 1997). In the  
86 SRZ, C<sub>4</sub> plants dominate plant communities (Vogel et al., 1978; Rebelo et al., 2006; Radloff,  
87 2008). In the WRZ, however, with the exception of a few common plant communities (e.g.,  
88 strandveld, renosterveld) that contain species that utilize the C<sub>4</sub> pathway, C<sub>3</sub> vegetation  
89 dominates in the form of the low-height, shrubby, fire-adapted fynbos (Cowling, 1992). This  
90 unique vegetation system primarily within the WRZ, classified as the Cape Floral Region (CFR),  
91 is host to nearly 9,000 plant species, a majority (69%) of which are endemic (Cowling, 1992;  
92 Cowling and Lombard, 2002; Goldblatt and Manning, 2002; see Marean, 2010 for summary).  
93 Within the CFR, differences in the proportion of C<sub>3</sub> and C<sub>4</sub> vegetation are primarily related to the  
94 relative abundance of C<sub>3</sub> and C<sub>4</sub> grasses (Bar-Matthews et al., 2010). C<sub>3</sub> grasses are the most  
95 common grasses in the WRZ, while the YRZ contains a mixture of C<sub>3</sub> and C<sub>4</sub> grasses. In the  
96 SRZ, C<sub>4</sub> grasses are more abundant. The vegetative diversity within the CFR is not mirrored in  
97 mammalian diversity (Klein, 1983). Due to the dominance of nutrient-poor fynbos vegetation, the  
98 contemporary CFR does not support a sizable community of large-bodied grazing and browsing  
99 ungulates, but rather is dominated by small-bodied, browsing taxa (Skead, 1980; Klein, 1983).

100 Although C<sub>3</sub> plants are present in high frequencies in the modern vegetative  
101 communities in the CFR (Cowling, 1992), this may not always have been the case. The timing  
102 and underlying climatological drivers of plant distributions in the CFR remain enigmatic. Marine  
103 records from the region beginning in the Miocene indicate an overall increase in aridity with

104 multiple phases of vegetation change alongside relative stability in moisture availability (Maslin  
105 et al., 2012; Hoetzel et al., 2013, 2015). More recent stable carbon isotopic analyses of  
106 mammalian enamel suggest the presence of C<sub>4</sub> vegetation in the CFR during certain periods of  
107 the Quaternary (Luyt et al., 2000; Hare and Sealy, 2013). Much like elsewhere on the African  
108 continent, however, the integration of C<sub>4</sub> vegetation into the CFR plant biome would have likely  
109 been highly heterogeneous within a C<sub>3</sub> dominated system (Feakins et al., 2013). This scenario  
110 is supported by the lack of evidence for C<sub>4</sub> grasses at Langebaanweg approximately 5 Ma (Ma  
111 = million years ago; Franz-Odenal et al., 2002; Rossouw et al., 2009), and evidence of their  
112 presence at younger sites of Elandsfontein (Luyt et al., 2002) and Hoedjiespunt (Hare and  
113 Sealy, 2013) dating to approximately 1.0 – 0.6 Ma and 0.35 – 0.25 Ma respectively. Thus,  
114 although these data suggest that C<sub>4</sub> plants were represented in the CFR during the Quaternary,  
115 we understand little about their overall spatial and temporal distribution.

116         Much of the uncertainty about the relative contribution of C<sub>3</sub> and C<sub>4</sub> vegetation in the  
117 CFR during the Quaternary can be attributed to a spatially and temporally discontinuous  
118 terrestrial paleoclimatic record (Carr et al., 2006). Although the region is host to a rich record of  
119 mammalian fossils spanning the Miocene to Holocene (Singer and Heltne, 1966; Hendeby, 1974;  
120 Volman, 1978; Klein et al., 2007; Marean et al., 2010; Braun et al., 2013a), robust connections  
121 between climate and terrestrial ecosystem dynamics are limited to a few well-studied records  
122 that are geographically dispersed throughout the CFR. The fossil record suggests that the CFR  
123 was drastically different during the Quaternary and was populated with large grazing and  
124 browsing herbivores that are absent from the region today (Klein et al., 2007; Stynder, 2008). In  
125 addition, this region was host to some of the earliest populations of humans that exhibited  
126 ‘modern’ behavior in terms of their manufacture of artifacts and utilization of resources  
127 (Henshilwood et al., 2002; Marean et al., 2007; Brown et al., 2009). This unique and highly

128 dynamic system is unlike that of the region today and requires further investigation to provide  
129 insights into the ecosystem-level drivers of this disparity.

130

## 131 **1.2 Study site**

132 The mid-Pleistocene eolian sediments of Elandsfontein (EFT) present a unique  
133 opportunity to investigate the nature of paleoecosystems within the CFR during the past 1  
134 million years (Fig. 1). These deposits (approximately 11 km<sup>2</sup>) contain an extensive record of  
135 both hominin and non-hominin ecological and behavioral evolution between 1.0 and 0.6 Ma  
136 (Braun et al., 2013a). With *in situ* associated fossils and artifacts, EFT presents the prospect of  
137 illuminating the ecological dynamics within a WRZ paleocommunity during an enigmatic period  
138 in the southern African record (Fig. 2). Although there are localities in the region of older (Franz-  
139 Odendaal et al., 2002) and younger age (Berger and Parkington, 1995; Dietl et al., 2005;  
140 Matthews et al., 2005; Klein et al., 2007; Faith and Behrensmeyer, 2013; Hare and Sealy,  
141 2013), EFT represents a rare window into the ecosystem and faunal community of the CFR  
142 during a period unrepresented at other sites (Klein et al., 2007).

143

### **INSERT FIGURE 2**

144 Paleontological and archaeological research at EFT has occurred intermittently over the  
145 past 50 years. Initial investigations into the EFT deposits resulted in the recovery of a hominin  
146 calvarium referred to as the “Saldanha” or “Hopefield” specimen (Drennen, 1953), a number of  
147 large cutting tools from a site called Cutting 10 as well as a tremendous quantity of non-hominin  
148 mammalian fossils (Singer and Wymer, 1968; Deacon, 1998; Klein et al., 2007). Subsequent  
149 collections during the 1960s and 1980s were the result of non-systematic surface surveys over  
150 a relatively small portion (~3 km<sup>2</sup>) of the extent of the dunefield at EFT (Avery, 1989; Klein et al.,  
151 2007). More recently, analyses were focused on collections of contextually uncertain fossil  
152 material from deflation surfaces across the dunefield; this collection is referred to as  
153 “Elandsfontein Main” and consists of well over 20,000 identified specimens (Klein, 1988; Klein et



154 al., 2007). The collection consists of an extremely diverse mammalian fauna dominated by large  
155 browsing and grazing ungulates suggestive of a paleocommunity that was drastically different in  
156 both diversity and abundance from that present in the CFR today. In addition, an analysis of the  
157 stable carbon isotopic signature of mammalian enamel from the Elandsfontein Main collection  
158 suggests the presence of a small amount of C<sub>4</sub> vegetation in the diet of ungulates from the site  
159 (Luyt et al., 2000; Lehmann et al., *in Review*). Analyses of the mesowear patterns on these  
160 teeth indicate that many large mammals had unexpected dietary adaptations to herbivory based  
161 on their taxonomy (Stynder, 2009). Although these investigations suggest a vegetation  
162 community different than that of contemporary EFT, due to the lack of precise context,  
163 questions regarding the spatial and temporal nature of these patterns remain unresolved.

164 Most recently, beginning in 2008, systematic excavations and collections were  
165 undertaken at EFT to provide a contextual link between environmental and hominin behavioral  
166 data (Braun et al., 2013a; 2013b). These recent efforts have produced a high-resolution  
167 stratigraphic framework for fossils and artifacts across the EFT dunefield and indicate that 1)  
168 there are *in situ* assemblages of mammalian fossils and behaviorally associated artifacts, 2) the  
169 majority of these *in situ* deposits are associated with a nodular layer in pedogenically modified  
170 sands, 3) there is an older, calcretized sand horizon which also contains mammalian fossils but  
171 these fossils are not abundant and are not associated with any artifacts, 4) distinguishing  
172 between *in situ* materials and deposits that reflect ancient episodes of deflation is  
173 straightforward using systematic excavation procedures and geologic observations (Rick, 2002),  
174 and 5) hominin toolmakers transported stone to EFT for the production and use of stone tools  
175 (Braun et al., 2013a).

176 The recent collections at EFT (2008-2015) have resulted in the recovery of a large  
177 sample of fossil Cape dune mole-rats (*Bathyergus suillus*), which is the focus of this study. The  
178 fossil remains of this relatively large, subterranean rodent (780-955 g; Bennett et al., 2009) are  
179 found in substantial frequencies in many excavations in the Pleistocene sediments at EFT and

180 provide the opportunity to characterize localized vegetative environment at EFT due to the  
181 restricted home range of *B. suillus*. Unlike most large mammalian ungulates that range over  
182 vast territories in search of seasonally available resources, small mammals live (and die) within  
183 a highly restricted space (Andrews, 1990; Reed, 1997). Before employing rodents and other  
184 small mammals as indicators of paleoenvironments, however, it is crucial to determine the  
185 agent/s of accumulation within a fossil assemblage (Andrews, 1990). Although small mammals  
186 may die and be preserved within or close to their home range in life, their remains may be  
187 transported away from their original environmental context by mammalian and avian predators  
188 (Matthews et al., 2006a; Reed, 2007; Terry, 2007). If the mode of accumulation can be  
189 confidently established, small mammals may provide an excellent proxy for localized  
190 paleoenvironments. This study uses the stable carbon isotopic composition of *in situ* Cape dune  
191 mole-rat enamel to provide the first analysis of the structure of the EFT vegetative environment  
192 between 0.6 and 1.0 Ma.

193

### 194 **1.3 Modern *Bathyergus suillus* ecology**

195 The genus *Bathyergus* consists of two extant species endemic to southern Africa:  
196 *Bathyergus suillus* (the Cape dune mole-rat) and *Bathyergus janetta* (the Namaqua dune mole-  
197 rat). *B. suillus* is primarily confined to the coastal soils of the Western Cape Province, with a  
198 single record from Rondawel near Groenrivier in the Northern Cape Province (Bennett et al.,  
199 2009). *B. janetta* occurs in the Northern Cape Province, particularly in the Namaqualand  
200 Hardeveld bioregion, Namaqualand Sandveld bioregion and some parts of the Namib desert  
201 (IUCN Red List; Herbst et al., 2004). To date, fossil *B. suillus* remains are only known from sites  
202 from within its historic range, the majority of which are younger than 130 Ka (Klein, 1991).  
203 Previous authors have attributed fossil mole-rat material from the earlier sites of Elandsfontein  
204 (Klein, 1991) and Duinefontein 2 (Klein, 1976) to *B. suillus*.

205 *Bathyergus* is largely solitary (Van Daele et al., 2007) with its spatial distribution  
206 influenced primarily by resource availability. *B. suillus* abundance varies in coastal fynbos and  
207 grassland settings, with high densities in grassland environments (Davies and Jarvis, 1986).  
208 Additionally, the species is large-bodied relative to other African mole-rats (780-955 g) (Bennett  
209 et al., 2009) and dig extensive burrows, some of which can include >400 m of interconnected  
210 tunnels, and typically live within a single burrow system throughout their life (Davies and Jarvis,  
211 1986).

212 Much like other African mole-rats, *B. suillus* feeds upon the underground storage organs  
213 (geophytes) of certain plant species (e.g., *Othonna*, *Wachendorfia*; see Yeakel et al., 2007 for  
214 summary). Unlike other African mole-rats, however, which are primarily subterranean feeders,  
215 more than 60% of the diet of *B. suillus* originates from aerial vegetation pulled into the burrow  
216 via the roots (Bennett et al., 2009). Robb et al. (2012) used stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen  
217 ( $\delta^{15}\text{N}$ ) isotope ratios to illuminate the diet of extant mole-rats in the CFR. The authors conclude  
218 that although geophytes make up a significant proportion of the species' diets, *B. suillus* had a  
219 substantially more generalized diet, including C<sub>4</sub> grasses, than the other mole-rat taxa of  
220 *Cryptomys hottentotus* and *Georchus capensis* from the CFR.

