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## Assessment of comminution capacity related to molar intercuspidation in catarrhines using a chewing simulator

### *Évaluation de la capacité de comminution lors de l'intercuspidation des molaires chez les catarrhines à l'aide d'un simulateur de mastication*

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Cette note fait suite à une communication présentée lors des 1846<sup>es</sup> journées de la Société d'Anthropologie de Paris dans le cadre de la session "Humanité(s) : définition(s), diversités et limites"

**Abstract** – Mammalian molars play a central role during chewing, or food comminution, through cyclic dental occlusion. Mammals fragment food items with varying degrees of efficiency depending on their dental morphology, suggesting an adaptive link that is yet to be assessed. Here, we test the effect of molar morphology at maximum intercuspidation (centric occlusion), i.e., between phases I and II, on the comminution of five food items that correspond to different mechanical challenges encountered by catarrhines. Using a chewing simulator, we experimentally measured the number of food fragments produced after five successive intercuspidations with two different forces, in order to assess their influence. The sample includes cercopithecoid and hominid specimens encompassing the main dental occlusal patterns and dietary habits displayed by extant and fossil catarrhines. We show that increasing bite force results in better food item degradation overall although we report some exceptions, notably for ductile and tough foods (apples, ginger and leaves). Brittle and complex foods (hazelnuts and crickets) are fragmented by intercuspidation. This experiment showed that proper occlusion and bite force are sufficient only to fragment brittle food and that additional movements are necessary to fragment tough foods (leaves and grasses). It also highlights the masticatory capacities of various occlusal patterns in primates and our ability to test these with robotics, a breakthrough that will allow investigations of important anthropological questions concerning the evolution of dental morphology.

**Keywords** – chewing performance, molar, primate, diet, adaptation

**Résumé** – Les molaires des mammifères jouent un rôle central lors de la mastication, ou la fragmentation des aliments par l'occlusion dentaire cyclique. Les mammifères

fragmentent les aliments avec un degré d'efficacité variable en fonction de leur morphologie dentaire, cela suggère qu'il existe un lien adaptatif à estimer. Dans cette étude, nous testons l'effet de la morphologie des molaires lors de l'intercuspidation en occlusion centrée, c'est-à-dire entre les phases I et II, sur la fragmentation de cinq aliments qui correspondent à différents défis mécaniques rencontrés par les catarrhiniens. En utilisant un simulateur de mastication, nous mesurons expérimentalement le nombre de particules alimentaires produits après cinq intercuspidations successives pour deux forces différentes, afin d'évaluer leur influence. L'échantillon comprend des spécimens de cercopithèques et d'hominidés englobant les principaux modèles d'occlusion dentaire et les habitudes alimentaires des catarrhiniens actuels et fossiles. Nous montrons que l'augmentation de la force de morsure entraîne globalement une meilleure dégradation des aliments, mais des exceptions sont signalées notamment pour les aliments ductiles et coriaces (pommes, gingembres et feuilles). L'intercuspidation fragmente les aliments fragiles et complexes (noisettes et grillons). Cette expérience a permis de montrer que seules une occlusion et une force de morsure appropriées sont suffisantes pour fragmenter les aliments fragiles et que des mouvements supplémentaires sont nécessaires pour fragmenter les aliments coriaces (feuilles et herbes). Elle met également en évidence les capacités masticatoires de différents modèles d'occlusion chez les primates et notre capacité à les tester avec la robotique. Cette nouvelle avancée permettra d'étudier des questions anthropologiques majeures portant sur l'évolution de la morphologie dentaire.

**Mots clés** – performance de mastication, molaire, primate, régime alimentaire, adaptation

## Introduction

### *Dental morphology*

Teeth are the focus of many palaeoanthropological studies (e.g. Berthaume et al., 2019; Déroit et al., 2019; Joannes-Boyau et al., 2019; Veneziano et al., 2019). They are highly mineralized organs that are preferentially preserved during fossilization and therefore form a significant part of the primate fossil record. Both taxonomic and phylogenetic data can be retrieved from the dental morphology of primates, since mineralized dental tissues do not remodel after dental eruption except through wear and show high heritability (Rathmann et al., 2017). Furthermore, dental morphology affects what a primate can or cannot eat and can thus be used to draw palaeoecological inferences (e.g. Meldrum and Kay, 1997; Ungar, 2004; Merceron et al., 2006; Thiery et al., 2017a). This is especially true for molars, which are complex teeth composed of several elements or features (cusps, crests, basins...) that come into occlusion, acting as tools to perform different food processing actions such as crushing, shearing or puncturing (Sheine and Kay, 1982; Rosenberger, 1992; Thiery et al., 2017b). While they may be used during food ingestion e.g., to crush seed shells open (Thiery and Sha, 2020), molars play a central role during chewing.

### *Background: chewing*

Chewing (or food comminution through cyclic occlusion of the teeth) is a crucial step in the digestion process of mammals (Lucas, 2004). Humans and other extant and fossil primates are no exception since they rely, or relied, extensively on molars to chew foods. Reducing food items into smaller particles increases the surface area upon which enzymes can act, hence the potential adaptive link between molar morphology, its capacity to fragment food and the subsequent energy release during the digestive process (e.g. Kay, 1975; Pérez-Barbería and Gordon, 1998). The underlying assumption that molar morphology was selected by the nature of the most commonly chewed foods explains why molars have been used extensively to draw palaeoecological inferences (e.g. Meldrum and Kay, 1997; Ungar, 2004; Merceron et al., 2006; Thiery et al., 2017a).

