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1 **Humans and climate as possible drivers of the morphology and function of the mandible of**
2 ***Suncus etruscus* in Corsica.**

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13 **Abstract**

14 Human-induced environmental changes have increased rapidly during the Holocene and have reached
15 alarming levels today. Consequently, it is crucial to better understand the impact of humans and
16 climate on the faunas and floras through time. Understanding the direct and underlying effect of past
17 human activity not only contributes to improving our knowledge of human history but also provides
18 insights for the future. We here investigate the effect of the human-induced environmental changes
19 that took place during the modern era (14-19th century AD) on the mandible of a small mammal, *Suncus*
20 *etruscus*, in Corsica. We detected rapid morphological changes in mandible shape over the relatively
21 short period of time included in our study, suggesting a strong human impact on the island. The
22 morphological changes observed had functional consequences as they are related to changes in the
23 mechanical potential of the principal masticatory muscle, the temporalis that, in turn, reflects shifts in
24 the animal's diet over time. These results highlight the effect that the 600-year human agricultural
25 activity shifts had on the island and its fauna. The integration of the body and the ramus of the
26 mandible appears to be related to the mechanical potential of the temporalis muscle but does not
27 constitute an indicator of human-induced environmental change. Whether these morphological
28 changes are the result of natural selection (genetic processes) or of phenotypic plasticity (epigenetic
29 processes) remains to be elucidated.

30 **Keywords:** Mandible; Morphometrics; Shape; Bite force; Corsica; Shrew; Integration

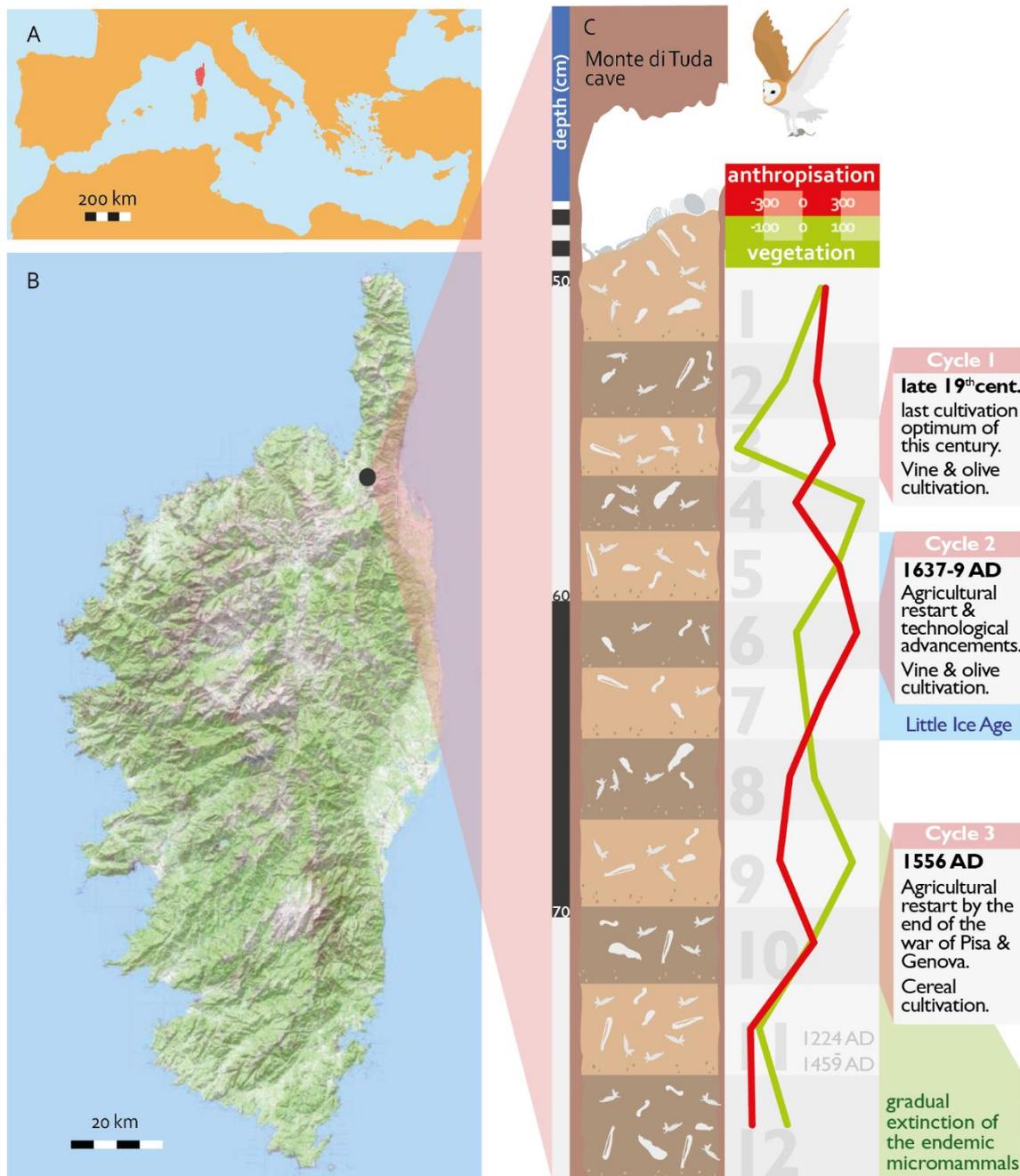
31 **1. Introduction**

32 We live in an era of rapid and global environmental change where man is the principal driver of changes
33 in the environment, largely because of the expansion of industry and agriculture, as well as population
34 growth (Vitousek et al., 1997). The impact of humans on natural ecosystems has dramatically increased
35 from the Holocene to recent times and has gone hand in hand with climate change. This has had
36 enormous repercussions on ecosystems worldwide (Barnosky et al., 2004) resulting in the so-called
37 sixth mass extinction (Pimm & Brooks, 2000; Barnosky et al., 2011; MacPhee & Sues, 2013; Ceballos et
38 al., 2015). It is therefore crucial to better understand past human activity in conjunction with its direct
39 and indirect impacts on natural landscapes and the organisms that inhabit these. The study of past
40 environmental changes and their impact on fauna and flora may provide us with valuable insights for
41 the future (Blois & Hadly, 2009). Understanding the direct and indirect effects of past human activity on
42 ecosystems provides valuable information that not only improves our understanding of human history
43 but also provides insights on how human activity can impact future ecosystems.

44 An important aspect is the phenotype of an organism as it typically reflects the environmental context it
45 lives in as form (shape and size) is intimately linked to function (Anderson et al., 2008). For example, the
46 form of the mandible is intimately linked to bite force generation and may thus provide insights into
47 diet, anti-predator defense and/or competition in animals (Anderson et al., 2008). As such, mandible
48 shape may be used as a marker of environmental change. This is true for all vertebrates, but especially
49 so for small mammals that are likely constrained in their diet by their absolute bite force (Atchley, 1993;
50 Aguirre et al., 2003; Renaud et al., 2009). As such, we hypothesize that bite force should be related to
51 environmental changes. We also hypothesize that the environmental changes may impact mandibular
52 integration and modularity. Integration is defined as the relation between anatomical structures often
53 referred to as modules. Modules are defined when the different anatomical structures inside the
54 module co-vary more strongly among themselves than with any anatomical structure outside the
55 module (Olson & Miller, 1958; Klingenberg et al., 2004; Schlosser & Wagner, 2004; Callebaut & Rasskin-
56 Gutman, 2005; Mitteroecker & Bookstein, 2007; Klingenberg, 2008; Goswami & Polly, 2010). Hanot et
57 al. (2018), for example, found that artificial selection had an impact on the patterns of integration of
58 the appendicular skeleton of domestic horses. Moreover, Hanot et al. (2017) showed that integration is
59 stronger in the cases where functional constraints are strong, suggesting that the degree of integration
60 of the mandible might provide insights in the strength of selection on this structure.