221 *Bathyergus suillus* is preyed upon by avian, mammalian and reptilian predators (Bennett  
222 et al., 2009); however, the archaeological record indicates some degree of exploitation by  
223 human populations in southern Africa (Henshilwood, 1997). This species is particularly  
224 vulnerable to predation when above ground and may be preyed upon by both avian and  
225 mammalian carnivores. When underground, *B. suillus* is frequently predated upon by mole  
226 snakes (*Pseudapis cana*) and Cape cobras (*Naja nivea*) (Bennett et al., 2009).

227

#### 228 **1.4 Study Objectives**

229 In this study, we use carbon stable isotope data from *in situ* mid-Pleistocene *B. suillus*  
230 remains systematically collected at EFT between 2008 and 2014 and address the following  
231 questions:

- 232 1. Do  $\delta^{13}\text{C}$  values of *B. suillus* enamel at EFT reflect the same information about mid-  
233 Pleistocene vegetation as the carbon isotope data from large mammals at EFT?
- 234 2. Can we use the carbon isotope data from the fossil teeth at EFT to identify spatial  
235 patterns in vegetation across the EFT dunefield?
- 236 3. What are the implications of these findings for understanding hominin paleobiology in  
237 the CFR between 1.0 and 0.6 Ma?

238

## 239 **2. Materials and Methods**

### 240 **2.1 Collections**

241 All *B. suillus* material was collected as part of archaeological and paleontological  
242 excavations or systematic trenches (“shovel test pits” or STPs) across the EFT dunefield  
243 between 2008 and 2014 (see Braun et al., 2013a). Collections were distributed spatially based  
244 upon what are referred to as Collection “Bays” which refer to deflation hollows between large  
245 modern dune crests (see Braun et al., 2013a; Fig. 3).

246

### **INSERT FIGURE 3**

247 From this collection, we selected 150 *B. suillus* upper (maxillary) incisors as candidates  
248 for stable isotopic and taphonomic analyses. All *B. suillus* material analyzed here originated  
249 from the artifact and fossil-rich zone (see Braun et al., 2013a). Due to their unique morphology  
250 (Fig. 4), maxillary incisors can be used to distinguish the isolated incisors of *B. suillus* from  
251 those of other relatively large rodent taxa (e.g., *Otomys*) in the EFT collection. We therefore  
252 focused on isolated upper incisors for this study. To preclude the potential of comingling of

253 modern and fossil material, this analysis does not include any specimens recovered from the  
254 artifact- and fossil-rich horizons that were in the upper ~10 – 15 cm of the STPs or excavations.

## 255 INSERT FIGURE 4

### 256 2.2 Taphonomic Analysis

257 Previous researchers have considered *B. suillus* remains from EFT to be  
258 contemporaneous with other fossils and artifacts from the site (Klein, 1991). However, we  
259 recognize three possibilities regarding the origin of *B. suillus* fossils within the EFT Pleistocene  
260 sedimentary units: 1) *B. suillus* remains were deposited and preserved in primary context with  
261 the artifacts and the other associated large mammal fossils as a result of normal mortality of *B.*  
262 *suillus*, 2) *B. suillus* remains were deposited by avian and mammalian predators living at EFT  
263 around the time of deposition of other fossils and artifacts from the site and are thus  
264 contemporaneous with them and, 3) the *B. suillus* fossils are younger than the other materials in  
265 the fossil- and artifact-rich horizons at EFT, as a product of *B. suillus* burrowing into those  
266 horizons subsequent to deposition. Given that these three scenarios result in two alternative  
267 temporal relationships between *B. suillus* remains and the other archaeological and  
268 paleontological collections at EFT, we conducted a detailed taphonomic analysis of a subset of  
269 *B. suillus* incisors prior to isotopic analyses.

270 To investigate the likelihood of secondary deposition of incisors (i.e., that the fossils  
271 originated from mammalian scats or avian pellets) within the EFT collection, 33 upper incisors  
272 were studied for traces of digestion and rounding on the enamel surface. When animal remains  
273 pass through the digestive system of a predator, digestive acids leave a distinct signature on the  
274 surface of bone or enamel in the form of etching or rounding, particularly in the area of contact  
275 between enamel and dentine (Andrews, 1990; Fernandez-Jalvo and Andrews, 1992). This  
276 signature can be easily discerned with a dissecting microscope. For this analysis, we use a  
277 systematic protocol for evaluating the degree of etching and rounding on rodent incisors

278 (Matthews 2002; 2006b; Table 1). This methodology is akin to that of Fernandez-Jalvo and  
279 Andrews (1992), however categories used here were specifically developed for the incisors of  
280 *Bathyergus* and other southern African rodents. Using this protocol, each incisor within our  
281 subset was photographed under magnification and rated on a scale of 0 – 4 based upon the  
282 degree of etching and rounding on the enamel surface. To remove the possibility of confusion  
283 with other taphonomic processes, such as etching caused by acidic/alkaline soil, specimens  
284 were only scored if there was unquestionable evidence of digestion (refer to Table 1). Acid and  
285 alkaline soils may also cause corrosion and etching on both enamel and dentine (Andrews,  
286 1990; Fernandez-Jalvo, 1995), and could possibly be confused with digestion (see Fig. 4D, 4E,  
287 4F), although there are generally differences in the manner in which this occurs. To avoid any  
288 such errors, analysis erred on the conservative side and only included specimens that showed  
289 clear evidence of having passed through the digestive tract of an avian or mammalian predator  
290 (see Fig. 4B, 4C).

291         To further investigate the stratigraphic relationship between the fossils of *B. suillus* and  
292 the other materials recovered from systematic excavations at EFT, we reviewed the  
293 stratigraphic frequency of *B. suillus* fossils in relation to other materials found in these  
294 excavations. Previously we conducted a related analysis to document the fact that similar finds  
295 (<1cm) are found in similar frequencies as larger finds (Braun et al., 2013a). This analysis was  
296 based on previous work documenting these types of patterns in the Channel Islands (Rick,  
297 2002). Here we test whether the frequency of *B. suillus* fossils track the frequency of other finds  
298 in these excavations. We excluded samples recovered from localities where formal  
299 standardized excavations were not conducted (i.e., material was recovered from shovel test  
300 pits). If the abundance of *B. suillus* fossils through the stratigraphic section closely tracks the  
301 frequency of other fossils in the excavations at EFT, it would suggest that the deposition of the  
302 *B. suillus* fossils and the other materials were the result of similar processes. If the frequency of  
303 these two types of material deviate through the stratigraphic section, however, then there is the

304 possibility that the *B. suillus* fossils were deposited through either 1) a natural mortality event  
305 occurring after mole-rats burrowed down into Pleistocene deposits or 2) deflation of younger  
306 sediments that were previously stratigraphically above the Pleistocene sediments.

307

## 308 **2.3 Stable Isotopic Analysis**

### 309 **2.3.1 Analytical Methods**

310 A subset of 19 *B. suillus* incisors from EFT was analyzed for carbon and oxygen stable  
311 isotope ratios using a laser ablation gas chromatograph system, coupled to a Thermo MAT 253  
312 isotope ratio mass spectrometer in the Department of Earth and Planetary Sciences at Johns  
313 Hopkins University. Although typically less precise than conventional, phosphoric acid digestion  
314 methods (Passey and Cerling, 2006), laser ablation approaches were first used on the EFT *B.*  
315 *suillus* material because they are less destructive and require less sample material than  
316 conventional methods. Because the laser ablation technique samples all material in the laser  
317 ablation pit, and does not select for the carbonate component, it is common to attempt removal  
318 of surface organics prior to analysis (Passey and Cerling, 2006). Here, we used three different  
319 approaches to evaluate the influence of contaminants on the surface of teeth: 1) gentle abrasion  
320 of the surface enamel with a high speed rotary drill to remove secondary material, 2) soaking  
321 the incisors for 15 minutes in 3% hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) to remove organic material and 3) a  
322 control group in which nothing was done to the enamel surface. We analyzed a subset of teeth  
323 targeted for carbon and oxygen isotopes of tooth enamel using the phosphoric acid digestion  
324 method (see methods below) such that we could develop an understanding of the offset in the  
325 results between these two methods that is specific to these samples, as is necessary for laser  
326 ablation studies of fossil teeth.

327 In addition to the dataset of incisors analyzed for comparison to the data obtained from  
328 laser ablation technique (n = 19), a large dataset of *B. suillus* upper incisors were analyzed  
329 using phosphoric acid digestion method (n = 62). As with the laser ablation technique, only

330 upper incisors were analyzed. All incisors were photographed prior to sampling with a high-  
331 speed rotary drill fitted with a diamond bit. Enamel powder was treated for 15 minutes with 3%  
332 H<sub>2</sub>O<sub>2</sub> to remove organic material and rinsed 3 times with distilled water prior to a 15 minute  
333 treatment with 0.1M buffered acetic acid to remove secondary carbonate. Following this  
334 treatment, samples were rinsed 3 times with distilled water and dried overnight at 60°C.  
335 Samples were then loaded into silver capsules and digested in a 100% phosphoric acid bath at  
336 90°C for 10 minutes. Samples were cryogenically cleaned using a custom-built automated  
337 system (Passey et al., 2010) and the resulting CO<sub>2</sub> was analyzed for δ<sup>13</sup>C and δ<sup>18</sup>O on a  
338 Thermo MAT 253 mass spectrometer. An acid fractionation factor of 1.00725 (90°C) was used  
339 for tooth enamel following Passey et al., (2007).

340 Stable isotope ratios for all phosphoric acid digestion and laser ablation samples are  
341 reported as δ values relative to Vienna Pee Dee Belemnite (VPDB) using standard per mil (‰)  
342 notation, where  $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ , and  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the ratios of  
343 heavy to light isotopes (e.g., <sup>13</sup>C/<sup>12</sup>C, <sup>18</sup>O/<sup>16</sup>O) of the sample and the standard, respectively.  
344 During both types of stable isotope analyses, internal working enamel standards were analyzed,  
345 normalized to the carbonate standard NBS-19, routinely to monitor instrument performance. For  
346 the phosphoric acid method, Carrara marble, normalized to NBS-19, was also routinely  
347 measured as an internal working standard. δ<sup>13</sup>C standard deviation of internal standards was  
348 0.3‰, while that of δ<sup>18</sup>O was 0.2‰.

349 Lastly, we compare δ<sup>13</sup>C enamel values obtained from acid-etched, non-acid etched,  
350 laser ablated and phosphoric acid digestion. Although we include the oxygen isotope results for  
351 completeness in the tables of this paper, we do not discuss them in depth and instead focus on  
352 the carbon isotope data.

353

### 354 **2.3.3 Dietary Reconstructions**



355 We use an isotopic dietary mixing model to estimate the potential contribution of C<sub>3</sub>, C<sub>4</sub>  
356 and Crassulacean acid metabolism (CAM) vegetation to the diet of *B. suillus* at EFT. We use  
357 the following equation:

358

$$359 \quad \delta^{13}C_{B.suillus} = (fC_3 * \delta^{13}C_{C_3(veg)}) + (fC_4 * \delta^{13}C_{C_4(veg)}) + (fCAM * \delta^{13}C_{CAM(veg)})$$

360

361 where *f* indicates the fraction of the different dietary inputs from plants that use the three  
362 photosynthetic pathways and δ<sup>13</sup>C indicate published average δ<sup>13</sup>C values for each (Radloff,  
363 2008; Kohn, 2010; Boom et al., 2014).

