Author for correspondence:
David S. Strait
e-mail: dstrait@wustl.edu

[†]These authors contributed equally.

THE ROYAL SOCIETY
PUBLISHING

Mechanical compensation in the evolution of the early hominin feeding apparatus

Justin A. Ledogar[1,†], Sascha Senck[2,†], Brian A. Villmoare[3,†], Amanda L. Smith[4], Gerhard W. Weber[5,6], Brian G. Richmond[7], Paul C. Dechow[8], Callum F. Ross[9], Ian R. Grosse[10], Barth W. Wright[11], Qian Wang[8], Craig Byron[12], Stefano Benazzi[13], Kristian J. Carlson[14,15], Keely B. Carlson[16], Leslie C. Pryor McIntosh[17], Adam van Casteren[18] and David S. Strait[19,20]

[1]Department of Health Sciences, East Tennessee State University, Johnson City, TN 37614, USA
[2]Research Group Computed Tomography, University of Applied Sciences Upper Austria, 4600 Wels, Austria
[3]Department of Anthropology, University of Nevada, Las Vegas, NV 89154, USA
[4]Department of Anatomy, Pacific Northwest University of Health Sciences, Yakima, WA 98901, USA
[5]Department of Evolutionary Anthropology and [6]Human Evolution and Archaeological Sciences (HEAS), University of Vienna, 1030 Vienna, Austria
[7]Unaffiliated
[8]Department of Biomedical Sciences, Texas A&M University College of Dentistry, Dallas, TX 75246, USA
[9]Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA
[10]Department of Mechanical and Industrial Engineering, University of Massachusetts, Amherst, MA 01003, USA
[11]Department of Surgery, University of Kansas Medical Center, Kansas City, KS 66106, USA
[12]Department of Biology, Mercer University, Macon, GA 31207, USA
[13]Department of Cultural Heritage, University of Bologna, Ravenna 48121, Italy
[14]Department of Integrative Anatomical Sciences, Keck School of Medicine, University of Southern California, Los Angeles, CA 90033, USA
[15]Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg 2050, South Africa
[16]Department of Anthropology, Texas A&M University, College Station, TX 77843, USA
[17]Department of Bio-Medical Sciences, Philadelphia College of Osteopathic Medicine South Georgia, Moultrie, GA 31768, USA
[18]School of Biological Sciences, University of Manchester, Oxford Road, Manchester, UK
[19]Department of Anthropology, Washington University in St. Louis, St. Louis, MO 63103, USA
[20]Palaeo-Research Institute, University of Johannesburg, Auckland Park, Johannesburg, Gauteng, South Africa

(iD) BAV, 0000-0003-1012-9388; ALS, 0000-0002-8290-7348; CFR, 0000-0001-7764-761X; CB, 0000-0001-8673-9196; SB, 0000-0003-4305-6920; LCPM, 0000-0002-0509-6860; AvC, 0000-0002-2993-8874; DSS, 0000-0002-3572-1663

Australopiths, a group of hominins from the Plio-Pleistocene of Africa, are characterized by derived traits in their crania hypothesized to strengthen the facial skeleton against feeding loads and increase the efficiency of bite force production. The crania of robust australopiths are further thought to be stronger and more efficient than those of gracile australopiths. Results of prior mechanical analyses have been broadly consistent with this hypothesis, but here we show that the predictions of the hypothesis with respect to mechanical strength are not met: some gracile australopith crania are as strong as that of a robust australopith, and the strength of gracile australopith crania overlaps substantially with that of chimpanzee crania. We hypothesize that the evolution of cranial traits that increased the efficiency of bite force production in australopiths may have simultaneously weakened the face, leading to the compensatory evolution of additional traits that reinforced the facial skeleton. The evolution of facial form in early hominins can therefore be thought of as an interplay between the need to increase the efficiency of bite force production and the need to maintain the structural integrity of the face.

1. Introduction

Within early hominins, there is a clear trend towards increasingly heavily built crania that may be proportionally large or exhibit traits that may 'buttress' or

otherwise structurally reinforce the facial skeleton against the forces associated with feeding (e.g. [1,2]). Such traits in hominins include bony pillars framing the nasal cavity entrance, laterally inflated and anteriorly positioned zygomatic bones, and tall, wide, orthognathic faces. The conventional hypothesis explaining why these features evolved is that a heavily built cranium is an adaptation for consuming foods that are mechanically challenging to eat. This hypothesis rests on the biomechanical premise that such crania are structurally strong (well suited to withstand high and/or repetitive forces associated with consuming such foods) and able to efficiently generate high bite forces [1,3]. A high bite force might facilitate the fracturing of foods by inducing high stresses within them, or allow large teeth with expanded occlusal areas to process large amounts of food without a loss in occlusal pressure [4] (= bite force divided by occlusal area). Here, we present mechanical evidence that is inconsistent with key predictions of this hypothesis and propose a novel interpretation of the evolution of early hominin cranial biomechanics.

Gracile australopiths (a group of Plio-Pleistocene hominins from Africa) possess a moderately derived, varying combination of the traits described above (e.g. [1,4,5]) compared to non-human apes. Robust australopiths (a group of Pleistocene hominins from Africa that are almost certainly descended from one or more gracile species (e.g. [5–13]) exhibit the most extreme expression of these traits [1]. The conventional explanation of early hominin form and function makes the following biomechanical predictions: (i) the facial skeletons of robust australopiths are structurally stronger than those of gracile australopiths, which are in turn stronger than those of non-human apes; (ii) robust australopiths produce bite force more efficiently than gracile australopiths, which in turn produce bite force more efficiently than non-human apes; and (iii) robust australopiths, gracile australopiths and non-human apes should produce similar occlusal pressures.

Structural strength involves geometry, stress (and associated strain) and material strength. Defined simply, stress is internal force divided by area and strain is deformation measured as a change in length divided by original length. Strain can be measured experimentally in living organisms and is a reasonable proxy for stress. The strength of a given material corresponds to the stress at which it begins to yield (deform plastically). When material properties, size and applied loads are held constant, then differences in stress and strain in objects of different shape should reflect differences in structural strength, where the object exhibiting lower strains is structurally stronger. The key strains to examine are those within local strain concentrations, as these are the loci within which structural failure may occur; global metrics summarizing 'overall' strain within an entire object (e.g. average von Mises strain) do not capture specific risks to structural integrity.

The efficiency of bite force production is simply mechanical advantage (MA), namely, the ratio of the bite force at a given tooth divided by the summed forces applied by the masticatory muscles. In other words, efficiency can be expressed as a simple ratio of force outputs to force inputs. Occlusal pressure can be roughly approximated as the bite force at a given tooth divided by the occlusal area of the tooth, estimated as the product of the tooth's width and length.

