ANTHROPOLOGY

The cost of chewing: The energetics and evolutionary significance of mastication in humans

Adam van Casteren[1,2]*, Jonathan R. Codd[1], Kornelius Kupczik[2,3], Guy Plasqui[4], William I. Sellers[5], Amanda G. Henry[6]

Any change in the energetic cost of mammalian mastication will affect the net energy gain from foods. Although the energetic efficiency of masticatory effort is fundamental in understanding the evolution of the human masticatory system, nothing is known currently about the associated metabolic costs of chewing different items. Here, using respirometry and electromyography of the masseter muscle, we demonstrate that chewing by human subjects represents a measurable energy sink. Chewing a tasteless odorless gum elevates metabolic rate by 10 to 15% above basal levels. Energy expenditure increases with gum stiffness and is paid for by greater muscle recruitment. For modern humans, it is likely that mastication represents a small part of the daily energy budget. However, for our ancestors, before the onset of cooking and sophisticated food processing methods, the costs must have been relatively high, adding a previously unexplored energetic dimension to the interpretation of hominin dentofacial fossils.

INTRODUCTION

Our ancestors' ability to effectively acquire, process, and consume food underpinned their survival, and changes in their masticatory system played a key role in the evolution of our own species. The efficiency of the feeding system is of high importance for all endothermic animals, such as mammals, that maintain a high and relatively constant temperature. The need to optimize feeding, so as to extract maximal energy from food sources without wasting it on processing costs, is one of the main driving forces behind the evolution of mammalian mastication (*1*, *2*) and has led to substantial morphological innovations in mammalian teeth, jaws, pharynges, and masticatory muscles (*1*, *3*). Mastication is a kinematically complex process involving both vertical and lateral movements of the mandible in a cyclical manner with repetitive closure of the jaws, forcing the working surfaces of the teeth onto food particles, so reducing them to a fraction of their original size. Chewing evolved some 260 million years ago and is associated with a range of vertebrate taxa (*4*, *5*). However, the precise occlusion and lateral movements that distinguish mammalian mastication as a remarkable evolutionary novelty have driven diversification in diet and are thought to have contributed to the global radiation of mammals (*1*, *4*).

An essential outcome of mastication is the comminution of a food into small particles, lubricating them with saliva, so promoting the formation of a bolus (a ball of particles bound together by saliva) that can be swallowed easily (*2*) and then digested (*6*, *7*). Teeth break foods down mechanically in the oral cavity via the initiation and propagation of fractures that are often resisted by the internal mechanical properties of these foods (*8*, *9*). The energy needed to reduce food particles from their ingested size down to what is swallowed defines the efficiency of the process (*10*). Variation in mammalian diets is thought to have driven the evolution of variably complex tooth morphologies and masticatory kinematics (*9*, *11*) as adaptive changes in masticatory morphology are thought, at least in part, to deliver reductions in the work needed to produce a given food particle size (*9*). For mammals consuming foods where nutrients are not readily available, such as in many plant-based resources, the ability to chew effectively, reducing food to small particles for minimal effort, and perhaps within a reasonable time period depending on the exact selection pressures acting on the individual, is vital. Evidence from a range of placental and marsupial mammals indicates that degradation in an individual's ability to chew can have a detrimental effect on an animal's survival (*12*–*14*).

The importance of food acquisition and processing has given rise to a vast literature aimed at understanding the energetic and biomechanical nuances of the mammalian masticatory system. Nowhere is this more salient than in the study of human evolution, where most primate and hominin fossil evidence is made up of craniodental elements. In hominoids, the major work for fracturing foods is performed by the large masticatory muscles that elevate the mandible: the temporalis, the masseter, and the medial pterygoid muscles. Jaw opening is facilitated by the lateral pterygoid, the digastrics, geniohyoid, and mylohyoid (*9*). However, the act of chewing also engages the tongue, which continually pushes food onto the molars for further comminution, and the buccinator, which contracts, causing the cheek to tense, pushing food into the path of the occluding teeth (*9*). Mastication in hominoids therefore involves a suite of many muscles that will be engaged to varying degrees when processing foods.

While there is a substantial body of work that has measured and estimated the bite forces and kinematic actions produced during mastication (*15*–*19*), there is little to no work focused on masticatory energetics. This oversight is unexpected because changes in energetics have been used to explain the evolution of many musculoskeletal systems in humans, especially when such systems are associated with uniquely human traits such as bipedalism. However, these tend to be large, energy-hungry systems, such as locomotion or digestion, that account for a high percentage of a hominin's total

[1]School of Biological Sciences, University of Manchester, Manchester, UK. [2]Max Planck Weizmann Center for Evolutionary Anthropology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. [3]Department of Anthropology, Faculty of Social Sciences, University of Chile, Santiago de Chile, Chile. [4]Department of Nutrition and Movement Sciences, NUTRIM School of Nutrition and Translational Research in Metabolism, Maastricht University Medical Centre+, Maastricht, Netherlands. [5]School of Natural Sciences, University of Manchester, Manchester, UK. [6]Faculty of Archaeology, Leiden University, Leiden, Netherlands.
*Corresponding author. Email: adam.vancasteren@gmail.com

energy expenditure (TEE) (*20*, *21*). Although the modern human masticatory system is highly derived when compared to that of our extinct or extant relatives, with modern humans having smaller and more gracile dentofacial features (*22*, *23*), there has been little focus on whether the evolution of this reduced form has equated to meaningful differences in TEE. Without measurements of the metabolic cost of chewing, we cannot ascertain to what extent natural selection has energetically optimized the human chewing apparatus, making evolutionary predictions of the role of energetics in shaping the masticatory system of modern humans somewhat precarious.

Here, we seek to determine whether the metabolic costs of using the masticatory system are measurable and notable in modern humans. We examine the metabolic costs of chewing in humans and assess the influence that a relative change in the physical properties of items being masticated may have on these costs. To isolate the metabolic costs associated specifically with chewing and not the overall metabolic costs of feeding, it was necessary to control confounding metabolic costs such as those associated with digestion and the stimulus response from smell, taste, and familiarity; all of which may have influenced the findings (*24*). This was achieved by having subjects chew odorless and tasteless gum bases of different mechanical properties (soft and stiff). Prolonged bouts of mastication on these gum bases allowed us to test the hypothesis that differences in gum base mechanical properties lead to significant differences in the energetic cost of chewing. We also determined how this relates to muscle activation of the masseter and the magnitude of the energetic cost of chewing as a fraction of human TEE. In answering these questions, we can provide a context into how the energetic costs of chewing may pertain to evolutionary changes in hominin masticatory systems through human evolution.