However, our ability to infer diet from the molars of extinct species is notably challenged by the complexity of chewing behaviour. During the power stroke in chewing, the lower molars move upwards and lingually across the upper molars (e.g. Hiiemae, 1978). Two components have been recognized in the power stroke in mammals, called phase I and phase II (Kay and Hiiemae, 1974; Kullmer et al., 2020). In primates, phase I ends when the lingual surface of the hypoconid meets the buccal surface of the protocone of the opposite tooth, crushing the food. The lower teeth are then at their highest position and are said to be in centric occlusion, corresponding to maximum intercuspation (Crompton and Kielan-Jaworowska, 1978; Butler, 2007; Kullmer et al., 2020). The lingual movement continues in

phase II, and past the centric position, so that the hypoconid retains contact with the protocone during the early phase of the opening stroke in which the opposite teeth separate. In primates, the phase II movement is directed more anteriorly than the phase I movement, as the centre of rotation of the jaw shifts towards the lingual side of the mouth (Butler, 2007).

During the chewing cycle, the dental elements at the surface of the molar are expected to affect its ability to fragment different kinds of food items. For instance, shearing crests would improve the ability of molars to shear leaf-like foods, especially during the bucco-lingual movements of the power stroke (Kay, 1975). However, accurately testing this hypothesis requires measuring the contribution to food fragmentation of each component of a chewing cycle (i.e., phase I, centric occlusion and phase II). Chewing motions can be estimated in fossils from the orientation of molar wear facets (von Koenigswald et al., 2012), but these estimations obviously cannot be compared with behavioural reports.

In addition, the ability to chew food is usually measured in two ways: chewing performance assesses the size distribution of food particles once chewed for a given number of strokes, and chewing efficiency counts the number of chewing cycles required to reduce food to a certain particle size (Bates et al., 1976; van der Bilt et al., 1987). However, these estimates cannot tell apart the contribution of each component of chewing. Other ways of capturing the full complexity of chewing behaviour therefore have to be devised.

### *State of the art: chewing experiments*

Chewing experiments involving volunteer humans have shown that chewing efficiency is affected by molar area (Laird et al., 2016), but also by pre-oral processing (Zink and Liberman, 2016) and the physical properties of food (Agrawal et al., 1997). In the wild, King et al. (2005) estimated the chewing performance of four Milne-Edward's sifakas (*Propithecus edwardsi*) from the number of seed particles found in their faeces. They found that chewing performance, molar slope and shearing quotient decreased concurrently. At present, the standard estimate of chewing performance in field ecology is the mean faecal particle size (Fritz et al., 2009; Venkataraman et al., 2014; He et al., 2020). However, the contribution of dental morphology *per se* is not directly tested, mostly because of the difficulty of matching the molar morphology of individuals with their faeces in the wild. Besides, a form-function approach (rather than an ecological approach) better suits the study of dental efficiency in the extant and fossil record.

In this context, experimental approaches using chewing simulators could provide significant insights into the effects of molar morphology on chewing efficiency. Chewing simulators have been used to investigate oral processing of manufactured food (Salles et al., 2007; Arvisenet et al., 2008; Mishellany-Dutour, 2011; Chen et al., 2022) or the effect of chewing on dental wear (Kern et al., 1999; Karne et al., 2016; Jeannin et al., 2019; Alemzadeh, 2020;

Krueger et al., 2021). Other devices modelling vertical movements have been used to test the effect of dental morphology on food fracturing (Lucas et al., 1994; Evans and Sanson, 1998; Anderson and LaBarbera, 2008; Berthaume et al., 2010), but to our knowledge, there has been no attempt to simulate food fracturing during non-vertical chewing motion.

## Objectives

This study aimed to estimate the effect of dental morphology on food fragmentation independently of chewing kinematics. It has been proposed that shearing crests would improve the ability of molars to shear leaf-like food. In order to test this hypothesis, we decided to decompose the chewing cycle in order to focus on one specific part of it, centric occlusion, i.e., removing the influence of the shearing or grinding motions related to phases I and II of the mastication cycle. We aimed to test the effect of molar morphology on the comminution of five food items that correspond to different mechanical challenges encountered by extant and fossil catarrhines. Using a chewing simulator, we experimentally processed a selection of foods eaten by catarrhines after successive intercuspatations mirroring centric occlusions with two different forces, in order to assess their influence. Furthermore, we chose to use a decomposition approach by removing most aspects of the system in order to model only one, the effect of dental morphology. The sample includes cercopithecoid and hominid specimens encompassing the main dental occlusal patterns and dietary habits displayed by catarrhines that may also correspond to fossil dental morphology and diets. Following the assumption that tough and elastic foods are fragmented by shearing movements and hard food by crushing movements, we chose to include leaves to test this hypothesis. We expected centric occlusion to be sufficient for fragmenting brittle food, but that fragmenting tough and complex foods would require additional movements (shearing and grinding) and therefore that centric occlusion will not be sufficient (Lucas, 2004; Berthaume et al., 2010; Swiderski and Zelditch, 2022).

## Materials & methods

### Specimens

The sample was composed of one pair of opposite upper and lower second molars representing a M2/M2 masticatory complex in four specimens (figure 1A1-A2). Four catarrhines were selected: two cercopithecoids (*Procolobus verus*: RMCA\_86002\_M50; *Theropithecus gelada*: MNHN\_1969-450) and two hominids (*Gorilla beringei graueri*: RMCA\_27755; *Homo sapiens*: AG-3 ZE 26 and AG-3 ZE 36). All the individuals selected presented low to moderate tooth wear.