Strain, MA and occlusal pressure can all be extracted from finite element analysis (FEA) (e.g. [14–17]), a physics-based modelling and analysis technique that can be used to examine how objects of complex geometry and material properties respond to load. Prior FEA [18–20] of one gracile and one robust australopith, as well as a sample of chimpanzees (the non-human ape that is the closest living relative to hominins), produced results that appeared to be consistent with the strength and efficiency predictions, above, but inconsistent with the occlusal pressure prediction. However, the predictions have yet to be evaluated against the full range of australopith morphology. Here, we show that biomechanical analysis of the *A. afarensis* cranium requires a re-interpretation of why australopith facial features evolved.

A finite element model (FEM) of fossil specimen A.L. 444-2 [12] (an adult male *A. afarensis*) was constructed (electronic supplementary material) and compared to already existing models of specimens Sts 5 (an adult female *A. africanus* [18]), MH1 (a subadult male *A. sediba* [21]) and OH 5 (an adult male *Paranthropus boisei* [20]). The former three specimens are gracile australopiths, while the last specimen is a robust australopith. The hominin models were compared to models of six chimpanzees chosen to represent extremes of chimpanzee craniofacial morphology following shape-space principal component analysis of a matrix of 709 Procrustes coordinates (digitized onto 21 specimens) to identify the individuals at the extremes of the first three principal components [19]. Insofar as morphological variation may produce biomechanical variation, this sample provides a coarse estimate of the range of mechanical variation that might be expected within a single ape species, thereby providing a comparative context for interpreting biomechanics within and between fossil hominins. All models were subjected to external forces and constraints simulating maximal bites on the third premolar and second molar. A common set of bone material properties collected from chimpanzee and gorilla crania was assigned to all models. Forces representing the muscles of mastication were scaled to remove the effects of size, meaning that all strain differences between the models are a consequence solely of differences in shape [22]. Note that in this context, 'shape' includes 'relative size'. Thus, a change in proportion in particular cranial elements (as when bony features evolve to be larger or smaller in relation to the rest of the skull) would be associated with stress and strain differences that would be detected using this scaling method.

2. Results

Strain maps of the FEMs (figure 1; electronic supplementary material, figures S5–S9) indicate that although the fossil specimens represent four different species of australopiths, they exhibit variation in the magnitude and distribution of strain that is broadly comparable to that seen within a morphologically diverse sample of chimpanzees. Strain maps summarize strain magnitudes from thousands of elements while preserving spatial information about how those strains are distributed. These maps demonstrate that chimpanzee crania differing profoundly in shape can differ markedly in strain magnitude while exhibiting similar distributions (i.e. spatial patterns) in strain [19]. Strain magnitudes in australopiths also vary (with strains generally being highest in *A. africanus*), although the magnitude of these differences is not obviously greater than that seen among chimpanzees.

Strain data extracted from the FEMs corroborate these observations (figure 2). When strains are sampled from homologous locations across the face, it is clear that von Mises
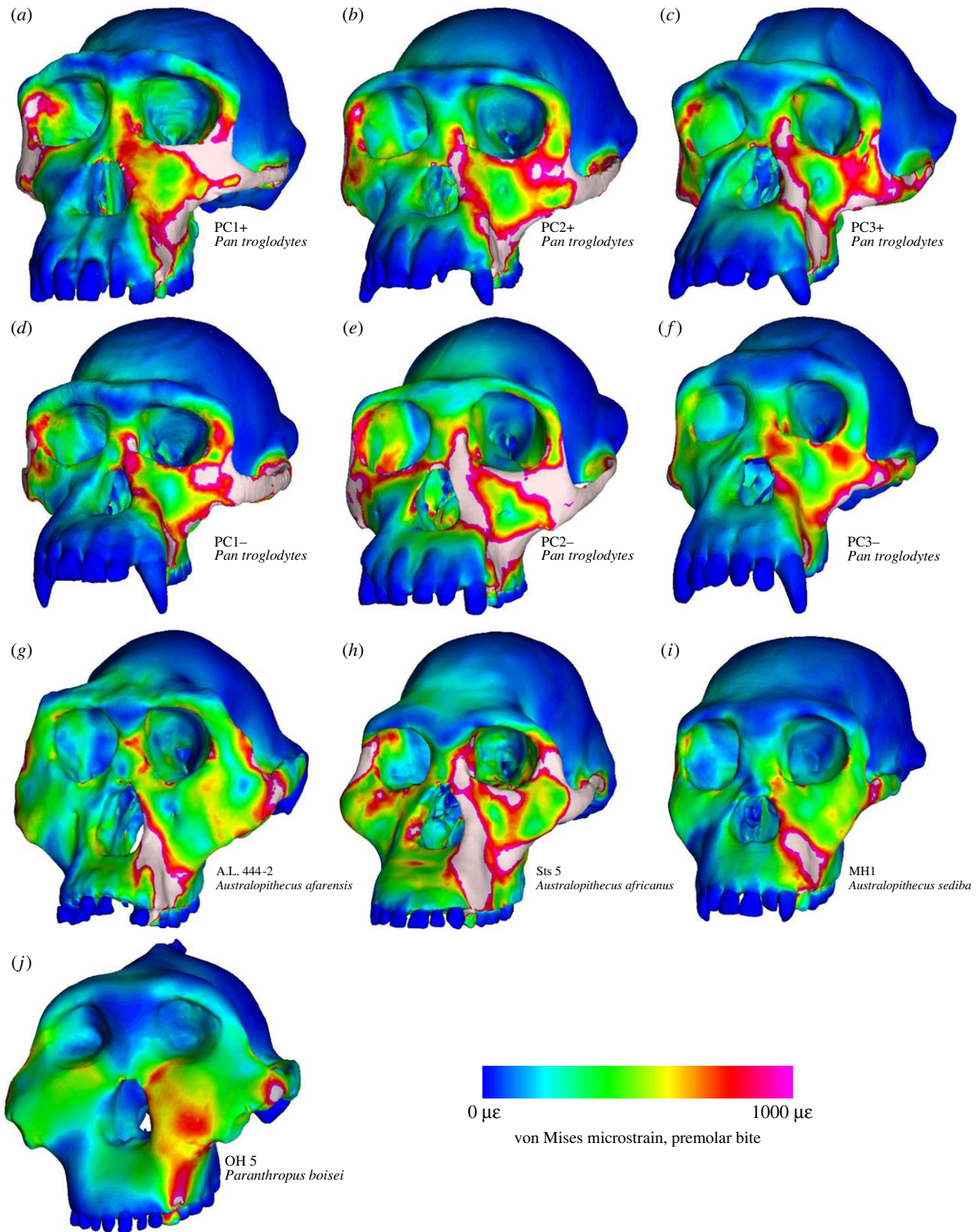
Figure 1. Colour mapping of von Mises strain in FEMs of chimpanzees (*a–f*), gracile australopiths (*g–i*) and a robust australopith (*j*) during maximal bites on the upper third premolar. Chimpanzee crania were intentionally selected to be morphologically different from each other [19] and are labelled according to whether or not they represent the extreme positive or negative ends of the range of variation along three principal components of shape. Colours correspond to strain magnitude, with white indicating strains greater than 1000 microstrain. (Online version in colour.)

strain magnitudes in *A. africanus* (Sts 5) fall within or just above the chimpanzee range, with the exception that strains are notably higher in *A. africanus* at the anterior pillar during premolar biting (figure 2*a*, location 12) and at the zygomatic root during molar biting (figure 2*a*, location 8). Strain magnitudes at several of these locations in *A. afarensis*, *A. sediba* and *P. boisei* are lower, falling near or just below the chimpanzee range. *A. afarensis* specimen A.L. 444-2 often exhibits the lowest-magnitude strains.