RESULTS

Metabolic cost of chewing

Metabolic measurements were made using indirect calorimetry. Oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) were measured using a ventilated hood system (Omnical, Maastricht University, Maastricht, Netherlands). First, a baseline basal metabolic rate (BMR) was recorded while the subject was in a post-absorptive state, reclining on a bed, limiting any movements to an absolute minimum for circa 45 min. The subject was randomly assigned one of two gum bases (soft or stiff) and asked to chew for 15 min. After this period had elapsed, the subject had a 5-min rest before being asked to chew the remaining gum base for a further 15 min (Fig. 1).

The average BMR among our mixed-sex sample (n = 21; Table 1) was 4.27 SD 0.53 kJ/min. Chewing of either gum provoked a substantial increase in energy expenditure (EE) compared to BMR, with the stiffer gum requiring more energy (4.91 SD 0.59 kJ/min) than the softer one (4.69 SD 0.53 kJ/min) (Fig. 2). A repeated-measures one-way analysis of variance (ANOVA) showed that EE was significantly different for each test condition [$F_{(2, 28)} = 290.4$, $P \leq 0.0001$] (Fig. 2). A Bonferroni post hoc test revealed that all the pairwise differences, between test conditions, were statistically significantly different ($P \leq 0.0001$). Of the confounding test variables (weight, sex, day, bed, and order of gums chewed), only sex had any influence on the results [$F_{(1, 14)} = 5.5$, $P \leq 0.05$] (see supplementary information S4 for the outputs of the model summaries).

Muscle activation

To investigate how muscle activation influenced EE, electromyography (EMG) activity was recorded from one of the subject's masseter muscles while chewing both the soft and stiff gums for 2 min (Fig. 3A). Raw EMG (Fig. 3B) was digitally filtered to extract the amplitude envelope; amplitude peaks were recorded as representing activation of the muscle (Fig. 3C). Frequency of activation was then calculated by generating a power spectrum via a Fourier transform (Fig. 3D). EMG results showed that the softer gum was chewed at a slightly higher mean frequency (1.15 SD 0.18 Hz) but lower mean peak amplitude (72 SD 2.7 μV) than the stiffer gum (frequency: 1.06 SD 0.18 Hz; mean peak amplitude:126 SD 4.6 μV). For statistical analysis, values were converted into ratios of stiff gum/soft gum. If there were no differences, we would expect the ratio to be 1.0. A one-sample t test comparing the value to 1.0 showed both the chewing frequency and the peak EMG values to be significantly different (frequency: $t = -3.3226$, $P = 0.0036$; EMG peak

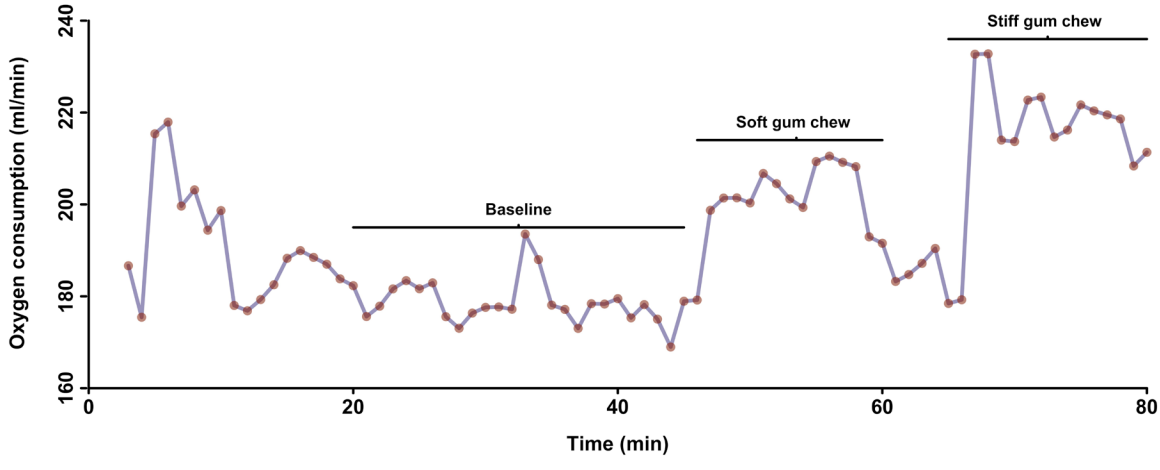

Fig. 1. Example of a typical respirometry trace. Oxygen consumption reduces to stable levels during the initial baseline acquisition phase (circa 45 min). There is an initial spike due to the subject acclimatizing to breathing in the mask, followed by a drop to a baseline resting level, and oxygen consumption shows a clear increase when the subject is chewing the gum bases, and these increases are proportional to the gum stiffness.

Table 1. Participant attributes. The physical attributes of participants. F, female; M, male.

Subject	Sex	Height (cm)	Weight (kg)
S01	F	158.0	51.0
S02	M	174.5	84.1
S03	F	164.8	57.0
S04	F	177.5	63.3
S05	F	166.0	56.6
S06	F	174.8	63.4
S07	F	170.8	62.1
S08	M	168.7	80.3
S09	F	172.5	58.2
S10	F	168.9	69.1
S11	M	175.2	69.0
S12	F	165.0	87.3
S13	F	164.8	54.0
S14	M	176.2	74.4
S15	M	182.5	107.2
S16	F	159.2	54.5
S17	F	167.2	66.1
S18	M	183.1	72.7
S19	F	183.0	78.2
S20	F	169.0	60.6
S21	F	173.1	63.5

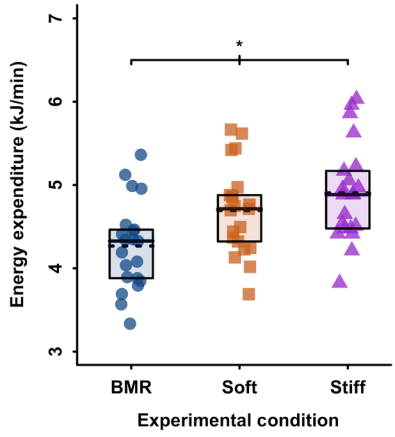

Fig. 2. Average respirometry data for BMR and both chewing conditions. Chewing has a measurable effect on the energy expenditure in humans, always demonstrating a significant increase [$F_{(2, 28)} = 290.4$, $^*P \leq 0.0001$] in energy expenditure compared to BMR (blue circles). Chewing the stiff (purple triangles) gum base induces higher energy expenditure than the same masticatory action performed on more compliant substrates (soft, orange squares). Solid lines represent medians, and dashed lines represent means; boxes represent the 25th and 75th quartiles.

$t = 8.4814$, $P \leq 0.0001$). The higher EE of stiffer gums indicates that, under our experimental conditions, it is force production rather than chewing frequency that drives energy consumption.