61 Islands are often considered “natural laboratories” allowing the study of ecosystems in relation to
62 environmental changes as well as a better understanding of evolutionary mechanisms and extinction
63 and speciation events as insular ecosystems are simple and sensitive to changes and moreover (Darwin,
64 1845; Wallace, 1860; Losos et al., 1997; Whittaker & Fernández-Palacios, 2007). In this context, the

65 island of Corsica (Fig. 1a, b) appears a good model to study the relationship between humans and their
66 environment through time and the subsequent impacts thereof on the fauna (Vigne et al., 1997; Vigne,
67 1999). The first arrival of man on most Mediterranean islands took place in the last 12,000 years and
68 this was more often than not, followed by the extinction of endemic species and their replacement with
69 newly introduced taxa (e.g. Alcover et al., 1981; Davis, 1984; Vigne & Alcover, 1985; Kouvari & van der
70 Geer, 2018). Corsica is a great example as the impact of humans on the endemic fauna and flora is
71 exceptionally well documented (Vigne, 1990, 1992, 1996, 1999; Vigne & Valladas, 1996). While the
72 megafauna extinction on Corsica took place soon after the first arrival of man, smaller endemic
73 mammals went extinct much later (Vigne, 1988, 1990, 1992). Humans involuntarily introduced many
74 small mammals that became established on the island (Vigne, 1988, 1990, 1992; Vigne & Valladas,
75 1996).



76

77 Figure 1. (a) Map of the Mediterranean Sea showing Corsica in red, (b) Geomorphological map of Corsica, and (c)
 78 an illustration of the layers of the Monte di Tuda cave, their depth, the vegetation and anthropisation indices and
 79 information on the dating, anthropisation cycles and other important events. Modified after Vigne & Valladas
 80 (1996). Mediterranean map based on outlines from © d-maps.com. Corsica map from © IGN Planet Observer.

81 The Monte di Tuda site is an archaeological site in the Nebbio Basin in the North of the island (Fig. 1a,
 82 b). The site consists of a cave that served as an owl nest (probably *Tyto alba*) for the last 2500 years and
 83 provides an exceptional accumulation of micromammal remains through time (Vigne & Valladas, 1996).
 84 Vigne & Valladas (1996) studied these remains and the changes therein through time. They
 85 distinguished biozones, and calculated an anthropisation and vegetation index for each layer. More
 86 specifically, they studied the cave sediment stratigraphy, distinguished the different layers present, and
 87 dated (^{14}C) some of them. They studied the faunal assemblages by calculating the minimum number of

88 individuals (MNI) of each species in each layer. Based on the previous and in conjunction with the
89 known ecological preference of the species, they ran a correspondence analysis (CA) between species
90 and layers (their faunal compositions) in order to observe the potentially existing patterns of ecological
91 significance. From this, the first axis distinguished between anthropophilic species while the second
92 between species preferring “natural” medium maquis vegetation and those preferring low vegetation.
93 They thus used the CA layer coordinates of the F1 axis as an anthropisation index and those on the F2
94 as a vegetation index. Finally, based on those vegetations and anthropisation indices along with the
95 information on the dated layers and the history of Corsica, the authors distinguished anthropisation
96 cycles, characterized by important local events.

97 This exceptional stratigraphic sequence in Monte di Tuda brought valuable evidence on the landscape,
98 faunal and human evolution in Northern Corsica (Vigne & Valladas, 1996). Three sub-sequences were
99 identified. The first and oldest one (864-409 BC to 322-283 AD) is characterized by the increase of
100 human-induced impacts (often due to intense cereal cultivation) and habitats consisting of high-
101 medium maquis. The second one (taking place until 1224-1459 AD) is characterized by an acceleration
102 of human impacts in the region coupled with clearing of vegetation. Finally, the third and last sub-
103 sequence includes a drastic intensification of deforestation resulting in a landscape not very different of
104 that of today. The extinction of the endemic small mammals is also recorded in this sub-sequence at
105 this last step and is hypothesized to have happened due human-induced habitat alteration in northern
106 Corsica (Vigne & Valladas, 1996). This last sub-sequence is the focus of our study (Fig. 1c).

107 Small mammals are often good markers of the environment they live in (Bar-Yosef & Tchernov, 1966;
108 Brothwell & Jones, 1978; Chaline, 1979; Marquet, 1989; Rofes et al., 2014; Weissbrod, 2010; Stoetzel et
109 al., 2011). We studied one of the smallest species, the white-toothed shrew *Suncus etruscus* (Savi,
110 1822) (Soricidae) (Fig. 2a). This shrew is one of the smallest extant mammals by mass (only 1.8 g;
111 Jürgens, 2002) and reached Corsica, as well as most other Mediterranean islands, through human-
112 mediated transport (Dobson, 1998; Chen & Koprowski, 2018). It is a synanthropic/anthropophilic
113 species as it thrives in human-transformed habitats such as olive groves and vineyards (Dobson, 1998).
114 It is an opportunistic species feeding principally on invertebrates but also occasionally on small
115 vertebrates (Nowak & Paradiso, 1999; Kingdon et al., 2013). We here specifically focus on its mandible
116 (Fig. 2a) as this structure is directly linked to diet (Badyaev & Foresman, 2004) and interspecific
117 competition (Cornette et al., 2015c) through its impact on bite force generation. Shrew mandibles also
118 show exceptional phenotypic plasticity (Young et al., 2010) i.e. non-heritable morphological variation as
119 a response to environmental pressures (Price et al., 2003). Phenotypic plasticity has been investigated
120 in laboratory-raised mice (Anderson et al., 2014; Garland & Kelly, 2006; Renaud et al., 2010) but has
121 also been observed in shrews fed on different diets (Young & Badyaev, 2010). Bite force is an

122 ecologically relevant performance trait as it is directly related to prey capture and manipulation and as
123 such determines the type and size of prey that can be consumed (Aguirre et al., 2003; Anderson et al.,
124 2008). We here estimated the mechanical advantage of the two primary masticatory muscles, the
125 temporalis and the masseter. These two muscles are particularly relevant as they are optimized to
126 generate force at different gape angles (masseter = low gape; temporalis = high gape; Cornette et al.,
127 2013). Consequently, if shifts in prey size occur through time this may be reflected in the relative
128 contribution on these two muscles to biting.

129 Human activity and its direct effects on islands, and in particular in Corsica, are well known. However,
130 the full range of the underlying consequences of these impacts has not been extensively studied to
131 date. In this paper, we investigated the effects of human-induced environmental changes in Corsica,
132 taking as a case study the Etruscan shrew. We hypothesized that environmental changes will impact the
133 integration of the mandible and tested whether phenotypic integration is a marker of environmental
134 change in an archeological context. Integration (i.e. the link between different modules of the same
135 anatomical structure) can change in two ways: via direct interactions (cell groupings or signaling
136 pathways change) and via parallel variation due to selection on function (Klingenberg & Zaklan 2000;
137 Klingenberg et al. 2003; Klingenberg 2005). The first type of integration is difficult to change as it
138 requires developmental and genetic “rewiring”. The second type of integration mostly drives the
139 evolution of population level variation (for example, Cheverud 1982, 1996; Wagner 1996; Wagner &
140 Altenberg 1996). Zelditch et al. (2009) suggested that while the mandible can be a highly modular
141 system from a developmental point of view, it is a functionally integrated system as the mandible as a
142 whole takes part in all its functions like the capture of prey and mastication. Here, we test whether the
143 integration between the body and ramus of the mandible (Fig. 2a) changes in response to the rapid
144 environmental changes observed at our study site through time. In summary, we attempt to define
145 morpho-functional markers of environmental change due to human activity. More specifically, we test
146 if, even over a short period of time at the start of the modern era the impact of environmental changes
147 is visible on the phenotype of the mandible of *Suncus etruscus*, in terms of its form and function.