364 To reconstruct the ingested vegetation, we use a diet-tissue fractionation factor (ε\*<sub>enamel-</sub>  
365 diet) of 11.1‰, which has been shown to be appropriate for small mammals (Podlesak et al.,  
366 2008). The incorporation of CAM vegetation into this analysis is especially important given: 1)  
367 the broad and often poorly understood isotopic signature of CAM vegetation in southern Africa  
368 (Boom et al., 2014), and 2) their well-documented abundance in the CFR (Peters and Vogel,  
369 2005). To incorporate CAM vegetation into our model, we use carbon isotopic values derived  
370 directly from CAM vegetation in the CFR. Boom et al. (2014) characterized the isotopic  
371 signature of 36 taxa of CAM plants from within the CFR. We use the average δ<sup>13</sup>C value for all  
372 CAM plants from the CFR (-19.7 ± 4.0‰; Boom et al., 2014) because we do not know the  
373 specific CAM plants that were prevalent in the region around EFT during the mid-Pleistocene.  
374 For C<sub>3</sub> vegetation we used a δ<sup>13</sup>C value of -27.1 ± 1.6‰ obtained from the large (n = 480),  
375 global compilation of C<sub>3</sub> plants by Kohn et al. (2010). For C<sub>4</sub> vegetation we used a δ<sup>13</sup>C value of  
376 -12.8 ± 1.3‰ obtained by Radloff et al. (2008) for C<sub>4</sub> grasses in the CFR.

377 We estimate the percentage of C<sub>4</sub> vegetation consumed by large mammals at EFT  
378 following a two-member version of the above mixing model, assuming that only C<sub>3</sub> and C<sub>4</sub>  
379 plants contributed to large mammal diets, where *f*<sub>CAM</sub> = 0. For these estimates we use a ε\*<sub>enamel-</sub>

380 diet of 14.1‰ following Cerling and Harris (1999) and compare these values to those obtained  
381 from the *B. suillus* model ( $\epsilon^*_{\text{enamel-diet}} = 11.1\text{‰}$ ; Podelsak et al., 2008) that also considers the  
382 influence of CAM vegetation.

383

### 384 **3. Results**

#### 385 **3.1 Taphonomic Analysis**

386 In the taphonomic sample (n = 33), 18% of EFT *B. suillus* incisors in our taphonomic  
387 subsample (n = 33) showed extreme signs of enamel and dentine etching as a result of  
388 predation (Fig. 4; Table S1). Of the etched specimens, 5 scored greater than 1, with scores of 3  
389 being the most prevalent. Many specimens, especially within the unetched category showed  
390 clear signs of root marks (etching) as well as small, circular areas where both enamel and  
391 dentine were dissolved (see Fig. 4). The latter could be related to intestinal etching, soil  
392 microbes, or soil acidity, but additional actualistic studies are needed to confirm this possibility.

393 Our analysis of the frequency of specimens through the stratigraphic sequence suggests  
394 that the fossils remains of *B. suillus* and those of other fossils from EFT are the result of similar  
395 depositional processes. A clear indication of differences in depositional context is when smaller  
396 specimens increase in frequency while larger specimens decrease (Rick, 2002). The upper 40  
397 cm of the excavation at the 0313 locality shows this pattern suggesting the upper part of this  
398 excavation is representative of a variety of depositional processes. In all other localities in this  
399 analysis, however, the abundance of *B. suillus* fossils tracks that of large mammals at the EFT  
400 Collection Bays (Fig. 5). Braun et al., (2013a) used the relationship between large and small  
401 mammal remains within EFT excavated localities to suggest that there is little evidence of  
402 deflation at certain localities. There have been previous suggestions that the fossiliferous  
403 sediments at EFT represent multiple episodes of deflation and reburial in the past (Klein et al.,  
404 2007). The fact that the frequency of *B. suillus* fossils follows the patterns exhibited by the larger  
405 fossils suggest that 1) these assemblages do not represent ancient deflated surfaces and 2)

406 that the depositional processes that are responsible for the burial and preservation of the large  
407 mammal fossils is also responsible for the presence of the *B. suillus* fossils. If the *B. suillus*  
408 fossils represented instances where younger (or modern) mole-rats burrowed down into the  
409 older Pleistocene sediments and died there, it is highly unlikely that they would preferentially be  
410 buried in the same horizons that also had the highest frequencies of fossils.

## 411 INSERT FIGURE 5

### 412 3.2.1 Laser Ablation vs. Acid Digestion

413 Nearly all enamel surfaces sampled by laser ablation charred significantly, which  
414 suggests a high proportion of impurities on the enamel surface as well as within the enamel  
415 matrix.  $\delta^{13}\text{C}$  values obtained by laser ablation and phosphoric acid digestion of EFT *B. suillus*  
416 enamel ( $n = 19$ ) are compared in Table 2. Average isotopic enrichment ( $^{13}\text{C}\epsilon^*_{\text{laser-acid}}$ ) was  $-5.9 \pm$   
417  $2.2\text{‰}$  and ranged from  $-9.5\text{‰}$  to  $-2.4\text{‰}$ . Acceptable values, as detailed in Passey and Cerling  
418 (2006) are:  $^{13}\text{C}\epsilon^*_{\text{laser-acid}} = -0.5 \pm 0.8\text{‰}$ . The majority of the  $\delta^{13}\text{C}$  values for EFT *B. suillus* incisors  
419 fall outside of the acceptable values obtained by Passey and Cerling (2006). This was true even  
420 for samples treated prior to sampling with either diluted  $\text{H}_2\text{O}_2$  or abrasion of the enamel surface.  
421 As a result, we do not use any of the laser ablation data in any of the following analyses. Due to  
422 the specific preservation circumstances of the *B. suillus* fossils at EFT, laser ablation is an  
423 inappropriate technique for isotopic analysis. The standard deviation of  $\delta^{13}\text{C}$  of JHU internal  
424 tooth enamel standards analyzed in the same laser ablation sessions as the EFT *B. suillus* teeth  
425 was  $0.9\text{‰}$  for  $\delta^{13}\text{C}$  and  $0.5\text{‰}$  for  $\delta^{18}\text{O}$ , which suggests that the poor performance of EFT *B.*  
426 *suillus* incisors is related to the characteristics of the EFT *B. suillus* teeth themselves and not  
427 related to the performance of the laser ablation system. Enamel standards analyzed on the  
428 system had an average  $^{13}\text{C}\epsilon^*_{\text{laser-acid}}$  of  $-1.2 \pm 0.3\text{‰}$ . The poor performance on the laser system  
429 may be due to the nature of preservation of fossil teeth at EFT. Previous analyses have noted  
430 the low carbonate content of EFT fossil teeth (Luyt et al., 2000; Lehmann et al., *In Review*). This  
431 serves as an instructive example that not all samples are appropriate for analysis by laser

432 ablation approaches. All subsequent analyses will be based on data obtained from phosphoric  
433 acid digestion.

434

### 435 **3.2.2 Phosphoric Acid Digestion**

436

#### **INSERT FIGURE 6**

437 EFT *B. suillus*  $\delta^{13}\text{C}$  enamel values ( $n = 81$ ) average  $-7.9 \pm 1.4 \text{ ‰}$  and range from  $-10.4$

438 to  $-4.1 \text{ ‰}$  (Tables 3, S2), while  $\delta^{18}\text{O}$  enamel values ( $n = 81$ ) average  $-0.8 \pm 1.2 \text{ ‰}$  and range

439 from  $-4.1 \text{ ‰}$  to  $2.6 \text{ ‰}$ . When these samples are pooled by Collection Bay, we do not observe a

440 significant correlation between median  $\delta^{13}\text{C}$  value and latitude ( $p = 0.35$ ; Spearman's Rank

441 Correlation) or longitude ( $p = 0.69$ ; Spearman's Rank Correlation) values at EFT (Fig. 6 A,B).

442 We do, however, recognize statistically significant differences between  $\delta^{13}\text{C}$  ratio distributions ( $p$

443  $= 0.01$ , Kruskal-Wallis test of equal medians) across Collection Bays, which suggests significant

444 isotopic heterogeneity across the dune field. It is important to consider, however, that sample

445 sizes for some Bays are especially low (Table 3) and additional targeted sampling is needed to

446 further confirm these patterns.

447 We find no statistically significant differences in the mean ( $p = 0.32$ , ANOVA;  $p = 0.32$ ,

448 Wilcoxon-Mann-Whitney Rank Sum Test) or variance ( $p = 0.52$ , F test for equal variance) of

449  $\delta^{13}\text{C}$  values between the subset of acid-etched and unetched incisors (Fig. 6C).  $\delta^{13}\text{C}$  of etched

450 incisors ( $n = 6$ ) average  $-6.7 \pm 1.2 \text{ ‰}$  and range from  $-8.2$  to  $-5.0 \text{ ‰}$ , while unetched incisors ( $n =$

451  $27$ ) average  $-7.4 \pm 1.2 \text{ ‰}$  and range from  $-10.1$  to  $-4.1 \text{ ‰}$ . Additionally, we find no difference in

452 the mean ( $p = 0.41$ , ANOVA;  $p = 0.28$ , Wilcoxon-Mann-Whitney Rank Sum Test) of  $\delta^{18}\text{O}$  values

453 of acid-etched and unetched incisors. We do, however, find a significant difference in the

454 variance ( $p = 0.003$ , F test for equal variance) in  $\delta^{18}\text{O}$  values of acid-etched and unetched

455 incisors. The similarities in isotopic values between the etched and unetched specimens further

456 support the assertion that all of the EFT *B. suillus* incisors analyzed here originated from the  
457 same fossil population.

### 458 **INSERT FIGURE 7**

459 Fossil EFT *B. suillus* incisors are significantly ( $p < 0.001$ , ANOVA;  $p < 0.001$  Wilcoxon-  
460 Mann-Whitney Rank Sum Test) enriched in  $\delta^{13}\text{C}$  when compared to contemporaneous large  
461 mammals ( $n = 194$ ; Luyt et al., Lehmann et al., *In Review.*) from the site (Fig. 7).  $\delta^{13}\text{C}$  values of  
462 large mammals average  $-10.2 \pm 1.3\text{‰}$  and range from  $-13.3\text{‰}$  to  $-6.9\text{‰}$ . The Lehmann et al. (*In*  
463 *Review*) large mammal dataset from EFT consists of samples from taxonomically (i.e., 8  
464 families) and ecologically (i.e., browsers and grazers) diverse taxa.

465

### 466 **3.2.3 Estimates of C<sub>4</sub> dietary contribution**

467 Even when considering the potential contribution of CAM vegetation, we find that the  
468 mean  $\delta^{13}\text{C}$  value ( $-7.9\text{‰}$ ) for *B. suillus* teeth at EFT would require diets between 20 and 52% C<sub>4</sub>  
469 vegetation (Fig. 7). This is consistent with dietary estimates based upon stable isotopic analyses  
470 for modern *B. suillus* obtained by Robb et al. (2012). It should be noted that the  $\delta^{13}\text{C}$  values for  
471 the modern mole-rats may indicate the consumption of grasses that are not native to the CFR.  
472 This variable diet is consistent with descriptions of modern populations in southern Africa  
473 (Bennett et al., 2009) and agrees with previous studies that indicate the presence of at least  
474 some C<sub>4</sub> vegetation within the EFT vegetative community (Luyt et al., 2000; Lehmann et al., *In*  
475 *Review*).

476

### 477 **3.2.4 Implications for Hominin Paleobiology**

478 The isotopic variation in the fossil *B. suillus* specimens likely reflects some variation in  
479 vegetation in the past. To better understand the relationship between this variation in ancient  
480 vegetation and hominin behavior we investigate the frequency of excavated artifacts at EFT and  
481 the  $\delta^{13}\text{C}$  signature of *B. suillus* from the various localities at EFT. We find that there is a positive

482 relationship (Kendall's Tau = 0.54;  $p = 0.05$ ) between artifact density (count/m<sup>2</sup>) and the median  
483 *B. suillus*  $\delta^{13}\text{C}$  signature when binned by Collection Bay (Fig. 8). We use the non-parametric  
484 Kendall's Tau correlation due to its conservative significance estimates with small sample size  
485 (refer to Table 3).