The metabolic equivalent of task [MET; EE (kilojoules per minute) during chewing divided by the EE (kilojoules per minute) of BMR] provides a measure of energy consumption that is comparable among individuals. We used it to assess whether the size of the masticatory musculature influences energy consumption during mastication. Linear regressions of the MET for each gum plotted against relaxed masseter thickness (Fig. 4) show no significant relationship for either gum type [softer: $F_{(1, 19)} = 2.131$, $P = 0.1607$; stiffer: $F_{(1, 19)} = 1.938$, $P = 0.1799$]. This indicates that a larger masseter muscle does not lead to disproportionately higher chewing costs on a chew-per-chew basis, but a larger masseter does contribute to higher absolute chewing costs. Therefore, masseter size is not a good predictor of the relative energetic cost of chewing.

DISCUSSION

Mechanically different substrates influence the cost of mastication

Our results are the first to demonstrate that the energy expended in human chewing is substantial and that the stiffness of the substrate has an appreciable effect on the metabolic cost of mastication. When chewing the softer gum, subjects increased their energetic expenditure by an average of 10.2% relative to their BMR, rising to 15.1% above BMR for the stiffer gum (Fig. 2). If we use the EMG mean voltage amplitudes as a proxy for mechanical power, our data show that metabolic energy change correlates with changes in the work being done by the masseter muscle.

We can contextualize these results by framing them in the context of daily chewing times and TEE. Chewing times for humans have been well investigated, and Organ *et al.* (*25*) composed a dataset of chewing times for 26 groups of adult modern humans. The lowest observed daily chew time is 7.2 min, while the maximum is more than 10 times higher at 75.7 min, with the mean value of 35.3 min/day. Generalized values of TEE for extant apes (including humans) can also be found in the literature (*26*). It is therefore possible to use our respirometry data in combination with published chewing times and values of TEE to predict the percentage of daily EE that an average human male (TEE = 11,385 kJ) or female (TEE = 9163 kJ) would consume chewing either of our substrates for a whole day of feeding (Fig. 5). Although masticating any of our experimental substrates does elicit a notably higher energetic rate compared to BMR, the daily cost of chewing, for even the longest chewing times reported in humans, is relatively small, well below 1% of the TEE.

With tools, food processing, cooking, and agriculture, modern humans are liberated from lengthy bouts of daily mastication. These differences can be seen when comparisons are made to the great apes that chew considerably more than humans, ranging from 4.5 hours in *Pan* to 6.6 hours in *Pongo* (*27*). Such chewing regimes are likely more representative of how much mastication an earlier hominin species may have needed to perform. Substituting ape chewing times into our calculations for % TEE of mastication allows us to predict how much of TEE would be required for humans with ape-like mastication regimes. Understandably, these estimations should be treated with some caution as real-world nonhuman great ape masticatory energetics is likely nonsynonymous with those of modern humans, but in the absence of any comparative data on chewing energetics, they offer a best guess to the energetic regimes

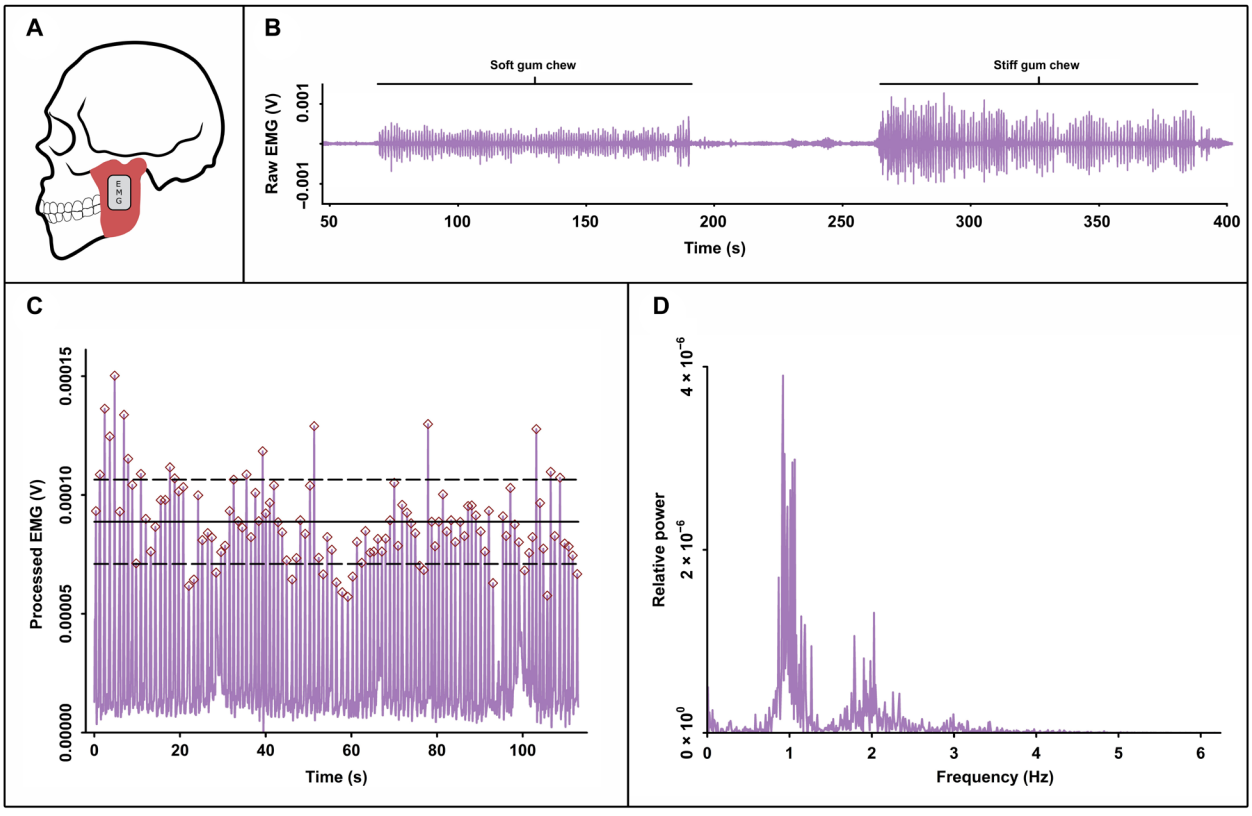

Fig. 3. Example of EMG data processing. EMG signal was recorded from surface electrodes placed on one of the masseter muscles (shown in red) (**A**). During chews of both the soft and stiff gums, electrical activity was recorded, and visual assessment of these data clearly demonstrates differences in muscle activation between the two chewing conditions (**B**). To quantify these visual differences, the raw data were split by chewing bout and then filtered, and the peak amplitudes were identified (**C**). This allowed the calculation of a mean (solid line) and SD (dashed lines) amplitude for each gum chewed. This peak amplitude equates to the mean muscle recruitment for each chewing bout. To assess differences in chewing frequency, a Fourier transformation of the data was performed, and this reveals the clear preferred chewing frequency (**D**).

of extinct hominins. Given this assumption, ape-like chewing times represent an appreciable rise in the daily EE dedicated to mastication, up to 2.6% in the case of the stiffer gum base (Table 2). We suggest that before the onset of cooking and sophisticated extra-oral processing, the mastication of food could have required a much larger proportion of a daily energy budget.

