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Experimental assessment of the relationship between diet and mandibular morphology: new insights for the paleodietary reconstructions of early hominins using a pig model

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Abstract

Dietary habits exert significant selective pressures on anatomical structures in animals, leading to substantial morphological adaptations. Yet, the relationships between the mandible and diet are still unclear raising issues for paleodietary reconstructions notably. To assess the impact of food hardness and size on morphological structures, we used an experimental baseline using a model based on the domestic pig, an omnivorous mammal with bunodont, thick-enameled dentition, and chewing movements similar to hominids. We hypothesized that the consumption of different types of seeds would result in substantial differences in the morphology of the mandible despite similar overall diets. The experiment was conducted on four groups of juvenile pigs fed with mixed cereal and soy flours. The control group received only flours. We supplemented the four others with either 10 hazelnuts, 30 hazelnuts, 30% barley seeds or 20% corn kernels per day. We investigated the shape differences between the controlled-fed groups using three-dimensional geometric morphometrics. Our results provide strong evidence that the supplemental consumption of a significant amount of seeds for a short period (95 days) substantially modify the mandibular morphology of pigs. Our analyses suggest that this shape differentiation is due to the size of the seeds, requiring high and repeated bite force, rather than their hardness. These results provide new perspectives for the use of mandibular morphology as a proxy in paleodietary reconstructions complementing dental microwear textures analyses.

Keywords: mandible, experimental study, paleodiet, durophagy, geometric morphometrics

1 Introduction

Dietary habits can exert significant selective pressures on anatomical structures in animals, leading to substantial morphological adaptations (Anapol & Lee, 1994; Kinzey, 1992; Smith et al., 2015). The mandible is one of the main bones involved in masticatory functions and several studies established a link between mandibular shape and diet in extant and extinct taxa, notably in primates (Daegling, 1992; Taylor, 2006; Wroe et al., 2010). In contrast, other analyses established no straightforward relationship between dietary categories and the morphology of the mandible (Arbour et al., 2019, Meloro et al., 2015; Raia et al., 2010; Tamagnini et al., 2021; Turnbull, 1970, Zelditch et al., 2017) underlining the absence of a clear link between the type of food and the shape of the masticatory apparatus. This lack of a clear relationship can be explained as dietary habits and adaptations to certain types of food are not equivalent. Indeed, mandibular morphology represents the potential diet of an animal (i.e. what it is capable of eating) rather than its actual diet (Gailer et al., 2016; Tütken et al., 2013, van Casteren et al., 2019). Several studies showed indeed that there is no clear relationship between the food items eaten by a given taxa and the trophic morphology for which it appears adapted (Grine & Daegling, 2017; Lambert et al., 2004; Norconk & Veres, 2011). This phenomenon, known as “Liem’s Paradox” (Liem, 1980) is a major issue for paleodietary reconstructions based on mandibular morphology. For instance, in numerous early hominins, a robust mandible with thick-enameled and bunodont cheek teeth has been traditionally considered as reflecting durophagy. The diet of the genus *Paranthropus* in particular was thought to consist primarily of hard foods (e.g. nuts and seeds; Rak, 1978; Robinson, 1954; Ward & Molnar, 1980). This interpretation based in part on mandibular morphology led to the view that *Paranthropus* fed specifically on hard-objects. Yet, later works focusing on the biogeochemical composition of enamel and the texture of dental microwear challenged this hypothesis. The robust condition has been associated with an adaptation to abrasive/fibrous foods for the eastern African *P. boisei* (Cerling et al., 2011; Scott et al., 2012; Ungar et al., 2008) and to the occasional consumption of hard items as fallback foods (Marshall et al., 2009) for the southern African *P. robustus* (Peterson et al., 2018; Scott et al., 2005; Ungar & Sponheimer, 2011). Fallback foods have been described as resources specifically consumed during food scarcity periods when easier-to-process items are unavailable (Marshall et al., 2009). They are generally mechanically challenging and have been recognized as potential selective drivers of trophic morphologies (Potts, 2004; Robinson and Wilson, 1998).

Overall, the relationship between diet and mandibular shape is poorly defined (Ross & Iriarte-Diaz, 2014; Ross et al., 2012). Whether mandible shape changes can be associated with differences in type of foods, and specifically in food hardness, therefore remain to be clarified. Previous experimental studies focusing on controlled-fed rodents and lagomorphs associated several mandibular shape changes with the consumption of hard food (e.g. extension of the coronoid and angular processes, reduction of the corpus length, and increase of the width between the dental arches; Anderson et al., 2014; Beecher & Corruccini, 1981; Ödman et al., 2008). Prior studies underline the great phenotypic plasticity of the mandible as it modelled throughout life to resist mechanical changes in the environment (Brassard et al., 2020; Fabre et al. 2018, Frost et al., 2001). Among these changes, several studies demonstrated that food mechanical properties are among the major cause of cortical bone remodelling (Bouvier and Hylander 1981; Lieberman et al. 2004; Scott et al. 2014; Ravosa et al. 2015). Here, to explore the link between diet and mandibular shape variations, we also used an experimental approach. We investigate mandibular changes related to diet on 28 controlled-fed domestic pigs (*Sus scrofa*), deciphering the role that phenotypic plasticity plays in the interpretation of shape variations in this context, focusing on seed consumption. This study allows avoiding the limitations associated with other animal models, particularly with respect to the specifics of their food oral processing. Indeed, contrary to rodents and lagomorphs, pigs are omnivorous mammals with bunodont, thick-enameled dentition morphologically closer to what is observed in hominids. Chewing movements are also broadly, although not exactly, similar between pigs and hominids (Herring, 1976; Menegaz et al., 2015). In addition, the size of the seeds used in our study (e.g. hazelnuts) is comparable to the size of the seeds that hominins can process, which is a significant improvement over previous studies. Finally, seeds have been hypothesized as important sources of food for early hominins (Rak, 1978), although dental microwear evidence suggests otherwise (Cerling et al., 2011; Peterson et al., 2018; Ungar et al., 2008). Focusing on one species, and therefore on intraspecific variations, this experiment will avoid the confounding factors associated with phylogeny and “Liem’s Paradox”, clarifying the connections between mandibular shape and food properties. We hypothesized that the consumption of various types of seeds leads to significant differences in the morphology of the mandible despite similar overall diets. More specifically, as it has been shown in experimental studies in rodents and lagomorphs (Anderson et al., 2014; Beecher & Corruccini, 1981; Ödman et al., 2008), we expect that the specimens fed with the hardest seeds will significantly differ from the control population.