## 486 **INSERT FIGURE 8**

487

## 488 **4. Discussion**

489

### 490 **4.1 Taphonomic history of *B. suillus* at EFT**

491 The taphonomic data demonstrate that at least 18% of *B. suillus* incisors from EFT  
492 display evidence of digestion (i.e., acid etching), indicating that they were prey items of avian or  
493 mammalian carnivores and became associated with the site through the deposition of pellets or  
494 scats (Fig. 4). The  $\delta^{13}\text{C}$  values from the acid-etched incisors are indistinct from  $\delta^{13}\text{C}$  values of  
495 teeth for which there is no evidence of acid digestion (Fig. 4C). This is also the case for  $\delta^{18}\text{O}$   
496 values. We conclude that the material analyzed here appears to have originated from a fossil  
497 population that has a similar depositional history as the other fossils and artifacts at EFT. This  
498 finding, originally suggested by Braun et al. (2013a), is supported by our analysis of the relative  
499 stratigraphic abundance of *B. suillus* and large mammal fossils at EFT (Fig. 5). We note that we  
500 cannot completely rule out the possibility that some of the fossil *B. suillus* material at EFT  
501 represents geologically later incursions into older deposits.

502

### 503 **4.2 Vegetative variability at EFT during the mid-Pleistocene**

504 The  $\delta^{13}\text{C}$  signature of *B. suillus* suggests significant vegetative variability (i.e., plants  
505 utilizing the C<sub>3</sub>, C<sub>4</sub> and CAM photosynthetic pathways) at EFT during the mid-Pleistocene. The  
506 ubiquity of *B. suillus*, a species with high dietary flexibility (Bennett et al., 2009), at the site,

507 combined with  $\delta^{13}\text{C}$  values spanning approximately 6‰ suggest the ancient local ecosystems  
508 varied significantly. For comparison, the range of  $\delta^{13}\text{C}$  values for *Aepyceros melampus*, a wide-  
509 ranging mixed-feeding bovid, in eastern Africa is approximately 10‰ (Cerling et al., 2003). The  
510 diet of *A. melampus* is directly related to the proportional representation of  $\text{C}_3$  and  $\text{C}_4$  vegetation  
511 across ecotones, such that as these proportions change, so does the diet of *A. melampus*.  
512 Thus,  $\delta^{13}\text{C}$  variation in *B. suillus* from EFT is consistent with findings in modern representatives  
513 (Robb et al., 2012) and suggests that the taxon was a relatively opportunistic feeder in ancient  
514 times and incorporated an isotopically diverse range of vegetation into its diet.

515 Our analyses of the  $\delta^{13}\text{C}$  signature of *B. suillus* (Fig. 6) suggest that the distribution of  
516 vegetation at EFT was highly heterogeneous across space. The spatial distribution of vegetation  
517 types at EFT could be related to highly localized landscape features (e.g., springs). The  
518 heterogeneous nature of the environment at EFT, and the resources available within it, is  
519 supported by the diversity of the large mammal fauna (Klein et al., 2007; Braun et al., 2013a).  
520 Alternatively, the variation that we have identified may be related to the particular taphonomy of  
521 this region. This is attributable to a combination of two possible factors: 1) some degree of time  
522 averaging within the assemblages, and 2) a majority of *B. suillus* material originated from avian  
523 pellets or mammalian scat that were deposited in locations a distance away from the area in  
524 which the material was caught. Although there are clear fossil horizons at EFT (Braun et al.,  
525 2013a), the depositional time represented by these horizons across the dunefield remains  
526 unclear. Dynamic climatic and geologic variables may have resulted in shifting ecotones at EFT;  
527 therefore a fossil sample originating from within one Collection Bay at EFT potentially  
528 represents an accumulation of time-averaged sediment as is the case with almost all  
529 Pleistocene archaeological sites (Shick 1987). Thus, each locality likely represents a unique  
530 window into the ecosystem at a particular time in the dunefield's depositional history. Secondly,  
531 predators may have transported the remains of *B. suillus* across the EFT dunefield, thus

532 decreasing the spatial fidelity of the sample. We suggest that it is likely that a combination of  
533 these factors contributed to the lack of spatial patterning in the  $\delta^{13}\text{C}$  signature of *B. suillus* at  
534 EFT.

535

#### 536 **4.3 Large mammals versus *Bathyergus suillus* at EFT**

537 The  $\delta^{13}\text{C}$  data indicate significant dietary differences between large mammals and *B.*  
538 *suillus* at EFT (Fig. 7). Based upon our dietary mixing model, even after considering the  
539 potential contribution of CAM vegetation, *B. suillus* at EFT consumed significant quantities of  $\text{C}_4$   
540 vegetation. To obtain the mean EFT *B. suillus*  $\delta^{13}\text{C}$  value ( $-7.9 \pm 1.4$  ‰), the diets of individual  
541 mole-rats would have had to included 20 - 52%  $\text{C}_4$  vegetation. In contrast,  $\delta^{13}\text{C}$  values from  
542 large mammals at EFT indicate that individuals had diets with 0-35%  $\text{C}_4$  vegetation (Lehmann et  
543 al., *In Review*), which is significantly less than that of contemporaneous *B. suillus*. This  
544 comparison clearly demonstrates that mole-rat diet at EFT was different than that of large  
545 mammals. Although it is difficult to assess the particular types of plants that contributed to the  
546  $\text{C}_4$  component to *B. suillus* diets (e.g., grasses or sedges), the diet of extant *B. suillus* from the  
547 CFR can potentially shed light on this issue. Although the diet of the species is especially  
548 variable relative to other African mole-rat genera, more than 60% of the diet of modern *B. suillus*  
549 is derived from the blades and rhizomes of *Cynodon dactylon*, a  $\text{C}_4$  grass (Davies and Jarvis,  
550 1986; Bennett and Jarvis, 1995, Smith and Winter, 1996; Yeakel et al., 2007). Although  
551 *Cynodon dactylon* is not endemic to South Africa, it does suggest that *B. suillus* readily  
552 consumes  $\text{C}_4$  resources if available on the local landscape. Thus, we suggest that it seems  
553 more likely that  $\text{C}_4$  grasses and sedges, rather than CAM plants, were the primary source of  
554 relatively high  $\delta^{13}\text{C}$  values in *B. suillus* teeth relative to those of large mammals at EFT.

555 It is also important to consider how variation in the carbon isotope diet-tissue  
556 fractionation factor ( $\epsilon^*_{\text{enamel-diet}}$ ) affects dietary reconstructions, especially between large and  
557 small mammals that potentially have different digestive physiologies (Passey et al., 2005). Here



558 we use a  $\epsilon^*_{\text{enamel-diet}}$  of 11.1‰ which has been suggested appropriate for small mammals  
559 (Podelsak et al., 2008). It is also important to consider, however, a scenario where  $\epsilon^*_{\text{enamel-diet}}$  for  
560 *B. suillus* was closer to that proposed for large mammals (i.e., 14.1‰; Cerling and Harris, 1999).  
561 If the  $\epsilon^*_{\text{enamel-diet}}$  for *B. suillus* were 14.1‰, then *B. suillus* at EFT during the mid-Pleistocene  
562 consumed slightly greater proportions of C<sub>4</sub> vegetation than we suggest in Section 3.2.3 (Fig.  
563 S1). Thus, the estimates provided here for the proportion of C<sub>4</sub> vegetation in the diet of *B.*  
564 *suillus* are conservative, minimum values given uncertainties in  $\epsilon^*_{\text{enamel-diet}}$  for *B. suillus* and other  
565 mole-rats.

566 The carbon isotope data presented here indicate that *B. suillus* consumed significantly  
567 more C<sub>4</sub> vegetation than large mammals at EFT in the mid-Pleistocene. We consider this to be  
568 reflective of elevated concentrations of C<sub>4</sub> vegetation at EFT relative to the surrounding, C<sub>3</sub>  
569 vegetation dominated, CFR. Because large-bodied mammals migrate seasonally and have  
570 more expansive home ranges, their isotopic signature is likely to reflect the vegetation in a  
571 larger geographic region than that of *B. suillus*. Given the relatively small spatial extent of EFT  
572 (~11 km<sup>2</sup>), it is likely that large mammals ranged both within and outside of site and as a result  
573 incorporated vegetation from outside of the bounds of EFT. Even considering post-mortem  
574 predatory transport estimates for avian predators of 1.5 km<sup>2</sup> (Colvin, 1984; Taylor, 1994), the  
575  $\delta^{13}\text{C}$  data from *B. suillus* at EFT represents vegetation from a more limited geographic range  
576 than that of the larger mammals, which in some cases could be greater than 50 km<sup>2</sup> (Klingel,  
577 1969). It is difficult to assess the impact of mammalian carnivore predation on the distribution of  
578 *B. suillus* remains at EFT, but it is unlikely that small carnivores transported mole rats far from  
579 the area in which they were caught. Previous work at EFT suggests a high diversity of  
580 mammalian carnivores at the site (Klein et al., 2007). Although mammalian carnivores can have  
581 extensive ranges based upon body size, metabolic requirements, habitat and diet (Gittleman  
582 and Harvey, 1982), our taphonomic analysis revealed that less than 20% of *B. suillus* incisors  
583 showed definitive evidence of digestion. Therefore, we find it implausible that the  $\delta^{13}\text{C}$  values of

584 fossil EFT *B. suillus* incisors reflect a geographic space equivalent in size to that of the home  
585 range of large mammalian carnivores.

586 An additional possibility is that the C<sub>4</sub> component of *B. suillus* diet is related to the  
587 consumption of C<sub>4</sub> sedges rather than C<sub>4</sub> grasses. Existing work by Mucina et al., (2006) and  
588 Radloff et al., (2008) indicates that wetlands within the WRZ support locally abundant C<sub>4</sub>  
589 biomass. Spring features on the ancient EFT landscape could have provided the water needed  
590 to fuel the growth of C<sub>4</sub> sedges during hot summer months in the CFR. Wetlands associated  
591 with spring features could have also supported C<sub>4</sub> grasses and it has been demonstrated that  
592 certain large ungulate taxa in the CFR preferentially target these grasses when available  
593 (Radloff, 2008). If this behavior was consistent in the past, the presences of C<sub>4</sub> grasses at EFT  
594 may have concentrated large ungulate taxa at the site and may explain the C<sub>4</sub> component of  
595 EFT large mammal diet reported by Lehmann et al., (*In Review*). If these wetland areas,  
596 however, supported only C<sub>4</sub> sedges, which are less likely to be consumed by large herbivores, it  
597 may explain the significantly enriched  $\delta^{13}\text{C}$  values of *B. suillus* relative to those of EFT large  
598 mammals.

#### 599 **4.4 C<sub>4</sub> vegetation in the Cape Floral Region**

600 Although the contemporary CFR lies well within the WRZ and is dominated by C<sub>3</sub>  
601 vegetation, we understand little about the evolution of this climatic system throughout the  
602 Quaternary (Chase and Meadows, 2007). Previous research suggests that C<sub>4</sub> vegetation was  
603 not a major component of CFR ecosystems at 5 Ma (Franz-Odendaal et al., 2002; Rossouw et  
604 al., 2009; Dupont et al., 2011, 2013; Hoetzel et al., 2013, 2015), however analyses of enamel  
605 from large mammals (Luyt et al. 2000; Hare and Sealy, 2014; Lehmann et al., *In Review*)  
606 suggest a minor presence of C<sub>4</sub> vegetation in the mid-Pleistocene, potentially related to  
607 decreased atmospheric  $p\text{CO}_2$  conditions during glacial periods. Our study suggests that a C<sub>4</sub>  
608 signal within the CFR during this period may be somewhat masked by the wide-ranging nature  
609 of large mammals. The carbon isotope data from *B. suillus* at EFT, which sample relatively

610 small geographic regions (<1.5 km<sup>2</sup>) indicate that some regions in the CFR potentially had  
611 greater proportions of C<sub>4</sub> vegetation than is indicated by carbon isotope data from large  
612 mammals alone.

613         It is important to consider the effect of glacial and interglacial climatic cycles on the δ<sup>13</sup>C  
614 signatures of herbivores at EFT (Hare and Sealy, 2013). The crossover model of Ehleringer  
615 (1997) and Cerling (1998) predicts that during glacial periods, atmospheric pCO<sub>2</sub> is lower and  
616 C<sub>4</sub> plants should have a distinct advantage over C<sub>3</sub> plants. Thus, it is hypothesized that during  
617 glacial periods in the CFR, C<sub>4</sub> vegetation would have been a more significant proportion of the  
618 plant biome than during interglacial periods (Hare and Sealy, 2013). Current geochronological  
619 models of EFT make it impossible to ascertain if the sediments at EFT represent a glacial or  
620 interglacial period. Both large and small mammals were collected from within a single fossil- and  
621 artifact-rich horizon at EFT that could represent glacial or interglacial cycles or a combination of  
622 both. Regardless of the specific time period represented, EFT large and small mammals  
623 represent similar depositional circumstances and were likely aggregated over a similar time  
624 interval (Fig. 5).