Diet-wise, *P. verus* mainly feeds on young leaves and has a sacculated stomach, which enhances the breakdown of cellulose (Oates, 1988). The diet of *T. gelada* mainly consists of grass rhizomes and blades (Dunbar, 1977;

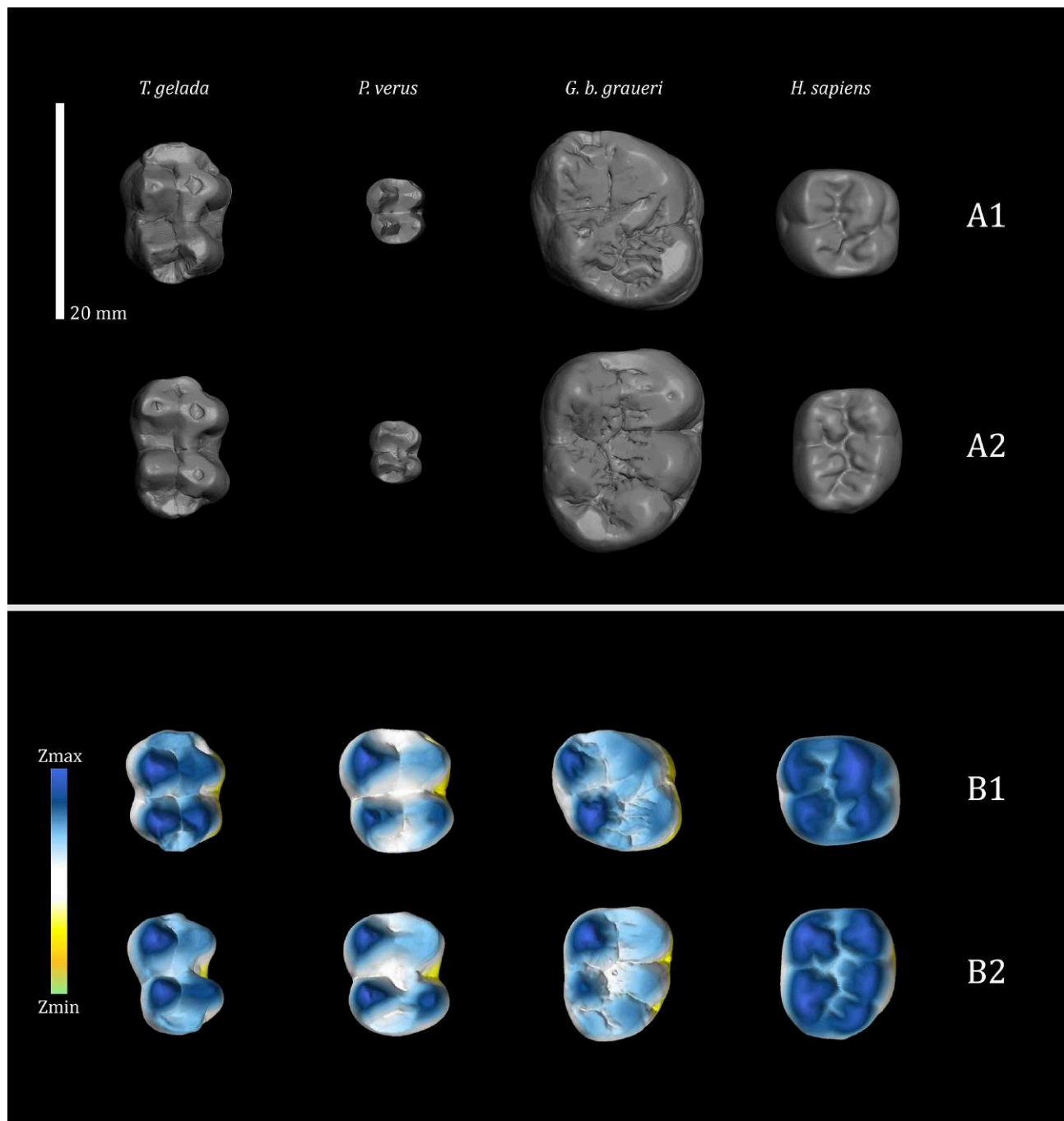
Venkataraman et al., 2014). *G.b. graueri* also relies on terrestrial herbaceous vegetation, but may include significant amounts of fruits in its diet (Yamagiwa et al., 2005). *H. sapiens* is classically defined as omnivorous.

Even though *G.b. graueri*, *P. verus* and *T. gelada* are all herbivorous, they are representative of three different kinds of dietary specializations, with differences in their dental morphology: the molars of *P. verus* are low-crowned (figure 1B1-B2; see also supplementary information A1 and table A2 for topographic characterizations) with four high and pointed cusps connected transversely by well-marked lophs; the molars of *T. gelada* are relatively high-crowned (figure 1B1-B2; see also supplementary information A1 and table A2) with four low rounded cusps connected by longitudinal ridges and transversal lophs interrupted by longitudinal grooves, whereas the molars of *G.b. graueri* display the characteristic hominoid pattern with four (upper) and five (lower) bunodont cusps bearing well-developed cuspal crests (figure 1B1-B2; see also supplementary information A1 and table A2). We expected the teeth of *G.b. graueri*, *P. verus* and *T. gelada* to be adapted to fragmenting foods for a high energy release rate (leaves) with a minimum number of chews i.e., that their chewing performance would be greater than in most primates for their specialized food range (M'Kirera and Ungar, 2003; Venkataraman et al., 2014). In contrast, *H. sapiens* rely less on fibrous and high energy-release rate foods, and their teeth need to perform different tasks, including the fragmentation of brittle food. This is associated with a different dental morphology: modern humans share with *G.b. graueri* the typical hominoid dental pattern, albeit with smaller molars with thicker enamel and tightly packed and non-wrinkled cusps (figure 1B1-B2; see also supplementary information A1 and table A2).