2 Material and methods

2.1 Experimental design

The controlled-food experiments were carried out at the experimental unit UE1372 GenESI (Pig Innovative Breeding Experimental Facility, France; DOI: 10.15454/1.5572415481185847E12) of the *Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement* (INRAE). Experimentations were conducted on pigs (large-white cross breed Piétrain), designed by G.M. and S.F. (agreement number: APAFiS 155/2015012117162897, *Ministère de l'Enseignement Supérieur, de la Recherche et de l'Innovation*), and have been described thoroughly previously (Louail et al., 2021). We considered 28 juvenile pigs (i.e. mandibular M2 fully erupted but M3 not visible for the oldest specimens) fed with five different diets *ad libitum* (Fig. 1, Supplementary data 1). Pigs were weaned at about 28 days old and were raised on concrete floors. Each animal had access to an individual trough except for the 'hazelnut 30' group having collective troughs. All pigs were kept together in groups of five to six pigs according to their diet. Before they were given their dedicated diets, they were all fed daily with a dry base diet (manufactured by ALICOOP) composed of 90% of wheat (*Triticum ssp.*), barley (*Hordeum vulgare*), and triticale (*X Triticosecale*) flour, and 10% of soybean (*Glycine max*) flour. This period lasted at least 48 days. The 'control' group (n = 6) was then fed exclusively with the same base diet described above for at least another 30 days before death. This base diet, composed of ground cereal and soy seeds, is expected to have little impact on mandibular shape and represents a baseline for comparing dietary signals among the experimental groups. The four other groups then received seeds of different size and hardness (Fig. 1, Supplementary data 1) in addition to the base diet. A 4-day period of adaptation to the new diet (with a progressive intake of seeds) was carried out on these four groups just before the dietary switch. The hazelnut groups were fed with the same amount of flours than the control group and received respectively 10 ('hazelnut 10' group; n = 6) and 30 ('hazelnut 30' group; n = 5) hazelnuts in shell (*Corylus avellana*; endosperm and shell used but leafy involucre removed) per pig each day for around 30 days before slaughter. The 'corn' group (n = 6) was fed with 60% of the base diet and 20% of corn (*Zea mays*) flour, supplemented with 20% (as dry matter weight) of corn kernels. The barley group (n = 5) was fed with 30% of barley seeds and 70% of the base diet. The 'corn' and 'barley' groups received their dedicated diet for at least another 95 days before death. Each group was approximately sex-balanced (Supplementary data 1). None of the pigs lost weight during the experiments. As planned by the experimental unit, pigs were slaughtered from six and a half months to nine and

a half months old when they reached their target weight (about 150–200 kg; females slaughtered a month after males) and were all sold for meat. Pig skulls were then boiled for 4 h in water to remove the flesh, and dried in an oven for 24 h at 40°C.

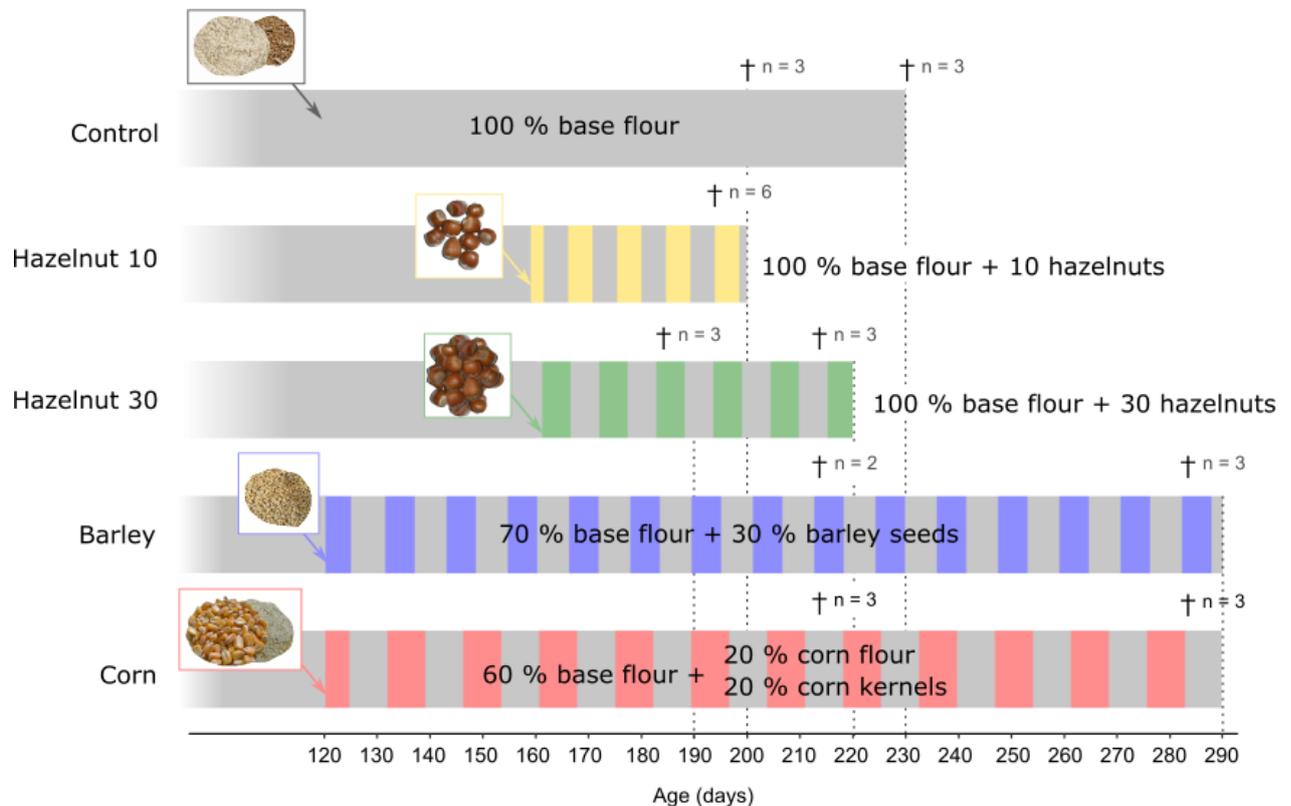


Figure. 1. Representation of the controlled-feeding experiment on domestic pigs (*Sus scrofa*). We carried out a 4-day period of adaptation to the new diet, that is not represented on the figure, before the dietary switch. Each time point specified by † indicates the age and number of pigs slaughtered. Modified after Louail et al. (2021).