148 **2. Material & Methods**

149 2.1 Material

150 We here focus on the modern era (14th-19th century AD), a short period of about 600 years. During this
151 time interval, Vigne & Valladas (1996) identified twelve layers at Monte di Tuda, each corresponding to
152 a different depth in the sediment (Fig. 1c). They dated layer eleven at 1224-1459 AD (610 ± 120 years
153 BP) and related the other layers with historical events, more specifically layer ten with the end of the
154 war of Pisa (1556 AD), layer six with the agricultural development of the Genovese people (1637-1639

155 AD; Arrighi, 1990) and layer three to the last cultivation optimum of the 19th century in Corsica (Vigne
 156 & Valladas, 1996). This period is characterized by a good resolution of environmental changes and
 157 human activity through time and shows a gradual intensification of human activity, the predominance
 158 of human transformed environments, and a short period of colder and wetter climate called the “Little
 159 Ice Age” (~1300-1850 AD) with minimal temperatures occurring around 1645-1715 AD; (Le Roy Ladurie,
 160 1967; Lamb, 1969; Schneider & Mass, 1975; Fagan, 2002).

161 We included 411 complete and fragmented mandibles (Appendix A.1) coming from the twelve different
 162 layers of the Monte di Tuda site (also included in the study of Vigne & Valladas, 1996). We also included
 163 26 present-day mandibles from different localities (Appendix A.2).

164 2.2 Methods

165 Specimens were sorted, numbered and the lingual sides were photographed using a NIKON D5500
 166 camera (with a NIKKOR 60mm lens).

167 2.2.1 Fragment types

168 We categorized our specimens by fragmentation pattern and defined fragment types in order to include
 169 a maximum number of specimens in our analysis. We defined different fragment types described in
 170 Table 1 and Fig. 2b. Fragment types were based on Cornette et al. (2015a, b) and divided in types SC,
 171 COMP, CMM, ABC, MM. For the present study we also added types A and B (Fig. 2b). For fragments
 172 COMP, CMM and B we also added sub-categories for the presence of the anterior part of the mandible
 173 (CMMi, Bi) and the angular process (COMPan) (Fig. 2b).

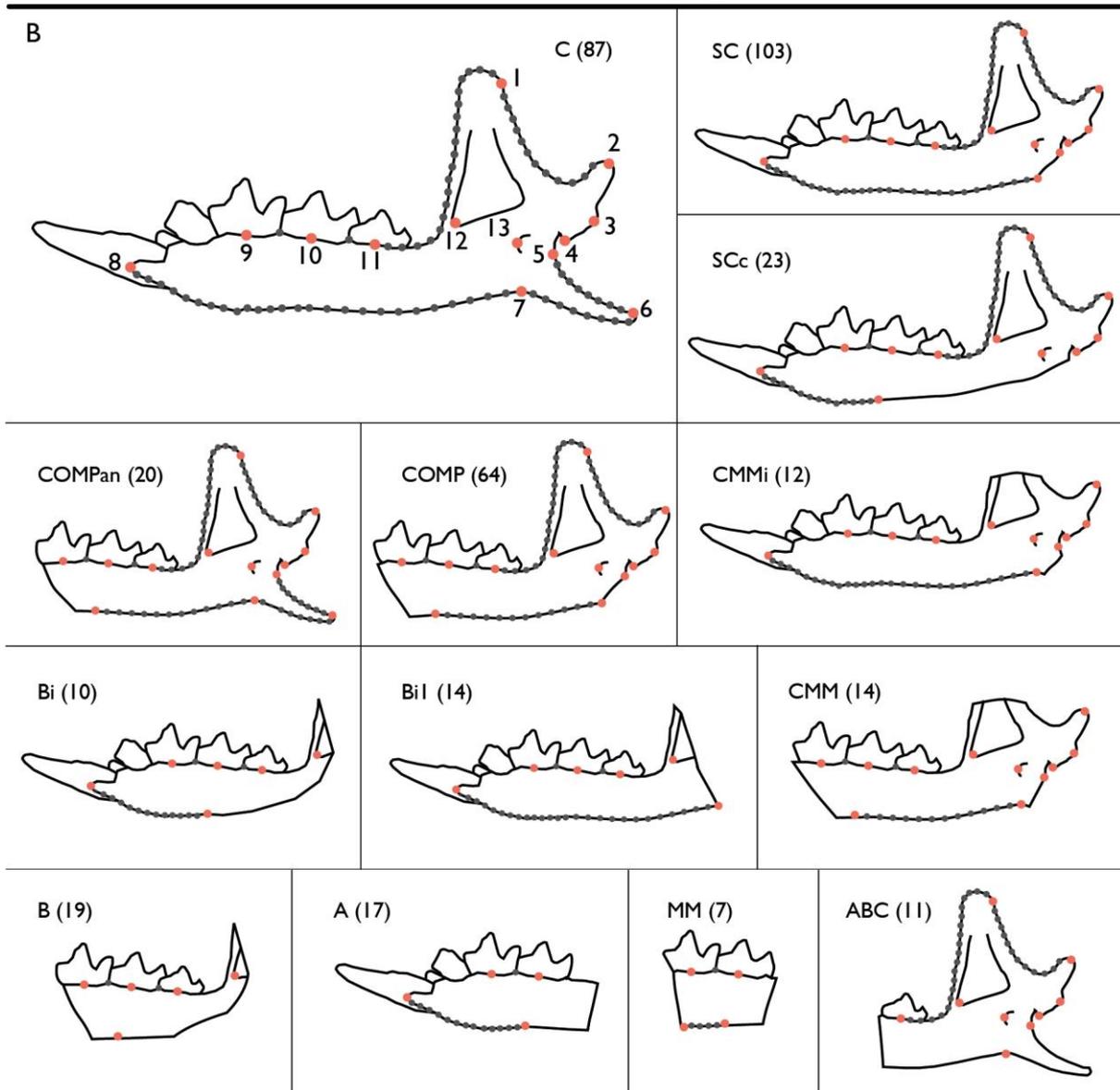
Groups	Anatomical localization
C	Complete mandibles
SC	Mandibles missing the angular process
SCc	SC missing the posteroventral curvature
COMPan	Mandibles missing the anterior part
COMP	COMPan missing the angular process
CMMi	Mandibles missing the angular and coronoid processes
CMM	CMMi missing the anterior part
ABC	Mandibles including the coronoid and angular processes
Bi1	Mandibles missing the angular and coronoid processes as well as the articular condyle
Bi	Bi1 missing the posteroventral curvature

B	Mandibles only containing the medial parts along with the anterior corner of the coronoid fossa
A	Mandibles only containing the anterior part
MM	Very fragmentary specimens containing a fragment of the middle of the mandible containing the m1 and m2 tooth insertions

174 Table 1. Anatomical localisation and description of the different fragment types starting with complete specimens
175 and finishing with the most fragmented types.

176 2.2.2 Analysis of mandible shape

177 The description of shape was performed using geometric morphometrics, and more specifically the use
178 of anatomical landmarks and semi-landmarks on curves (Bookstein, 1997; Gunz et al., 2005; Cornette et
179 al., 2013). Semi-landmarks were slid using a bending energy minimization procedure and can thus be
180 considered spatially homologous (Bookstein, 1997; Slice, 2007; Mitteroecker & Gunz, 2009).



181

182 Figure 2. (a) *Suncus etruscus* (photographed by © Jose B. Ruiz) with a scale that corresponds to a 2-Euro coin and
 183 the anatomical parts of its mandible. (b) Types of fragments and their landmarks (red) and semi-landmarks (grey).
 184 The number in brackets corresponds to the number of specimens of each fragment type.