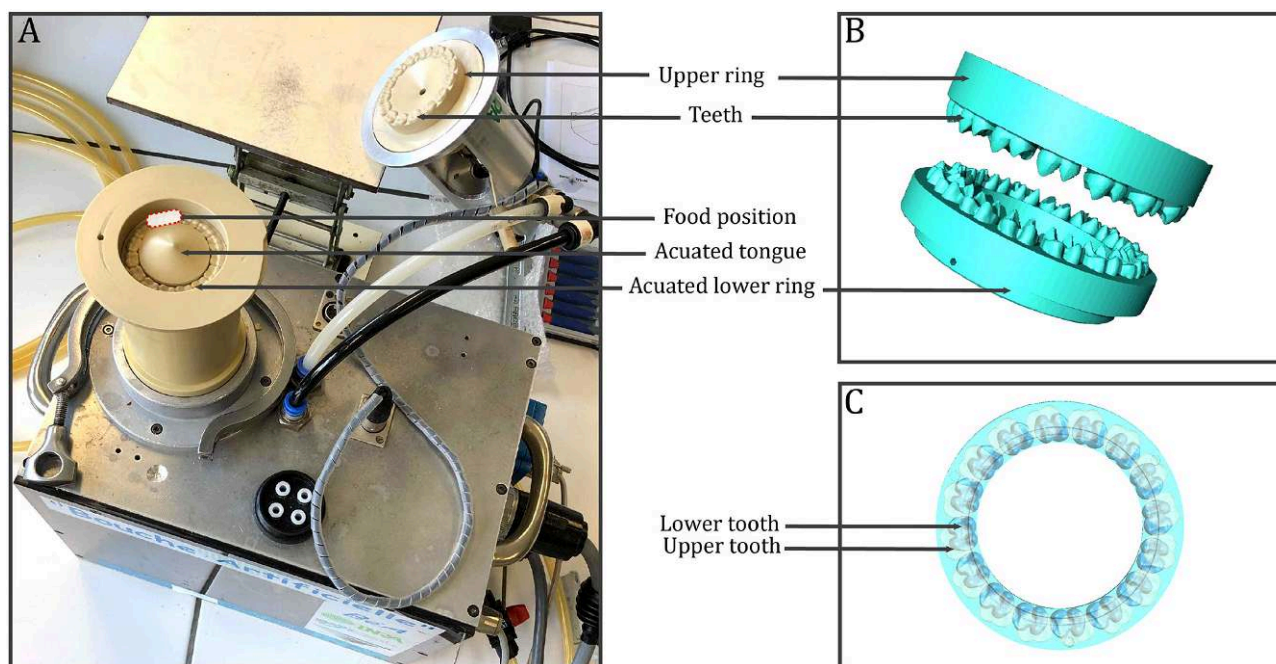
### Polygonal dental surfaces and replicas

The opposite molars selected were scanned using an Easytom microtomograph to produce virtual 3D dental volumes with an isovoxel size ranging from 0.013 to 0.076 mm, depending on the size of the original tooth. The enamel caps were extracted using semi-automatic segmentation and converted into polygonal surfaces (Avizo software). The resulting meshes were corrected and processed to obtain regular printable surfaces of about 250,000 polygons. The molar sets were oriented, resized (isometric scaling), replicated 14 to 16 times depending on original tooth size and spaced equally along a circular path (figure 2A-B), resulting in two dental rings interlocking with each other (figure 2C). The models were 3D printed by fused deposition modelling (Additive Manufacturing) in ASA material (acrylonitrile styrene acrylate) at the PLATEFORM3D (IUT du Creusot, France). Additionally, five topographic variables were computed for each mesh and analyzed to characterize each dental pattern (supplementary information A1) and build topographic maps (figure 1B1-B2, supplementary information A1).





**Figure 1.** Three-dimensional morphometric maps and associated chromatic colour scales of the elevation for OES (Occlusal Enamel Surface, e.g. Guy et al., 2013). The molars shown correspond to a subsample of four M2/M2 masticatory complexes in four species (from left to right): *T. gelada*, *P. verus*, *G. b. graueri* and *H. sapiens*. A1: Grey scale upper molar; A2: Grey scale lower molar; B: elevation (B1: upper molar and B2: lower molar). To improve readability, the size of the molar representations have been rescaled by length in B; refer to the grey scale molars (A) for relative and absolute size / *Cartes morphologiques 3D et échelles de couleurs chromatiques associées à l'élevation pour OES (Occlusal Enamel Surface, p. ex. Guy et al., 2013)*. Les molaires représentées correspondent à un sous-échantillon de quatre complexes masticatoires M2/M2 chez quatre espèces (de gauche à droite) : *T. gelada*, *P. verus*, *G. b. graueri* et *H. sapiens*. A1 : molaire supérieure en niveau de gris ; A2 : molaire inférieure en niveau de gris ; B : élévation (B1 : molaire supérieure et B2 : molaire inférieure). Pour améliorer la lisibilité, la taille des représentations des molaires a été redimensionnée en fonction de la longueur en B ; se référer aux molaires en niveau de gris (A) pour la taille relative et absolue



**Figure 2.** The chewing simulator BA and example of associated dental replica rings. A: View of the chewing simulator with positioned upper and lower human dental replica rings; B: 3D virtual meshes of upper and lower dental replica rings, *P. verus* example; the inner ring diameter is 40 mm and the outer diameter 60 mm; C: Cuspal interlocking between upper and lower dental replica rings, *P. verus* example / *Le simulateur de mastication et un exemple de couronnes dentaires associées. A : Simulateur de mastication avec les répliques dentaires supérieure et inférieure positionnées ; B : Image virtuelle 3D des répliques dentaires supérieure et inférieure, exemple de P. verus ; le diamètre intérieur de l'anneau est de 40 mm et le diamètre extérieur de 60 mm ; C : Imbrication des cuspidés entre les répliques dentaires supérieure et inférieure, exemple de P. verus*

### Chewing experiments

The models for each individual were positioned in a chewing simulator (BA, *Centre de Sciences du Goût et de l'Alimentation* - INRA, Dijon, France; figure 2A) consisting of two rings of replicated opposite upper and lower teeth (Salles et al., 2007). With the simulator starting from an open position, BA operates (1) a closing movement in order to reach occlusion, (2) a relative rotation of the lower ring (bearing lower teeth) to facilitate cusp interlock and (3) a reopening movement to return to the initial position. Before each starting cycle, food items are positioned on the molars of the lower ring and the simulator is sealed, bringing the upper ring close to the lower one. Following Tarrega et al. (2019), the rotation of the upper jaw during the cycles was fixed at 3° to facilitate cusp interlocking. While this probably introduced a shearing component in addition to the orthal cusp interlock, its effect on food fragmentation cannot be equated with a grinding/shearing phase. An actuated tongue consisting of a complete cylinder with a conical end directed upward and running inside the lower dental ring remobilizes the food towards the dental row after each reopening (Salles et al., 2007).