2.2 Data acquisition and analyses

We scanned the mandibles with a surface laser scanner (Artec Space Spider) and we reconstructed them using the Artec Studio 15 software to create three-dimensional (3D) digital model. We used 10 homologous landmarks and 72 semilandmarks placed on the 3D surfaces to describe the morphology. We digitized the anatomical landmarks and semilandmarks using IDAV Landmark v3.0 software (Wiley et al., 2005). The upper part of the ramus (i.e. the head and neck regions) was sawed during the preparation of most of the specimens. Therefore, we adapted previously published landmark definition protocols (Neaux et al., 2021a; Neaux et al., 2020), removing the landmarks from this area (Supplementary data 2). All the analyses were performed in the R environment (R Core Team, 2019). We removed variation related to their initial arbitrary position along the curves by sliding semilandmarks along the tangent of the curves, minimizing bending energy (Gunz & Mitteroecker, 2013). We aligned coordinates

using a generalized Procrustes superimposition (Rohlf & Slice, 1990), implemented in the `procSym` function of the package ‘Morpho’ (Schlager & Jefferis, 2020) to obtain a new set of shape variables (Procrustes coordinates) and the centroid size.

We visualized the multivariate ordination of the aligned specimen by performing a Principal Component Analysis (PCA) on the Procrustes coordinates. We visualized the shape differentiation between the studied groups with a Canonical Variate Analysis (CVA), computed on a reduced dataset after the PCA (i.e. PCA scores accounting for 95% of the variance) to avoid the dangers of over-fitting data caused by small sample size and a high number of variables (Kovarovic et al., 2011) following Evin et al. (2013). We computed shape deformations for both PCA and CVA warping the surface of one of the pig specimens at +3 and -3 standard deviations of the principal components (PC) and linear discriminants (LD) using `tps3d` (‘Morpho’). We evaluated the significance of shape differences between groups by performing a Procrustes ANOVA on aligned Procrustes coordinates using the `procD.lm` function of the package ‘geomorph’ (Adams et al., 2019). We tested the difference in centroid size between groups and visualized it with box plots. We also tested for the influence of life duration and weight at feeding change on shape and size. We investigated the allometric component of shape variation using a Procrustes ANOVA, with size computed as the logarithm of centroid size (Collyer et al., 2015). We also tested the difference between the allometric slopes of the 5 studied groups testing the interaction factor `size*group` with an ANCOVA.

3 Results

In the PCA, PC1 and PC2 account respectively for 18.4% and 13.4% of the total variance (Fig. 2.a). The ‘control’, ‘hazelnut 10’, and ‘hazelnut 30’ groups are localized toward positive scores for PC1 and negative scores for PC2 while the ‘barley’ and ‘corn’ groups are mostly restrained to negative scores for PC1 and positive scores for PC2. Each following PC represents less than 10% of the total variance and are less informative (Supplementary data 3). The mandibular shape changes toward positive scores along PC1 are expressed by three main traits: (1) a reduced gonial angle (i.e. the angle between the mandibular ramus and corpus), (2) an anteroposteriorly larger ramus, and (3) an anteroposteriorly longer corpus resulting in a longer symphysis region. The mandible shape changes along PC2 towards positive scores were characterized by (1) a superoinferiorly shorter, anteroposteriorly larger, and less upright ramus, (2) a global shape moving from a ‘V shape’ to a ‘U shape’ in dorsal view and, (3) a mediolaterally wider mandible especially in the lower part of the ramus.

