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

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ABSTRACT

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

1. Introduction

We live in an era of rapid and global environmental change where man is the principal driver of changes in the environment, largely because of the expansion of industry and agriculture, as well as population growth (Vitousek et al., 1997). The impact of humans on natural ecosystems has dramatically increased from the Holocene to recent times and has gone hand in hand with climate change. This has had enormous repercussions on ecosystems worldwide (Barnosky et al., 2004) resulting in the so-called sixth mass extinction (Pimm and Brooks, 2000; Barnosky et al., 2011; MacPhee and Sues, 2013; Ceballos et al., 2015). It is therefore crucial to better understand past human activity in conjunction with its direct and indirect impacts on natural landscapes and the organisms that inhabit these. The study of past environmental changes and their impact on fauna and flora may provide us with valuable insights for the future (Blois and Hadly, 2009). Understanding the direct and indirect effects of past human activity on ecosystems

provides valuable information that not only improves our understanding of human history but also provides insights on how human activity can impact future ecosystems.

The phenotype is an important aspect of an organism as it typically reflects the environmental context it lives in as form (shape and size) is intimately linked to function (Anderson et al., 2008). For example, the form of the mandible is intimately linked to bite force generation and may thus provide insights into diet, anti-predator defense and/or competition in animals (Anderson et al., 2008). As such, mandible shape may be used as a marker of environmental change. This is true for all vertebrates, but especially so for small mammals that are likely constrained in their diet by their absolute bite force (Atchley, 1993; Aguirre et al., 2003; Renaud et al., 2009). As such, we hypothesize that bite force should be related to environmental changes. We also hypothesize that the environmental changes may impact mandibular integration and modularity. Integration is defined as the relation between anatomical structures often referred to as modules. Modules are defined when the

different anatomical structures inside the module co-vary more strongly among themselves than with any anatomical structure outside the module (Olson and Miller, 1958; Klingenberg et al., 2004; Schlosser and Wagner, 2004; Callebaut and Rasskin-Gutman, 2005; Mitteroecker and Bookstein, 2007; Klingenberg, 2008; Goswami and Polly, 2010). Hanot et al. (2018), for example, found that artificial selection had an impact on the patterns of integration of the appendicular skeleton of domestic horses. Moreover, Hanot et al. (2017) showed that integration is stronger in the cases where functional constraints are strong, suggesting that the degree of integration of the mandible might provide insights in the strength of selection on this structure.

Islands are often considered "natural laboratories" allowing the study of ecosystems in relation to environmental changes as well as a better understanding of evolutionary mechanisms, extinction and speciation events as insular ecosystems are simple and sensitive to changes (Darwin, 1845; Wallace, 1860; Losos et al., 1997; Whittaker and

Fernández-Palacios, 2007). In this context, the island of Corsica (Fig. 1a and b) appears a good model to study the relationship between humans and their environment through time and the subsequent impacts thereof on the fauna (Vigne et al., 1997; Vigne, 1999). The first arrival of man on most Mediterranean islands took place in the last 12,000 years and this was more often than not, followed by the extinction of endemic species and their replacement with newly introduced taxa (e.g. Alcover et al., 1981; Davis, 1984; Vigne and Alcover, 1985; Kouvari and van der Geer, 2018). Corsica is a great example as the impact of humans on the endemic fauna and flora is exceptionally well documented (Vigne, 1990, 1992, 1996, 1999; Vigne and Valladas, 1996). While the megafauna extinction on Corsica took place soon after the first arrival of man, smaller endemic mammals went extinct much later (Vigne, 1988, 1990, 1992). Humans involuntarily introduced many small mammals that became established on the island (Vigne, 1988, 1990, 1992; Vigne and Valladas, 1996).
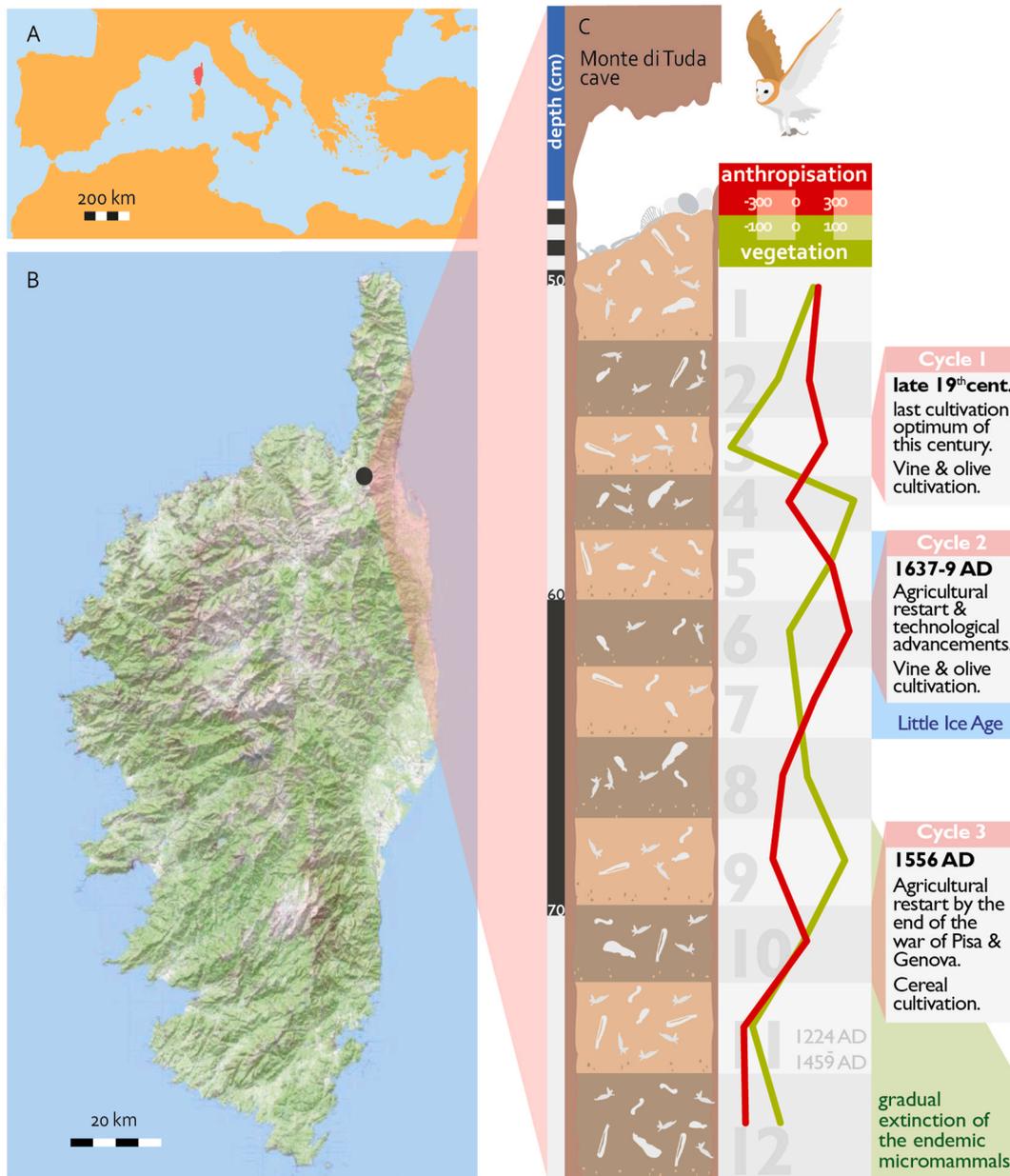