Classically, the chewing simulator operates in a salivary context, but we chose to run these experiments in a dry context in order to remove the influence of chemical interactions with the food items (Yven et al., 2010; Swackhamer and Bornhorst, 2019). BA allows chewing force ranging from

1 N to 350 N. For our experiments, the chewing force was fixed at 100 N (experiment #1) and 300 N (experiment #2) in order to evaluate the influence of bite pressure on the fragmentation of food items. For each trial, each food item and each bite pressure, we performed one chew (control test: one closing and one reopening) (supplementary information A2) and five successive intercusations (fragmentation test), which are presented here. The latter were always repeated five times (5 experiments). The duration of the fragmentation test was about 5 seconds. Overall, 240 trials were conducted, covering all species and food items.

### Food samples

The food items selected were: mature ficus tree leaves (*Ficus benjamina*), shelled hazelnuts (*Corylus avellana*), apples (var. Granny Smith), ginger root (*Zingiber officinale*) and crickets (75% hydrated *Gryllus campestris*). These correspond roughly to five types of foods consumed by primates in the wild (Lucas et al., 2000; Vincent and Wegst, 2004; Dominy et al., 2008) and to different physical food properties (stiffness, hardness, energy release rate):

- *Leaf-like foods*, which are expected to be flat and ductile, with low stiffness and hardness but a medium to high energy release rate;
- *Nut-like foods*, which are expected to be bulky, brittle and moderately stiff, with a low energy release rate and relatively anisotropic properties;

- *Fruit-like foods*, which are expected to be bulky, brittle and soft, with low stiffness and a low energy release;
- *Tuber-like foods*, which are expected to be bulky and ductile, with low to moderate stiffness and hardness, but a high energy release rate due to highly isotropic properties;
- *Insect-like foods*, which are expected to be complex and ductile, with low to high stiffness but a high energy release rate and again, isotropic properties.

Apple and ginger root samples were taken using a 7-mm diameter die cutter in order to obtain samples 20 mm in length. The ficus tree leaves were cut with a scalpel along the main vein to produce a 10 × 20 mm sample. Similarly, the crickets were cut to obtain 20 mm long samples by taking off the head and part of the thorax. The hazelnuts were longitudinally split in half and their convex side was levelled to obtain a 3 mm thick rectangle with a surface of about 200 mm<sup>2</sup>. Each food item was positioned with its major axis parallel to the occlusal plane in the mesio-distal direction in order to normalize the relative starting position of the food throughout the experimentation (figure 2A).

### Analysis

For each trial, after opening the chewing cell, the food particles were carefully collected using a spatula, pliers and brush, then analyzed. After each trial, the chewing cell was rinsed with de-ionized water and dried with a paper towel. Before analysis, the food residuals were immersed in containers with 150 mL of glycerol diluted at 80% in order to scatter the particles. The glycerol and its contents were poured onto a glass plate, which was placed in a colour-calibrated scanner (Epson perfection V750 PRO) and then digitized to standard size (A4), and resolution (400 dpi). The resulting images were processed with Fiji software (Schindelin et al., 2012). Depending on the type of residuals obtained, 192 analyses were carried out.

Each image was binarized using a threshold value based on the initial colour-standardized scanner parameter. The “particles analysis” plugin was applied to the binarized images. The number of fragments (Nf), their respective area (Af) and the total area (At) were recorded. In order to remove background noise, any particle smaller than 0.05% of the total area was discarded. For the least brittle food (i.e. apple and ginger), the crushing coefficient of the food item was also measured as the ratio (Ar) of the total area of the chewed food item (At) over the maximum area of the initial food item (Ai). As the chewed leaves showed neither fragmentation nor significant crushing deformation, they were treated separately. The number of pits (Np: small marks corresponding to localized compressions of the leaf sample) and cracks (Nc: fissures propagating from the outer edge of the leaf sample towards its centre) were visually numbered. Each count was repeated five times over five days and the average value was retained. A qualitative observation (punctuation, perforation, tears of the leaf) was also carried out. Statistical analyses (Dunn’s test) were performed with R 4.0.4 (R Core Team, 2021).

## Results

### Crickets

The particle count ranged from 1 to 150 (figure 3A). Increasing the chewing force from 100 to 300 N increased the number of particles (Dunn’s test shows a significant difference,  $Z=-3.95$  at  $p<0.001$ ). At 100 N, the highest numbers of particles were obtained by the human teeth (Dunn’s test:  $Z=-2.14$ ,  $p<0.001$ ), while at 300 N they were obtained by the cercopithecoid teeth, especially *T. gelada* (Dunn’s test:  $Z=-3.62$ ,  $p<0.001$ ) (figure 3A). Increasing chewing force greatly impacts reduction of the particles for all taxa except humans, whose teeth chip but do not fragment the crickets.

### Ginger

The number of fragments (Nf) ranged from 1 to 50 and the crushing coefficient (Ar) from 0.8 to 2.52 (figure 3B-C). Contrary to crickets, fewer particles were produced and deformation of the ginger was mainly ductile. After 5 cycles, greater chewing force increased the crushing coefficient (Ar) for all except the human teeth, which had already reached the maximum Ar (Dunn’s test:  $Z=-2.70$ ,  $p<0.001$ ). At 100 N, the human and cercopithecoid teeth obtained higher crushing coefficient scores than the gorilla teeth (Dunn’s test  $Z=3.18$ ,  $p<0.001$ ). The human teeth present relatively higher crushing coefficients than for the other taxa. At 300 N, the crushing coefficient does not differ significantly across taxa.

Both the highest and the lowest values were recorded for the human teeth. Considering fragmentation (Nf), the number of particles is associated with chipping, which mainly isolates fibres but also small fragments. The number of particles produced remains low on average ( $Nf<30$ ) whatever the taxa considered. The number of fragments increases between 100 N and 300 N except for *H. sapiens* and *P. verus*.