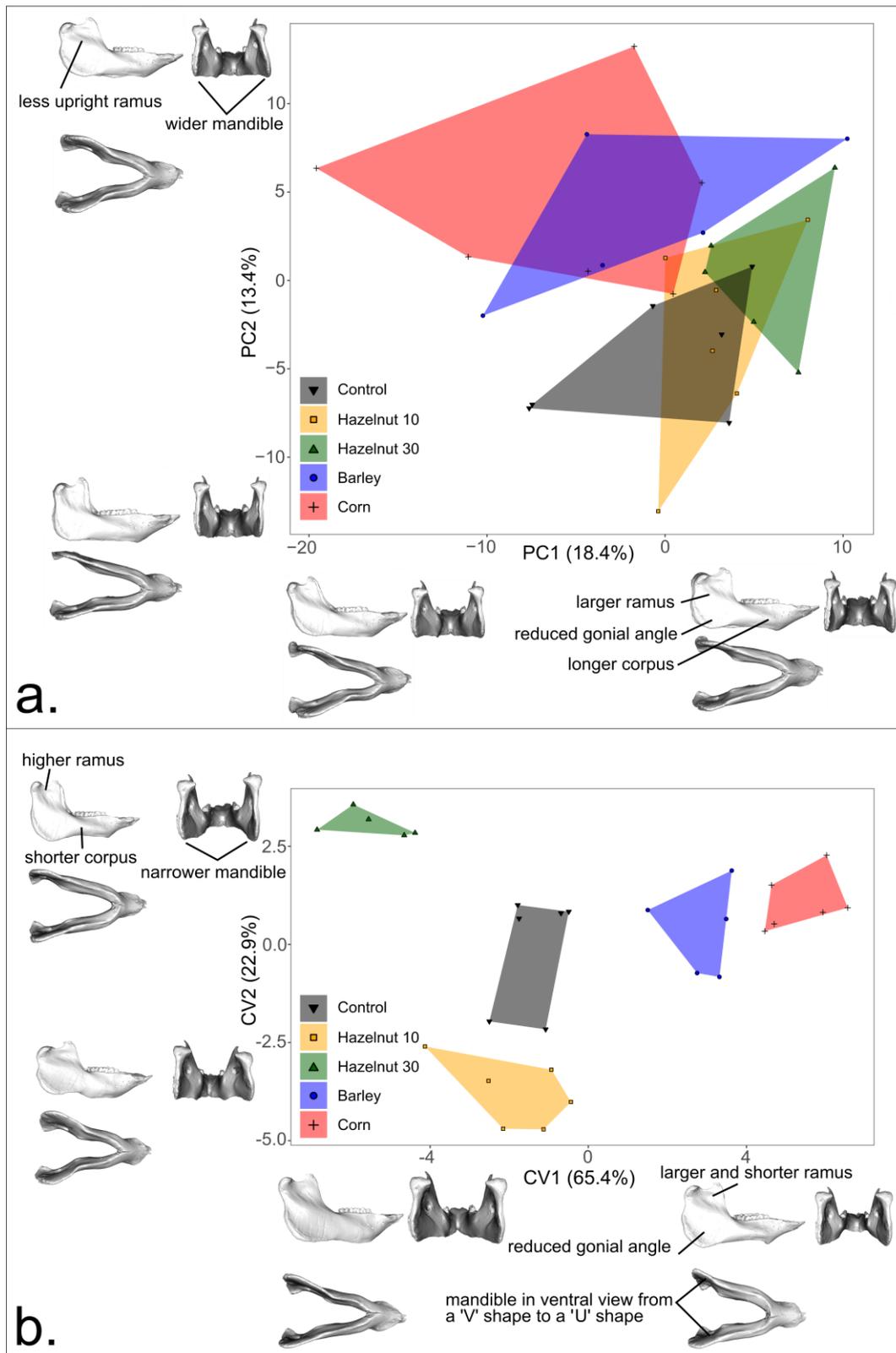


Figure 2.a. Principal component analysis in the PC1-PC2 shape space. b. Canonical Variate Analysis (CVA) displaying discriminant axes CV1 and CV2. Shape changes are depicted in lateral, ventral and posterior views.

We performed the CVA on the first 18 PC of the PCA accounting for 95% of the variance. The CVA was strongly dominated by CV1, accounting for 65.4% of the total variance (Fig. 2.b). CV1 was driven by the strong divergence between the ‘hazelnut 30’ group towards negative scores and the ‘corn’ group towards positive scores. CV2 mainly separated the ‘hazelnut 10’ and ‘hazelnut 30’ groups. The shape changes along CV1 were expressed by three traits: (1) a reduction of the gonial angle, (2) an anteroposteriorly larger and superoinferiorly shorter ramus, and (3) a global shape moving from a ‘V shape’ to a ‘U shape’. Shape changes along CV2 involved three main shifts: (1) a superoinferiorly higher ramus, (2) an anteroposteriorly shorter corpus and (3) a mediolaterally narrower mandible. We found significant differences in shape ($F = 1.57$; $R^2 = 0.21$; $df: 4$; $p = 0.02$) and in size ($F = 5.96$; $R^2 = 0.51$; $df: 4$; $p < 0.01$; Fig. 3) between the diet groups. Also, life duration does not influence significantly shape ($F = 0.90$; $R^2 = 0.03$; $df: 1$; $p = 0.484$) but influence size ($F = 39.75$; $R^2 = 0.60$; $df: 1$; $p < 0.01$). In the same way, weight at feeding change does not influence significantly shape ($F = 1.84$; $R^2 = 0.66$; $df: 1$; $p = 0.06$) but influence size ($F = 11.15$; $R^2 = 0.30$; $df: 1$; $p < 0.01$). Allometry explains only 3.24% of the total variance of the shape variation in the mandible and is not significant ($F = 0.91$; $df: 1$; $p = 0.49$). The allometric slopes did not differ between the studied groups ($F = 0.79$; $df: 4$; $p = 0.78$).

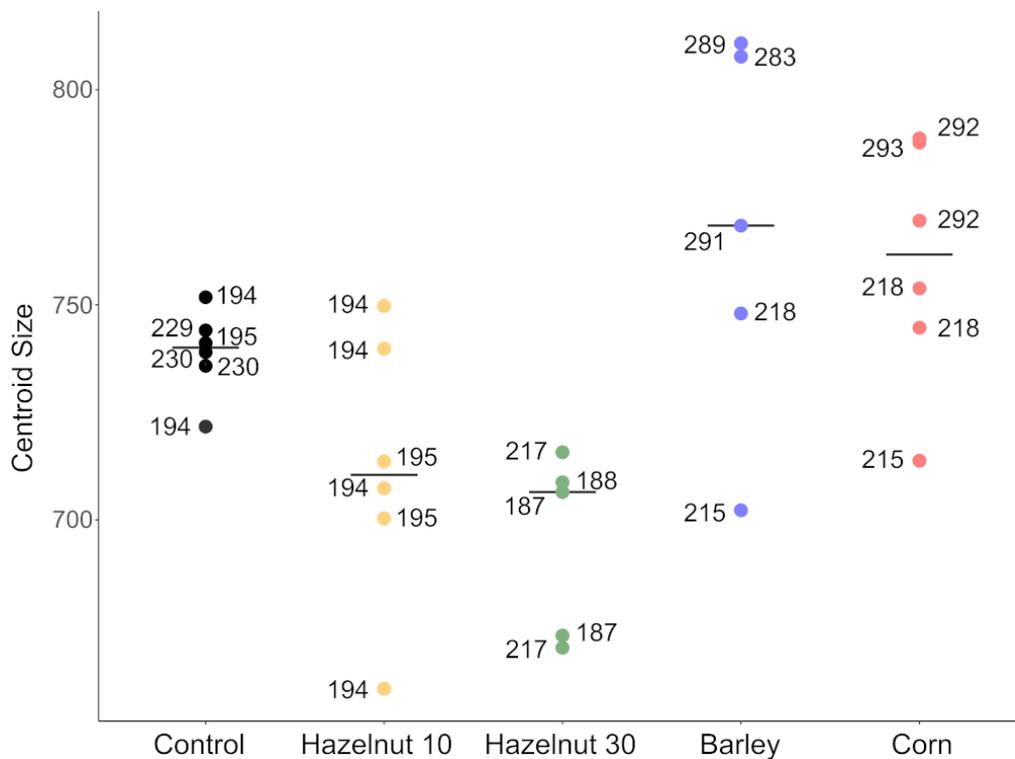


Figure 3. Centroid sizes. The dots are the values of centroid size for each specimen. The horizontal lines are the median. For each point, the corresponding number is the age at slaughter.