Fig. 1. (a) Map of the Mediterranean Sea showing Corsica in red, (b) geomorphological map of Corsica, and (c) an illustration of the layers of the Monte di Tuda cave, their depth, the vegetation and anthropisation indices and information on the dating, anthropisation cycles and other important events - modified after Vigne and Valladas (1996). Mediterranean map based on outlines from © d-maps.com. Corsica map from © IGN Planet Observer. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The Monte di Tuda site is an archeological site in the Nebbio Basin in the North of the island (Fig. 1a and b). The site consists of a cave that served as an owl nest (probably *Tyto alba*) for the last 2500 years and provides an exceptional accumulation of micromammal remains through time (Vigne and Valladas, 1996). Vigne and Valladas (1996) studied these remains and the changes therein through time. They distinguished biozones, and calculated an anthropisation and vegetation index for each layer. More specifically, they studied the cave sediment stratigraphy, distinguished the different layers present, and dated (^{14}C) some of them. They studied the faunal assemblages by calculating the minimum number of individuals (MNI) of each species in each layer. Based on the previous and in conjunction with the known ecological preference of the species, they ran a correspondence analysis (CA) between species and layers (their faunal compositions) in order to observe the potentially existing patterns of ecological significance. From this, the first axis distinguished between anthropophilic species while the second between species preferring "natural" medium maquis vegetation and those preferring low vegetation. They thus used the CA layer coordinates of the F1 axis as an anthropisation index and those on the F2 as a vegetation index. Finally, based on those vegetations and anthropisation
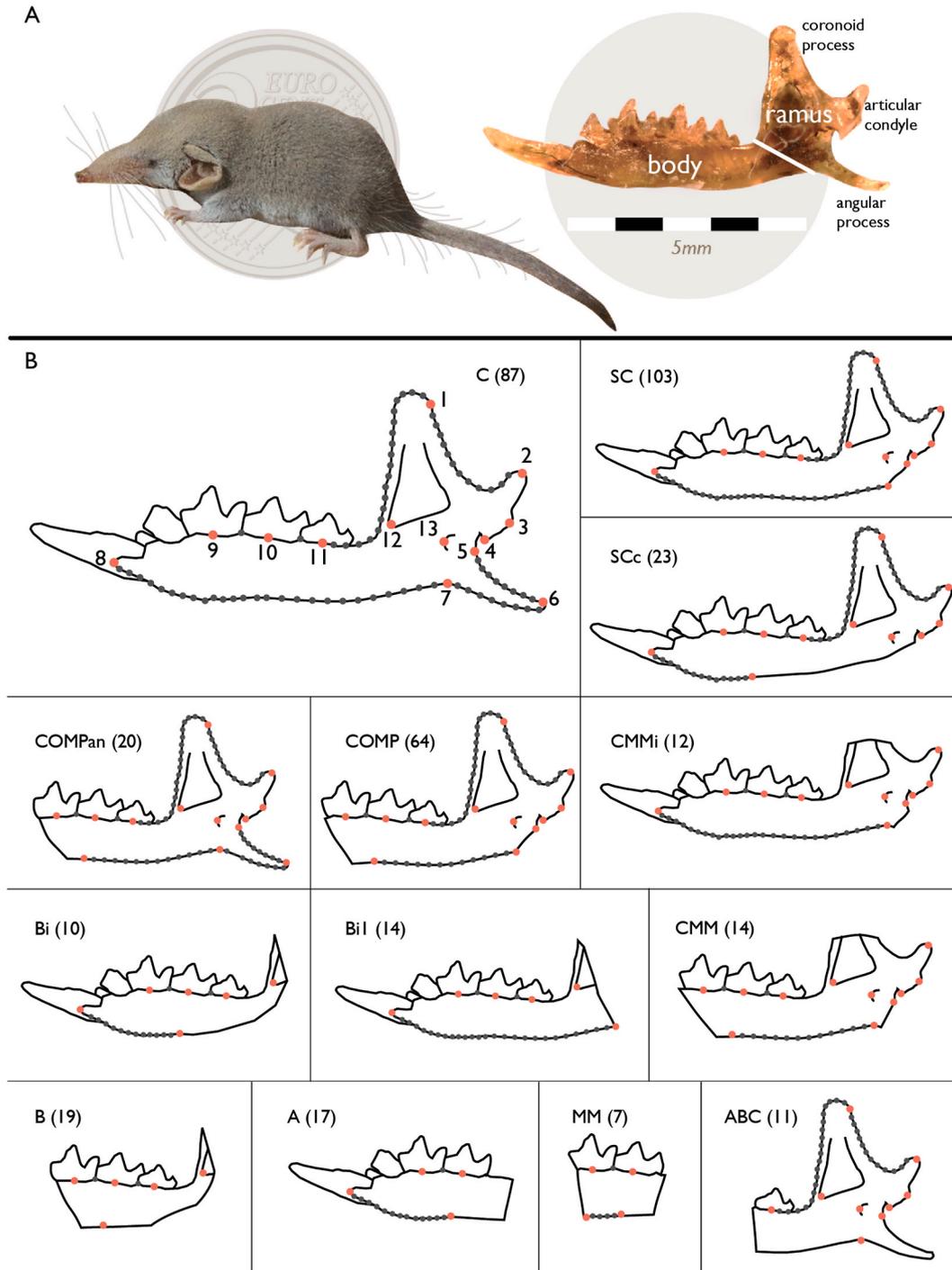