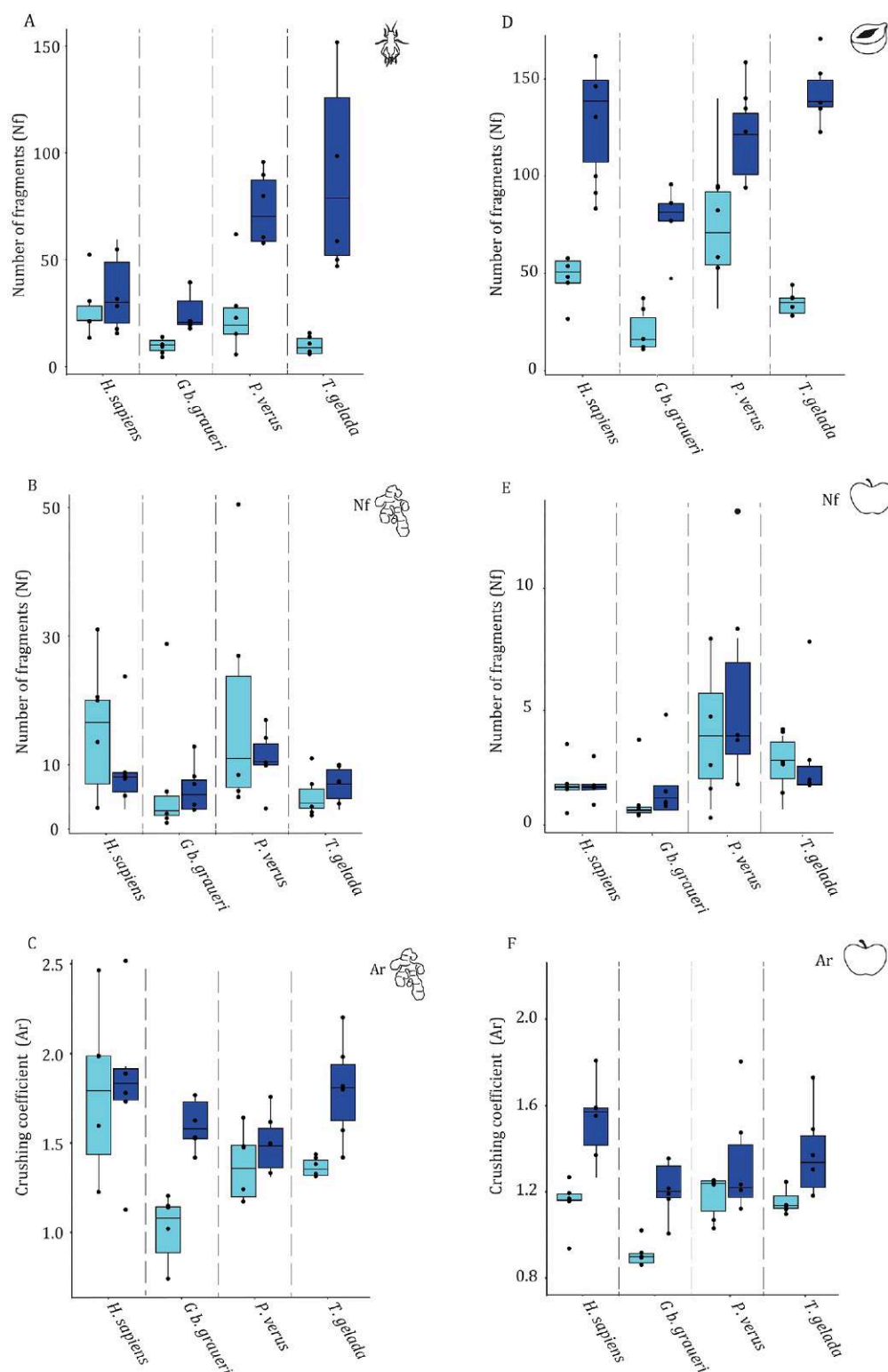
### Hazelnuts

The particle count for hazelnut ranges from 1 to 170 (figure 3D). As with crickets, increasing the chewing force from 100 N to 300 N increases the number of particles (Dunn’s test:  $Z=-4.49$ ,  $p<0.001$ ). The largest numbers of particles are obtained by human and cercopithecoid molars at 100 N and 300 N (Dunn’s test, 100 N:  $Z=-2.75$ ,  $p<0.001$ ; 300 N:  $Z=-2.92$ ,  $p<0.001$ ). *G.b. graueri* molars produce fewer particles. However, increasing the chewing force greatly impacts reduction of the particles for these taxa (figure 3D).

### Apple

The number of fragments (Nf) ranged from 1 to 13 and the crushing coefficient (Ar) from 0.8 to 1.8 (figure 3E-F). After 5 cycles, greater chewing force increased the crushing





**Figure 3.** Quantification of chewing residuals for hazelnuts, crickets, apples and ginger according to species and bite force. Box-and-whisker diagrams (median, first and third quartiles and full range of values) for 5 cycles. A: number of fragments (Nf) of crickets; B: number of fragments (Nf) of ginger; C: crushing coefficient (Ar) for ginger; D: number of fragments (Nf) of hazelnuts; E: crushing coefficient (Ar) for apples; F: number of fragments (Nf) of apples. Light blue is for 100 N; dark blue is for 300 N / Quantification des résidus de mastication pour les noix, les grillons, les pommes et le gingembre en fonction de l'espèce et de la force de morsure. Boîtes à moustaches (médiane, premier et troisième quartiles et gamme complète des valeurs) pour 5 cycles. A : nombre de fragments (Nf) de grillons ; B : nombre de fragments (Nf) de gingembre ; C : coefficient d'écrasement (Ar) du gingembre ; D : nombre de fragments (Nf) de noix ; E : coefficient d'écrasement (Ar) de pommes ; F : nombre de fragments (Nf) de pommes. Les boîtes à moustaches bleu clair correspondent à 100 N et les boîtes à moustaches bleu foncé correspondent à 300 N