4 Discussion

Our results clearly suggest that the supplemental consumption of a significant amount of seeds for a short period influences substantially the mandibular morphology of pigs. Yet, the main difference observed is between the ‘barley’ and ‘corn’ groups on one hand and the hazelnuts and ‘control’ groups on the other hand. The rupture forces averaged by Louail et al. (2021) from the literature show that the seed hardness of barley (rupture force of 140.51 N; Jangi et al., 2011; Markowski et al., 2010) and corn (164.42 N; Kalkan et al., 2011; Tran et al., 1981) are lower than the hardness of hazelnut (331.26 N; Delprete & Sesana, 2014; Ercisli et al., 2011) and therefore cannot be considered as a sufficient factor to explain our results. Previous experimental studies in rodents and lagomorphs associated hard food feeding with an extension of the angular processes, a reduction of the corpus length, and an increase of the width between the dental arches (Anderson et al., 2014; Beecher & Corruccini, 1981; Ödman et al., 2008). In our study, the increase of the gonial angle, corresponding anatomically to the angular process, and the reduction of the corpus length are associated with the hazelnuts and ‘control’ groups, while the increase of the width between the dental arches is associated with the ‘barley’ and ‘corn’ groups. This also indicates that food hardness may not be the main factor involved in mandibular shape changes. If the hardness of the food consumed can have a major impact on mandible shape (Anderson et al., 2014; Daegling, 1992; Marcé-Nogué et al., 2017), other factors, such as food geometric properties (e.g. size and flatness) and dietary abrasiveness, have to be considered to better assess the relationships between seed consumption and mandibular shape (Ross et al., 2012; Schulz et al., 2013). In this regard, it has been suggested that smaller particles of food resources (Lucas, 2004), as well as bolus containing large amounts of small resources (van Casteren et al., 2020), might require high and repeated bite force for oral processing. This assertion is in line with our results as barley and corn are smaller seeds and possess a higher density (i.e. number of seeds/kg; Louail et al., 2021) than hazelnut. In a controlled-food experiment on sheep (*Ovis aries*), Ramdarshan et al. (2016) also found a higher microwear complexity in smaller but softer seeds (barley), confirming the prominence of seed size over seed hardness in masticatory properties. The shape changes described toward the ‘barley’ and ‘corn’ groups are similarly in favor of a high and repeated bite force in these specimens as a reduced gonial angle and a more upright ramus have been previously associated with an increase in masticatory frequency and force in wild boar (*Sus scrofa*; Neaux et al., 2021a) and in humans (*Homo sapiens*; von Cramon-Taubadel, 2011; Sella-Tunis et al., 2018). The relationship between muscle activity, enlargement of attachment areas, and bone

remodelling in response to stress loads is well documented, notably for masseter muscle inserted on the inferior part of the ramus, i.e. at the gonial angle of the mandible (Cornette et al. 2015; Dinu 2009; Wolff 1986). Previous experiments in wild boar evidences a clear relationship between chewing activity, increase of the masseter size, and the setting of a reduced gonial angle and a more upright ramus (Neaux et al., 2021a; 2021b). Conversely, in humans suffering from myotonic dystrophy of the masticatory muscles a greater gonial angle was reported (Kiliaridis, Mejersjö, & Thilander, 1989). This suggests that robust mandibles features, such as a reduction of the gonial angle and a more upright ramus, are not necessarily related to hard food but rather to an increase of chewing activity. Interestingly, these characteristics (reduced gonial angle and tall and upright ramus) are among the main features defining the robust morphology of *Paranthropus* (Rak and Hylander, 2008). In this sense, our experimental results in pigs are in line with previous studies on *Paranthropus* finding that the unique mandibular morphology of this taxa is not a specialization toward a hard-object diet as previously thought (Jolly, 1970; Kay, 1985; Robinson, 1954). Instead, *Paranthropus* mandibular shape is more likely an adaptation (1) to abrasive/fibrous foods (including small seeds) for *P. boisei* (Cerling et al., 2011; Scott et al., 2012; Ungar et al., 2008) or (2) to the occasional consumption of hard items as fallback foods for *P. robustus* (Peterson et al., 2018; Scott et al., 2005; Ungar & Sponheimer, 2011). More broadly, our study underlines the significant role of seeds, which are often fallback foods, in modifying mandibular shape variations after a dietary shift of only few months, corresponding to the time period of a seasonal consumption of fallback foods (Marshall et al., 2009). It is in line with previous works stating that such items, generally mechanically challenging, are potential selective drivers of morphologies and that robust types could be due to the consumption of mechanically difficult foods during “fallback” episodes of resource stress (Scott et al., 2005; Ungar et al. 2012, Ungar and Daegling, 2013). This result contradicts, a previous experimental study on the jaw of rabbits (*Oryctolagus cuniculus*) finding a significant influence of challenging foods on mandibular structures when eaten year-round but not on short time periods (Scott et al., 2014). The fact that the stiffer food in this experiment was not seeds but hay and that the rabbit model is morphologically and in terms of diet more distant from hominids than the pig model may explain these differences. Our results based on intraspecific variations, also confirm the great plasticity of mandibular structures as we observed significant shape differences (Renaud et al. 2009, Anderson et al. 2014, Kamaluddin et al., 2019). This corroborates recent experimental studies showing that the constraints of a captive anthropogenic environment leave rapidly an anatomical imprint on the mandible shape of wild boar beyond the phenotypic variation range

observed in their natural habitat (Neaux et al., 2021a; Neaux et al., 2021b). This role of phenotypic plasticity as an important source of variation for natural selection may therefore explain the morphological variations observed among species at the interspecific level.