Fig. 2. (a) *Suncus etruscus* (photographed by © Jose B. Ruiz) with a scale that corresponds to a 2-Euro coin and the anatomical parts of its mandible. (b) Types of fragments and their landmarks (red) and semi-landmarks (grey). The number in brackets corresponds to the number of specimens of each fragment type. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

indices along with the information on the dated layers and the history of Corsica, the authors distinguished anthropisation cycles, characterized by important local events.

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

Small mammals are often good markers of the environment they live in (Bar-Yosef & Tchernov, 1966; Brothwell and Jones, 1978; Chaline, 1979; Marquet, 1989; Rofes et al., 2014; Weissbrod, 2010; Stoetzel et al., 2011). We studied one of the smallest species, the white-toothed shrew *Suncus etruscus* (Savi, 1822) (Soricidae) (Fig. 2a). This shrew is one of the smallest extant mammals by mass (only 1.8 g; Jürgens, 2002) and reached Corsica, as well as most other Mediterranean islands, through human-mediated transport (Dobson, 1998; Chen and Koprowski, 2018). It is a synanthropic/anthropophilic species as it thrives in human-transformed habitats such as olive groves and vineyards (Dobson, 1998). It is an opportunistic species feeding principally on invertebrates but also occasionally on small vertebrates (Nowak and Paradiso, 1999; Kingdon et al., 2013). We here specifically focus on its mandible (Fig. 2a) as this structure is directly linked to diet (Badyaev and Foresman, 2004) and interspecific competition (Cornette et al., 2015c) through its impact on bite force generation. Shrew mandibles also show exceptional phenotypic plasticity (Young et al., 2010) i.e. non-heritable morphological variation as a response to environmental pressures (Price et al., 2003). Phenotypic plasticity has been investigated in laboratory-raised mice (Anderson et al., 2014; Garland and Kelly, 2006; Renaud et al., 2010) but has also been observed in shrews fed on different diets (Young and Badyaev, 2010). Bite force is an ecologically relevant performance trait as it is directly related to prey capture and manipulation and as such determines the type and size of prey that can be consumed (Aguirre et al., 2003; Anderson et al., 2008). We here estimated the mechanical advantage of the two primary masticatory muscles, the temporalis and the masseter. These two muscles are particularly relevant as they are optimized to generate force at different gape angles (masseter = low gape; temporalis = high gape; Cornette et al., 2013). Consequently, if shifts in prey size occur through time this may be reflected in the relative contribution on these two muscles to biting.

Human activity and its direct effects on islands, and in particular in Corsica, are well known. However, the full range of the underlying consequences of these impacts has not been extensively studied to date. In this paper, we investigated the effects of human-induced environmental changes in Corsica, taking as a case study the Etruscan shrew. We hypothesized that environmental changes will impact the integration of the mandible and tested whether phenotypic integration is a marker of environmental change in an archeological context. Integration (i.e. the link between different modules of the same anatomical structure) can change in two ways: via direct interactions (cell groupings or signaling pathways change) and via parallel variation due to selection on function (Klingenberg and Zaklan 2000; Klingenberg et al., 2003; Klingenberg 2005). The first type of integration is difficult to change as it requires developmental and genetic "rewiring". The second type of integration mostly drives the evolution of population level variation (for example, Cheverud 1982, 1996; Wagner 1996; Wagner and Altenberg 1996).

Zelditch et al. (2009) suggested that while the mandible can be a highly modular system from a developmental point of view, it is a functionally integrated system as the mandible as a whole takes part in all its functions like the capture of prey and mastication. Here, we test whether the integration between the body and ramus of the mandible (Fig. 2a) changes in response to the rapid environmental changes observed at our study site through time. In summary, we attempt to define morpho-functional markers of environmental change due to human activity. More specifically, we tested if, even over a short period of time at the start of the modern era the impact of environmental changes is visible on the phenotype of the mandible of *Suncus etruscus*, in terms of its form and function.