coefficient (Dunn's test:  $Z=-3.86$ ,  $p<0.001$ ), especially in hominids. At 100 N, the human and cercopithecoid teeth displayed higher crushing coefficient scores than the gorilla teeth (Dunn's test:  $Z=3.09$ ,  $p<0.001$ ). At 300 N, Ar did not differ significantly across taxa. The highest values were seen in *H. sapiens* and the lowest values in *G.b. graueri*. Considering fragmentation (Nf), the number of particles was lower for apple than for the other food items. On average the number of particles produced remained low ( $Nf<5$ ) whatever the taxa considered. At 100 N, there was no significant difference between taxa. At 300 N, deformation was associated with chipping in the case of *P. verus* while only few agglomerate particles were obtained by *G.b. graueri*, *H. sapiens* and *T. gelada*. Overall, the ginger model showed greater variation than the apple model at 100 N (CVAr ginger=27.1%; CVArapple=11.6% all taxa included). Variation in the models is comparable between ginger and apple at 300 N (CVAr ginger=18.6%; CVAr apple=16.5% for all taxa).

### Leaves





The average number of indentation marks ranged from 0 to 7 and the average number of cracks from 0 to 2, which is rather low and implies that the chewing simulator is not tailored for leaf fragmentation (supplementary information A3). We observed four levels of leaf degradation:

1. the ficus leaf is neither perforated nor torn (figure 4A);
2. punctuations are present (figure 4B);
3. the ficus leaf is perforated (figure 4C);
4. cracks are observable (figure 4D).

After five chews at 100 N, most of the ficus leaves chewed by the human teeth do not show pits and/or cracks. All taxa except *H. sapiens* produced puncture marks, and only *P. verus* produced cracks (twice out of 5 chewing experiments). Increasing chewing force greatly impacts the production of pits/punctures and perforations for all taxa. At 300 N, there was a significant increase in pits (Dunn's test,  $Z=-2.74$  at  $p<0.001$ ) and cracks (Dunn's test:  $Z=-2.91$ ,  $p<0.01$ ). All taxa except the gorilla produced cracks (supplementary information A3), but the cercopithecoid teeth produced more cracks than the human teeth. Whatever the force, all species produced pits.

### Discussion

The classic hypothesis explaining the relationship between the masticatory apparatus and diet assumes that, in a masticatory context, selection will favour molars which have a better capacity to fragment food (Ungar et al., 2010). If this hypothesis is correct, then we would expect the molars of each primate studied to better fragment the food items within their respective dietary category. The results presented in this study tend to support this hypothesis. However, in addition to the form-function relationship between teeth and food items, other parameters contribute to the chewing process. In fact, the force required and its variation during a masticatory cycle, the duration of mastication and the chewing movement also play a role in food comminution (Pérez-Barbería and Gordon, 1998; Ross et al., 2016; Zink and Liberman, 2016), and this should be taken into account for future research.

	Undeteriorated	Punctuations	Perforations	Cracks
	<b>A</b> 	<b>B</b> 	<b>C</b> 	<b>D</b> 
100 N	<i>H. sapiens</i> 4/5 <i>P. verus</i> 2/5	<i>H. sapiens</i> 1/5 <i>P. verus</i> 2/5 <i>T. gelada</i> 5/5 <i>G. b. gorilla</i> 5/5		<i>P. verus</i> 1/5
300 N		<i>H. sapiens</i> 3/5 <i>G. b. gorilla</i> 5/5	<i>H. sapiens</i> 1/5 <i>T. gelada</i> 3/5	<i>H. sapiens</i> 1/5 <i>P. verus</i> 5/5 <i>T. gelada</i> 2/5

**Figure 4.** Effect of centric occlusion on leaves according to species and bite force. The upper row illustrates the four different patterns of leaf deterioration after five intercuspatations at 100 N (middle row) and 300 N (lower row). A: Undeteriorated; B: Punctuation, small imprint without perforation; C: Perforations; D: Cracks, propagating from the edge. In each panel, the count (light grey) for each pattern is indicated per species / *Effet de l'occlusion centrée sur les feuilles en fonction de l'espèce et de la force de morsure. La ligne supérieure illustre les quatre différents modèles de détérioration des feuilles après cinq intercuspatations à 100 N (ligne du milieu) et 300 N (ligne inférieure). A : Non détérioré ; B : Ponctuation, petite empreinte sans perforation ; C : Perforations ; D : Fissures, se propageant à partir du bord. Pour chaque espèce le nombre des différents modèles de détérioration est indiqué en gris clair*

### Effect of bite force

In our simulation, increasing the bite force resulted overall in greater degradation of the food item. We show that, at 300 N, this degradation can involve collapsing and/or supplementary cracks in addition to the initial indentation. However, because bite force is known to be controlled and to vary within the same chewing cycle and between chewing cycles (Takahashi et al., 2009), this result does not allow comparisons of relative chewing performance between species. This variation is important, but depends on the muscles and geometry of the masticatory apparatus of the animal considered (Takahashi et al., 2009), which cannot be modelled in the BA chewing simulator. In this study, the gorilla performs less well than other taxa at 300 N, but depending on the feeding actions, living gorillas can easily increase their bite force up to  $3,420 \pm 251$  N (Breuer et al., 2012; Eng et al., 2013). We conclude that bite force plays a significant role during food comminution and our results show that higher forces prevail over morphology for the fragmentation of brittle (nut-like, fruit-like) foods and tough (leaf-like, cricket-like and ginger-like) foods.