Finer scale sampling of strains along transects across the face reveals the extent to which strains in australopiths overlap with each other and with chimpanzees (figure 3; electronic supplementary material, figure S10). Although it is possible to find sections along the transects in which strains
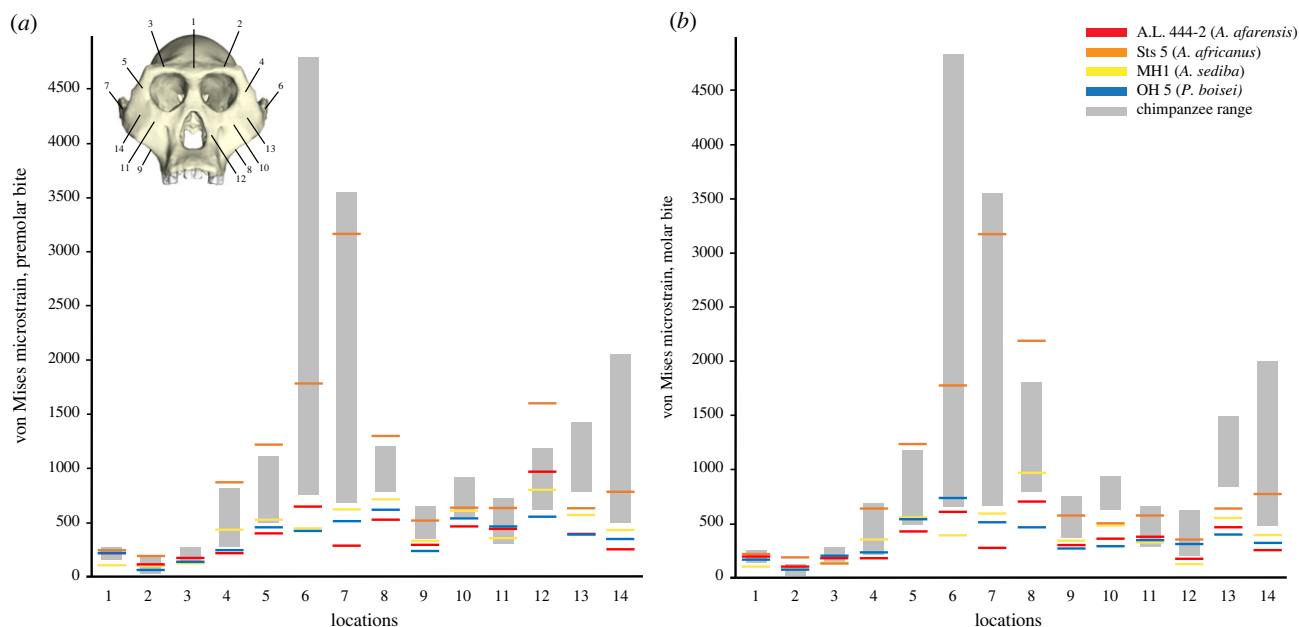
Figure 2. Plot of von Mises strain generated during maximal (*a*) premolar (P³) and (*b*) molar biting (M²) using bilaterally symmetrical muscle forces, recorded from 14 homologous locations across the craniofacial skeleton of FEMs of chimpanzees, and gracile and robust australopiths. Vertical grey bars represent the range of variation seen in chimpanzees, while horizontal coloured lines represent the values observed in individual hominin FEMs. (Online version in colour.)

in the australopiths are notably lower than those in chimpanzees, there are also transect sections in which australopiths exhibit the highest strains. Sections in which strains are lowest in robust australopiths, intermediate in gracile australopiths and highest in chimpanzees are rare and sample only small regions of the face.

If one were to focus only on regions of high strain, then it might appear that the face of the robust australopith *P. boisei* is stronger than those of the other taxa because high strain regions appear to be absent in this species. However, if one examines regions other than those typically of interest in studies of primate feeding biomechanics (e.g. [23,24]), then one finds that the face of this species is, in fact, subjected to high strains. During molar biting in the OH 5 model, an expansive area of the lateral wall of the maxilla superior to the alveolae and posterior to the zygomatic root is highly strained (electronic supplementary material, figure S12). This strain concentration occurs because the zygomatic root is both mediolaterally and anteroposteriorly offset relative to a molar bite point in this specimen, so the maxilla experiences shear and bending in both the coronal and sagittal planes. By contrast, the zygomatic root in most other models is positioned more nearly above the M² so that although the maxilla still experiences shear in coronal and sagittal planes, sagittal bending moments and associated strains associated with the bite force are reduced. Hence, strain is concentrated on the alveolar process between the inferior margin of the root and the bite point. The anteroposterior position of the root is intermediate in *A. sediba* specimen MH1, and this specimen experiences slightly elevated strains posterior to the root, as in *P. boisei.* Thus, the face of *P. boisei* does not lack high strain areas but rather those areas are atypically positioned.

The efficiency of bite force production (as measured by MA; electronic supplementary material, table S1) is broadly equivalent in all models during premolar biting, but is greatest in *P. boisei*, intermediate in *A. afarensis*, *A. africanus* and *A. sediba*, and least in *Pan troglodytes* during molar biting. By contrast,

occlusal pressures in australopiths are at or below the bottom of the chimpanzee range during both molar and premolar biting (electronic supplementary material, table S1).

3. Discussion

The results obtained here are inconsistent with the prediction that the faces of robust australopiths are stronger than those of gracile australopiths, which are in turn stronger than those of non-human apes. Rather, two gracile australopith crania (MH1 and A.L. 444-2) are roughly as strong as that of a robust australopith (OH 5), with a gracile specimen (A.L. 444-2) not infrequently being the one that exhibits the lowest strains (figures 1–3). Moreover, a different gracile australopith cranium (Sts 5) often exhibits strain magnitudes that are within or above the chimpanzee range. In addition, the dispersion of australopith strain values is often less than that of chimpanzees, even though the former data are being sampled from four species while the latter are intraspecific. One could reasonably conclude that the three specimens (A.L. 444-2, MH1, OH 5) with the most robust zygomatic bones are stronger than chimpanzees in that region of the face, but otherwise the strain data do not allow species to be sorted simply into obvious categories of cranial strength. Our earlier work [20] did not allow us to reject the cranial strength hypothesis because we had not modelled as many gracile australopith crania. The addition of A.L. 444-2 to our sample has been informative in this regard.