It must, however, be remembered that the food proxies used in this experiment provide a somewhat artificial chewing experience when compared to most actual foods and do not incorporate the fracture properties or mechanical behavior of an actual diet. Even the stiffest gum used in this experiment, which had a measured stiffness of 209 kPa, was less than 10% the stiffness of commonly consumed plant tissues such as apple pulp (3.41 MPa) (*28*) and raw carrot (4.57 MPa) (*29*). There is currently no data to help predict what the relationship between chewing energetics and food mechanical properties may look like, and this may be extremely difficult to obtain because chewing and eating real food will activate the digestive system, and disentangling the metabolic costs due to the chewing process alone would be challenging. However, given that, here, in the first quantitative measurements of chewing energetics in humans, we demonstrate a 5% increase in masticatory EE between two gum bases that varied in stiffness by only 120 kPa, it seems probable that even chewing relatively easy-to-process foods could induce much higher energetic costs. Future investigations would be needed to establish how the suite of dietary mechanical metrics contribute to masticatory energetics, but given the foundational results presented here, it seems likely that the real-world cost of chewing in the ancestors of modern humans is far from negligible.

Implications for human evolution

Our results indicate that the increase in EE while chewing is driven by the mechanical challenge of the food being consumed rather than the frequency of chewing. Plant foods consumed by animals, with a few exceptions such as fruit, are generally adapted to avoid being eaten (*30*). Biological structures and materials, including those eaten by primates, are often natural composites, hierarchical in nature, composed of two to three structural units that endow a material with extrinsic toughening mechanisms, making them energetically expensive to break down (*31*). In addition, plants often protect valuable nutrients with lignified structures requiring significant masticatory effort to break (*30*, *32*, *33*). Ancestral hominins likely consumed biological tissues that maintained their internal structural elements.

On the basis of our results, a hominin using its oral apparatus to consume relatively stiff foods, chew for chew, will consume more energy, therefore eliciting a stronger selective response for energy

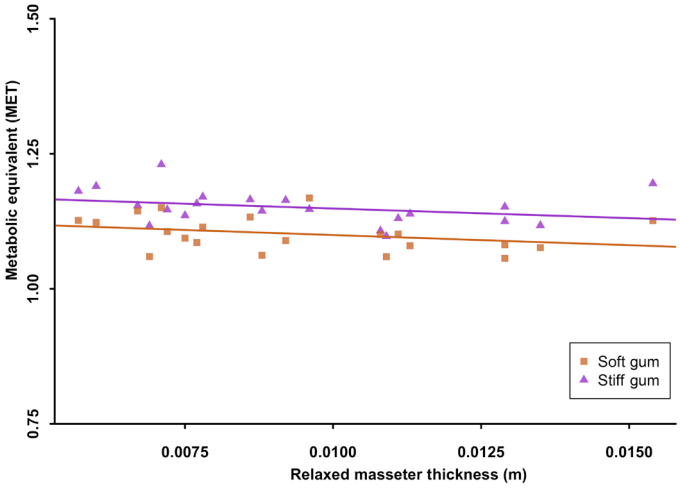

Fig. 4. Comparing normalized masseter sizes with MET while chewing on both the soft and stiff gums. Linear regressions indicate no significant relationship between masseter size and MET for both the soft [$F_{(1, 19)} = 2.131$, $P = 0.1607$] and stiff [$F_{(1, 19)} = 1.938$, $P = 0.1799$] gum bases. Therefore, masseter size is not a good predictor of the relative energetic cost of chewing.

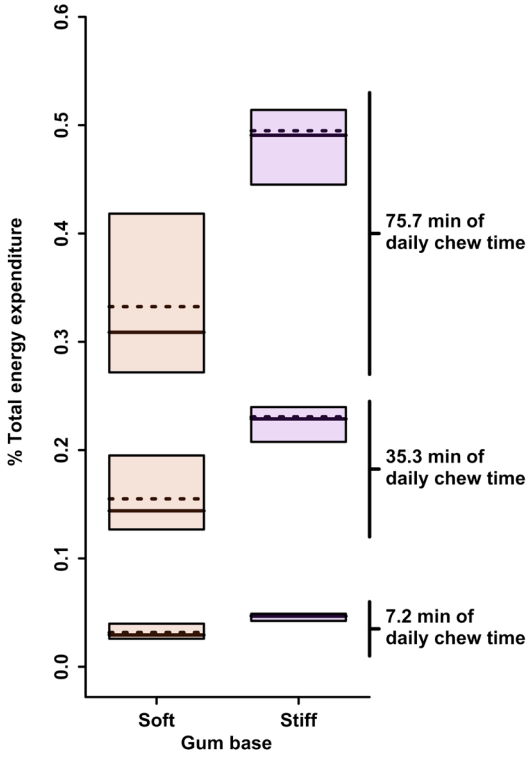

Fig. 5. The derived daily cost of chewing each gum based on our respirometry data. Combining chewing times and TEE values from the literature with our respirometry data allows us to derive the daily chewing costs of our two gums. Note that for both substrates and both sexes, the daily energetic cost of chewing is very low. Solid lines represent medians, and dashed lines represent means; boxes represent the 25th and 75th quartiles.

optimization of the masticatory system. This optimization is likely to manifest in two main ways: Either the musculoskeletal system used for chewing can be optimized for efficient use (*16*, *19*, *34*, *35*), and/or tooth morphology can be optimized for increased effectiveness in the breakdown of foods (*9*, *36*, *37*). Both strategies would improve chewing efficiency by reducing the work needed to process food and therefore increasing the net gain from dietary items. In this way, it is possible that the need to energetically optimize the masticatory system may have played a role in the evolution of the derived robust morphology of australopiths and early *Homo*.

However, modern humans and our more recent ancestors in the genus *Homo* have, over the past ~1 to 2 million years, routinely improved tool-assisted food processing technology, adopted habitual fire use, and, within the past circa 10,000 years, developed agriculture. These practices have led to improvements of the availability and quality of foods within their diets (*38*–*40*). Many modern foods consumed today are the end products of thousands of years of artificial selection, increasing the ease at which they are consumed. Hence, these foods require minimal masticatory action when compared to the ancestral human diet (*41*, *42*), as illustrated by the low estimates from our data of the percentage of TEE dedicated to chewing. However, foods consumed by foraging peoples and earlier members of *Homo* would have almost certainly required a greater masticatory effort to orally process (*19*, *35*). Currently, we cannot speak to how much major evolutionary milestones such as advanced tools, fire use, and agriculture have reduced the energetic demands of mastication and whether such advances have completely liberated the human feeding system from energetic selection pressures, although a simple thought experiment can illustrate how understanding the energetic cost of chewing may provide insights into dietary changes throughout human evolution.