### Effect of dental morphology

Three occlusal patterns for extant folivorous species (bilophodont with low crown, bilophodont with high crown and bunodont with cuspal crests) and one pattern for an extant omnivorous species (bunodont with small basin) were tested to evaluate the effect of dental morphology on food comminution. Classic hypotheses suggest that bunodont molars are adapted to hard food consumption (Evans and Pineda-Munoz, 2018), bilophodont molars to leaf consumption while insectivory is more commonly associated with sharp pointed teeth, an occlusal pattern not tested here (Kay, 1977; Evans and Sanson, 1998, 2003). *P. verus* and *T. gelada*, which are folivorous and herbivorous, are better at processing leaves than other primates in this study. Unexpectedly, these cercopithecids also showed an evident capacity for fragmenting hazelnuts, ginger, apples and crickets. *H. sapiens*, which consumes an omnivorous diet (albeit consisting mainly of cooked food items), showed an evident capacity for crushing and fragmenting most of the food items except leaves, and this capacity was frequently equivalent to that of *T. gelada* and *P. verus*. Overall, our results concur with the classic hypotheses for these taxa that explain dental morphology as an adaptive response to primary dietary components. *H. sapiens*, *P. verus* and *T. gelada* performed relatively well for most of the food items without showing any specialization for fragmenting particular food items. Conversely, *G.b. graueri* did not show any particular ability to crush and fragment selected food items except ginger, as far as only centric occlusion is considered. This could be due to the relatively low force applied as compared to the mean bite force measured for this species. In this study, we decided to simplify some aspects of mastication, for example by standardizing molar

size (i.e. the sizes of the teeth used in the chewing simulator are all equal). Nevertheless, tooth size has an influence on the fragmentation of certain types of food, in terms of mechanics (Lucas et al., 1986; Lucas, 2004; Berthaume et al., 2014).

### Role of intercuspatation in food fragmentation

The aims of our study were to test different dental occlusal patterns during simple intercuspatation, removing shearing and grinding movements to understand the specific contribution of centric occlusion during the chewing cycle. While centric occlusion damages all kinds of food items, we found that certain foods with particular physical properties (with high energy release rates) were never (leaf-like, see figure 4) or poorly (tuber-like, see figure 3B) fragmented whatever the dental morphology. In fact, some food items reacted differently depending on their geometry (leaf-like), composition (ginger and apple are composed of juice that can act as a binder) and physical properties. This is consistent with the literature, as some foods do not respond in the same way to stress: for example, tuber-like and leaf-like foods require relatively low stress but with larger amounts of displacement for the cracks to propagate (Lucas et al., 2000). Nevertheless, the presence of certain characteristics (cusps, lophs and shearing crests) and/or greater force is sufficient to fragment brittle foods during intercuspatation, but grinding or shearing movements need to be added to process hard or tough foods (Simpson, 1933, 1936; Gordon, 1984; Ungar and Sponheimer, 2011).

### Limitations

In order to study the effect of centric occlusion, a specific component of mastication, on the fragmentation of foods that depends on different occlusal patterns in primates, we simplified the chewing process using the BA chewing simulator. First, for methodological reasons, the experiments were run with standardized isolated food items in a dry environment, which does not take some aspects of natural masticatory processes into account (e.g. presence of saliva, more complex food item geometries, relative size and positioning), in order to focus solely on morphological aspects. Furthermore, tooth size was standardized and the row design was modified (dental ring) to fit into the BA simulator (supplementary information table A1). However, accurately reproducing chewing behaviour would require tooth replicas to scale as well as scalable dental motions, and dental rows similar to what is observed in nature. We observed that intercuspatation occurring at centric occlusion can be sufficient to fragment brittle foods, but it is important to study the effects of the other phases of the complete chewing cycle of primates (e.g. through functionally accurate phase I and phase II components, bite force magnitude and variation during mastication cycles, and proper emulation of slicing, grinding, shearing actions) (Kay, 1975, 1977; von Koenigswald et al., 2012; Thiery et al., 2017b; Montuelle

et al., 2018). The capacities of teeth to fragment selected food items as observed in this study apply only to molars with low to moderate wear, while studies show that dental performance can increase with wear to a certain extent (M'Kirera and Ungar, 2003). Lastly, the chewing time (frequency and duration) should also be considered. Trials were carried out (control test: supplementary information A2) but this needs to be further investigated. The design of a new chewing simulator that will improve the emulation of natural masticatory processes is underway. Other simulators under development (e.g. Jeannin et al., 2019; Alemzadeh et al., 2020; Krueger et al., 2021; Chen et al., 2022) may allow further studies of the form-function relationship of teeth.

## Conclusion

This study focuses on four extant primates with different dental occlusion patterns to model the variations observed in extant and fossil catarrhines. We investigated two bilophodont and two bunodont patterns, representing cercopithecids and hominids respectively. The differences between these species are mainly the height of the crown in cercopithecids and the addition of cuspal crests and cusp arrangement in hominids. Many studies are interested in the relationship between tooth morphology and the ability to fragment foods efficiently, because postcanine dentition probably evolved mostly in response to differences in the physical properties of diets (e.g. Lucas, 2004; Berthaume and Kupeczik, 2021). In this study, we experimentally tested how these morphologies differ in their ability to fragment various food items during centric occlusion. We show that molar performance can be investigated through recent developments in robotics. We also show that intercuspation occurring at centric occlusion will fragment brittle and complex food (hazelnuts and crickets) and that greater bite force results in higher food item degradation overall, although we report some exceptions, notably for ductile and tough foods (apples, ginger and leaves). This experiment showed that proper occlusion and bite force are sufficient only to fragment brittle food and that additional movements are necessary to fragment tough foods (leaves and grasses).

Studies of dental evolution and adaptation lack experimental data to test morpho-functional hypotheses. Protocols and methods to simplify mastication need to be developed in order to test the contribution of molar morphology during the different occlusal phases. If some limitations of the current protocol are improved, this chewing experiment could be applied to infer the effect of dental morphology on chewing ability across a wide range of primates, including humans and their ancestors. Such a breakthrough would allow investigations into major anthropological questions such as the diets of the Australopithecids and how climate can affect the evolution of dental morphology (e.g. Ungar, 2004; Cerling et al., 2011; Grine and Daegling, 2017; Wynn et al., 2020).

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## Supplementary information

Supplementary information is available at:  
<https://journals.openedition.org/bmsap/10104?file=1>

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