185

1	Maximum curve point of coronoid process
2	Dorsal most, posteroventral and ventral most aspect of the articular condyle
3	
4	
5	Ventral point of condylar neck
6	Most distal point of angular process
7	Inflexion point between angular process and body of mandible
8	Most anterior point of mandible body
9	Intersection point of mandible and m1
10	Intersection point of mandible and m2
11	Intersection point of mandible and m3
12	Anterior corner of coronoid fossa
13	Anterior most point of mandibular foramen

186 Table 2. Anatomical Landmarks and their description.

187 More specifically, 13 landmarks (Table 2) and 76 semi-landmarks were defined on complete specimens.
188 For fragmented mandibles we used the maximum number of landmarks present on the fragment (Fig.
189 2b). A repeatability test was performed on three specimens. Landmarks were positioned 20 times on
190 each specimen, followed by a General Procrustes Analysis (GPA) and a Principal Components Analysis
191 (PCA). This showed that the intra-specimen variability was lower than that between specimens.
192 Landmark digitization was done using the TPSDig2 software (Rohlf, 2010). The definition and sliding of
193 semi-landmarks, Procrustes superimposition (by Bending energy) and PCA were done with the
194 ‘Geomorph’ package (Adams et al., 2017) in R (R Development Core Team).

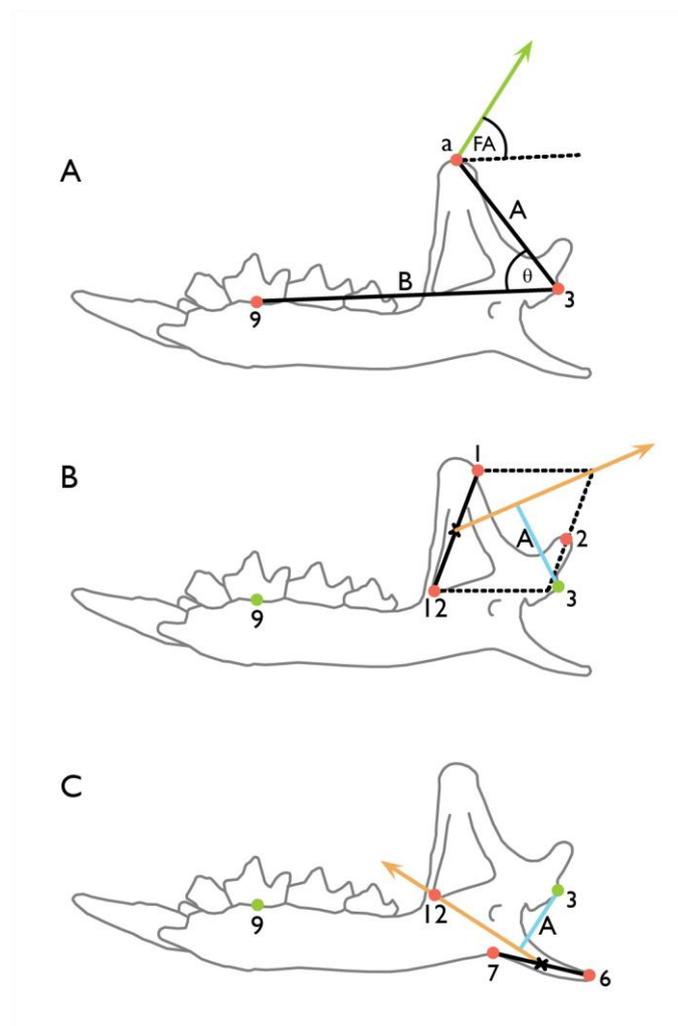
195 2.2.3 Neighbour-Joining trees of mean shapes

196 We performed a ‘Between group PCA’ (i.e. a PCA on the mean shapes of each layer; Boulesteix, 2005;
197 Mitteroecker & Bookstein, 2011) for each fragment type (Appendix B.1) as this allows to minimize the
198 shape variability within each layer and maximizes the variability between layers. This was done using
199 the ‘GroupPCA’ function in the ‘Morpho’ R package (Schlager, 2017). In order to better visualize the
200 morphological similarities between the layers and to take into consideration the total shape variability
201 we created Neighbour-Joining trees (Saitou & Nei, 1987; Studier et al., 1988) based on the Euclidian
202 distances between the mean shapes of each layer using the ‘nj’ function of the ‘ape’ R package (Paradis
203 et al., 2004). We did this for all fragment types, each time including the most complete specimens.

204 2.2.4 Mechanical Potential

205 We calculated the mechanical potential (MP) of the temporalis and masseter muscles on the complete
206 specimens as well as on the fragment types that allowed for these calculations (i.e. SC, SCc, COMP and

207 COMPan). We then calculated the mean for each layer. The MP of the temporalis was calculated
 208 following two methods. The first (MPtemp; figure 3a) is the method described by Carraway et al. (1996;
 209 see also Cornette et al., 2012, 2015c). Although this method has been widely used, it is not the best
 210 estimation of force transmission by the temporalis muscle as it does not present the line of action of
 211 the temporalis muscle realistically. As shown in figure 3a, in the original model, the temporalis bite
 212 force (arrow) originates from the tip of the coronoid process and extends dorso-posteriorly. However,
 213 in reality, the muscle attaches on the middle of the ramus and on the temporal bones of the skull that
 214 are situated posterior to the coronoid process. This is the reason why we introduce the second method
 215 referred to as MPtemp' (Fig. 3b) which provides a better estimate of the functional advantage of the
 216 temporalis muscle by including the calculation of the muscle moment arm.



217
 218 Figure 3. The biomechanical model of (a) MPtemp (by Carraway et al. 1996); (b) the new model for MPtemp' and
 219 (c) MPmas. For all models, B is the distance between landmark 3 and 9 (it is only represented in 3a because of lack
 220 of free space in the rest). Distance A is the distance between landmark 3 and the uppermost point of the coronoid
 221 process for (a), the perpendicular distance between landmark 3 and the muscle vector (orange) for (b) and (c). FA
 222 = $90^\circ - \theta^\circ$.

223 The mechanical potential of the masseter is calculated for the complete specimens as well as the
224 COMPan fragment using the method described below (Fig. 3c). For all analyses we used the \log_{10}
225 transformed mechanical potential values.

226 2.2.4.1 MPtemp

227 Based on Carraway et al. (1996) the mechanical potential of the temporalis muscle is calculated with
228 the following function (see also figure 3a).

$$229 \quad \text{MPtemp} = (A/B) \cos(\text{FA}) \text{ where } \text{FA}^\circ = 90 - \theta^\circ$$

230 2.2.4.2 MPtemp'

231 We calculated the moment arm of the temporalis muscle by creating a vector that takes its origin at the
232 mid-point between landmarks 1 and 12 and whose direction is defined by the intersection of the
233 parallel passing through landmarks 2 and 3 (Fig. 3b). The perpendicular between the center of rotation
234 and this vector provides the moment arm of the temporalis muscle. This assumes no variation in the
235 origin of the muscle on the cranium. The moment arm is dependent on the inclination of the coronoid
236 process relative to the axis of the mandible.

$$237 \quad \text{MPtemp}' = A/B$$

238 2.2.4.3 MPmas

239 This is a model of the estimation of the masseter moment arm (Fig. 3c). We calculated the moment arm
240 of the masseter by creating a vector which takes its origin at the mid-point between landmarks 6 and 7
241 and whose direction is defined by the position of landmark 12 (Fig. 3c). The perpendicular between the
242 center of rotation and this vector provides the moment arm of the masseter muscle. The moment arm
243 is dependent on the shape, length and position of the angular process relative to the axis of the
244 mandible.

$$245 \quad \text{MPmas} = A/B$$

246 2.2.5 Mandible Size

247 We used the centroid size to study size differences between mandibles of different layers and used the
248 \log_{10} transformed centroid size in our analyses. Centroid size equals the square root of squared
249 distances of all landmarks of a mandible from its centroid (center of mass, whose position is calculated
250 by the mean of the x and y coordinates of all landmarks; Klingenberg, 2016).