During the Pliocene/Pleistocene, hominins are thought to have adopted more meat into their diets (*43*, *44*). This dietary change has been associated with tool use and cooking, allowing our early ancestors to liberate themselves from lengthy chewing bouts by performing some preingestive processing (*39*). When consuming raw meat, extant great apes invest in lengthy chewing times. Some have suggested this as evidence against substantial meat consumption in early hominins, as lengthy masticatory bouts would be temporarily prohibitive to daily foraging (*44*, *45*). Our work here can add an energetic element to these arguments. Chimpanzees consume raw meat at an estimated 400 kcal/hour and orangutans at a substantially slower rate of 185 kcal/hour (*44*, *45*). If we assume that chewing meat exerts a similar energic cost to our stiffer gum, then chewing meat would cost 9.2 kcal/hour. This would result in a 2.3% reduction in energy gained from meat per hour for chimpanzees and a 5.0% decrease in the case of the orangutan. These numbers are speculative, and given the high mechanical challenge provided by the connecting tissues of actual meat, these estimates are also likely conservative. What this thought experiment does, however, is demonstrate that mastication for prolonged time periods in hominoids may represent an energy sink, and technologies used to tenderize meat would not only reduce chewing times but also increase the energetic returns of food. Much more comparative and experimental data are needed to facilitate a clearer understanding of the role of energetics in human mastication. While much research has focused on how food processing technologies (tools, fire, and agriculture) may have released early humans from the temporal and physical binds of oral food processing (*39*, *46*), our data suggest that there is also likely a significant energetic component to this dynamic.

Table 2. Human chewing energetics with ape-like chewing durations. If humans chewed for similar lengths of time as other great apes, this increased time chewing could see daily masticatory energetics taking up considerably more of the daily energy budget (% TEE).

Chewing time	Sex	Daily chew EE soft gum (kJ/day)	% TEE soft gum	Daily chew EE stiff gum (kJ/day)	% TEE stiff gum
0.35 hours (human-like)	M	15.4	0.1	25.1	0.2
	F	14.9	0.2	21.5	0.2
4.5 hours (*Pan*-like)	M	117.7	1.0	192.4	1.7
	F	114.2	1.2	164.5	1.8
6.5 hours (*Gorilla*-like)	M	170.1	1.5	278.1	2.4
	F	165.1	1.8	237.7	2.6
6.6 hours (*Pongo*-like)	M	172.6	1.5	282.2	2.5
	F	167.5	1.8	241.3	2.6

MATERIALS AND METHODS

Subjects

Twenty-one human subjects were recruited: 15 females and 6 males aged between 18 and 45 years. Each volunteer first filled out a self-assessment of their medical and dental health and was asked to proceed only if they identified no issues. Potential participants were asked not to proceed if they had major dental surgery within the past 12 months. The study was approved by the Medical Ethical Review Committee of Maastricht University (METC number 2017-0182), and each subject gave written informed consent to take part in the study.

Each subject had some basic scaling metrics taken. Height and weight were measured to the nearest 0.1 cm and 0.1 kg, respectively. In addition, the thickness of the masseter muscle, when tensed and relaxed, was measured by placing a handheld ultrasound wand (Terason T3000, Teratec Corporation, USA), connected to an ultrasound transducer (Terason 8MC4, Teratec Corporation, USA), over the center of the muscle. An average of three measurements of muscle thickness was taken in both tensed and relaxed states. The masseter was chosen as the muscle of interest due to its ease of measurement and central role on force production during mastication.

Selection of chewing substrate

We chose the substrates for these experiments to avoid the confounding influence of chewing real food items and to provide a meaningful test of the role of different stiffness on the cost of chewing and associated masseter muscle activation. Digestion in humans is energetically expensive, and physiological cues can kick-start digestive actions that consume large amounts of energy. Such EE of digestion may swamp any energetic signal produced by the musculature of mastication. Therefore, when measuring the energetics of mastication, it was essential to limit the actions of the digestive system to ensure accurate data collection. We asked the participants to fast overnight before the experiment, so they were in a post-absorptive state for measurements of BMR. From midnight before the morning of the experiment, they could take water or medication as needed but were instructed not to consume any foods or beverages other than water. Their compliance was confirmed immediately before the start of the experiment.

In addition, real food could not be used as a chewing substrate during the experiments as the sensory feedback of either taste or smell could initiate digestive action, and the mastication signal would be swamped. There may also be elements of prelearning the amount of effort required to chew specific food items, which would confound results. Therefore, food had to be replaced by an alternative chewing substrate that was both odorless and flavorless. We chose to use commercial gum bases as a chewing substrate, as these gums are readily available and produced of a reliable material suitable for use in human experiments with consistent and alterable mechanical properties. Gum bases are the base element of chewing gum and constitute a non-nutritive, flavorless, and tasteless material that provides the texture and masticatory properties of chewing gum. Gum bases are not a substitute for food as they likely behave rather differently in the mouth. Such chewing substrates, once chewed and heated within the oral cavity, form a variably shaped object composed of an extremely ductile material with low stiffness and high extensibility. Therefore, within the scope of this experiment, the gum bases simply provide physical presence between occluding teeth that had variation in compressive stiffness.

The two gum bases used in this study were produced by Cafosa (subsidiary of Mars Corporation, Barcelona, Spain). The soft gum was Suncom-T, which is a gum base designed for softer chewing gums such as bubble gum. It has a density of 1.10 g/cm^3 and a measured elastic modulus of 89 kPa (SD 47 kPa). The stiffer gum was Solsona-T, a gum base used for regular chewing gums, which has a density of 1.15 g/cm^3 and a measured elastic modulus of 209 kPa (SD 101 kPa). Elastic modulus was measured using a portable material testing machine (FLS-1, Lucas Scientific, Panama). For each gum base type, a hemispherical indenter of 3.175 mm radius was pressed into a gum that had been chewed for 2 min, with indentation occurring to ~10% of gum thickness. Ten measurements were made, and the elastic modulus (here termed "stiffness") was calculated following van Casteren *et al.* (*47*), who also give details of these tests. The gum bases differed significantly in stiffness (t test, $P = 0.003$). For ingestion by each subject in the study, a 2-cm square was cut from prerolled sheets of gum base provided by the manufacturer. This gave a per-tablet volumetric measurement of ~3 cm^3 for the soft gum base and ~2.75 cm^3 for the stiff gum base.