At present, therefore, one cannot conclude that australopith facial features evolved to make their crania structurally stronger overall. What, then, explains the evolution of such derived morphology? Our results are consistent with the hypothesis that certain aspects of australopith cranial form evolved instead to increase the efficiency of bite force production. During molar biting, gracile australopiths exhibit a higher MA than any chimpanzee, but a lower MA than the robust australopith. These species do not differ in MA
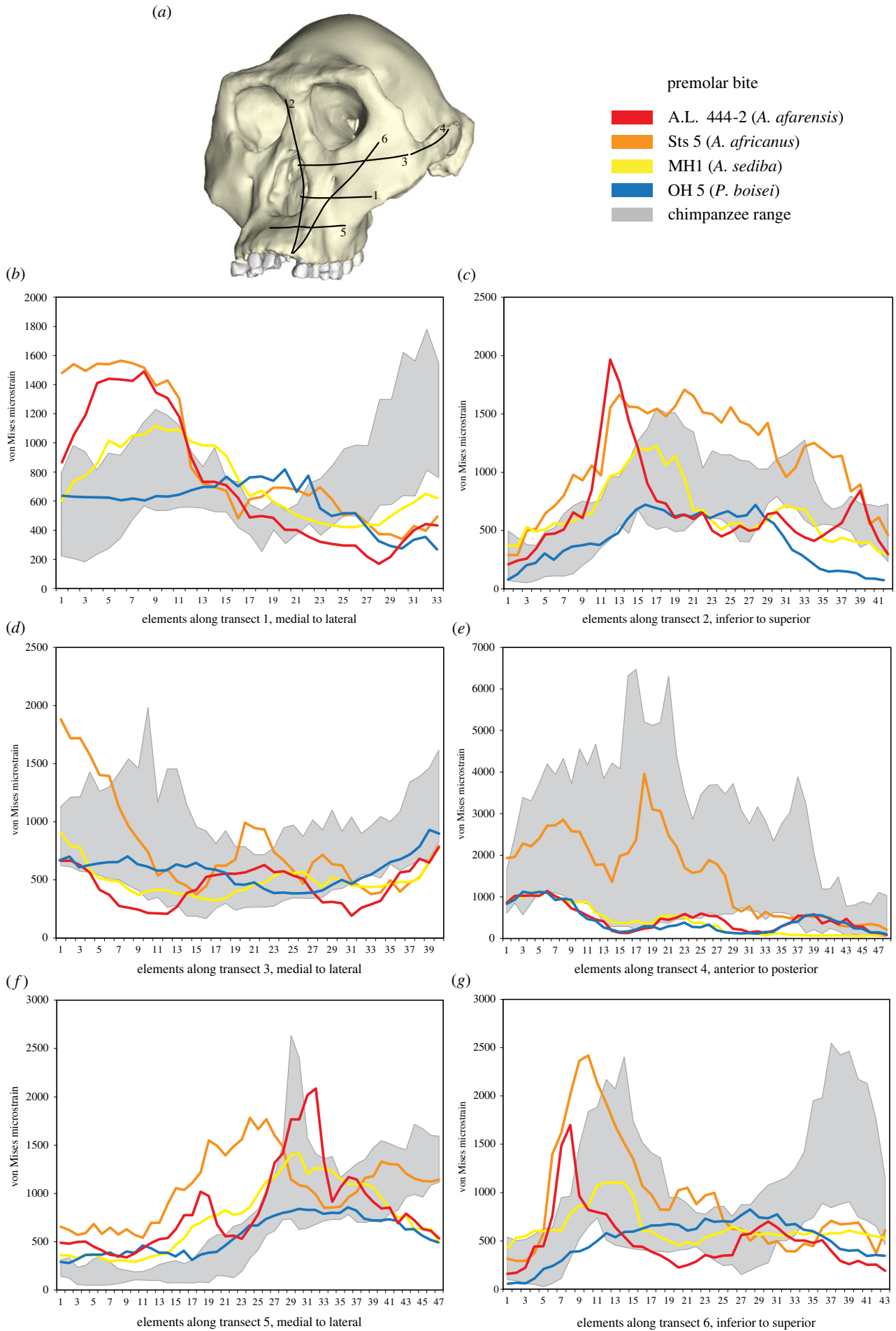
Figure 3. Line plots of von Mises strain were recorded along six transects across the face of each model during maximal P³ biting. Transects are shown (*a*) on A.L. 444-2, and line plots of the strain data in each model are shown separately by transect (*b*–*g*). Grey areas represent the range of variation seen in chimpanzees, while coloured lines represent the values observed in individual hominin FEMs. (Online version in colour.)

during premolar biting, but the australopiths have a much longer cheek tooth row owing to the large size of their molars and premolars. Thus, biting efficiency remains constant even though the load arm of the premolars has increased in australopiths. These data suggest that, as in other primate and mammalian taxa [25–32], a major influence on the evolution of australopith form is selection for bite force generation.

One might argue that these data imply that the robust australopith face is relatively stronger than that of gracile australopiths, which is relatively stronger than that of chimpanzees because stresses and strains are maintained at similar levels while being exposed to proportionally greater bite forces. This line of reasoning, however, depends critically on MA (which converts muscle force into bite force) and thus is in fact a further argument in favour of the hypothesis that australopith facial form is adapted to increase the efficiency of bite force production. Moreover, bite force is a reaction force, not an applied load. To consider strength in response to an applied load, one must normalize muscle forces rather than bite force, and in analyses presented here these are normalized in that all of the models are being subjected to isometrically scaled muscle forces. Thus, we do not view our findings as being consistent with the strength predictions tested here.

Finally, results are inconsistent with the hypothesis that high efficiency in bite force generation evolved to maintain occlusal pressures in australopiths relative to a non-human ape-like ancestral condition. Among the australopiths, occlusal pressure is greatest in specimen OH 5, but its value is only 81% of the chimpanzee average during premolar bites, and 72% during molar bites.

Do these results mean that australopith facial features traditionally thought to be structural reinforcements that strengthen the face are not, in fact, related to load bearing? Not necessarily. It has previously been found [33] that traits that increase MA can expose the facial skeleton to proportionally higher bite forces and change the bending moments around which the masticatory muscles act, potentially elevating stress and strain in the face and weakening it. Reinforcing features may then have evolved to compensate locally for the weakening caused by higher MA and/or bending moments. In engineering, compensation refers to the systems or structures designed to control or manage the side-effects of the primary function of a device. For example, heat might be a side-effect of the normal functioning of a transistor; if the heat is not managed, then the transistor might fail. Similarly, if evolution in the early hominin feeding apparatus has been driven primarily by selection to enhance the efficiency of bite force production, then elevated stress can be viewed as a side-effect related to elevated bite force and changes in shear forces and bending moments related to the positioning of the zygomatic root on the maxilla. The associated evolution of bony traits that structurally reinforce the facial skeleton can be thought of as compensatory mechanisms that 'control' or reduce what would otherwise be markedly elevated stresses. Thus, these traits do, in fact serve to reduce stress, but structural strength across the cranium remains broadly comparable to that of non-human apes. In this view, natural selection favoured the evolution of traits that increased MA for bite force production, requiring the evolution of traits that reinforce the facial skeleton to avoid it being weakened.