251 2.2.6 Statistical Analysis

252 To evaluate the effect of MPtemp, MPtemp', size, and the layers on the shape of the complete
253 specimens we performed a 'Procrustes ANOVA' (Goodall, 1991) using the 'procD.lm' of the R package
254 'Geomorph' (Adams et al., 2017). To understand what shape variation corresponds to mechanical
255 potential and size variation we visualized shapes corresponding to maximum and minimum MPtemp
256 and MPmas and size using multivariate regressions (Monteiro, 1999). Next, we also visualized
257 allometry. The presence of allometry indicates the existence of an effect of size on shape (Huxley, 1924;
258 Huxley et al., 1932; Cock, 1966; Gould, 1966; Calder, 1984; Schmidt-Nielsen, 1984; Klingenberg, 2016).
259 Visualizations were done with the 'plotRefToTarget' function of the R package 'Geomorph' (Adams et
260 al., 2017).

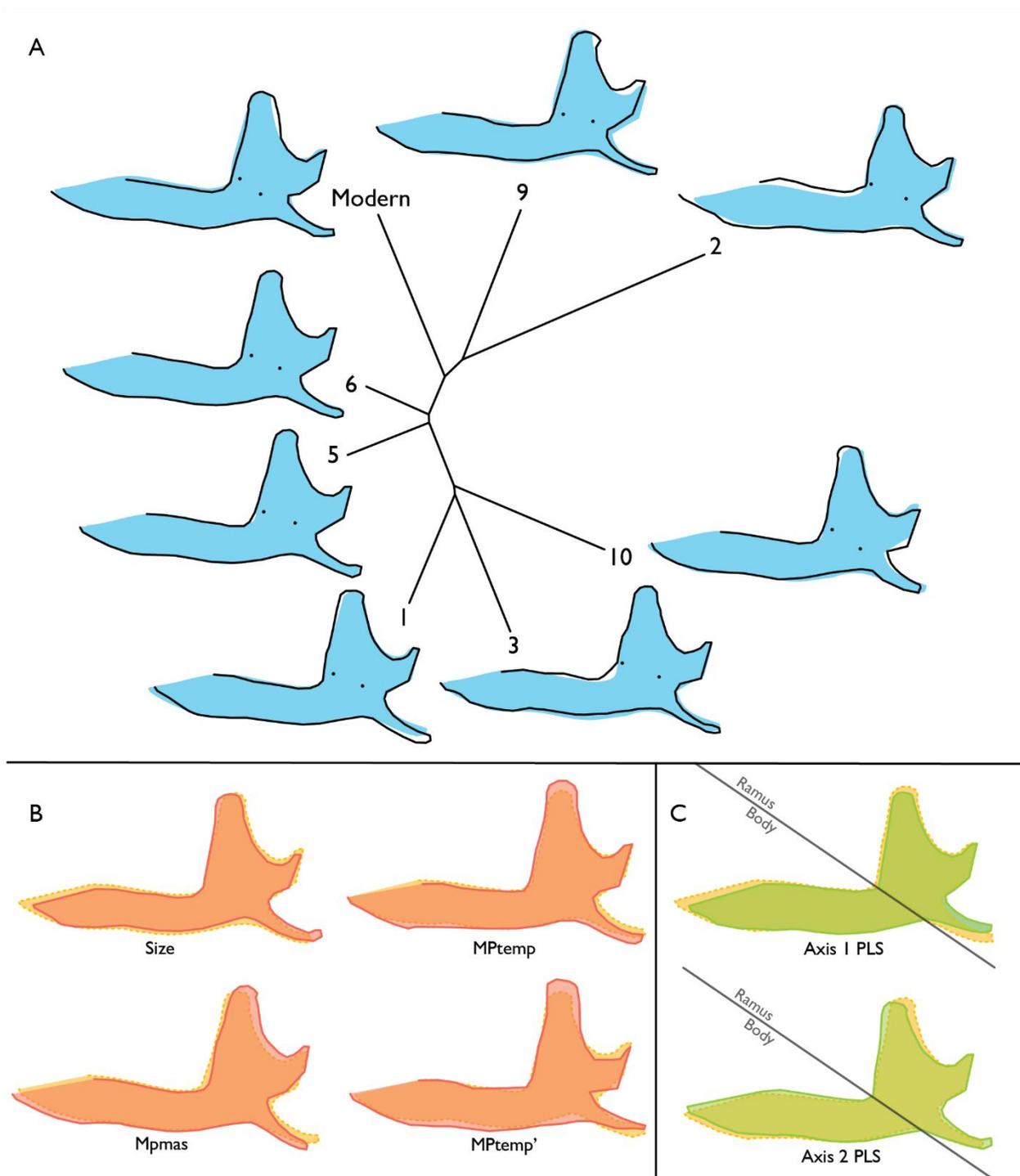
261 To evaluate the effect of size as well as vegetation and anthropisation indexes on MPs we performed
262 simple regressions. To test the relation between MPtemp and MPtemp' and MPtemp' and MPtemp
263 with MPmas we performed correlations (Pearson's correlation) for each case. Regressions and
264 correlations were done using the 'lm' et 'cor' functions in R. To study how MPs and size change through
265 time, we calculated the mean of each layer and presented box-plots (Appendix B.3) in order to present
266 variation between each layer.

267 In order to study modularity and integration of the mandible, we first defined the body and ramus as
268 the two modules of the mandible (Fig. 2a) based on previous studies (Cheverud et al., 1997; Mezey et
269 al., 2000; Klingenberg et al., 2003). We performed a modularity test ('Modularity.test' function of the
270 'Geomorph' package; Adams et al., 2017) to compare the degree of modularity between two modules
271 defined using the covariance ratio or CR coefficient (Adams, 2016). If the CR coefficient obtained by our
272 pre-defined structure is smaller than the CRs obtained by the random permutations, then our
273 hypothesis is valid (Adams, 2016). The definition of the modules was performed using the
274 'define.modules' function in 'Geomorph' (Adams et al., 2017). In order to test whether modules are
275 integrated we performed an integration test using the 'Integration.test' function of 'Geomorph' (Adams
276 et al., 2017). The two-block partial least squares (2b-PLS) test quantifies the degree of integration
277 between the two modules (Adams & Collyer, 2016). In addition, we visualized the shape of each module
278 corresponding to the maximum and minimum of each axis of covariation using the 'shape.predictor'
279 function of 'Geomorph' (Adams et al., 2017). In order to test functional consequences of integration we
280 plotted all variables (MPs, size, vegetation and anthropisation indexes) on the first PLS axis. P-values
281 were considered significant if smaller than or equal to 0.05. For the analyses that include multiple
282 tests/comparisons, we applied a Bonferroni correction according to which alpha (critical value) is used
283 to judge the significance of the results and is equal to 0.05 divided by the number of tests performed
284 for each analysis (Rice, 1989).

285 **3. Results**

286 3.1 Global morphological patterns

287 The Euclidian distance tree for complete specimens is represented in figure 4a and the rest are
288 represented in Appendix B.1. The tree in figure 4a shows a separation of the layers that correspond to a
289 recolonization of vegetation or high vegetation (nine and two) in contrast to layers characterized by a
290 high degree of anthropisation (one, three, and ten). Layers five and six correspond to the “Little Ice
291 Age” and are characterized by the presence of very low vegetation (Vigne & Valladas, 1996). The
292 mandibles of the first group have a more posteriorly slanted coronoid process, a more anterior articular
293 condyle and a more ventral angular process while those of the third group have a shorter body and a
294 more anterior coronoid process.