2. Material & methods

2.1. Material

We here focus on the modern era (14th−19th century AD), a short period of about 600 years. During this time interval, Vigne and Valladas (1996) identified twelve layers at Monte di Tuda, each corresponding to a different depth in the sediment (Fig. 1c). They dated layer eleven at 1224–1459 AD (610 ± 120 years BP) and related the other layers with historical events, more specifically layer ten with the end of the war of Pisa (1556 AD), layer six with the agricultural development of the Genovese people (1637–1639 AD; Arrighi, 1990) and layer three to the last cultivation optimum of the 19th century in Corsica (Vigne and Valladas, 1996). This period is characterized by a good resolution of environmental changes and human activity through time and shows a gradual intensification of human activity, the predominance of human transformed environments, and a short period of colder and wetter climate called the "Little Ice Age" (~1300–1850 AD) with minimal temperatures occurring around 1645–1715 AD; (Le Roy Ladurie, 1967; Lamb, 1969; Schneider and Mass, 1975; Fagan, 2002).

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

2.2. Methods

Specimens were sorted, numbered and the lingual sides were photographed using a NIKON D5500 camera (with a NIKKOR 60 mm lens). All data and analyses are available in Kouvari et al. (2021).

2.2.1. Fragment types

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

2.2.2. Analysis of mandible shape

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

More specifically, 13 landmarks (Table 2) and 76 semi-landmarks were defined on complete specimens. For fragmented mandibles we used the maximum number of landmarks present on the fragment (Fig. 2b). A repeatability test was performed on three specimens.

Table 1

Anatomical localization and description of the different fragment types starting with complete specimens and finishing with the most fragmented types.

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

Table 2

Anatomical Landmarks and their description.

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

Landmarks were positioned 20 times on each specimen, followed by a General Procrustes Analysis (GPA) and a Principal Components Analysis (PCA). This showed that the intra-specimen variability was lower than that between specimens. Landmark digitization was done using the TPSDig2 software (Rohlf, 2010). The definition and sliding of semi-landmarks, Procrustes superimposition (by Bending energy) and PCA were done with the 'Geomorph' package (Adams et al., 2017) in R (R Development Core Team, 2008).

2.2.3. Neighbour-Joining trees of mean shapes

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

2.2.4. Mechanical potential

We calculated the mechanical potential (MP) of the temporalis and masseter muscles on the complete specimens as well as on the fragment types that allowed for these calculations (i.e. SC, SCc, COMP and COMPan). We then calculated the mean for each layer. The MP of the temporalis was calculated following two methods. The first (MPtemp; Fig. 3a) is the method described by Carraway et al. (1996; see also Cornette et al., 2012; 2015c). Although this method has been widely
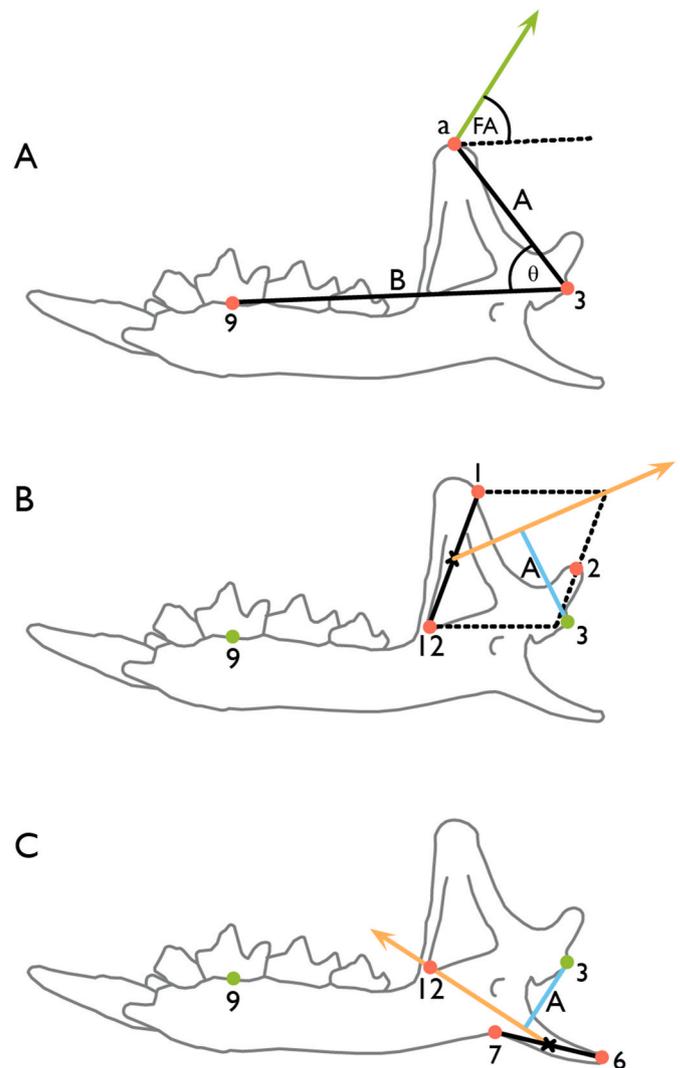

Fig. 3. The biomechanical model of (a) MPtemp (by Carraway et al., 1996); (b) the new model for MPtemp' and (c) MPmas. For all models, B is the distance between landmark 3 and 9 (it is only represented in 3a because of lack of free space in the rest). Distance A is the distance between landmark 3 and the uppermost point of the coronoid process for (a), the perpendicular distance between landmark 3 and the muscle vector (orange) for (b) and (c). FA = 90° - θ°. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

used, it is not the best estimation of force transmission by the temporalis muscle as it does not present the line of action of the temporalis muscle realistically. As shown in Fig. 3a, in the original model, the temporalis bite force (arrow) originates from the tip of the coronoid process and extends dorso-posteriorly. However, in reality, the muscle attaches on the middle of the ramus and on the temporal bones of the skull that are situated posterior to the coronoid process. This is the reason why we introduce the second method referred to as MPtemp' (Fig. 3b) which provides a better estimate of the functional advantage of the temporalis muscle by including the calculation of the muscle moment arm.