Metabolic measurements

Metabolic measurements were made using indirect calorimetry. Oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) were measured continuously using a ventilated hood system (Omnical, Maastricht University, Maastricht, Netherlands), where a subject's

whole head is encapsulated in a Perspex hood, and respiratory gases are measured from samples of air that flows through the hood. The hood is ventilated with a continuous flow of fresh air at a rate of approximately 80 liters/min. The system measures total airflow passing the participant's face and determines gas concentrations of O_2 and CO_2 for inspired and expired air with a representative resolution of ≤0.001% (open-circuit respirometry—diluted flow) (*48*). Flow of sample is typically 1 to 2% of total flow through the hood, allowing optimal sample flow for drying and pressure regulation of samples through the analyzer. All gas samples are dried by a first-stage condensation dryer and then dried in a chain of second-stage membrane dryers (Perma Pure) with its outer hull continuously flushed with pure and dry nitrogen. The gas analysis is done with ABB (Hartmann & Braun) and Servomex 19″-rack analyzers. The analyzers were calibrated automatically every 15 to 30 min using nitrogen gas to set the zero and a mixture of ~18% O_2 and 0.8% CO_2 for calibration. The Omnical is validated weekly using a methanol burn. The current Omnical system is an updated version of the previously described system [for more detail, see (*49*)]. The Omnical with its full capture of exhaled gasses and its intermittent calibrations has been extensively validated and has shown high reproducibility, accuracy, and ease of use (*50*–*53*). Energy expenditure was then calculated from $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ data using the formula of Weir (*54*).

Each subject followed a set of experimental procedures. First, BMR was measured. After an overnight fast, the subject reclined and rested on a bed for 45 min under thermoneutral conditions, reducing movements to an absolute minimum while gas exchange was monitored. Immediately following this initial BMR measurement, the first chewing experiment was undertaken. Here, the subject was given a tablet of gum base and told to chew it continuously for 15 min, allowing a steady-state measurement of EE to be reached for that given substrate. Following this first chew, the subject was instructed to rest for 5 min before the second chew was undertaken to limit the effects of fatigue. After the rest period, the subject was then asked to chew the second chewing substrate for a further 15 min. The order in which each subject chewed the two chewing substrates (soft or stiff) was randomized for each subject within the study.

BMR was calculated by averaging $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ data over the last 25 min of the 45-min period, where the first 15 min was not used for analysis to allow the subject to come to a complete rest. For each 15-min chewing period, the first 3 min was eliminated, and EE was calculated by averaging $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ data over the last 12 min.

EMG measurements

EMG measurements were not taken simultaneously with energetics to control for any influence of the attachment, weight, and feel of an EMG surface electrode placed over the masseter on the chewing behavior of an experimental subject. The experimental protocol was identical in both cases, which enabled us to directly correlate EMG activity with measurement of the metabolic cost of chewing. Here, we used wireless EMG electrodes (Tringo, Delsys Incorporated, USA) to measure electrical activity at a sample rate of 2000 Hz of the masseter when chewing different chewing substrates.

Following completion of the energetic experiments (approximately 5 min) and using the same protocol as that previously, each subject was equipped with EMG sensors that were adhered to the skin, via adhesive tape, of the thickest part of a tensed masseter as derived from visual surface palpation (Fig. 3A). The subject was then given a gum base and told to chew for 2 min while continuous measurements of masseter electrical activity were made. After this initial chewing time, the subject was given a 1-min rest period before repeating the process with the second chewing substrate. Once again, the order in which substrates (soft and stiff) were chewed was randomized for each subject. From these data, the frequency and maximum amplitude of masseter activation were calculated. A total of $n = 20$ EMG measurements were made as an equipment malfunction voided one subject's dataset.

The raw EMG data (Fig. 3B) were processed digitally by rectification followed by low-pass filtration at 5 Hz using a two-pass four-element Butterworth filter implemented in MATLAB (www.mathworks.com) to extract the amplitude envelope (*55*). Each peak of EMG activity represented the activation of the masseter muscle during a chew cycle. A power spectrum was generated via Fourier transformation, and each trial had an obvious preferred frequency, which was used for further analysis (Fig. 3D). The individual peaks from the amplitude data were extracted using the MATLAB findpeaks function with manual inspection to check that the correct locations were found. The mean of the peak values was then calculated to provide a measure of the overall activation of the masseter during chewing (Fig. 3C).

Statistical analysis

All statistical tests were run in R (version 4.1.3; R Core Team, 2022). It is well documented that EE may be affected by external confounding variables. Therefore, these confounding variables were built into the repeated-measures ANOVA to predict their influence on our results. The covariables considered were the sex of the participant ("sex"), the weight of the participant ("weight"), age of the participant ("age") the day on which the subject performed the experiment ("day," recorded as 1 to 8), the hood airflow system that the subject used ("bed," recorded as 1 or 2), the order that the subject chewed the gums ("order," 1 for soft gum first), and the time of day that the subject performed the experiment ("time," either "early" or "late") (see Supplementary information S1).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://science.org/doi/10.1126/sciadv.abn8351

View/request a protocol for this paper from *Bio-protocol*.

REFERENCES AND NOTES

1. A. G. S. Lumsden, J. W. Osborn, The evolution of chewing: A dentist's view of palaeontology. *J. Dent.* **5**, 269–287 (1977).
2. J. F. Prinz, P. W. Lucas, An optimization model for mastication and swallowing in mammals. *Proc. Biol. Sci.* **264**, 1715–1721 (1997).
3. K. K. Smith, The evolution of the mammalian pharynx. *Zool. J. Linn. Soc.* **104**, 313–349 (1992).
4. C. F. Ross, A. Eckhardt, A. Herrel, W. L. Hylander, K. A. Metzger, V. Schaerlaeken, R. L. Washington, S. H. Williams, Modulation of intra-oral processing in mammals and lepidosaurs. *Integr. Comp. Biol.* **47**, 118–136 (2007).
5. N. Rybczynski, R. R. Reisz, Earliest evidence for efficient oral processing in a terrestrial herbivore. *Nature* **411**, 684–687 (2001).
6. L. Day, J. Gomez, S. K. Øiseth, M. J. Gidley, B. A. Williams, Faster fermentation of cooked carrot cell clusters compared to cell wall fragments in vitro by porcine feces. *J. Agric. Food Chem.* **60**, 3282–3290 (2012).
7. M. Clauss, P. Steuer, K. Erlinghagen-Lückerath, J. Kaandorp, J. Fritz, K. H. Südekum, J. Hummel, Faecal particle size: Digestive physiology meets herbivore diversity. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **179**, 182–191 (2015).
8. S. Coiner-Collier, R. S. Scott, J. Chalk, S. M. Cheyne, P. J. Constantino, N. J. Dominy, A. A. Elgart, H. Glowacka, L. C. Loyola, K. Ossi-Lupo, M. Raguet-Schofield, M. Talebi,