625         Previous research has demonstrated that in addition to atmospheric pCO<sub>2</sub>, growing  
626 season temperature is the dominant climatic parameter that determines the abundance of C<sub>4</sub>  
627 vegetation within an ecosystem (Terri and Stowe, 1976; Epstein et al., 1997). These studies  
628 suggest that more elevated growing season temperatures result in higher proportions of C<sub>4</sub>  
629 plants within a particular system. As with all plants, however, water availability is crucial for the  
630 initiation of plant growth (Ehleringer et al., 1997). We hypothesize that the consistent presence  
631 of water near springs at EFT evident from spring deposits (Braun et al., 2013a) may have  
632 created conditions in which a significant proportion of C<sub>4</sub> vegetation could thrive during the hot,  
633 dry summers of the WRZ. We further hypothesize that the prevalence of C<sub>4</sub> vegetation would be  
634 elevated in areas with low-lying topography in close contact with the water table (i.e., spring  
635 features). This relationship between spring features and elevated C<sub>4</sub> vegetation has been

636 demonstrated in eastern Africa (Garrett, 2015). In the contemporary CFR, increased C<sub>4</sub>  
637 biomass, specifically *Sporobolus virginicus* and *Stenotaphrum secundatum*, has been  
638 documented in conjunction with estuaries and wetlands (Mucina et al., 2006; Radloff, 2008).  
639 Thus, it is highly plausible that spring features and the resulting availability of water during the  
640 dry summer months resulted in localized instances of C<sub>4</sub> vegetation at EFT during the mid-  
641 Pleistocene.

642 It is also important to consider that the C<sub>4</sub> vegetation component of *B. suillus* enamel  
643 values may have been affected by seasonal variation in the EFT ecosystem. Breeding in *B.*  
644 *suillus* has been shown to be highly seasonal and tied to periods elevated rainfall (Hart et al.,  
645 2006). The shorter life spans and enamel maturation periods in *B. suillus* relative to those of  
646 large mammals, means that the  $\delta^{13}\text{C}$  data from *B. suillus* is representative of relatively shorter  
647 periods of time compared to the  $\delta^{13}\text{C}$  data of large mammals at EFT. If the time of enamel  
648 maturation in *B. suillus* corresponds to a seasonal period in which C<sub>4</sub> vegetation is more  
649 abundant, then the EFT mole-rat  $\delta^{13}\text{C}$  data could represent a bias towards this particular aspect  
650 of the ecosystem. Carbon isotopic data from large mammals at Hodjiespunt (Hare and Sealy,  
651 2013) and EFT (Lehmann et al., *In Review*) however, suggest that the differential winter rainfall  
652 seen in the modern winter rainfall zone was active during the mid-Pleistocene. Thus, C<sub>3</sub>  
653 vegetation is more likely to have increased in the WRZ during instances of increased rainfall.  
654 This scenario would manifest in the enamel of *B. suillus* that would reflect greater amounts of C<sub>3</sub>  
655 vegetation during these periods. This is the opposite of the pattern exhibited in the *B. suillus*  
656 specimens in this study.

657 The connection between C<sub>4</sub> vegetation and standing water could represent an important  
658 insight into the ecological mechanisms behind the elevated diversity and abundance of  
659 mammalian fossils at EFT (Klein et al., 2007). The consistent presence of water would have  
660 been an extremely valuable resource for animals, especially the obligate drinkers during the  
661 relatively long, hot and dry summers in the WRZ. In turn, the seasonal consumption of

662 vegetation from these areas at EFT could be responsible for the small amount of C<sub>4</sub> vegetation  
663 in the diet of large mammals from the site (Luyt et al., 2000; Lehmann et al., *In Review*).

664

#### 665 **4.5 Implications for hominin ecology at EFT**

666 The fossil and archaeological deposits at EFT provide a rare glimpse into hominin  
667 behavior between 1.0 and 0.6 Ma, a period of human history that is poorly understood in Africa  
668 (Patterson et al., 2014). Previous research suggests that hominin occupation at EFT can be  
669 best explained by the complex interplay of availability of stone to make artifacts and the  
670 variability in food resources (Archer and Braun, 2010; Braun et al., 2013a). Our findings suggest  
671 a previously undocumented diversity of vegetative resources at EFT and support this conclusion  
672 on two fronts: 1) EFT likely represented a rare, resource-rich landscape within a broader  
673 regional ecosystem that was relatively resource poor, and 2) this landscape presented an  
674 adaptive scenario for mid-Pleistocene hominins in the Western Cape that is substantially  
675 different from the summer rainfall ecosystems represented in the vast majority of similarly aged  
676 deposits on the African continent.

677 Although we understand little about the position of mid-Pleistocene hominins within the  
678 broader mammalian community in the CFR, EFT provides important clues into hominin  
679 paleoecology during this period. Directly associated artifacts and fauna at EFT (Braun et al.,  
680 2013a) suggests that hominins capitalized on meat resources and were likely drawn to EFT by  
681 what may have been consistently available water and vegetation. Additionally, the incredible  
682 diversity of mammalian carnivores preserved at EFT (Klein et al., 2007; Braun et al., 2013a),  
683 suggests that hominins were a part of the large carnivore guild by this time, a process that  
684 potentially began at least 1 million years earlier on the continent (Werdelin and Lewis, 2013).  
685 Recent work by Forrest et al. (2015) suggests a higher frequency of cut marked bones which is  
686 likely an underestimate due to poor bone surface preservation resulting from the Aeolian

687 depositional setting at the site, at EFT than that indicated by previous studies (Klein et al.,  
688 2007).

689         The isotopic disparity between EFT *B. suillus* and EFT large mammals suggests a  
690 landscape that provided hominins with locally distinct and consistent resources (i.e., water and  
691 associated C<sub>4</sub> vegetation) during periods of resource scarcity in the broader CFR, particularly  
692 during the dry summer months. Although the CFR may have been climatically dynamic during  
693 the mid-Pleistocene (Chase and Meadows, 2007), we hypothesize that the resources available  
694 at EFT may have provided a buffer against broader environmental, and resource instability in  
695 the CFR.

696         Lastly, our analysis contributes to our understanding of intra-landscape hominin behavior  
697 at EFT. Although lithic evidence indicates that hominin behavior varied in intensity across the  
698 EFT dunefield (Braun et al., 2013a), we know little about the ecology of these patterns.  
699 Preliminarily, our analyses suggest that the presence of C<sub>4</sub> resources, could have contributed to  
700 this concentration. Our data indicate a positive relationship between artifact density and median  
701  $\delta^{13}\text{C}$  of *B. suillus* from EFT. This finding suggests that the unique environmental conditions  
702 suitable for C<sub>4</sub> vegetation (i.e., water during the summer months) may have also contributed to  
703 the resultant discard of stone artifacts by hominin toolmakers at similar points on the landscape.  
704

## 705 **5. Conclusion and future directions**

706         We used a large sample (n = 81) of fossil *B. suillus* incisors to assess the distribution of  
707 vegetation at EFT. Our findings suggest that the paleolandscape of EFT contained a unique  
708 mixture of C<sub>4</sub>, C<sub>3</sub> and CAM vegetation relative to the broader fynbos-dominated C<sub>3</sub> ecosystem  
709 of the CFR.  $\delta^{13}\text{C}$  values of *B. suillus* are significantly different from those of contemporaneous  
710 large mammals from EFT and suggest a plant community with a significant presence of plants  
711 utilizing the C<sub>4</sub> photosynthetic pathway, even when the contribution of CAM vegetation in the  
712 diet of *B. suillus* is considered. We hypothesize that this geographically restricted landscape

713 provided abundant resources for both hominin and non-hominin taxa and potentially buffered  
714 these populations against larger environmental fluctuations and resource instability in the Cape  
715 Floral Region.

716 Future studies at EFT hope to increase the resolution with which we understand both  
717 hominin and large mammal behavior in the CFR. Strontium isotopic analysis of both large and  
718 small mammals at the site promises to provide insight into ranging patterns and the opportunity  
719 to further test many of the hypotheses presented here. In addition, geochemical sourcing of raw  
720 materials utilized by EFT hominins can potentially offer insights into the utilization of regionally  
721 available lithic resources (Braun et al. 2008). Lastly, increasing the chronological resolution of  
722 the EFT deposits is crucial to testing climatic hypotheses, especially the impact glacial and  
723 interglacial cycles on the CFR.

724

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733 Planetary Sciences at Johns Hopkins University.

734

## 735 **Figure Captions**

736 **Figure 1.** Modern rainfall seasonality in southern Africa. Inset: location of Elandsfontein (EFT)  
737 and other important archaeological locations along the west coast of southern Africa (rainfall  
738 data: [www.worldclim.org](http://www.worldclim.org); Inset: modified from Braun et al., 2013a).

739

740 **Figure 2.** Temporal distribution of WCP sites. Refer to Figure 1 for spatial distribution.

741

742 **Figure 3.** A) Map of EFT Collection Bays and small mammal collection strategies. B) Shovel  
743 test pit (STP) in Bay 0710; refer to Braun et al., (2013a) for further descriptions of geological  
744 context of EFT; C) 0313 excavation.

745

746 **Figure 4.** A) Modern *B. suillus* skull (NMNH 344067) from Mosselbaai, South Africa; B) WCRP  
747 46140 (acid etch score = 3); C) WCRP 46138 (acid etch score = 3); D) WCRP 45684 (acid etch  
748 score = 0); E) WCRP 45642 (acid etch score = 2; note potential root etching); F) WCRP 45548  
749 (acid etch score = 0); Arrows indicate anterior direction of specimen. Note differences in enamel  
750 surface modification in 3B, 3C, 3D, 3E, 3F. 3D, 3E and 3F could be related to soil acidity,  
751 microbes or both.

752

753 **Figure 5.** Altimetric analysis of the relationship between *B. suillus* fossils and large mammal  
754 fossils from EFT Collection Bays. EFT *B. suillus* fossils depicted with red triangles. EFT large  
755 mammal fossils depicted with black circles.

756

757 **Figure 6.** A) *B. suillus*  $\delta^{13}\text{C}$  values arranged by Collection Bay from north to south, B) *B. suillus*  
758  $\delta^{13}\text{C}$  values arranged by collection Bay from east to west, C) Comparison of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$   
759 values of etched and unetched incisors. Center line represents the sample median, box  
760 represents the 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers represent the sample range exclusive of  
761 outliers, circles represent outliers defined at 1.5 times the interquartile range.

762

763 **Figure 7.** Comparison of EFT large mammals and EFT *B. suillus*. Models of 100% C<sub>3</sub>, CAM and  
764 C<sub>4</sub> represent are associated with the diet of *B. suillus*, not EFT large mammals. Darker green,



765 hashed areas represent overlap between the two distributions. EFT large mammal grazer and  
766 browser mean values from Lehmann et al. (*In Review*).

767

768 **Figure 8.** Relationship between Collection Bay median *B. suillus*  $\delta^{13}\text{C}$  values and Bay artifact  
769 density. Line represents best fit line from median *B. suillus*  $\delta^{13}\text{C}$  values – artifact density linear  
770 model.

771

772 **Figure S1.**  $\epsilon^*_{\text{enamel-diet}}$  affect on EFT large mammal and EFT *B. suillus* distributions. A) Small  
773 mammal  $\epsilon^*_{\text{enamel-diet}}$  (11.1‰) following Podelsak et al., 2008, B) Large mammal  $\epsilon^*_{\text{enamel-diet}}$   
774 (14.1‰) following Cerling and Harris (1999).