296

297 Figure 4. (a) The Euclidian distance tree between mean shape by layer for complete specimens (mean shapes by
 298 layer are also presented (black outline) and compared to mean shape of all sample (blue shape)); (b) The
 299 theoretical shape that corresponds to the minimum (yellow) and maximum (red) of size, MPtemp, MPtemp' and
 300 Mpmas; (c) the theoretical shapes corresponding to the max (green) and minimum (yellow) of the first two PLS
 301 axis. Additional graphs in Appendix B.4.

302 Similar patterns emerge from trees established and based on different fragment types (Appendix B.1)
 303 including the distinction of layers eleven and seven, the grouping of layers five and six (trees SC, SCc,
 304 CMMi, ABC, Bi), and the distinction of layers two and ten from layers five and six (COMP, COMPan, SC,
 305 CMMi). However, different fragments do also show some additional patterns. The COMP tree separates

306 all layers with low vegetation from layers two and eleven with high vegetation and trees (Vigne &
307 Valladas, 1996). The SCc tree separates all layers from the layers nine and ten that correspond to cereal
308 cultivation and its recolonization period (Vigne & Valladas, 1996). The CMM tree (including COMP)
309 separates all layers from layers four, three and eleven, the first corresponding to maximum vegetation
310 and the two others to minimum vegetation (Vigne & Valladas, 1996). Finally, the ABC tree (including
311 COMP, COMPan, SC and C) separates all layers from layer seven (very humid climate and “Little Ice
312 Age”) and eleven (vegetation minimum) (Vigne & Valladas, 1996).

313 3.2 Morphological changes and functional consequences

314 A summary of the statistical analyses performed as well as their results can be found in Appendix B.2.
315 The results of the Procrustes ANOVA show a significant effect of layers ($P < 0.001$, $R^2 = 0.13$) and
316 MPtemp ($P < 0.001$, $R^2 = 0.06$) on shape. MPmas impacted shape only before the application of the
317 Bonferroni correction. To understand the nature of the effect of the mechanical potential and size on
318 shape, we calculated the theoretical shapes corresponding to the maximum and minimum values of the
319 variables (Fig. 4b).

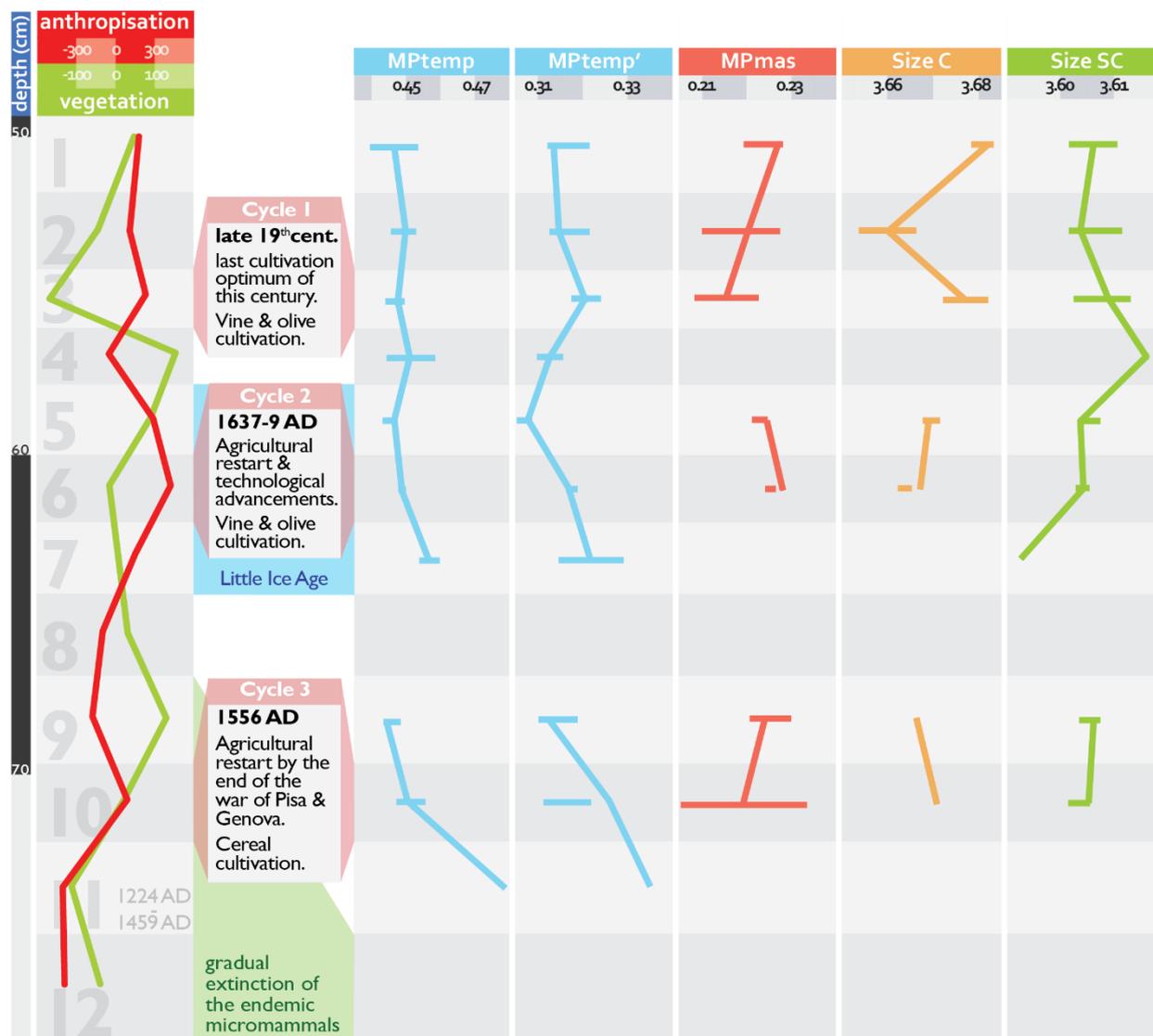
320 The shape corresponding to maximum size presents a shorter and finer ramus, a more anterior
321 coronoid, a more ventral articular condyle and a more stretched angular process (Fig. 4b). The shape
322 corresponding to the maximum MPtemp has a more curved anterior ramus, a more robust and
323 elongated coronoid and a more ventral angular process (Fig. 4b). The shape corresponding to the
324 maximum MPtemp' is similar to the latter but with a more sharply dorsally and ventrally defined
325 articular condyle and a posteriorly thinner, less ventrally positioned angular process. Finally, the shape
326 corresponding to the maximum MPmas presents a narrower body, a more posterior coronoid, a more
327 ventral articular condyle and a less robust and posterior and ventral angular (Fig. 4b). The changes in
328 shape have consequences on the mechanical potential, something that was expected, as we found that
329 6.5% of shape variability is explained by MPtemp and 4.2% by MPmas.

330 Our results also show a significant effect of size on MPmas ($P = 0.01$, $R^2 = 0.06$), a negative correlation
331 between MPtemp and MPmas ($P = 0.03$, $r = -0.23$), between MPtemp' and MPmas ($P = 0.023$, $r = -0.25$)
332 as well as a strong positive correlation between MPtemp' and MPtemp ($P < 0.001$, $r = 0.44$). The
333 regression results show an effect of the anthropisation index on MPtemp' ($P = 0.03$, $r = -0.04$) and
334 MPtemp ($P = 0.001$, $r = -0.01$), both decreasing with an increase in anthropisation.