In this scenario, the elevated efficiency of bite force production in australopiths is related to the position of the masseter origin. Gracile and, especially, robust australopiths

have a zygomatic root that is positioned further forward on the postcanine tooth row than in chimpanzees and gorillas [1,12,34], meaning that origin of the masseter muscle is positioned further forward as well. This increases the lever arm of the masseter relative to the temporomandibular joint and in a simple lever model should increase bite force outputs for a given muscle force input [35]. Modelling experiments confirm this principle in australopiths [33]. Moreover, simple metrics demonstrate that, in gracile australopiths compared to *Pan* and *Gorilla*, and robust compared to gracile australopiths, a greater proportion of the total length of the tooth row is 'covered' by the masseter muscle (electronic supplementary material), implying greater masseter leverage. An anterior positioning of the zygomatic root imposes a mechanical cost, however; modelling experiments show that such a root position is associated with elevated strains in parts of the face [33].

To compensate for elevated strains, it is proposed that australopiths evolved an inferolaterally expanded zygomatic root, the rounded inferior margin of which acts as a strut to resist shear as the masseter muscle deflects the zygomatic arch inferiorly relative to a more medially positioned bite point. Modelling experiments show that this reduces strains across the infraorbital region and zygomatic root [33]. Furthermore some australopiths (although not A.L. 444-2) exhibit an externally swollen anterior pillar along the lateral margins of the nasal cavity that acts as a strut in compression during premolar loading [33]. Modelling experiments show that removal of the pillar increases strains along the nasal margin and zygomatic root [33]. Moreover, the inferior aspect of the frontal process of the zygomatic flares laterally in most australopiths which should reduce stresses in the zygomatic angle as the masseter pulls down on the zygomatic arch. In addition, it has been hypothesized [36] that some robust australopiths evolved a posteriorly expanded zygomatic root to reduce shear stresses caused by bites on teeth that are positioned behind an anteriorly positioned zygomatic root.

This scenario implies that the evolution of australopith facial form can be explained by understanding why australopiths would need to efficiently generate bite force. In other words, what aspects of the australopith diet may have induced selection pressure leading to the evolution of enhanced masticatory MA? Foods like nuts and seeds (including grass seeds) would clearly be suitable candidates because they are stress-limited [37], meaning that they fail under the application of high external forces (which in turn create high stresses within the food object). Such foods are often considered 'hard', although hardness is more precisely defined as resistance to plastic deformation (e.g. as observed during an indentation test) whereas in this context hardness may be considered a sensory perception of objects that are both stiff and crack resistant [38]. Increases in MA should, for a given set of muscles, increase maximum bite force and potentially expand the range of stress-limited food items that could be consumed. This ought to provide a selective advantage, especially during periods when other food resources might be scarce. However, anterior placement of the masseter muscle constrains gape [39] so the extraordinary anterior placement of this muscle (and the concomitant high overall MA) in *P. boisei* suggests that selection to consume stress-limited foods may have been confined to items on the smaller end of the size spectrum.

An alternative hypothesis would be that high MA and high bite force evolved as adaptations for bulk feeding, namely, the

processing of high volumes of food on large cheek teeth with expanded occlusal areas [3,4]. In this view, increased bite force allowed australopiths to maintain occlusal pressures while processing foods like whole fruits (including exocarp, pulp and seeds). However, our estimates of occlusal pressures in australopiths would have been at or below the lower limit of values observed in chimpanzees, who are not obviously adapted for bulk feeding (electronic supplementary material, table S1). Thus, although australopiths may have engaged in bulk feeding behaviours, the biomechanical premise underlying this hypothesis seems unsupported. Bulk feeding, therefore, seems unlikely to have been an adaptation.

Another possibility would be that high MA evolved as an adaptation to process foods that are both compliant and crack resistant. These foods are displacement-limited in the sense that they fail not because of especially high levels of stress but rather because they are so deformable that their mechanical strength is exceeded only after their tissues are substantially displaced [37]. Such foods are often considered 'tough', although toughness is a term that, confusingly, is used differently in different mechanical contexts [37]. High force levels are not necessarily needed to fracture these foods, but the muscles of mastication must work over an extended time to propagate cracks through the food item. High MA may allow muscles to work at lower activity levels in order to provide the requisite work, thereby sparing the muscle from fatigue. This might be especially useful when masticating foods that are broken down only after many chewing cycles. The key argument against the hypothesis that early hominins are adapted to consume displacement-limited foods derives from tooth morphology (e.g. [18]). Among primates, folivorous species that are adapted to eat displacement-limited foods exhibit teeth with long, high, sharp ridges (so-called 'shearing crests', although they do not necessarily act to shear foods [37]). These ridges promote displacement of the plant tissues, making it easier to reach the strength limit of a given food during a chewing cycle. However, australopiths (and especially robust australopiths) have derived, bunodont teeth with rounded cusps that wear flat over time. These teeth are especially poorly configured to promote displacements within compliant foods, which would mean that at precisely the same time that the masticatory apparatus would have been evolving high MA to consume compliant/tough foods, the teeth would have been changing to be almost perfectly maladapted for processing those items. The contradiction inherent in this hypothesis is seemingly difficult to justify. It has been suggested [40] that loss of occlusal relief is a developmental by-product of having thick tooth enamel, and that the latter is an adaptation to prolong tooth life in the face of an abrasive diet. However, it is acknowledged [40] that there is no comparative evidence from living primates that is compatible with this hypothesis.

The primary objection to a hypothesis in which australopiths are adapted to consume stress-limited foods is that few australopith species exhibit a pitted, complex dental microwear signal that would indicate frequent consumption of such foods. However, traditional interpretations of dental microwear data have been challenged on mechanical grounds insofar as theoretical models and experimental evidence suggest that microwear signals are less strongly influenced by food material properties than they are by the mechanical properties of ingested non-food particles [41–46]. It has also been suggested that the ability of dental microwear analysis

to discriminate among primates with known diets is less efficacious than is generally supposed [20,47]. Consequently, a vigorous debate about the mechanics of microwear formation has ensued [44–46,48–60]. Key recent findings include observations of wild chimpanzee populations corroborating the hypothesis that microwear patterns are strongly influenced by the amount and nature of abrasive particles in the diet [57], and experiments on sheep and guinea pigs showing that the size of grit particles can dramatically affect microwear signals independent of diet [58,59]. *In vitro* experiments have further shown that even the hardest seed shell particles are nonetheless too soft to meaningfully abrade enamel to create marks on the scale of typical microwear features [46]. Thus, there is a reasonable (albeit contested) case to be made that an absence of pitted, complex microwear textures in many early hominins cannot be interpreted to mean that hard foods were not consumed by them.