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785 **List of Tables:**

786

787 **Table 1.** Protocol used for assigning EFT *B. suillus* upper incisors to acid-etching categories

788

789 **Table 2.**  $^{13}\text{C}_{\text{ε-laser-acid}}$  and  $^{18}\text{O}_{\text{ε-laser-acid}}$  for EFT *Bathyergus* enamel.  $^{13}\text{C}$  Offset<sup>1</sup> and  $^{18}\text{O}$  Offset<sup>1</sup>  
790 refer to difference between values obtained in this study and those of Passey and Cerling  
791 (2006)

792

793 **Table 3.** Summary of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  EFT *B. suillus* upper incisors arranged by Collection Bay

794

795 **Table S1.** Taphonomic analysis of EFT *B. suillus* upper incisors. Refer to Table 1 for etch  
796 scoring protocol.

797

798 **Table S2.**  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of EFT *B. suillus* upper incisors.

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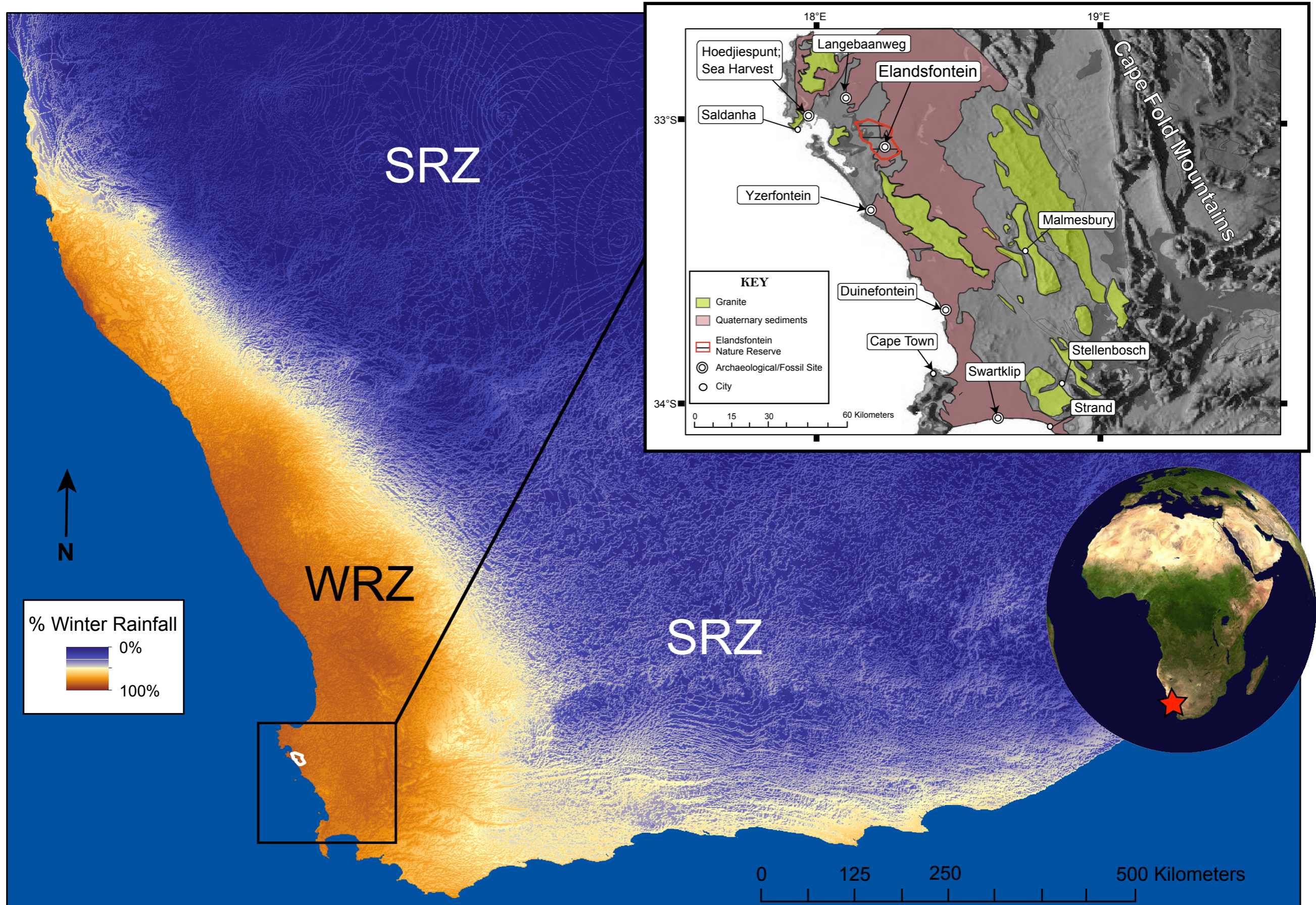
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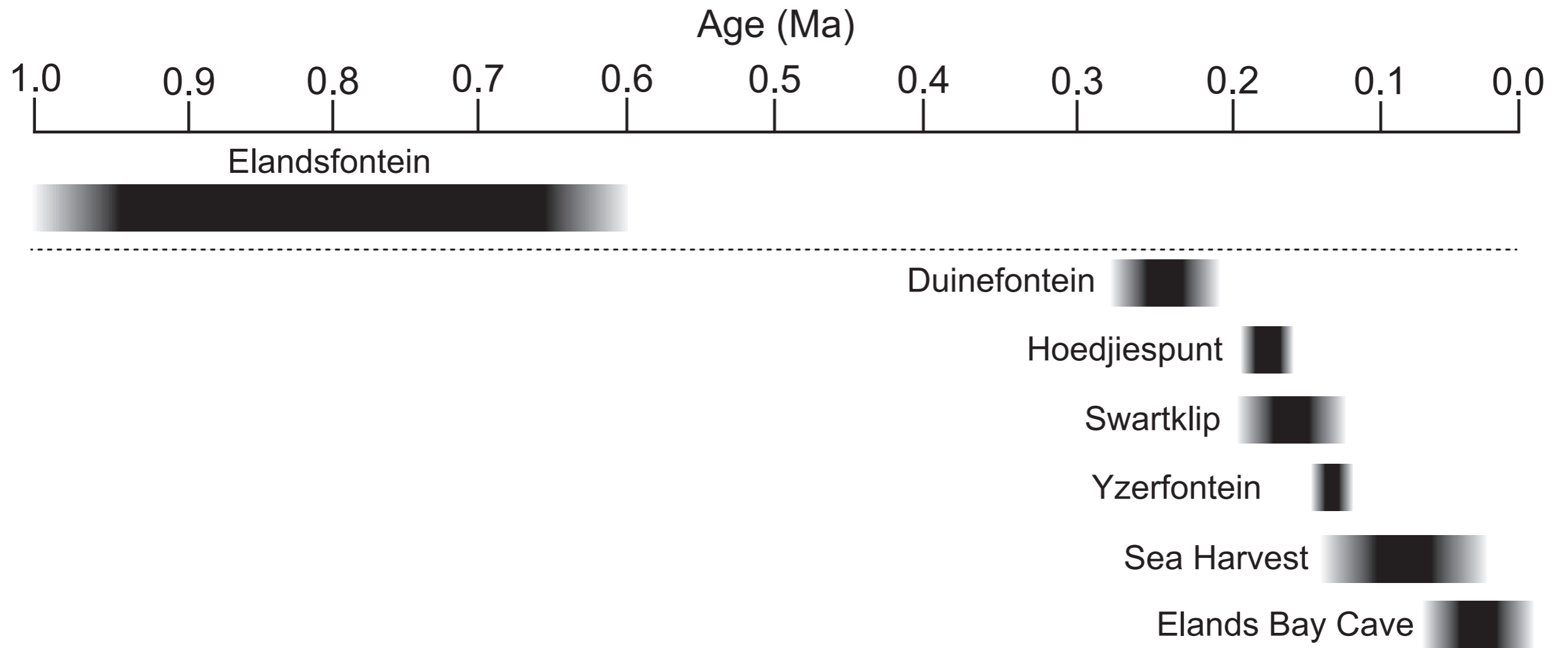
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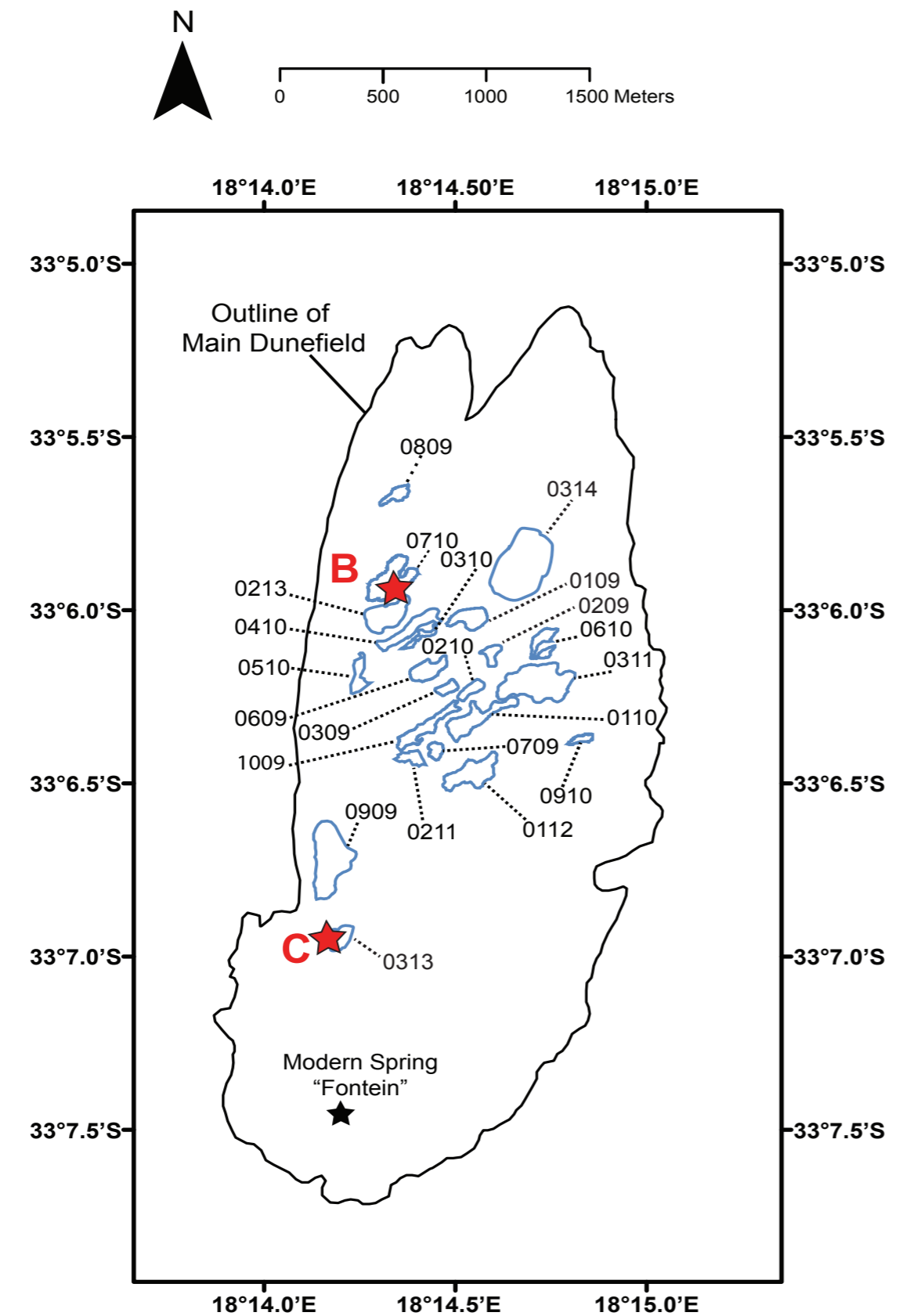
**Figure 1.** Modern rainfall seasonality in southern Africa. Inset: location of Elandsfontein (EFT) and other important archaeological locations along the west coast of southern Africa (rainfall data: [www.worldclim.org](http://www.worldclim.org); Inset: modified from Braun et al., 2013a).