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

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

MPtemp = (A/B) cosine (FA) where FA^o = 90 - θ^o

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

MPtemp' = A/B

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

MPmas = A/B

2.2.5. Mandible size

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

2.2.6. Statistical analyses

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

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

In order to study modularity and integration of the mandible, we first defined the body and ramus as the two modules of the mandible (Fig. 2a) based on previous studies (Cheverud et al., 1997; Mezey et al., 2000; Klingenberg et al., 2003). We performed a modularity test ('Modularity. test' function of the 'Geomorph' package; Adams et al., 2017) to compare the degree of modularity between two modules defined using the covariance ratio or CR coefficient (Adams, 2016). If the CR coefficient obtained by our pre-defined structure is smaller than the CRs obtained by the random permutations, then our hypothesis is valid (Adams, 2016). The definition of the modules was performed using the 'define.modules' function in 'Geomorph' (Adams et al., 2017). In order to test whether modules are integrated we performed an integration test using the 'Integration.test' function of 'Geomorph' (Adams et al., 2017).

The two-block partial least squares (2b-PLS) test quantifies the degree of integration between the two modules (Adams and Collyer, 2016). In addition, we visualized the shape of each module corresponding to the maximum and minimum of each axis of covariation using the 'shape. predictor' function of 'Geomorph' (Adams et al., 2017). In order to test functional consequences of integration we plotted all variables (MPs, size, vegetation and anthropisation indexes) on the first PLS axis. P-values were considered significant if smaller than or equal to 0.05. For the analyses that include multiple tests/comparisons, we applied a Bonferroni correction according to which alpha (critical value) is used to judge the significance of the results and is equal to 0.05 divided by the number of tests performed for each analysis (Rice, 1989).

3. Results

3.1. Global morphological patterns

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

Similar patterns emerge from trees established and based on different fragment types (Appendix B.1) including the distinction of layers eleven and seven, the grouping of layers five and six (trees SC, SCc, CMMi, ABC, Bi), and the distinction of layers two and ten from layers five and six (COMP, COMPan, SC, CMMi). However, different fragments do also show some additional patterns. The COMP tree separates all layers with low vegetation from layers two and eleven with high vegetation and trees (Vigne and Valladas, 1996). The SCc tree separates all layers from the layers nine and ten that correspond to cereal cultivation and its recolonization period (Vigne and Valladas, 1996). The CMM tree (including COMP) separates all layers from layers four, three and eleven, the first corresponding to maximum vegetation and the two others to minimum vegetation (Vigne and Valladas, 1996). Finally, the ABC tree (including COMP, COMPan, SC and C) separates all layers from layer seven (very humid climate and "Little Ice Age") and eleven (vegetation minimum) (Vigne and Valladas, 1996).

3.2. Morphological changes and functional consequences

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

The shape corresponding to maximum size presents a shorter and finer ramus, a more anterior coronoid, a more ventral articular condyle and a more stretched angular process (Fig. 4b). The shape corresponding to the maximum MPtemp has a more curved anterior ramus, a more robust and elongated coronoid and a more ventral angular process (Fig. 4b). The shape corresponding to the maximum MPtemp' is similar to the latter but with a more sharply dorsally and ventrally defined articular condyle and a posteriorly thinner, less ventrally positioned angular process. Finally, the shape corresponding to the maximum MPmas presents a narrower body, a more posterior coronoid, a more ventral articular condyle and a less robust and posterior and ventral
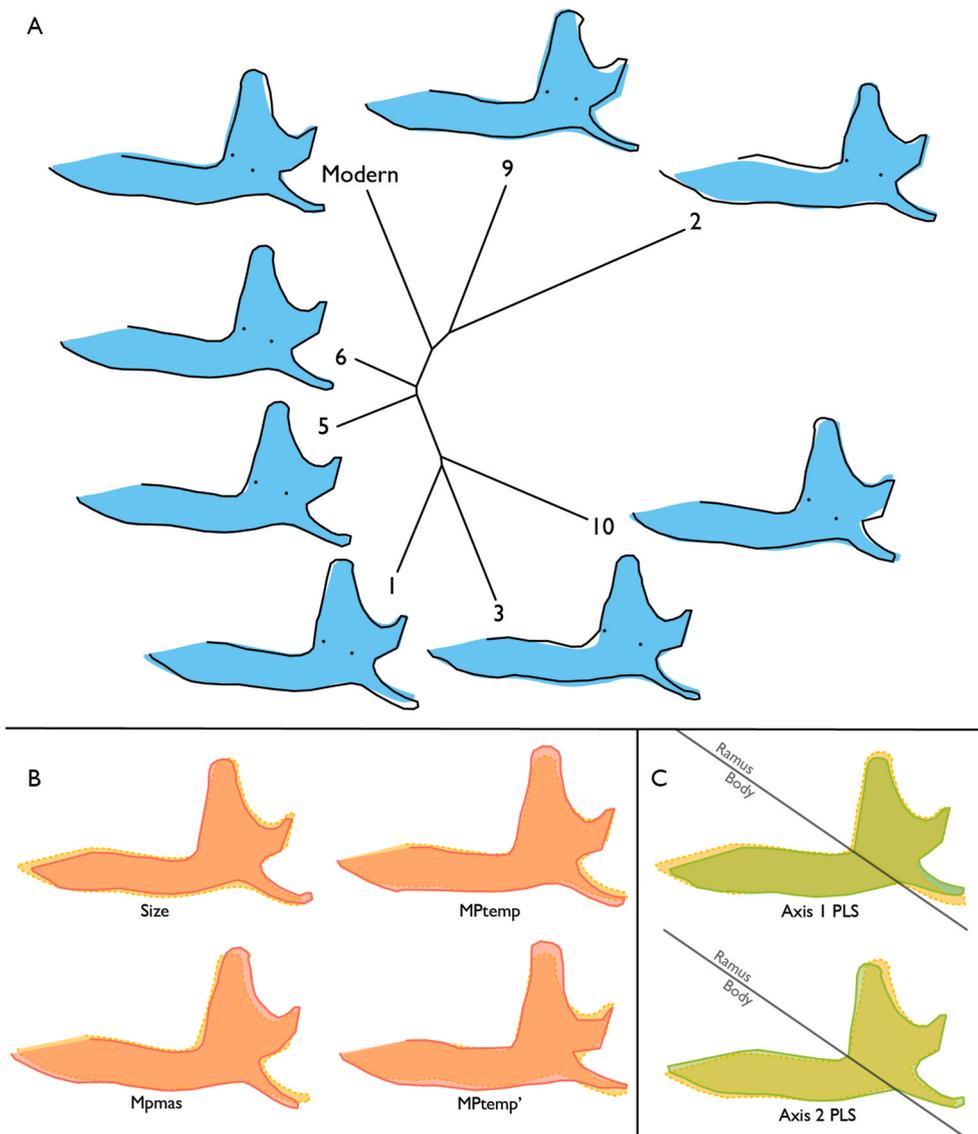
Fig. 4. (a) The Euclidian distance tree between mean shape by layer for complete specimens (mean shapes by layer are also presented (black outline) and compared to mean shape of all sample (blue shape)); (b) The theoretical shape that corresponds to the minimum (yellow) and maximum (red) of size, MPtemp, MPtemp' and MPmas; (c) the theoretical shapes corresponding to the max (green) and minimum (yellow) of the first two PLS axis. Additional graphs in Appendix B.4. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