335 3.3 Mechanical potential and size through time

336 The presentation of the mean MPtemp, MPtemp', MPmas, and size of complete and SC specimens by
337 layer is found in figure 5 (a box-plot version is found in Appendix B.3). The MPtemp of layers three,

338 seven and eleven seem to be different from other layers. There is a noticeable difference in MPtemp
 339 and MPtemp' between layers eleven and ten, however, the sample size for layer eleven is low. Notably,
 340 the MPtemp' for samples from layers six to four is significantly different to that for the next most recent
 341 layer. The MPtemp value for layer nine is significantly different than that of layer seven, and the latter is
 342 significantly different than the value of the next most recent layer. MPmas increases when MPtemp
 343 decreases (with the exception of layers five and six). However, there are missing values for several
 344 layers and the only significant difference between MPmas values is that between layer three and nine.



345
 346 Figure 5. The mean values of MPtemp, MPtemp', MPmas and size (C and SC) by layer and compared to
 347 anthropisation and vegetation indices and important historical events by layer (Vigne & Valladas, 1996). Error bars
 348 present the standard error of the mean (SE).

349 Regarding size, there are changes through time especially for fragment C. All the layers where enough
 350 samples were present to allow an estimate of error show that they are distinct from their adjacent

351 samples. The SC fragments are recovered from most layers and as such provide a more complete image
352 of changes over time. However, as the error bars overlap, no changes are present over time.

353 3.4 Modularity and Integration

354 A summary of the analyses as well as supplementary graphs are found in Appendix B.2 and B.4. There is
355 a statistically significant independence between the two modules of the mandible (body and ramus) (P
356 < 0.001 , $CR = 0.67$) compared to random divisions of the mandible. The integration results on the
357 totality of the samples show that the two modules are integrated ($P < 0.001$, $r\text{-PLS} = 0.729$). The
358 integration tests on each layer find similar levels of integration in the layers tested (Appendix B.2). The
359 first PLS axis that explains 50.6% of the total co-variation shows that when the coronoid process is more
360 robust, the angular becomes more ventral and the body more stretched.

361 In order to test whether morphological changes of the two modules have functional consequences, we
362 visualized the values of MPtemp, MPtemp', MPmas, size, layers as well as anthropisation and
363 vegetation indices on the first PLS axis plot (Appendix B.4). No clear separation of groups appears on
364 the PLS plot suggesting that the patterns of covariation are common to all groups. However, some
365 grouping can be observed relative to the mechanical potential of the temporalis with animals with a
366 higher MP segregating on the upper part of the PLS plot (Appendix B.4). Moreover, the maximum and
367 minimum theoretical shapes of MPtemp (Fig. 4b) can be considered presenting similarities (mostly
368 relative to the articular condyle) to the ones corresponding to the min and max of the first PLS axis (Fig.
369 4c).

370 4. Discussion

371 Our results show that even over a short period of time environmental changes may result in rapid
372 changes of mandible shape (i.e. in the phenotype) in a small insectivorous mammal (*Suncus etruscus*).
373 As such, the shape of the mandible appears a good indicator of environmental change (Anderson et al.,
374 2008). Shape was linked with the mechanical potential of the temporalis muscle (MPtemp) and this
375 (MPtemp and MPtemp') was linked to changes in anthropisation. These results show that shape
376 changes have functional consequences that most probably are linked to shifts in diet that, in turn, have
377 taken place due to habitat alteration mostly because of the changes in human activity or anthropisation
378 around the study area.

379 The morphofunctional relations observed in the present study (Fig. 4b) agree with those observed for
380 other shrews. For example, Cornette et al. (2015c) also found a shorter mandible and Cornette et al.
381 (2012) found a less robust body and more elongate angular process corresponding to an increased size.
382 Additionally, Cornette et al. (2015c) found a more elongate and robust coronoid process corresponding

383 to the maximum mechanical potential of the temporalis muscle, similarly to our results. However, these
384 relations were not investigated in relation to anthropisation changes. Additionally, our results extend
385 the knowledge on how the shape of the shrew mandible reacts to functional constraints imposed by
386 the masseter. The mechanical potential for the masseter muscle was not linked to any of the
387 environmental variables and only slightly impacted by variation in size. It is noteworthy to mention that
388 the MP_{mas} was calculated for a significantly fewer number of specimens (compared to that of the
389 temporalis) because it requires the presence of the angular process – a mandible part that is easily
390 broken off and thus rarely preserved. In this study, we used two biomechanical models to calculate the
391 mechanical potential of the temporalis muscle, one previously established (Carraway et al. 1996) and
392 one that we thought was more representative of the muscle insertion and orientation. The estimates
393 are, as expected, highly correlated. However, the results of the Procrustes ANOVA did not detect a
394 significant link between shape and MP_{temp'}. If it is true that MP_{temp'} is a better representation of the
395 function of the temporalis muscle than MP_{temp}, then this suggests that variation in MP_{temp} is not a
396 direct consequence of changes in shape. As such it may represent a more general shape change in the
397 coronoid rather than being linked specifically to the function of the temporalis muscle.

398 4.1 Modularity and Integration

399 Contrary to the mechanical potential, the integration of the two modules, body and ramus, does not
400 appear to be a marker of environmental change (Fig. 4c, 5; Appendix B.2). Previous studies have shown
401 that shifts in integration as a response to short-term environmental stress produced in the lab are
402 possible in shrews (Badyaev & Foresman 2004; Badyaev et al. 2005). The absence of integration shifts
403 through time in our data suggests that either the environmental changes and diet change were not
404 extreme enough to also alter the integration of the mandible during those 600 years (Klingenberg &
405 Zaklan 2000; Klingenberg et al. 2003; Klingenberg 2005) or that the mandible of *Suncus etruscus* is
406 highly integrated functionally (as the mandible as a whole partakes in the capture and mastication of
407 prey; Zelditch et al., 2009). It is also possible that integration change takes more time and would be
408 visible only on a larger timescale (like for example Monteiro et al. 2005).

409 4.2 On the relation of mandible shape and size with environmental change

410 Our results suggest differences between layers as well as groupings of layers with similar environmental
411 conditions. For example, layers three and ten or four and eleven correspond to the maximum and
412 minimum of the vegetation index (Fig. 4a and Appendix B.1). In addition, we found that these changes
413 are rapid as shape differences are detected even in successive layers (ANOVA results and Fig. 5). This is
414 of interest in the light of suggestions by previous authors (Sans-Coma et al., 1981) stating that *Suncus*
415 *etruscus* is a relatively homeomorphic species in the Mediterranean and Europe in general, with the

416 exception of Sardinia (Sans-Coma et al., 1985). Our results add the Corsican populations to that
417 exception. Similarities between Sardinia and Corsica are not uncommon, because of their shared
418 biogeographical past as well as their connection during periods of lower sea-level during the
419 Pleistocene and the beginning of Holocene (Vigne, 1993; Oggiano et al., 2009).

420 Our results show a significant albeit low allometry as size explains only 2.5% of the total shape
421 variability. Regarding variation in size through time, complete specimens show distinct sizes compared
422 to the adjacent layers while incomplete SC specimens are less distinct in size (Fig. 5). However, it is
423 interesting to note that layer four, corresponding to a vegetation maximum, and layer seven,
424 corresponding to one of the “cold” periods during the “Little Ice Age” (along with layer six) have the
425 biggest and smallest mandibles respectively. The fourth layer is characterized by the highest vegetation
426 level and by a reduction in agricultural activity (Vigne & Valladas, 1996). Large size could be an
427 advantage to capture and eat larger prey, as is the case for bats (Santana & Cheung, 2016), however,
428 this remains to be tested. Bergmann’s rule (see Bergmann, 1848; McNab, 1971) generally does not
429 apply to shrews (Lomolino, 1985; Ochocinska & Taylor, 2003) and the results of this study also support
430 this as the smallest mandibles are found in the coldest intervals of our study. Ochocinska & Taylor
431 (2003) also observed smaller shrews in colder climates, especially for the smallest species of their study,
432 *Sorex minutus*. They explained this observation by suggesting that a decrease in size may allow shrews
433 to increase their ability to find better micro-habitats to survive (Randolph, 1973). Additionally, shrews
434 lose a part of their mass during winter (Churchfield, 1990; Frafjord, 2008) and may change cranial shape
435 seasonally and with age (Lázaro et al., 2017). As an exception, Zaveloff & Boyce (1988) documented
436 bigger shrews in colder climates but their study was spatially restricted to mostly cold habitats in
437 Canada.