E. A. Sala, P. Sieradzy, A. B. Taylor, C. J. Vinyard, B. W. Wright, N. Yamashita, P. W. Lucas, E. R. Vogel, Primate dietary ecology in the context of food mechanical properties. *J. Hum. Evol.* **98**, 103–118 (2016).
9. P. W. Lucas, *Dental Functional Morphology: How Teeth Work* (Cambridge Univ. Press, 2004).
10. M. F. Laird, E. R. Vogel, H. Pontzer, Chewing efficiency and occlusal functional morphology in modern humans. *J. Hum. Evol.* **93**, 1–11 (2016).
11. J. Iriarte-Díaz, D. A. Reed, C. F. Ross, Sources of variance in temporal and spatial aspects of jaw kinematics in two species of primates feeding on foods of different properties. *Integr. Comp. Biol.* **51**, 307–319 (2011).
12. O. Pearson, Longevity of the short-tailed shrew. *Am. Midl. Nat.* **34**, 531–546 (1945).
13. F. P. Cuozzo, M. L. Sauther, Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): A function of feeding ecology, dental structure, and individual life history. *J. Hum. Evol.* **51**, 490–505 (2006).
14. M. Logan, G. D. Sanson, The effect of tooth wear on the feeding behaviour of free-ranging koalas (*Phascolarctos cinereus*, Goldfuss). *J. Zool.* **256**, 63–69 (2002).
15. A. L. Smith, S. Benazzi, J. A. Ledogar, K. Tamvada, L. C. Pryor Smith, G. W. Weber, M. A. Spencer, P. W. Lucas, S. Michael, A. Shekeban, K. Al-Fadhalah, A. S. Almusallam, P. C. Dechow, I. R. Grosse, C. F. Ross, R. H. Madden, B. G. Richmond, B. W. Wright, Q. Wang, C. Byron, D. E. Slice, S. Wood, C. Dzialo, M. A. Berthaume, A. van Casteren, D. S. Strait, The feeding biomechanics and dietary ecology of *Paranthropus boisei*. *Anat. Rec.* **298**, 145–167 (2015).
16. S. Wroe, T. L. Ferrara, C. R. McHenry, D. Curnoe, U. Chamoli, The craniomandibular mechanics of being human. *Proc. Biol. Sci.* **277**, 3579–3586 (2010).
17. A. B. Taylor, E. R. Vogel, N. J. Dominy, Food material properties and mandibular load resistance abilities in large-bodied hominoids. *J. Hum. Evol.* **55**, 604–616 (2008).
18. L. C. Fitton, J. F. Shi, M. J. Fagan, P. O'Higgins, Masticatory loadings and cranial deformation in *Macaca fascicularis*: A finite element analysis sensitivity study. *J. Anat.* **221**, 55–68 (2012).
19. C. M. Eng, D. E. Lieberman, K. D. Zink, M. A. Peters, Bite force and occlusal stress production in hominin evolution. *Am. J. Phys. Anthropol.* **151**, 544–557 (2013).
20. C. F. Ross, J. Iriarte-Diaz, What does feeding system morphology tell us about feeding? *Evol. Anthropol.* **23**, 105–120 (2014).
21. L. C. Aiello, P. Wheeler, The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199–221 (1995).
22. R. S. Lacruz, C. B. Stringer, W. H. Kimbel, B. Wood, K. Harvati, P. O'Higgins, T. G. Bromage, J. L. Arsuaga, The evolutionary history of the human face. *Nat. Ecol. Evol.* **3**, 726–736 (2019).
23. H. H. Stedman, B. W. Kozyak, A. Nelson, D. M. Thesier, L. T. Su, D. W. Low, C. R. Bridges, J. B. Shrager, N. Minugh-Purvis, M. A. Mitchell, Myosin gene mutation correlates with anatomical changes in the human lineage. *Nature* **428**, 415–418 (2004).
24. S. M. Secor, Specific dynamic action: A review of the postprandial metabolic response. *J. Comp. Physiol. B* **179**, 1–56 (2009).
25. C. Organ, C. L. Nunn, Z. Machanda, R. W. Wrangham, Phylogenetic rate shifts in feeding time during the evolution of *Homo*. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 14555–14559 (2011).
26. H. Pontzer, M. H. Brown, D. A. Raichlen, H. Dunsworth, B. Hare, K. Walker, A. Luke, L. R. Dugas, R. Durazo-Arvizu, D. Schoeller, J. Plange-Rhule, P. Bovet, T. E. Forrester, E. V. Lambert, M. E. Thompson, R. W. Shumaker, S. R. Ross, Metabolic acceleration and the evolution of human brain size and life history. *Nature* **533**, 390–392 (2016).
27. C. F. Ross, R. L. Washington, A. Eckhardt, D. A. Reed, E. R. Vogel, N. J. Dominy, Z. P. Machanda, Ecological consequences of scaling of chew cycle duration and daily feeding time in primates. *J. Hum. Evol.* **56**, 570–585 (2009).
28. S. H. Williams, B. W. Wright, Van Den Truong, C. R. Daubert, C. J. Vinyard, Mechanical properties of foods used in experimental studies of primate masticatory function. *Am. J. Primatol.* **67**, 329–346 (2005).
29. K. R. Agrawal, P. W. Lucas, The mechanics of the first bite. *Proc. Biol. Sci.* **270**, 1277–1282 (2003).
30. P. W. Lucas, I. M. Turner, N. J. Dominy, N. Yamashita, Mechanical defences to herbivory. *Ann. Bot.* **86**, 913–920 (2000).
31. E. Munch, M. E. Launey, D. H. Alsem, E. Saiz, A. P. Tomsia, R. O. Ritchie, Tough, bio-inspired hybrid materials. *Science* **322**, 1516–1520 (2008).
32. A. van Casteren, E. Wright, K. Kupczik, M. M. Robbins, Unexpected hard-object feeding in Western lowland gorillas. *Am. J. Phys. Anthropol.* **170**, 433–438 (2019).
33. A. van Casteren, V. M. Oelze, S. Angedakin, A. K. Kalan, M. Kambi, C. Boesch, H. S. Kühl, K. E. Langergraber, A. K. Piel, F. A. Stewart, K. Kupczik, Food mechanical properties and isotopic signatures in forest versus savannah dwelling eastern chimpanzees. *Commun. Biol.* **1**, 109 (2018).
34. J. A. Ledogar, P. C. Dechow, Q. Wang, P. H. Gharpure, A. D. Gordon, K. L. Baab, A. L. Smith, G. W. Weber, I. R. Grosse, C. F. Ross, B. G. Richmond, B. W. Wright, C. Byron, S. Wroe, D. S. Strait, Human feeding biomechanics: Performance, variation, and functional constraints. *PeerJ* **4**, e2242 (2016).
35. R. M. Godinho, L. C. Fitton, V. Toro-Ibacache, C. B. Stringer, R. S. Lacruz, T. G. Bromage, P. O'Higgins, The biting performance of *Homo sapiens* and *Homo heidelbergensis*. *J. Hum. Evol.* **118**, 56–71 (2018).
36. P. W. Lucas, P. J. Constantino, B. Wood, B. Lawn, Dental enamel as a dietary indicator in mammals. *Bioessays* **30**, 374–385 (2008).
37. P. J. Constantino, J. J. W. Lee, D. Morris, P. W. Lucas, A. Hartstone-Rose, W.-K. Lee, N. J. Dominy, A. Cunningham, M. Wagner, B. R. Lawn, Adaptation to hard-object feeding in sea otters and hominins. *J. Hum. Evol.* **61**, 89–96 (2011).
38. R. G. Allaby, C. Stevens, L. Lucas, O. Maeda, D. Q. Fuller, Geographic mosaics and changing rates of cereal domestication. *Philos. Trans. R. Soc. B Biol. Sci.* **372**, 20160429 (2017).
39. K. D. Zink, D. E. Lieberman, Impact of meat and Lower Palaeolithic food processing techniques on chewing in humans. *Nature* **531**, 500–503 (2016).
40. R. Wrangham, R. Carmody, Human adaptation to the control of fire. *Evol. Anthropol.* **19**, 187–199 (2010).
41. C. G. Forde, C. Leong, E. Chia-Ming, K. McCrickerd, Fast or slow-foods? Describing natural variations in oral processing characteristics across a wide range of Asian foods. *Food Funct.* **8**, 595–606 (2017).
42. R. S. Corruccini, R. M. Beecher, Occlusal variation related to soft diet in a nonhuman primate. *Science* **218**, 74–76 (1982).
43. E. P. Hoberg, N. L. Alkire, A. De Queiroz, A. Jones, Out of Africa: Origins of the Taenia tapeworms in humans. *Proc. Biol. Sci.* **268**, 781–787 (2001).
44. R. Wrangham, N. Lou Conklin-Brittain, Cooking as a biological trait. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **136**, 35–46 (2003).
45. M. E. Hardus, A. R. Lameira, A. Zulfa, S. S. U. Atmoko, H. Vries, S. A. Wich, Behavioral, ecological, and evolutionary aspects of meat-eating by Sumatran orangutans (*Pongo abelii*). *Int. J. Primatol.* **33**, 287–304 (2012).
46. R. W. Wrangham, *Catching Fire: How Cooking Made Us Human* (Basic Books, 2009).
47. A. van Casteren, V. Venkataraman, A. R. Ennos, P. W. Lucas, Novel developments in field mechanics. *J. Hum. Evol.* **98**, 5–17 (2016).
48. P. F. M. Schoffelen, G. Plasqui, Classical experiments in whole-body metabolism: Open-circuit respirometry-diluted flow chamber, hood, or facemask systems. *Eur. J. Appl. Physiol.* **118**, 33–49 (2018).
49. P. F. M. Schoffelen, K. R. Westerterp, W. H. M. Saris, F. Ten Hoor, A dual-respiration chamber system with automated calibration. *J. Appl. Physiol.* **83**, 2064–2072 (1997).
50. J. M. A. Alcantara, J. E. Galgani, L. Jurado-Fasoli, M. Dote-Montero, E. Merchan-Ramirez, E. Ravussin, J. R. Ruiz, G. Sanchez-Delgado, Validity of four commercially available metabolic carts for assessing resting metabolic rate and respiratory exchange ratio in non-ventilated humans. *Clin. Nutr.* **41**, 746–754 (2022).
51. S. Kaviani, D. A. Schoeller, E. Ravussin, E. L. Melanson, S. T. Henes, L. R. Dugas, R. E. Dechert, G. Mitri, P. F. M. Schoffelen, P. Gubbels, A. Tornberg, S. Garland, M. Akkermans, J. A. Cooper, Determining the accuracy and reliability of indirect calorimeters utilizing the methanol combustion technique. *Nutr. Clin. Pract.* **33**, 206–216 (2018).
52. M. P. E. Adriaens, P. F. M. Schoffelen, K. R. Westerterp, Intra-individual variation of basal metabolic rate and the influence of daily habitual physical activity before testing. *Br. J. Nutr.* **90**, 419–423 (2003).
53. P. F. M. Schoffelen, M. den Hoed, E. van Breda, G. Plasqui, Test-retest variability of VO_{2max} using total-capture indirect calorimetry reveals linear relationship of VO_2 and Power. *Scand. J. Med. Sci. Sport.* **29**, 213–222 (2019).
54. J. B. De B. Weir, New methods for calculating metabolic rate with special reference to protein metabolism. *J. Physiol.* **109**, 1–9 (1949).
55. D. A. Winter, *Biomechanics and Motor Control of Human Movement* (John Wiley and Sons, 1990).