Interestingly, there is one class of stress-limited foods that appears to be consistent with many aspects of australopith feeding biomechanics and dietary ecology: grass and sedge seeds. These seeds, when consumed several at a time, require high forces to process [46] yet would require highly repetitive chewing (thereby risking bone fatigue) because many seeds would need to be processed in order to satisfy daily dietary requirements. Such seeds are best processed with large, somewhat flat occlusal surfaces [61]. The feeding apparatuses of robust and, to a lesser extent, gracile australopiths are well suited to meet these mechanical demands. The seeds themselves are too soft to create pitted microwear textures, but the seeds of some species are populated with phytoliths that would be displaced in a radial fashion as the seed was compressed between occluding teeth [46], leading to microwear textures characterized by unaligned (i.e. isotropic) grooves, as is seen in some early hominins [62,63]. Many grass and sedge seeds are also produced by plants using the C4 photosynthetic pathway, which would lead to elevated stable carbon isotope values, as is observed in many australopiths (e.g. [64,65]). Moreover, the simultaneous consumption of multiple grass seeds would distribute bite force across many points of contact, making grass seed consumption unlikely to damage teeth through chipping and possibly explaining why chips are rare in some early hominins [66]. We hypothesize, as have others [20,46,67], that grass and sedge seed consumption may have been an adaptively significant behaviour for some early hominins.

4. Methods

(a) Virtual reconstruction of A.L. 444-2

We reconstructed the *Australopithecus afarensis* cranium of A.L. 444-2 using the toolkit of virtual anthropology and geometric morphometrics [68–71], including mirror imaging, reflected relabelling and thin-plate splines (electronic supplementary material). Our reconstruction uses a prior reconstruction [12] as a base guideline and augments it by virtually correcting for asymmetries and distortions of individual parts, and using a quantitative approach for reconstructing missing regions by reference specimens [69,70].

(b) Finite element analysis

Details regarding the construction and analysis of FEMs of OH 5, Sts 5, MH1 and the chimpanzees are provided elsewhere [19–21],

and the FEA of A.L. 444-2 followed the same procedures. Briefly, a watertight, tessellated surface model was converted into a mesh of tetrahedral finite elements. The model was assigned the material properties of bone and loaded with forces simulating the jaw adductor muscles. Muscle forces were applied to all FEMs for the anterior temporalis, superficial masseter, deep masseter and medial pterygoid. Force magnitudes were estimated from the physiological cross-sectional area of each of these muscles in an adult female chimpanzee [18], but were scaled to bone volume to the 2/3 power in each FEM to remove any size-related differences in strain pattern or magnitude [22]. This focuses our comparisons on the functional consequences of differences in shape alone. The muscle forces applied to the A.L. 444-2 model are as follows: anterior temporalis = 775.46 N; superficial masseter = 797.62 N; deep masseter = 118.63 N; medial pterygoid = 263.57 N. The forces applied to the other models are reported elsewhere [19–21]. These forces are coarse approximations of the forces that were produced in this specimen, and indeed all of the muscle forces applied to all of the fossil hominin models are first-order approximations at best. Indeed, no FEA of any fossil taxon can reconstruct strains corresponding to naturalistic feeding behaviour with especially high confidence. However, the isometric scaling of muscle forces [22] allows a modelling experiment that can confidently assess the biomechanical consequences of skeletal shape differences (electronic supplementary material). Nodes at the two articular condyles and a bite point on either the M^2 or P^3 were constrained from moving, producing reaction forces at those nodes. The reaction force at the bite point is the bite force. Maximum principal, minimum principal and von Mises strains were recorded at selected nodes throughout the model (see electronic supplementary material for more details).

References

1. Rak Y. 1983 *The ustralopithecine face*. New York, NY: Academic Press.

2. Prado FB, Freire AR, Rossi AC, Ledogar JA, Smith AL, Dechow PC, Strait DS, Voigt T, Ross CF. 2016 Review of *in vivo* bone strain studies and finite element models of the zygomatic complex in humans and non-human primates: implications for clinical research and practice. *Anat. Rec.* **299**, 1753–1778. (doi:10.1002/ar.23486)

3. Demes B, Creel N. 1988 Bite force, diet, and cranial morphology of fossil hominids. *J. Hum. Evol.* **17**, 657–670. (doi:10.1016/0047-2484(88)90023-1)

4. Walker A. 1981 Diet and teeth - dietary hypotheses and human evolution. *Phil. Trans. R. Soc. Lond. B* **292**, 57–64. (doi:10.1098/rstb.1981.0013)

5. Kimbel WH, White TD, Johanson DC. 1984 Cranial morphology of *Australopithecus afarensis*: a comparative study based on a composite reconstruction of the adult skull. *Am. J. Phys. Anthropol.* **64**, 337–388. (doi:10.1002/ajpa. 1330640403)

6. Tobias PV. 1967 *Olduvai Gorge: the cranium and maxillary dentition of Australopithecus (Zinjanthropus) boisei*, vol. 2. Cambridge, UK: Cambridge University Press.

7. Johanson DC, White TD. 1979 A systematic assessment of early African hominids. *Science* **203**, 321–330. (doi:10.1126/science.104384)

8. Walker AC, Leakey REF, Harris JM, Brown FH. 1986 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature* **322**, 517–522. (doi:10. 1038/322517a0)

9. Kimbel WH, White TD, Johanson DC. 1988 Implications of KNM-WT 17000 for the evolution of 'robust' australopithecines. In *Evolutionary history of the 'robust' australopithecines* (ed. FE Grine), p. 259. New York, NY: Aldine de Gruyter.

10. Strait DS, Grine FE, Moniz MA. 1997 A reappraisal of early hominid phylogeny. *J. Hum. Evol.* **32**, 17–82. (doi:10.1006/jhev.1996.0097)

11. Strait DS, Grine FE. 2004 Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. *J. Hum. Evol.* **47**, 399–452. (doi:10.1016/j.jhevol.2004.08.008)

12. Kimbel WH, Rak Y, Johanson DC. 2004 *The skull of Australopithecus afarensis*. Oxford, UK: Oxford University Press.

13. Mongle CS, Strait DS, Grine FE. 2019 Expanded character sampling underscores phylogenetic stability of *Ardipithecus ramidus* as a basal hominin. *J. Hum. Evol.* **131**, 28–39. (doi:10.1016/j.jhevol.2019.03.006)

14. Zienkiewicz OC, Taylor RL, Zhu JZ. 2005 *The finite element method: its basis and fundaments*, 6th edn. Oxford, UK: Elsevier.