A limitation of our study is the differences in feeding and dietary switch durations between the studied groups. Yet, the effect of allometry between groups is non-significant and the life duration as well as the weight at dietary switch does not significantly influence shape data. Furthermore, the youngest specimens from the ‘barley’ and ‘corn’ groups are not the closest to the hazelnuts and ‘control’ groups (Supplementary data 4). This suggests that the feeding and dietary switch duration differences do not affect meaningfully the obtained results. Our controlled-food experiment is not directly comparable to data from wild extant or extinct groups as controlled diets in experimental settings are much less diverse than diets in the wild (e.g. Schley & Roper, 2003). Yet, it seems to show that mandibular morphological changes potentially associated with high bite force are not necessarily associated with high level of seed hardness. To insure this assertion and confirm our results, direct evidences such as chewing counts, bite force or strain gauge measurements should be considered in future experimental analyses. In addition, the differences in the amount of seeds added to base flour can be another factor influencing our results as a larger amount of seeds may require a more repetitive oral processing. Therefore, it is not clear whether the hazelnut groups are similar to the control group because they are large seeds or because we did not consider enough seeds. Seed size may indeed not be the only factor influencing mandibular shape and the amount of seeds in the diet (i.e. number of seeds/kg) may also be another factor explaining the observed changes. If the amount of consumed seeds really influences mandibular morphology, future studies should consider including a greater amount of hard objects to test why the amount of seeds impact mandibular shape and whether the amount tested in this study (30 hazelnuts) is enough to be comparable to durophagous diets.

A recent dental microwear texture analysis (DMTA) on the same specimens (except the ‘hazelnut 30’ group) found slightly different results as it describes (1) significant differences between the three groups of seed-eaters (i.e. ‘hazelnut 10’, ‘barley’, and ‘corn’ groups) and (2) an overlap of the control group with both the ‘hazelnut 10’ and ‘corn’ groups (Louail et al., 2021). This difference between DMTA and mandibular shape comparisons is understandable as both proxies have different type of physical relationships with the food items (direct vs. indirect) and record different time scales (Davis & Pineda-Munoz, 2016). Both methodologies underline the difficulty to detect occasional hard object feeding as in both case hazelnuts and

control groups are overlapping underlining the need for new approaches to detect durophagous diets. Conversely, both methods prove able to distinguish soft but tough seeds such as barley from the control groups. These slightly different results pointing toward similar conclusions underline the interest of mandibular morphology studies in addition to DMTA. The latter remains one of the more accurate proxies for dietary reconstructions but the study of mandibular shape changes may help to support DMTA results at a higher anatomical scale, especially for paleontological studies where there is no prior knowledge of dietary groups. These results underline the need for new approaches to detect durophagous diets as well as the necessity for more comprehensive studies including both dental microwear texture and mandibular shape analyses for a more complete comprehension of the dietary habits of extant and extinct taxa.

5 Conclusion

Our results provide strong evidence that the supplemental consumption of a significant amount of seeds for a short period influences substantially the mandibular morphology of pigs, confirming the very plastic nature of the mandible (Neaux et al., 2021a). Our analyses suggest that this shape differentiation is due to the size of the seeds rather than their hardness. This supports previous assertions that food resources of smaller particle size require enhanced bite force for oral processing (Lucas, 2004). Mandibular morphological changes associated with high and repeated bite force are therefore not necessarily associated with significant seed hardness. Our results on mandibular morphology are slightly different from the findings of a recent DMTA on the same specimens (Louail et al., 2021) underlining the interest of combining different proxies (e.g. mandibular morphology, dental microwear texture, gross toothwear, enamel biogeochemical composition) in future studies for a more comprehensive assessment of the diet of extant taxa as well as paleodietary reconstructions.

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Data accessibility statement

All the codes and data necessary to reproduce this work are freely available at: <https://doi.org/10.5281/zenodo.5549914>

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Experimental assessment of the relationship between diet and mandibular morphology: new insights for the paleodietary reconstructions of early hominins

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Supplementary data 1

Detailed description of the controlled-feeding experiments per individual. F: female, UM: uncastrated male, CM: castrated male.

Dietary group	Specimen	Birth date	Sex	Start of trial	Age at dietary switch (days)	Age at slaughter (days)	Total feeding duration (days)	Feeding duration after dietary switch (days)	Weight before the feeding change (kg)	Date of weighing
Control	870614	13/12/2018	UM	08/04/2019		194	78		84.3	14/05/2019
	870619	13/12/2018	UM	08/04/2019		194	78		84.6	14/05/2019
	870641	12/12/2018	UM	08/04/2019		195	78		98.2	14/05/2019
	870623	13/12/2018	F	08/04/2019		229	113		80.9	14/05/2019
	870638	12/12/2018	F	08/04/2019		230	113		103.8	14/05/2019
	870640	12/12/2018	F	08/04/2019		230	113		106.6	14/05/2019
Hazelnut 10	870601	13/12/2018	UM	08/04/2019	163	194	78	30	104.2	14/05/2019
	870603	13/12/2018	UM	08/04/2019	163	194	78	30	110.7	14/05/2019
	870609	13/12/2018	UM	08/04/2019	163	194	78	30	97.5	14/05/2019
	870610	13/12/2018	F	08/04/2019	163	194	78	30	71.8	14/05/2019
	870645	12/12/2018	F	08/04/2019	164	195	78	30	119.7	14/05/2019
	870649	12/12/2018	F	08/04/2019	164	195	78	30	112.6	14/05/2019
Hazelnut 30	970269	06/08/2019	UM	21/10/2019	155	188	112	33	100.9	06/01/2020
	970287	07/08/2019	F	21/10/2019	187	217	142	30	135.03	10/02/2020
	970296	07/08/2019	UM	21/10/2019	154	187	112	33	87.59	06/01/2020
	970286	07/08/2019	F	21/10/2019	187	217	142	30	126.24	10/02/2020
	970298	07/08/2019	UM	21/10/2019	154	187	112	33	88.6	06/01/2020
Barley	812073	17/06/2018	F	28/07/2018	120	215	174	95	68.67	15/10/2018
	811925	13/06/2018	CM	28/07/2018	124	293	248	169	48.72	15/10/2018
	812003	15/06/2018	F	28/07/2018	122	291	248	169	58.77	15/10/2018
	812078	17/06/2018	CM	28/07/2018	120	289	248	169	62.8	15/10/2018
	812031	14/06/2018	CM	28/07/2018	123	218	174	95	73.35	15/10/2018
Corn	812046	14/06/2018	CM	28/07/2018	123	218	174	95	75.67	15/10/2018
	812049	14/06/2018	CM	28/07/2018	123	218	174	95	80.4	15/10/2018
	812068	17/06/2018	F	28/07/2018	120	215	174	95	64.48	15/10/2018
	811916	13/06/2018	F	28/07/2018	124	293	248	169	58.15	15/10/2018
	811958	14/06/2018	CM	28/07/2018	123	292	248	169	67.25	15/10/2018
	812020	14/06/2018	F	28/07/2018	123	292	248	169	74.2	15/10/2018