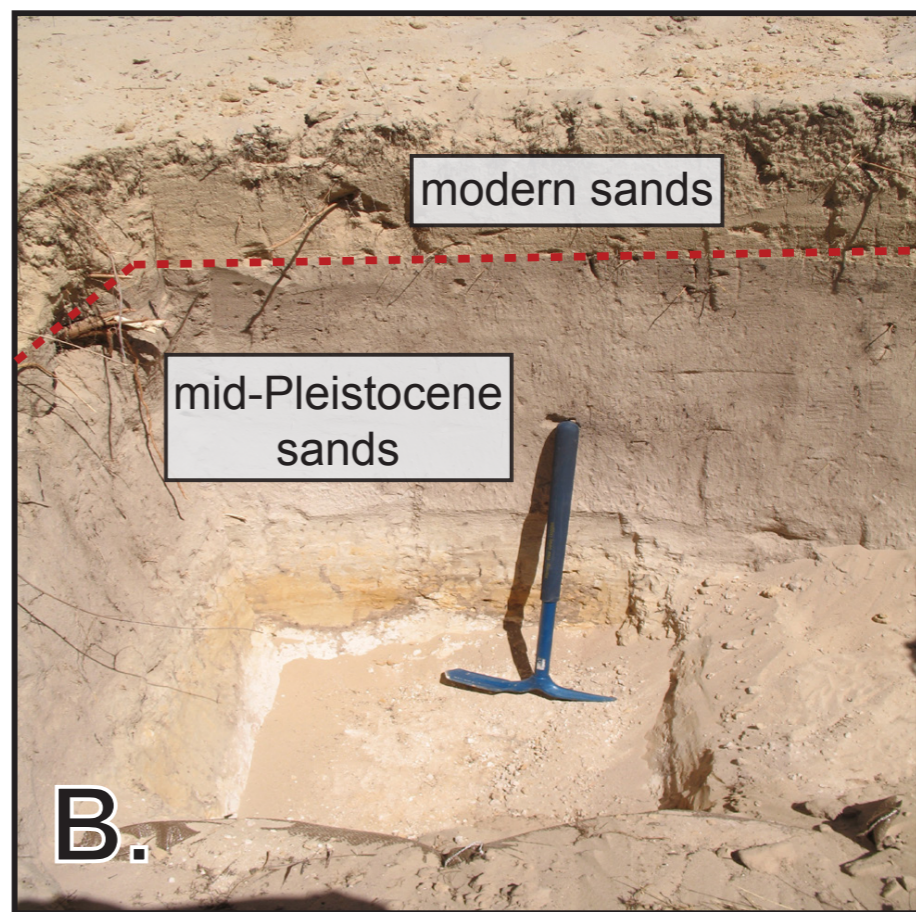
**Figure 2.** Temporal distribution of WCP sites. Refer to Figure 1 for spatial distribution.



**Figure 3.** A) Map of EFT Collection Bays and small mammal collection strategies. B) Shovel test pit (STP) in Bay 0710; refer to Braun et al., (2013a) for further descriptions of geological context of EFT; C) 0313 excavation.