15. Huiskes R. 1982 On the modelling of long bones in structural analyses. *J. Biomech.* **15**, 65–69. (doi:10. 1016/0021-9290(82)90036-7)

16. Richmond BG, Wright BW, Grosse I, Dechow PC, Ross CF, Spencer MA, Strait DS. 2005 Finite element analysis in functional morphology. *Anat. Rec.* **283A**, 259–274. (doi:10.1002/ar.a.20169)

17. Rayfield EJ. 2007 Finite element analysis and understanding the biomechanics and evolution of

living and fossil organisms. *Ann. Rev. Earth Planet. Sci.* **35**, 541–576. (doi:10.1146/annurev.earth.35.031306.140104)

18. Strait DS *et al*. 2009 The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proc. Natl Acad. Sci. USA* **106**, 2124–2129. (doi:10.1073/pnas.0808730106)

19. Smith AL *et al*. 2015 Biomechanical implications of intraspecific shape variation in chimpanzee crania: moving towards an integration of geometric morphometrics and finite element analysis. *Anat. Rec.* **298**, 122–144. (doi:10.1002/ar.23074)

20. Smith AL *et al*. 2015 The feeding biomechanics and dietary ecology of *Paranthropus boisei*. *Anat. Rec.* **298**, 145–167. (doi:10.1002/ar.23073)

21. Ledogar JA *et al*. 2016 Mechanical evidence that *Australopithecus sediba* was limited in its ability to eat hard foods. *Nat. Comm.* **7**, 10596. (doi:10.1038/ncomms10596)

22. Dumont ER, Grosse IR, Slater GJ. 2009 Requirements for comparing the performance of finite element models of biological structures. *J. Theor. Biol.* **256**, 96–103. (doi:10.1016/j.jtbi.2008.08.017)

23. Hylander WL, Picq PG, Johnson KR. 1991 Masticatory-stress hypotheses and the supraorbital region of primates. *Am. J. Phys. Anthropol.* **86**, 1–36. (doi:10.1002/ajpa.1330860102)

24. Ross CF *et al*. 2011 *In vivo* bone strain and finite-element modeling of the craniofacial haft in catarrhine primates. *J. Anat.* **218**, 112–141. (doi:10.1111/j.1469-7580.2010.01322.x)

25. Ross CF, Iriarte-Diaz J. 2019 Evolution, constraint, and optimality in primate feeding systems. In *Feeding in vertebrates* (eds V Bels, IQ Whishaw), pp. 787–829. Cham, Switzerland: Springer.

26. Santana SE, Dumont ER. 2009 Connecting behavior and performance: the evolution of biting behavior and bite performance in bats. *J. Evol. Biol.* **22**, 2131–2145. (doi:10.1111/j.1420-9101.2009.01827.x)

27. Dumont ER, Ryan TM, Godfrey LR. 2011 The *Hadropithecus* conundrum reconsidered, with implications for interpreting diet in fossil hominins. *Proc. R. Soc. B* **278**, 3654–3661. (doi:10.1098/rspb.2011.0528)

28. Dumont ER, Davis JL, Grosse IR, Burrows AM. 2011 Finite element analysis of performance in the skulls of marmosets and tamarins. *J. Anat.* **218**, 151–162. (doi:10.1111/j.1469-7580.2010.01247.x)

29. Dumont ER, Samadevam K, Grosse I, Warsi OM, Baird B, Davalos LM. 2014 Selection for mechanical advantage underlies multiple cranial optima in New World leaf-nosed bats. *Evolution* **68**, 1436–1449. (doi:10.1111/evo.12358)

30. Santana SE, Grosse IR, Dumont ER. 2012 Dietary hardness, loading behavior, and the evolution of skull form in bats. *Evolution* **66**, 2587–2598. (doi:10.1111/j.1558-5646.2012.01615.x)

31. Cox PG, Rinderknecht A, Blanco RE. 2015 Predicting bite force and cranial biomechanics in the largest fossil rodent using finite element analysis. *J. Anat.* **226**, 215–223. (doi:10.1111/joa.12282)

32. McIntosh AF, Cox PH. 2016 The impact of gape on the performance of the skull in chisel-tooth digging and scratch digging mole-rats (Rodentia: Bathyergidae). *R. Soc. Open Sci.* **3**, 160568. (doi:10.1098/rsos.160568)

33. Ledogar JA *et al*. 2017 The biomechanics of bony facial 'buttresses' in South African australopiths: an experimental study using finite element analysis. *Anat. Rec.* **300**, 171–195. (doi:10.1002/ar.23492)

34. Weber G, Krenn VA. 2017 Zygomatic root position in recent and fossil hominids. *Anat. Rec.* **300**, 160–170. (doi:10.1002/ar.23490)

35. Smith RJ. 1978 Mandibular biomechanics and temporomandibular joint function in primates. *Am. J. Phys. Anthropol.* **49**, 341–349. (doi:10.1002/ajpa.1330490307)

36. Martin JM *et al*. 2021 Drimolen cranium DNH 155 document microevolution in an early hominin species. *Nat. Ecol. Evol.* **5**, 38–45. (doi:10.1038/s41559-020-01319-6)

37. Lucas PW. 2004 *Dental functional morphology: how teeth work*. Cambridge, UK: Cambridge University Press.

38. Kim EHJ, Corrigan VK, Wilson AJ, Waters IR, Hedderley DI, Morgenstern MP. 2012 Fundamental fracture properties associated with sensory hardness of brittle solid foods. *J. Texture Stud.* **43**, 49–62. (doi:10.1111/j.1745-4603.2011.00316.x)

39. Hylander WL. 2013 Functional links between canine height and jaw gape in catarrhines with special reference to early hominins. *Am. J. Phys. Anthropol.* **150**, 247–259. (doi:10.1002/ajpa.22195)

40. Ungar PS, Hlusko LJ. 2016 The evolutionary path of least resistance. *Science* **353**, 29–30. (doi:10.1126/science.aaf8398)

41. Lucas PW *et al*. 2013 Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *J. R. Soc. Interface* **10**, 20120923. (doi:10.1098/rsif.2012.0923)

42. Lucas PW *et al*. 2014 The role of dust, grit and phytoliths in tooth wear. *Ann. Zool. Fennici* **51**, 143–152. (doi:10.5735/086.051.0215)

43. Lucas PW *et al*. 2016 Dental abrasion as a cutting process. *J. R. Soc. Interface Focus* **6**, 2016008.

44. van Casteren A *et al*. 2018 Evidence that metallic proxies are unsuitable for assessing the mechanics of microwear formation and a new theory of the meaning of microwear. *R. Soc. Open Sci.* **5**, 171699. (doi:10.1098/rsos.171699)

45. van Casteren A *et al*. 2019 Metallic proxies remain unsuitable for assessing the mechanics of microwear formation: reply to comment on van Casteren *et al*. (2018). *R. Soc. Open Sci.* **6**, 190572. (doi:10.1098/rsos.190572)