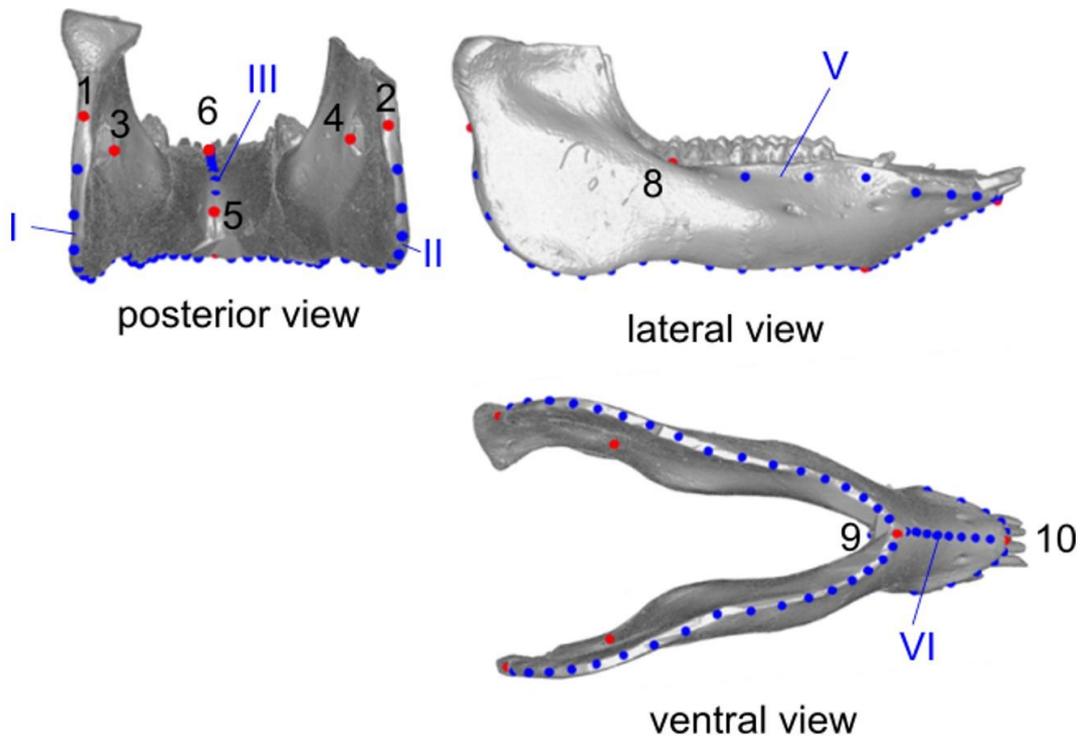
1 **Supplementary data 2**

2 a. Definitions of mandibular homologous landmarks (1-10) and curves (I-VI).

Landmarks and curves	Definition
1, 2	Most anterior point of the curve between the condyle and the gonial angle, above the insertion of the pterygoideus medialis
3, 4	Most anterior point of the mandibular foramen
5	Most dorsal, posterior point of the mandibular symphysis
6	Most dorsal, anterior point of the mandibular symphysis
7, 8	Most lateral point at the maximum of curvature between the mandibular ramus and corpus
9	Most ventral, posterior point of the mandibular symphysis
10	Most ventral, anterior point of the mandibular symphysis
I	from LM 1 to LM 9
II	from LM 2 to LM 9
III	from LM 5 to LM 6
IV	from LM 7 to LM 10
V	from LM 8 to LM 10
VI	from LM 9 to LM 10

3

- 4 b. Pig (*Sus scrofa*) mandible showing the homologous landmarks (red dots and Arabic numerals)
5 and semilandmarks (blue dots and Roman numerals) used in the study.

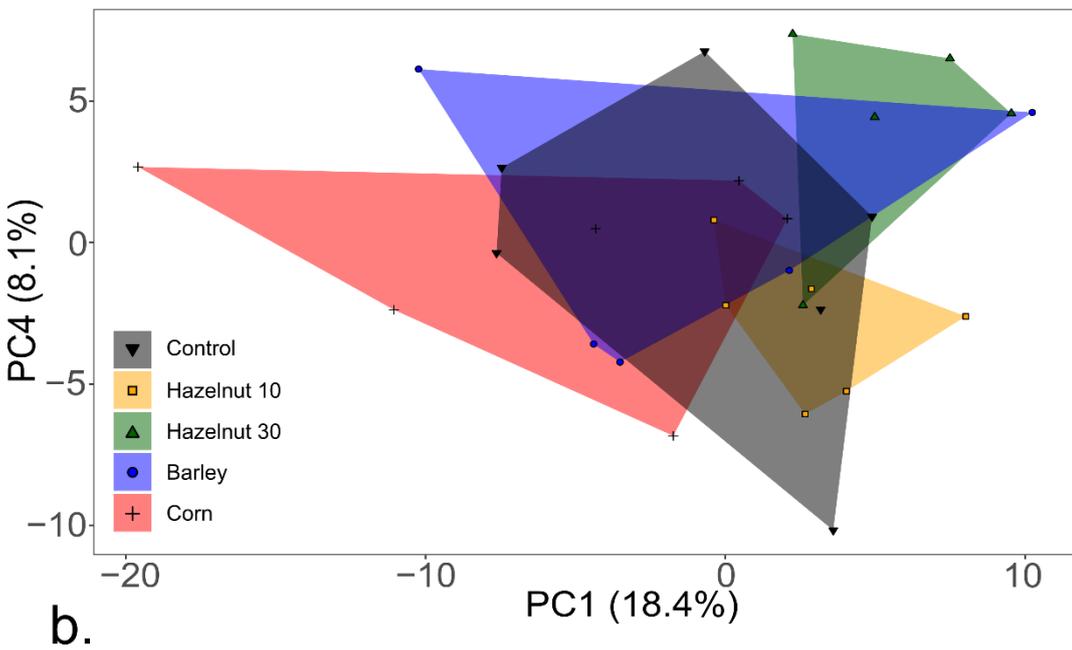
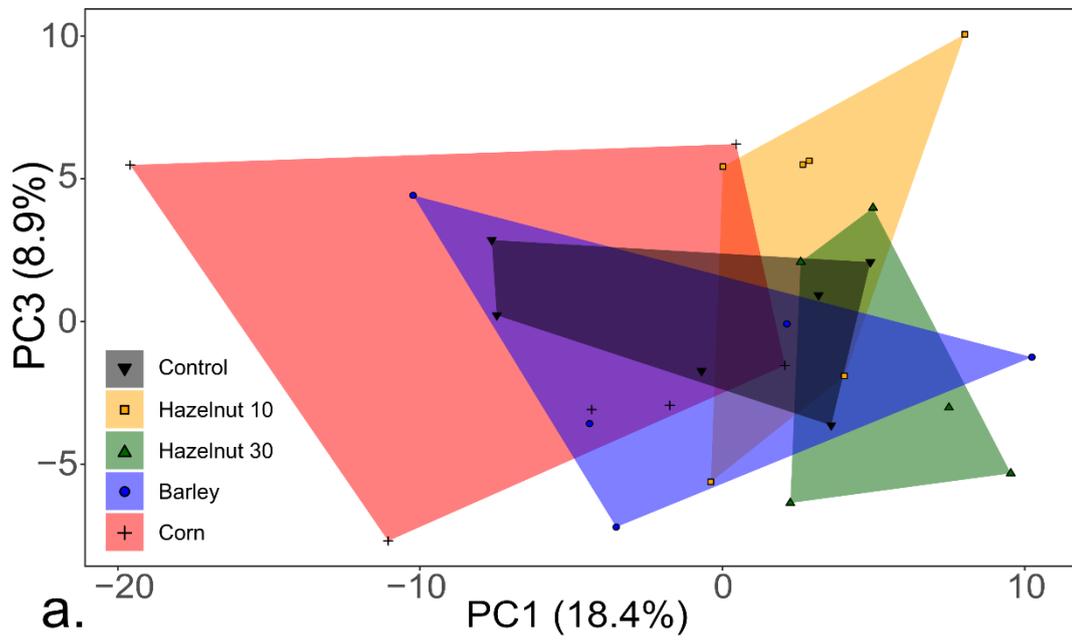