angular (Fig. 4b). The changes in shape have consequences on the mechanical potential, something that was expected, as we found that 6.5% of shape variability is explained by MPtemp and 4.2% by MPmas.

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

3.3. Mechanical potential and size through time

The presentation of the mean MPtemp, MPtemp', MPmas, and size of complete and SC specimens by layer is found in Fig. 5 (a box-plot version is found in Appendix B.3). The MPtemp of layers three, seven and eleven seem to be different from other layers. There is a noticeable difference in MPtemp and MPtemp' between layers eleven and ten, however, the sample size for layer eleven is low. Notably, the MPtemp' for samples from layers six to four is significantly different to that for the next most recent layer. The MPtemp value for layer nine is significantly different than that of layer seven, and the latter is significantly different than the value of the next most recent layer. MPmas increases when MPtemp

decreases (with the exception of layers five and six). However, there are missing values for several layers and the only significant difference between MPmas values is that between layer three and nine.

Regarding size, there are changes through time especially for fragment C. All the layers where enough samples were present to allow an estimate of error show that they are distinct from their adjacent samples. The SC fragments are recovered from most layers and as such provide a more complete image of changes over time. However, as the error bars overlap, no significant changes are present over time.

3.4. Modularity and integration

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

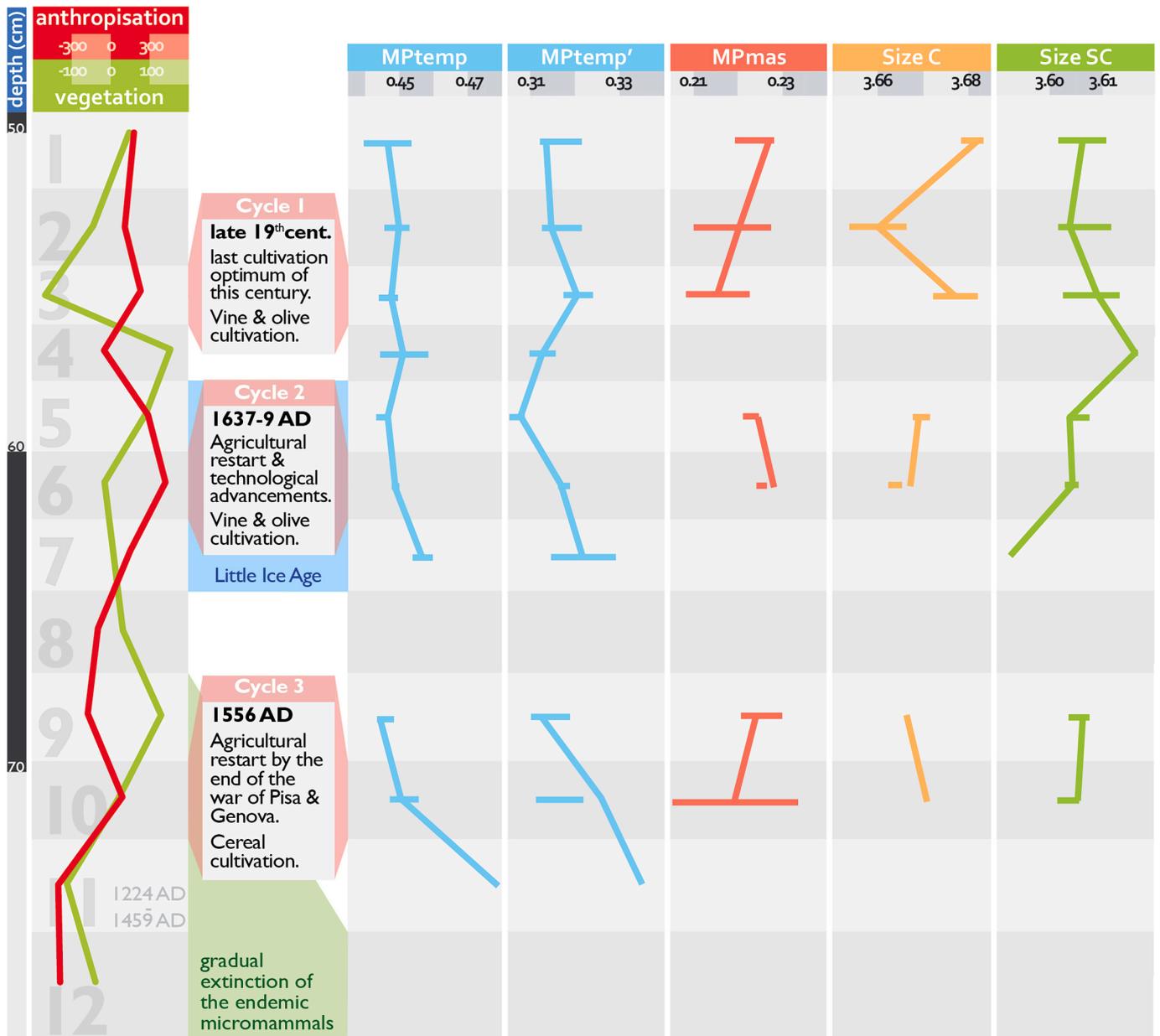In order to test whether morphological changes of the two modules