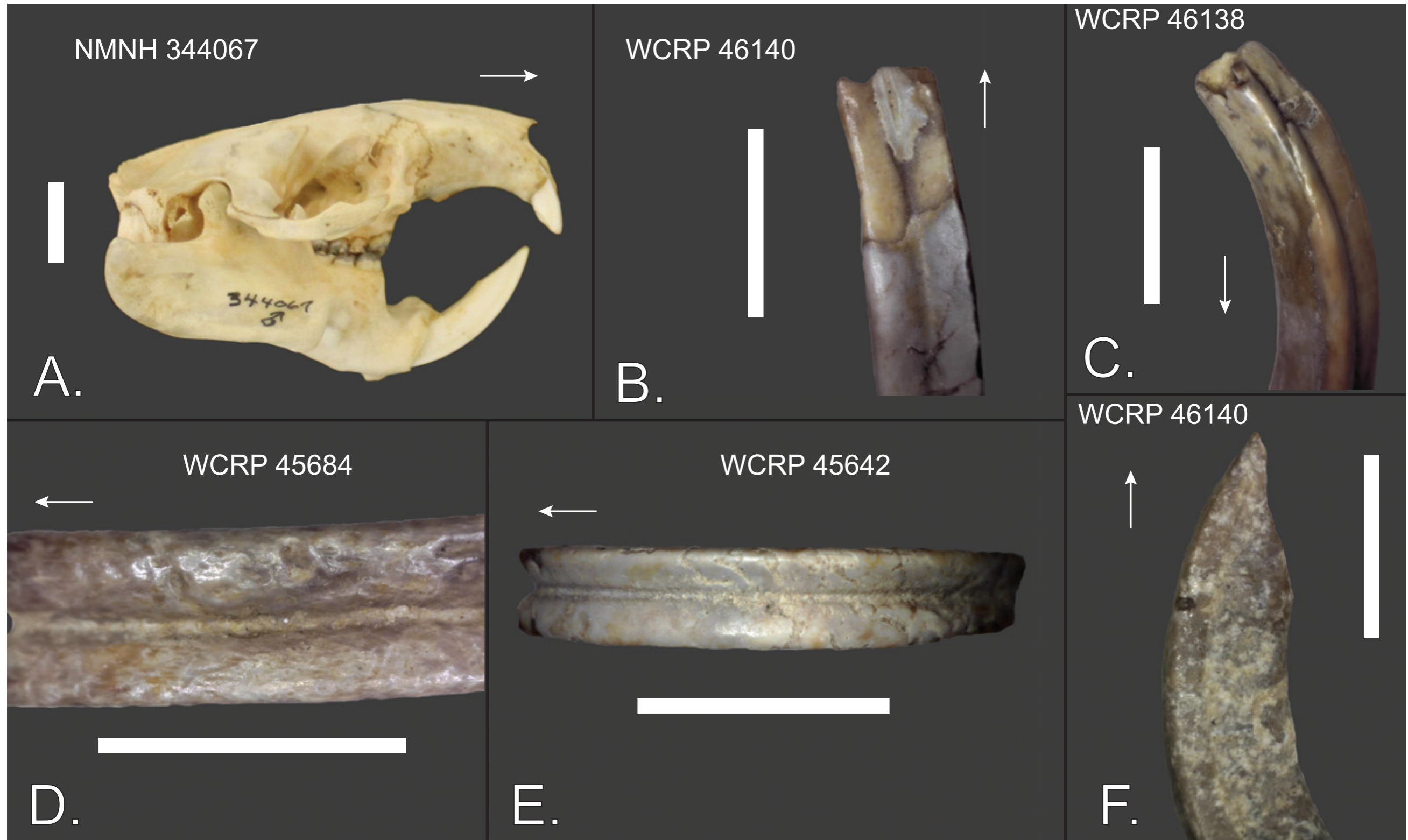
**A.**



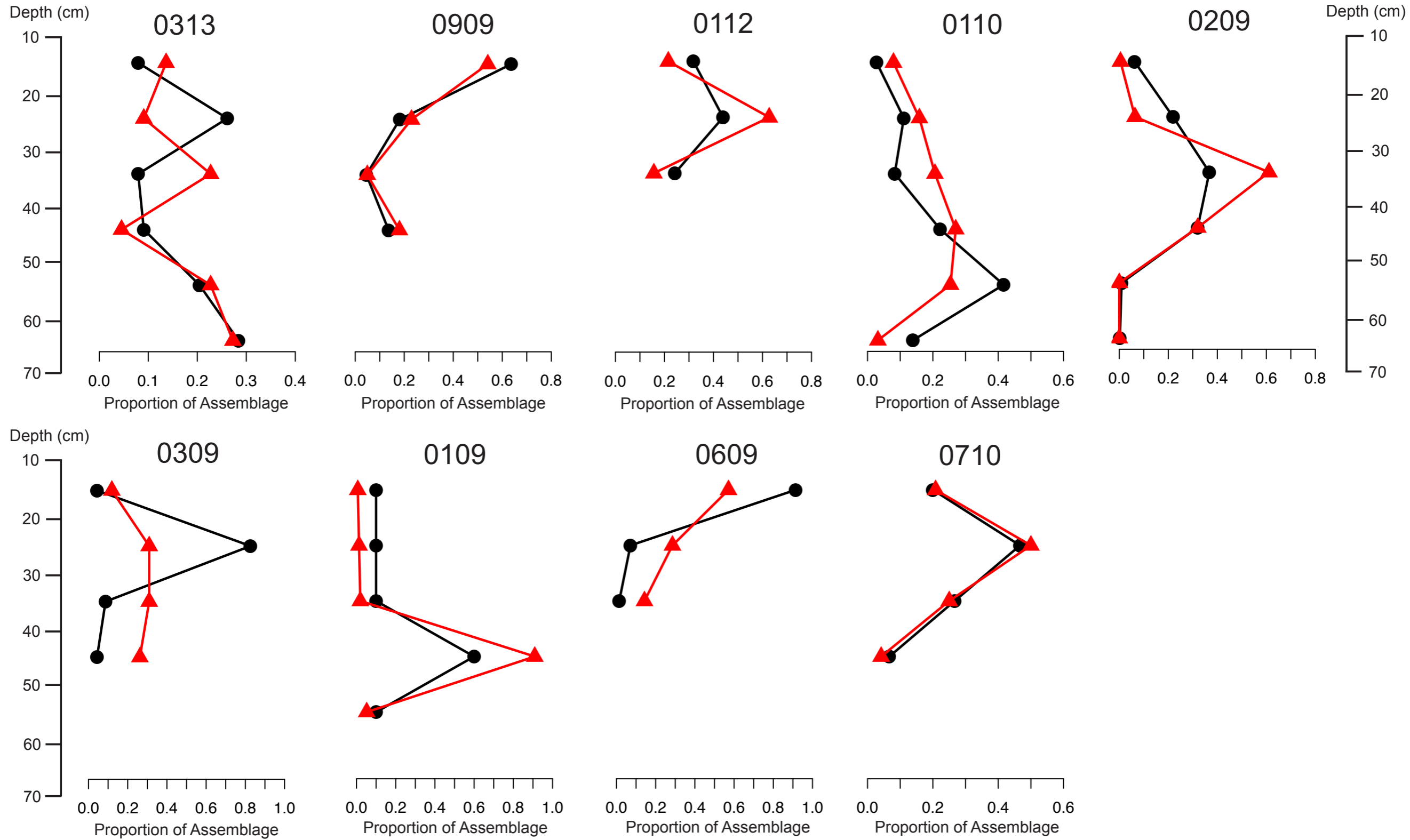
**C.**



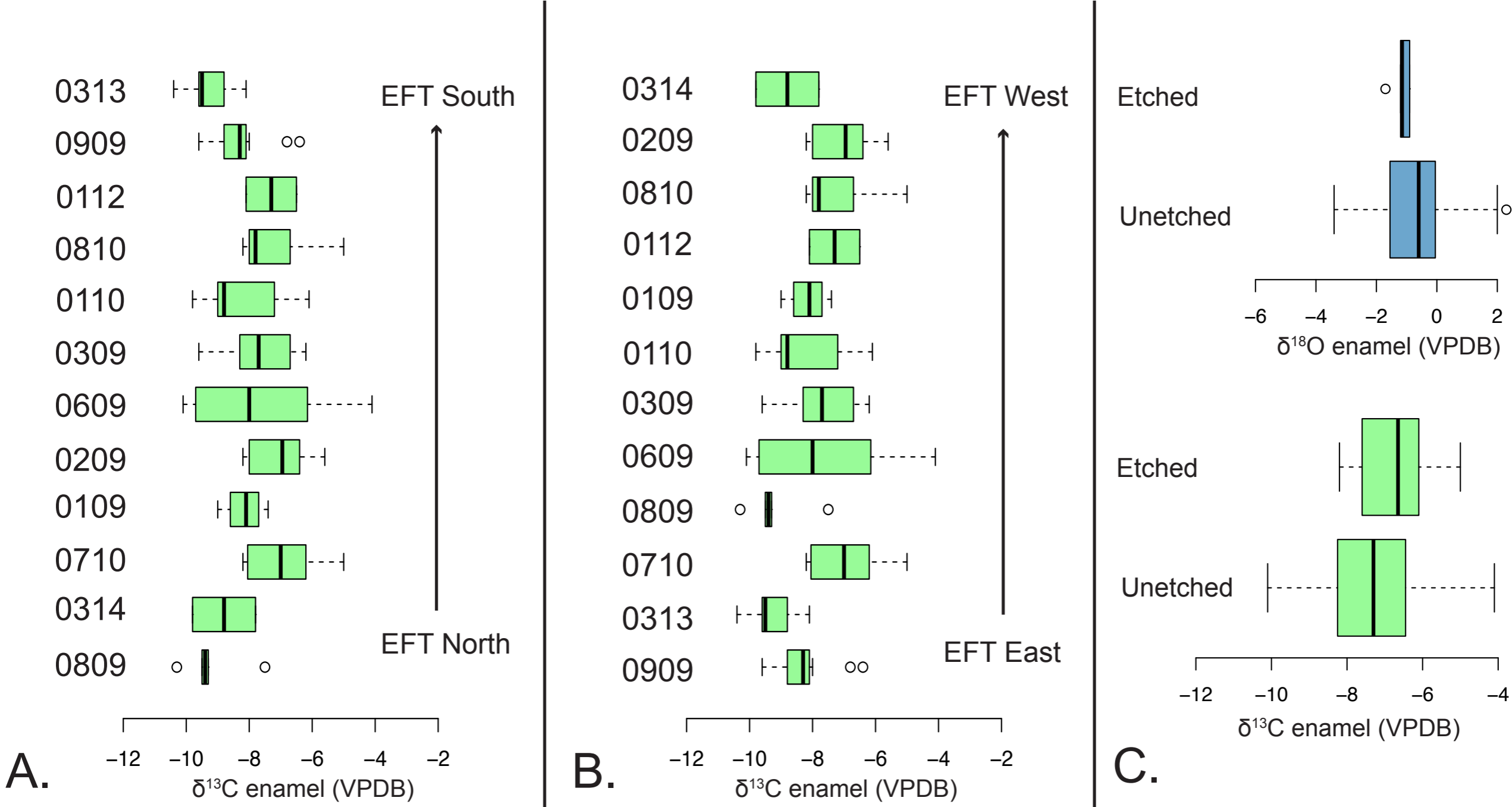
**Figure 4.** A) Modern *B. suillus* skull (NMNH 344067) from Mosselbaai, South Africa; B) WCRP 46140 (acid etch score = 3); C) WCRP 46138 (acid etch score = 3); D) WCRP 45684 (acid etch score = 0); E) WCRP 45642 (acid etch score = 2; note potential root etching); F) WCRP 45548 (acid etch score = 0); Arrows indicate anterior direction of specimen. Note differences in enamel surface modification in 3B, 3C, 3D, 3E, 3F. 3D, 3E and 3F could be related to soil acidity, microbes or both.



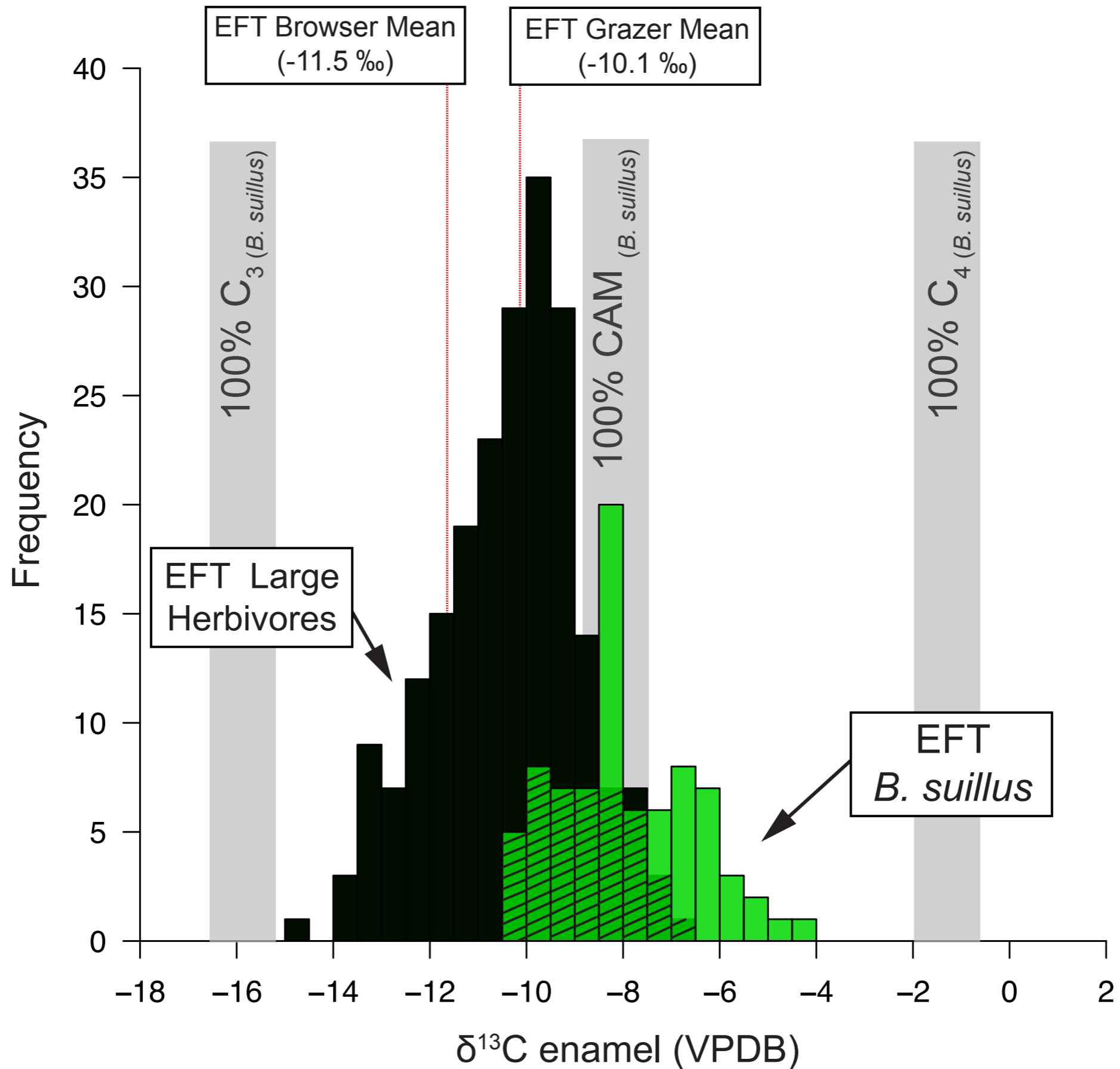
**Figure 5.** Altimetric analysis of the relationship between *B. suillus* fossils and large mammal fossils from EFT Collection Bays. EFT *B. suillus* fossils depicted with red triangles. EFT large mammal fossils depicted with black circles.



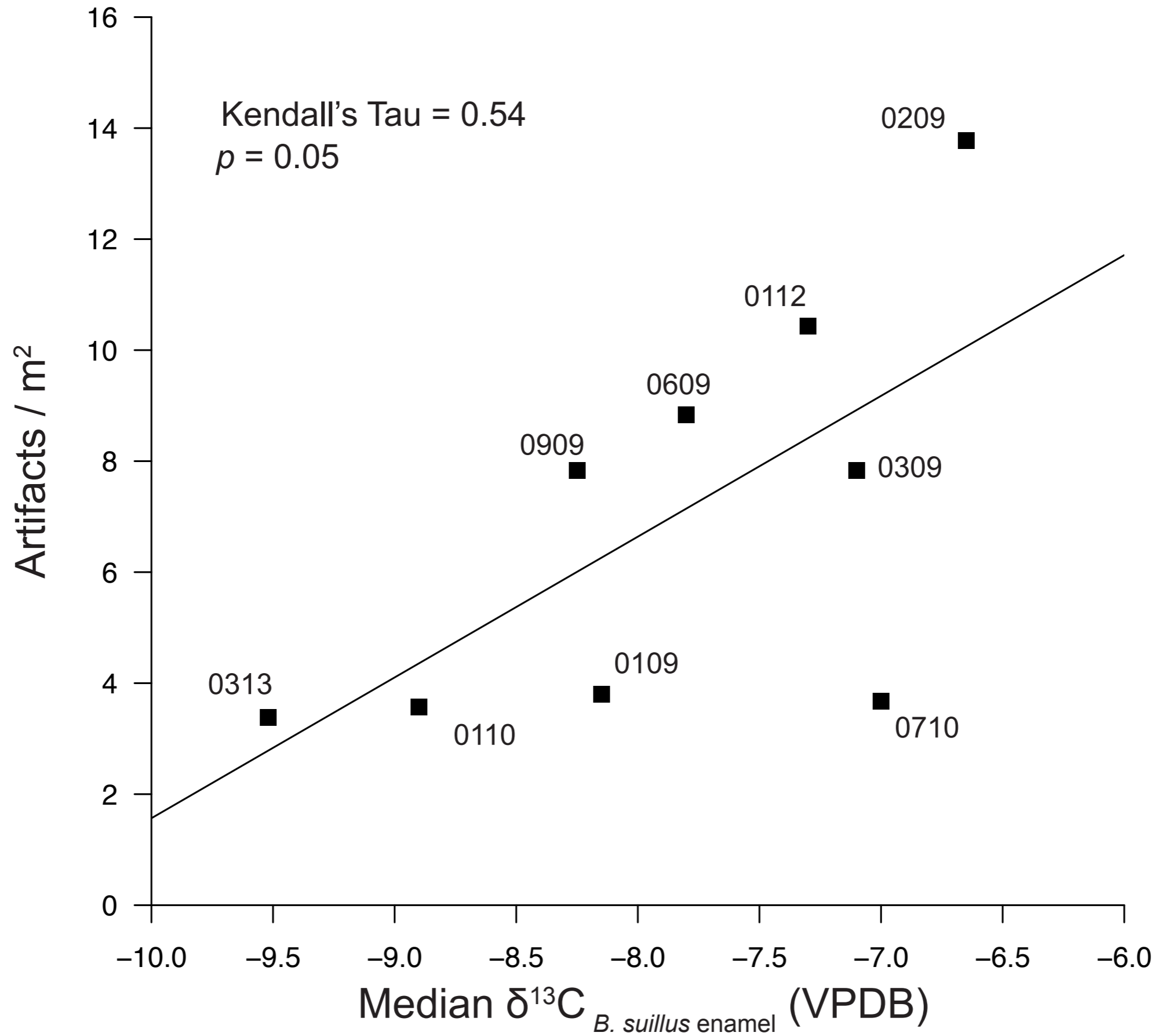
**Figure 6.** A) *B. suillus*  $\delta^{13}\text{C}$  values arranged by Collection Bay from north to south, B) *B. suillus*  $\delta^{13}\text{C}$  values arranged by collection Bay from east to west, C) Comparison of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  ratios of etched and unetched incisors. Center line represents the sample median, box represents the 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers represent the sample range exclusive of outliers, circles represent outliers defined at 1.5 times the interquartile range.



**Figure 7.** Comparison of EFT large herbivores and EFT *B. suillus*. 100% C<sub>3</sub>, CAM and C<sub>4</sub> represent are associated with the diet of *B. suillus*, not EFT large herbivores. Darker green, hashed areas represent overlap between the two distributions. EFT large mammal grazer and browser mean values from Lehmann et al. (*In Review*).



**Figure 8.** Relationship between Collection Bay median *B. suillus*  $\delta^{13}\text{C}$  values and Bay artifact density. Line represents best fit line from median *B. suillus*  $\delta^{13}\text{C}$  values – artifact density linear model.



**Figure S1.**  $\epsilon^*_{\text{enamel-diet}}$  effect on EFT large herbivore and EFT *B. suillus* distributions. A) Small mammal  $\epsilon^*_{\text{enamel-diet}}$  (11.1‰) following Podelsak et al., 2008, B) Large mammal  $\epsilon^*_{\text{enamel-diet}}$  (14.1‰) following Cerling and Harris (1999).