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8 **Supplementary data 3**

9 Principal component analyses for the mandible in the PC1-PC3 (a) and PC1-PC4 (b) shape space.

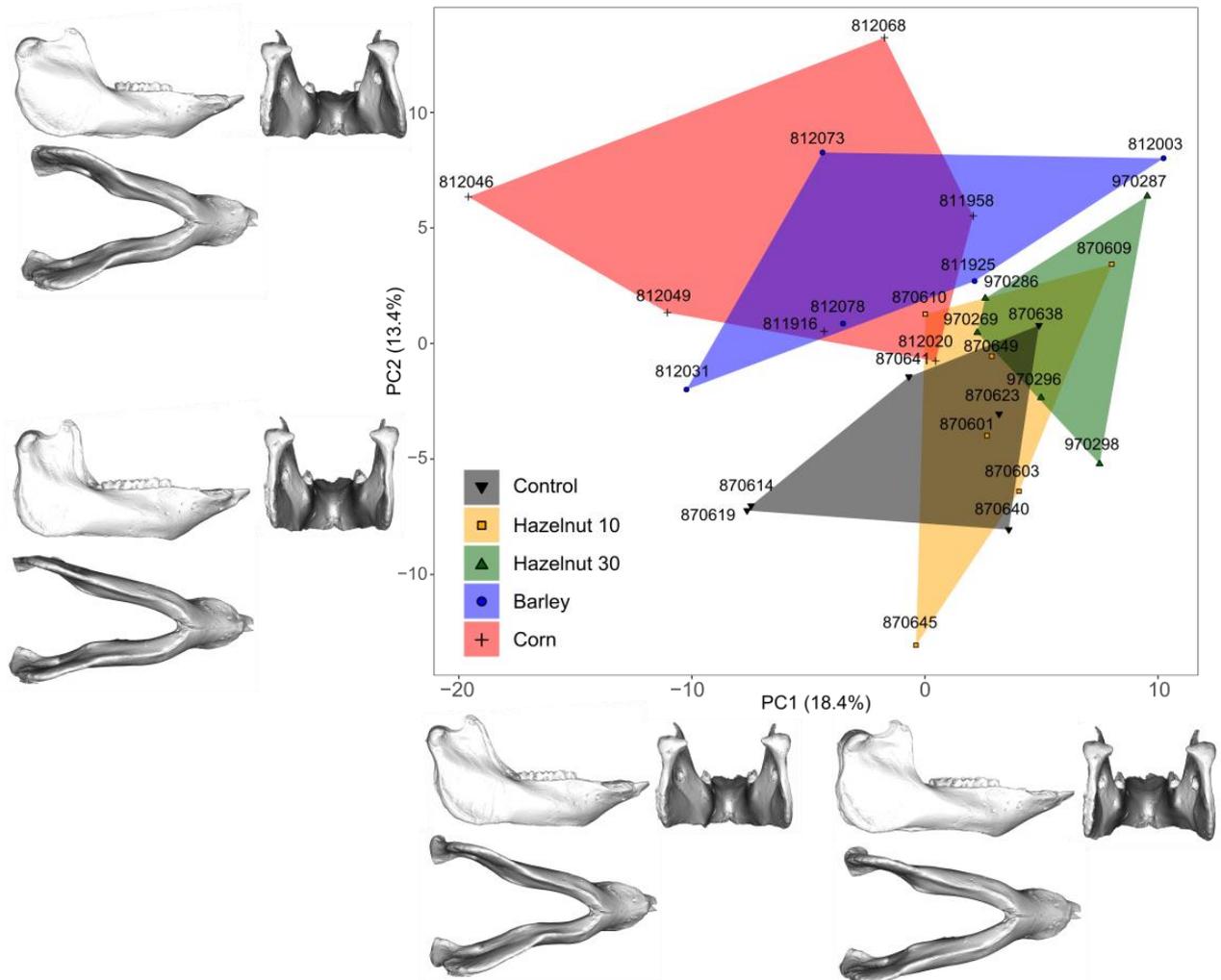


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12 **Supplementary data 4**

13 Principal component analyses for the mandible in the PC1-PC2 shape space including the
14 identifications of the specimens (see Supplementary data 1). Shape changes are depicted in lateral,
15 ventral and posterior views.



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