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

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

4. Discussion

Our results show that even over a short period of time environmental changes may result in rapid changes of mandible shape (i.e. in the phenotype) in a small insectivorous mammal (*Suncus etruscus*). As such, the shape of the mandible appears a good indicator of environmental

change (Anderson et al., 2008). Shape was linked with the mechanical potential of the temporalis muscle (MPtemp) and this (MPtemp and MPtemp') was linked to changes in anthropisation. These results show that shape changes have functional consequences that most probably are linked to shifts in diet that, in turn, have taken place due to habitat alteration mostly because of the changes in human activity or anthropisation around the study area.

The morphofunctional relations observed in the present study (Fig. 4b) agree with those observed for other shrews. For example, Cornette et al. (2015c) also found a shorter mandible and Cornette et al. (2012) found a less robust body and more elongate angular process corresponding to an increased size. Additionally, Cornette et al. (2015c) found a more elongate and robust coronoid process corresponding to the maximum mechanical potential of the temporalis muscle, similarly to our results. However, these relations were not investigated in relation to anthropisation changes. Additionally, our results extend the knowledge on how the shape of the shrew mandible reacts to functional constraints imposed by the masseter. The mechanical potential for the masseter

muscle was not linked to any of the environmental variables and only slightly impacted by variation in size. It is noteworthy to mention that the MPmas was calculated for a significantly fewer number of specimens (compared to that of the temporalis) because it requires the presence of the angular process – a mandible part that is easily broken off and thus rarely preserved. In this study, we used two biomechanical models to calculate the mechanical potential of the temporalis muscle, one previously established (Carraway et al., 1996) and one that we thought was more representative of the muscle insertion and orientation. The estimates are, as expected, highly correlated. However, the results of the Procrustes ANOVA did not detect a significant link between shape and MPtemp'. If it is true that MPtemp' is a better representation of the function of the temporalis muscle than MPtemp, then this suggests that variation in MPtemp is not a direct consequence of changes in shape. As such it may represent a more general shape change in the coronoid rather than being linked specifically to the function of the temporalis muscle.

4.1. Modularity and integration

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

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

Our results suggest differences between layers as well as groupings of layers with similar environmental conditions. For example, layers three and ten or four and eleven correspond to the maximum and minimum of the vegetation index (Fig. 4a and Appendix B.1). In addition, we found that these changes are rapid as shape differences are detected even in successive layers (ANOVA results and Fig. 5). This is of interest in the light of suggestions by previous authors (Sans-Coma et al., 1981) stating that *Suncus etruscus* is a relatively homeomorphic species in the Mediterranean and Europe in general, with the exception of Sardinia (Sans-Coma et al., 1985). Our results add the Corsican populations to that exception. Similarities between Sardinia and Corsica are not uncommon, because of their shared biogeographical past as well as their connection during periods of lower sea-level during the Pleistocene and the beginning of Holocene (Vigne, 1993; Oggiano et al., 2009).

Our results show a significant albeit low allometry as size explains only 2.5% of the total shape variability. Regarding variation in size through time, complete specimens show distinct sizes compared to the adjacent layers while incomplete SC specimens are less distinct in size (Fig. 5). However, it is interesting to note that layer four, corresponding to a vegetation maximum, and layer seven, corresponding to one of the "cold" periods during the "Little Ice Age" (along with layer six) have the biggest and smallest mandibles respectively. The fourth layer is characterized by the highest vegetation level and by a reduction in agricultural activity (Vigne and Valladas, 1996). Large size could be an advantage to capture and eat larger prey, as is the case for bats (Santana and Cheung, 2016), however, this remains to be tested. Bergmann's rule (see Bergmann, 1848; McNab, 1971) generally does not apply to shrews

(Lomolino, 1985; Ochocinska and Taylor, 2003) and the results of this study also support this as the smallest mandibles are found in the coldest intervals of our study. Ochocinska and Taylor (2003) also observed smaller shrews in colder climates, especially for the smallest species of their study, *Sorex minutus*. They explained this observation by suggesting that a decrease in size may allow shrews to increase their ability to find better micro-habitats to survive (Randloph, 1973). Additionally, shrews lose a part of their mass during winter (Churchfield, 1990; Frafjord, 2008) and may change cranial shape seasonally and with age (Lázaro et al., 2017). As an exception, Zeveloff and Boyce (1988) documented bigger shrews in colder climates but their study was spatially restricted to mostly cold habitats in Canada.