438 4.3 On the relation of mechanical potential and environmental change

439 As previously mentioned, bite force is linked to diet in many animals (Aguirre et al., 2003; Anderson et
440 al., 2008). Consequently, the study of the relative shifts of the mechanical potential of the temporalis
441 and masseter muscles may provide information on the type of prey eaten. First, an increase in the
442 mechanical potential of the muscles suggests an increase in bite force which may allow an expansion of
443 the dietary spectrum of an animal (i.e. allowing the animal to consume bigger or harder prey; Young et
444 al., 2007; Cornette et al., 2015c). A possible case where the reduction of the dietary spectrum could
445 have taken place is during layers six to five where the MP of both muscles seems to decrease (Fig. 5).
446 Second, an increase of masseter and decrease of temporalis mechanical potential, as in layers ten to
447 nine, and three to two, suggests a shift in diet to one with more small/soft prey (Cornette et al., 2013).
448 The strong negative correlation of the mechanical potential of the temporalis and masseter also
449 supports this. MP shifts in shrews have also previously been linked with shifts in diet (Cornette et al.,

450 2012). However, it is noteworthy that MP could also give an advantage in competition between
451 individuals of the same or different species. Competition and aggression in shrews is common (mainly
452 involving biting) as they are very territorial (Churchfield, 1990; Kirkland, 1991; Cornette et al., 2015b,
453 2015c). As such, competition can also be expected to drive an increase in the mechanical potential of
454 the temporalis muscle, more specifically as during aggressive interactions biting likely takes place at
455 large gape.

456 Climate and man are both important factors that cause drastic changes to the environment and may
457 affect wildlife. Climate change involves fluctuations in the mean temperature and humidity of the area
458 that affect vegetation and fauna. Changes in human activity, however, can be faster and can equally
459 impact vegetation according to differences in land use. In both cases, changes in vegetation affect the
460 availability of prey and the efficacy of predation which may lead to changes in diet (Geier & Best, 1980;
461 Churchfield, 1990). Human-induced vegetation shifts have been found to affect the phenotype of
462 shrews (example Badyaev et al. 2000). In our study it remains difficult to prove which (climate or man)
463 was the primary driver of the observed changes in shape through time. However, during the period of
464 our study only one important climatic change event took place, the “Little Ice Age”, restricted to the
465 time that corresponds to layers seven to five. However, our results show continuous shifts in shape and
466 mechanical potential from Medieval times to the late 19th century AD. Vigne & Valladas (1996) also
467 found extensive shifts in small mammal abundances during that time. Knowing that that interval was
468 characterized by the intense human activity on the northern part of Corsica (Vigne & Valladas, 1996)
469 this suggests that humans were the primary drivers of habitat change which may have resulted in
470 changes in diet leading to selection on mechanical potential and resulting in changes in shape. More
471 specifically, our results show that anthropisation (the presence of human activity or not) and not
472 vegetation (the presence of natural medium maquis versus low vegetation found in man-made
473 cultivation habitats) affects the mechanical potential of the temporalis. For example, the highest value
474 of temporalis MP is found in the oldest layer (but the sample size is small). The mean MP_{mas} appears to
475 increase through time as well (Fig. 5), possibly suggesting a shift to a diet containing smaller prey
476 (Cornette et al. 2013).

477 While human impacts on the Corsican habitats around Monte di Tuda were already present from the
478 Roman period onwards (Vigne & Marinval-Vigne, 1989; Istria, 1994; Vigne & Valladas, 1996) they
479 intensified/accelerated just before the 13th century with a drastic deforestation (corresponding to the
480 oldest layers of this study). This is illustrated by the Monte di Tuda mammal assemblage but also by the
481 construction of a small castrum on the same hill in 1289 AD, known to have been used for agricultural
482 and pastoral purposes in Corsica (Istria, 1994). In northern Corsica, the establishment of this
483 intensification is marked by cycle 3 – but similar patterns/events took place in southwestern Corsica as

484 well (Vella et al., 2019). This cycle coincides with the Pisa Peace and the subsequent human population
485 increase in the whole of Corsica (Vigne & Valladas 1996; Perry, 1967). However, the drastic and
486 intensified deforestation wave was not only visible in Corsica but in the whole western Europe (in
487 eastern Spain (Planchais & Parra Vergara, 1984; Riera-Mora & Esteban-Amat, 1994), Southern France
488 (Planchais, 1985; Durand & Vernet, 1987; Diot & Laborie, 1989; Chabal, 1991; Durand, 1991; Durand &
489 Leveau, 2004), French Alps (Colardelle & Vedrel, 1993), Puglia (Martin, 1984) and Sicily (Bossard-Beck,
490 1984)). It is interesting to note that this drastic intensification event is also coupled with the extinction
491 of the small mammal endemics like *Prolagus*, *Tyrrhenicola* and *Rhagomys* (Vigne & Valladas, 1996). The
492 endemic extinctions have been linked to this intensification of agricultural activities of Corsicans in the
493 area of Monte di Tuda (Vigne, 1987; Vigne & Marival-Vigne, 1991). At a larger spatial scale these
494 extinctions are more likely to have taken place across a longer time period and to be linked to more
495 than one factor (Vigne, 2014). It is also interesting to note that whereas the arrival of humans on
496 Corsica eventually led to the extinction of endemic small mammals, it left other groups like reptiles
497 almost unimpacted (Vigne & Alcover, 1985; Vigne et al., 1997).

498 4.4 Final thoughts and perspectives

499 The presence of humans has been an important factor shaping the environment of Corsica since their
500 first arrival; however, the intensity of their impact fluctuated through time (Vigne et al., 1997). The
501 results of this study show that human activity in northern Corsica was so intense that its impact is
502 visible on the shape of the mandible of the smallest mammal. The shape and mechanical potential of
503 the main masticatory muscle appear to be indicators of the fluctuations in human activity in the region.
504 This study focused on a local scale, but it is expected that the human impact may be detectable in the
505 micromammal fauna of the rest of the island. Corsica can also serve as an analogue for what happened
506 to the rest of the Mediterranean islands in the sense that the first arrival of man happened early and
507 with this, the introduction of new animals and plants and the anthropisation of the environment (Vigne,
508 1992). However, each Mediterranean island also has its unique human-habitat evolution (Vigne, 1996).
509 It would be interesting to explore whether human impacts can be detected on the fauna of other
510 islands and whether other small mammals reacted to this impact in the similar ways to *Suncus etruscus*.

511 5. Conclusion

512 In a short period of only 600 years, human exploitation resulted in environmental changes on the island
513 of Corsica that had important underlying effects on the fauna. Human-induced environmental change
514 likely resulted in rapid changes in the morphology of the mandible in a small shrew, *Suncus etruscus*.
515 The changes in shape had functional consequences as they are strongly related to changes in the
516 mechanical potential of the primary masticatory muscle, the temporalis. Its negative correlation with

517 the second most important masticatory muscle, the masseter, as well as their link with the
518 anthropisation index suggest a shift in the diet of this shrew species through time linked to human
519 activity. Finally, the integration of the two modules of the mandible seems to be linked to the function
520 of the temporalis muscle but is not a reliable marker of human-induced environmental change.

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