Acknowledgments: We wish to extend our thanks to P. W. Lucas, whose work and discussions were central to this project's inception and for reading and commenting on early drafts of the paper. P. Lucas' deep research legacy, ideas, and connections provided the framework on which this project was based, but especially, his story, related to both A.v.C. and A.G.H., of the attempt to consume large volumes of carrots in a respirometry chamber inspired us to try to measure the costs of chewing. Thanks also to S. Gur Arieh and N. Stephens whose discussion over chewing times at the lunch table inspired us to revisit P. Lucas' hypotheses. **Funding:** This work was supported by the European Research Council (ERC) [grant number STG–677576 ("HARVEST")], Max Planck Weizmann Center for Integrative Archaeology and Anthropology (funded by the Max Planck Society), and Biotechnology and Biosciences Research Council BBSRC BB/G011338/1 and BB/I021116/1. **Author contributions:** Conceptualization: A.v.C., A.G.H., and K.K. Methodology: A.v.C., A.G.H., J.R.C., W.I.S., and G.P. Investigation: A.v.C., A.G.H., J.R.C., and W.I.S. Data analysis: A.v.C., W.I.S., G.P., and A.G.H. Writing—original draft: A.v.C. and A.G.H. Writing—review and editing: A.v.C., A.G.H., J.R.C., W.I.S., G.P., and K.K. **Competing interests:** The authors declare that they have no competing influences. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.

Submitted 24 December 2021
Accepted 1 July 2022
Published 17 August 2022
10.1126/sciadv.abn8351

ScienceAdvances

The cost of chewing: The energetics and evolutionary significance of mastication in humans

Adam van CasterenJonathan R. CoddKornelius KupczikGuy PlasquiWilliam I. SellersAmanda G. Henry

Sci. Adv., 8 (33), eabn8351. • DOI: 10.1126/sciadv.abn8351

Science Advances (ISSN) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science Advances* is a registered trademark of AAAS.