4.3. On the relation of mechanical potential and environmental change

As previously mentioned, bite force is linked to diet in many animals (Aguirre et al., 2003; Anderson et al., 2008). Consequently, the study of the relative shifts of the mechanical potential of the temporalis and masseter muscles may provide information on the type of prey eaten. First, an increase in the mechanical potential of the muscles suggests an increase in bite force which may allow an expansion of the dietary spectrum of an animal (i.e. allowing the animal to consume bigger or harder prey; Young et al., 2007; Cornette et al., 2015c). A possible case where the reduction of the dietary spectrum could have taken place is during layers six to five where the MP of both muscles seems to decrease (Fig. 5). Second, an increase of masseter and decrease of temporalis mechanical potential, as in layers ten to nine, and three to two, suggests a shift in diet to one with more small/soft prey (Cornette et al., 2013). The strong negative correlation of the mechanical potential of the temporalis and masseter also supports this. MP shifts in shrews have also previously been linked with shifts in diet (Cornette et al., 2012). However, it is noteworthy that MP could also give an advantage in competition between individuals of the same or different species. Competition and aggression in shrews are common (mainly involving biting) as they are very territorial (Churchfield, 1990; Kirkland, 1991; Cornette et al., 2015b, 2015c). As such, competition can also be expected to drive an increase in the mechanical potential of the temporalis muscle, more specifically as during aggressive interactions biting likely takes place at large gape.

Climate and man are both important factors that cause drastic changes to the environment and may affect wildlife. Climate change involves fluctuations in the mean temperature and humidity of the area that affect vegetation and fauna. Changes in human activity, however, can be faster and can equally impact vegetation according to differences in land use. In both cases, changes in vegetation affect the availability of prey and the efficacy of predation which may lead to changes in diet (Geier and Best, 1980; Churchfield, 1990). Human-induced vegetation shifts have been found to affect the phenotype of shrews (example Badyaev et al., 2000). In our study it remains difficult to prove which (climate or man) was the primary driver of the observed changes in shape through time. However, during the period of our study only one important climatic change event took place, the "Little Ice Age", restricted to the time that corresponds to layers seven to five. However, our results show continuous shifts in shape and mechanical potential from Medieval times to the late 19th century AD. Vigne and Valladas (1996) also found extensive shifts in small mammal abundances during that time. Knowing that interval was characterized by the intense human activity on the northern part of Corsica (Vigne and Valladas, 1996) this suggests that humans were the primary drivers of habitat change which may have resulted in changes in diet leading to selection on mechanical potential and resulting in changes in shape. More specifically, our results show that anthropisation (the presence of human activity or not) and not vegetation (the presence of natural medium maquis versus low vegetation found in man-made cultivation habitats) affects the mechanical potential of the temporalis. For example, the highest value of temporalis MP is found in the oldest layer (but the

sample size is small). The mean MPmas appears to increase through time as well (Fig. 5), possibly suggesting a shift to a diet containing smaller prey (Cornette et al., 2013).

While human impacts on the Corsican habitats around Monte di Tuda were already present from the Roman period onwards (Vigne and Marinval-Vigne, 1989; Istria, 1994; Vigne and Valladas, 1996), they intensified/accelerated just before the 13th century with a drastic deforestation (corresponding to the oldest layers of this study). This is illustrated by the Monte di Tuda mammal assemblage but also by the construction of a small castrum on the same hill in 1289 AD, known to have been used for agricultural and pastoral purposes in Corsica (Istria, 1994). In northern Corsica, the establishment of this intensification is marked by cycle 3 – but similar patterns/events took place in south-western Corsica as well (Vella et al., 2019). This cycle coincides with the Pisa Peace and the subsequent human population increase in the whole of Corsica (Vigne and Valladas 1996; Perry, 1967). However, the drastic and intensified deforestation wave was not only visible in Corsica but in the whole western Europe (in eastern Spain (Planchais and Parra Vergara, 1984; Riera-Mora and Esteban-Amat, 1994), Southern France (Planchais, 1985; Durand and Vernet, 1987; Diot and Laborie, 1989; Chabal, 1991; Durand, 1991; Durand and Leveau, 2004), French Alps (Colardelle and Vedrel, 1993), Puglia (Martin, 1984) and Sicily (Bossard-Beck, 1984)). It is interesting to note that this drastic intensification event is also coupled with the extinction of the small mammal endemics like *Prolagus*, *Tyrrhenicola* and *Rhagomys* (Vigne and Valladas, 1996). The endemic extinctions have been linked to this intensification of agricultural activities of Corsicans in the area of Monte di Tuda (Vigne, 1987; Vigne and Marinval-Vigne, 1991). At a larger spatial scale these extinctions are more likely to have taken place across a longer time period and to be linked to more than one factor (Vigne, 2014). It is also interesting to note that whereas the arrival of humans on Corsica eventually led to the extinction of endemic small mammals, it left other groups like reptiles almost unimpacted (Vigne and Alcover, 1985; Vigne et al., 1997).

4.4. Final thoughts and perspectives

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

5. Conclusion

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

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

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendices A and B. Supplementary data

Supplementary material to this article can be found online at https://doi.org/10.1016/j.jas.2021.105434

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