46. van Casteren A *et al*. 2020 Hard plant tissues do not contribute meaningfully to dental microwear: evolutionary implications. *Sci. Rep.* **10**, 582. (doi:10.1038/s41598-019-57403-w)

47. Strait DS *et al*. 2013 Diet and dietary adaptations in early hominins: the hard food perspective. *Am. J. Phys. Anthropol.* **151**, 339–355. (doi:10.1002/ajpa.22285)

48. Xia J, Zheng J, Huang D, Ryan Tian Z, Chen L, Zhou Z, Ungar PS, Qian L. 2015 New model to explain tooth wear with implications for microwear formation and diet reconstruction. *Proc. Natl Acad. Sci. USA* **112**, 10 669–10 672. (doi:10.1073/pnas.1509491112)

49. Hua LC, Brandt ET, Muellenet JF, Zhou ZR, Ungar PS. 2015. An in vitro study of dental microwear formation using the BITE Master II chewing machine. *Am. J. Phys. Anthropol.* **158**, 769–775. (doi:10.1002/ajpa.22823)

50. Karme A, Rannikko J, Kallonen A, Clauss M, Fortelius M. 2016 Mechanical modeling of tooth wear. *J. R. Soc. Interface* **13**, 20160399. (doi:10.1098/rsif.2016.0399)

51. Merceron G *et al*. 2016 Untangling the environmental from the dietary: dust does not matter. *Proc. R. Soc. B* **283**, 20161032. (doi:10.1098/rspb.2016.1032)

52. Ungar PS, Scott JR, Steininger CM. 2016 Dental microwear differences between eastern and southern African fossil bovids and hominins. *S. Afr. J. Sci.* **112**, 1–5. (doi:10.17159/sajs.2016/20150393)

53. Daegling DJ, Hua LC, Ungar PS. 2016 The role of food stiffness in dental microwear feature formation. *Arch. Oral Biol.* **71**, 16–23. (doi:10.1016/j.archoralbio.2016.06.018)

54. Teaford MF, Ungar PS, Taylor AB, Ross CF, Vinyard CJ. 2020 The dental microwear of hard-object feeding in laboratory *Sapajus apella* and its implications for dental microwear formation. *Am. J. Phys. Anthropol.* **171**, 439–455. (doi:10.1002/ajpa.24000)

55. Rodrigues-Rojas F, Borrero-Lopez O, Constantino PJ, Henry AG, Lawn BR. 2020. Phytoliths can cause tooth wear. *J. R. Soc. Interface* **17**, 20200613. (doi:10.1098/rsif.2020.0613)

56. Schulz-Kornas E *et al*. 2020 Everything matters: molar microwear texture in goats (*Capra aegagrus hircus*) fed diets of different abrasiveness. *Palaeogeog. Paleoclimat. Palaeoecol.* **552**, 109783. (doi:10.1016/j.palaeo.2020.109783)

57. Schulz-Kornas E, Stuhlträger J, Clauss M, Wittig RM, Kupczik K. 2019 Dust affects chewing efficiency and tooth wear in forest dwelling Western chimpanzees (*Pan troglodytes verus*). *Am. J. Phys. Anthropol.* **2019**, 1–12. (doi:10.1002/ajpa.23808)

58. Ackermans NL, Winkler DE, Martin LF, Kaiser TM, Clauss M, Hatt JM. 2020 Dust and grit matter: abrasives of different size lead to opposing dental microwear textures in experimentally fed sheep (*Ovis aries*). *J. Exp. Biol.* **223**, jeb220242. (doi:10.1242/jeb.220442)

59. Winkler DE, Tütken T, Schulz-Kornas E, Kaiser TM, Müller J, Leichliter J, Weber K, Hatt JM, Clauss M. 2020 Shape, size, and quantity of ingested external abrasives influence dental microwear texture formation in guinea pigs. *Proc. Natl Acad. Sci. USA* **117**, 22 264–22 273. (doi:10.1073/pnas.2008149117)

60. Louail M, Ferchaud S, Souron A, Walker AEC, Merceron G. 2021 Dental microwear textures differ

in pigs with overall similar diets but fed with different seeds. *Palaeogeog. Palaeoclimat. Palaeoevol.* **572**, 110415. (doi:10.1016/j.palaeo.2021.110415)

61. Lucas PW, Corlett RT, Luke DA. 1985 Plio-pleistocene hominid diets: an approach combining masticatory and ecological analysis. *J. Hum. Evol.* **14**, 187–202. (doi:10.1016/S0047-2484(85)80006-3)

62. Ungar PS, Grine FE, Teaford MF. 2008 Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei. PLoS ONE* **3**, e2044. (doi:10.1371/journal.pone.0002044)

63. Ungar PS, Scott RS, Grine FE, Teaford MF. 2010 Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis. Phil. Trans. R. Soc. B* **365**, 3345–3354. (doi:10.1098/rstb.2010.0033)

64. Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, Leakey MG, Sponheimer M, Uno KT. 2011 Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc. Natl Acad. Sci. USA* **108**, 9337–9341. (doi:10.1073/pnas.1104627108)

65. Sponheimer M *et al*. 2013 Isotopic evidence of early hominin diets. *Proc. Natl Acad. Sci. USA* **110**, 10 513–10 518. (doi:10.1073/pnas.1222579110)

66. Constantino PJ, Konow KA. 2021 Dental chipping supports lack of hard object feeding in *Paranthropus boisei. J. Hum. Evol.* **156**, 103015. (doi:10.1016/j.jhevol.2021.103015)

67. Jolly CJ. 1970 Seed-eaters - new model of hominid differentiation based on a baboon analogy. *Man* **5**, 5–26. (doi:10.2307/2798801)

68. Slice DE. 2005 *Modern morphometrics in physical anthropology*. Boston, MA: Springer.

69. Gunz P, Mitteroecker P, Neubauer S, Weber GW, Bookstein FL. 2009 Principles for the virtual reconstruction of hominin crania. *J. Hum. Evol.* **57**, 48–62. (doi:10.1016/j.jhevol.2009.04.004)

70. Weber GW, Bookstein FL. 2011 *Virtual anthropology: a guide to a new interdisciplinary field*. New York, NY: Springer.

71. Senck S, Bookstein FL, Benazzi S, Kastner J, Weber GW. 2015 Virtual reconstruction of modern and fossil hominoid crania: consequences of reference sample choice. *Anat. Rec.* **298**, 827–841. (doi:10.1002/ar.23104)

72. Ledogar JA *et al*. 2022 Data from: Mechanical compensation in the evolution of the early hominin feeding apparatus. Dryad Digital Repository. (https://doi.org/10.5061/dryad.4b8gthtd7)

73. Ledogar JA *et al*. 2022 Mechanical compensation in the evolution of the early hominin feeding apparatus. FigShare. (doi:10.6084/m9.figshare.c.6011795)